Biodiversity, redundancy and resilience of riparian vegetation under different land management regimes

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by

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Abstract

Biodiversity is widely thought to enhance resilience in ecosystems by providing 'insurance' which buffers the effects of disturbances on ecosystem functioning. However, little empirical evidence is available to support this assumption. Biodiversity and resilience are both complex, multifaceted concepts, and the mechanisms underlying the relationship between them are far from clear. However, understanding this relationship is important because resilience underpins the ability of ecosystems to continue to provide essential 'goods and services' in the face of increasing human pressure and an uncertain future.

In this thesis I address two properties thought to be important in determining the resilience of ecological assemblages, namely functional redundancy (similarities in ecological functioning between species) and response disparity (differences in species' responses to disturbance). Both are related to biodiversity, being determined by the degree of similarity or difference among the species in an assemblage. After developing a conceptual framework for understanding the relationship between biodiversity and resilience, I provide a critical evaluation of existing methods for measuring redundancy and response disparity, and develop measures of these two properties that better reflect the continuous, multidimensional nature of differences between species. A key element of my approach is the use of different sets of functional traits to describe individual species' contributions to different ecological functions. This is valuable because it explicitly recognises that species have multiple functional roles, an obvious fact that is often overlooked and a source of much misunderstanding about redundancy and disparity. I then use these methods to measure redundancy and response disparity in riparian plant assemblages from different–sized streams and under different land management regimes, providing some of the first empirical evidence for these aspects of resilience in real, species–rich assemblages. In particular, I provide the first empirical confirmation of two hypotheses about the roles of redundancy and response disparity in the resilience of plant assemblages, namely (1) that minor species in the tail of the abundance distribution provide redundancy for functions performed by the dominant species, and (2) that groups of species that provide redundancy for each others' functioning differ in their response traits, thus providing response disparity (Walker *et al.*, 1999, *Ecosyst.* 2:95–113).

This thesis also contributes to our understanding of the effects of land management practices on the resilience of riparian systems, something which is poorly understood but of critical interest to conservation and land managers. Ecosystem–based approaches to management place emphasis on maintaining desirable functioning in ecosystems. However, often it is very difficult for managers to assess whether this is being achieved (the 'manager's dilemma'). The resilience measures developed here are valuable because they provide a measure of the long–term sustainability of the various functions performed by species assemblages.

Both redundancy and response disparity were present in the riparian assemblages studied. Species in the tail of the abundance distribution were particularly important providers of redundancy. These tail species, often inadequately sampled or left out of functional diversity analyses, provided 53–100% (mean 82%) of the redundancy for the functioning of the more abundant species. For most functions performed by a particular species, between 5 and 20 other species were potentially able to perform that function in a similar way, thus providing redundancy. However, all assemblages also had species (1–40%) with low redundancy for one or more functions, suggesting that certain particular aspects of functioning may lack resilience, even in assemblages with high overall resilience.

Species providing redundancy for a particular function were seldom very similar in their contributions to other functions. Functional 'analogues' (species identical or very similar in all functions) were relatively uncommon (42–71% of species across different management regimes and stream sizes had no analogues for the small number of functions studied, and this number was shown to increase with the number of functions considered). Redundancy was usually provided by a large number of *partially similar* species rather than by a few identical species. Redundancy and disparity were therefore simultaneously present in each assemblage, because each species contributed both to redundancy (for some functions) and disparity (for others). This suggests that the commonly held view of redundancy provided by 'identical copies' is far too one–dimensional, and successfully lays to rest the debates about its existence and the concerns that promoting redundancy will somehow be detrimental to diversity. I therefore propose that it is time to put redundancy back on the research agenda as an important aspect of functional organisation which leads to resilience.

The highly distributed nature of redundancy, involving many partially similar species, also has important implications for our understanding of change in ecosystems. It means that functional compensation will seldom be a simple matter of species replacing each other as 'drop–in replacements'. Rather, compensatory changes in species composition or abundance will have knock–on effects that affect many other species and lead to many 'readjustments' in species' functioning, responses to disturbance, interactions and abundances. The results of this study have shown that the way changes in species composition or diversity affect resilience are often idiosyncratic, depending on which particular species are involved. It is therefore not appropriate to try to model the impacts of changes in biodiversity on ecosystem resilience deterministically.

However, ecosystem managers require information about resilience to implement ecosystem–based management. This information needs to be simple enough to be useful, but flexible anough to account for the fact that idiosyncratic species effects frequently make considering the details of a particular situation unavoidable. In this thesis I outline an approach that involves the judicious use of generalisations together with a flexible means of combining compositional, functional and resilience perspectives on species assemblages, allowing exploration of the relationship between diversity and resilience in a particular system. This approach is more flexible, and allows a wider range of questions to be addressed, than commonly used approaches using indices of diversity or ecosystem health. Rather than summarising a large amount of detailed information in the form of an index, my approach retains the detail but concentrates on making it easier to interpret. This provides a flexible way of using the detail to answer specific management questions, thus increasing its usefulness to managers.

The finding of a generally positive relationship between redundancy and species richness in this study is a useful generalisation for managers trying to implement an ecosystem–based approach to conservation and land management. It suggests that, in general, maintaining species–rich assemblages will tend to maintain redundancy. However, this relationship varied with growth form (woody vs herbaceous), stream order (small streams vs main river) and the function being considered. The amount of redundancy and response disparity associated with each species for each function were also highly variable, pointing to the need to use generalisations with care.

Comparison of assemblages under the different land management regimes (Kruger National Park, privately–owned reserves and communal rangeland) suggested that management practices in river catchments do affect the resilience of riparian vegetation, but not always in the manner expected. Management practices in the conservation areas did not necessarily promote higher diversity or resilience than management practices in the communal area, which may come as a surprise to many conservationists. While assemblages from the main river were less resilient in the communal area than in the reserves, assemblages from the small streams were more diverse and resilient than those in the reserves, even though communal rangeland areas are not managed specifically for biodiversity conservation. Far from being 'degraded' as is usually assumed, small streams within these communally managed areas are in fact valuable as biodiversity hotspots, and this should be reflected in conservation planning and ecosystem service assessments in the region.

Declaration

I declare that this thesis is my own, unaided work. It is being submitted for the degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other university.

AKotschy

K A Kotschy

This 4th day of October 2013 in Johannesburg.

For
Paulie, Anna, Robyn and the "great proleteriat" of species

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Appropriately, this project was made possible by an extremely diverse group of people with diverse skills and functions. Like an ecological assemblage, this community of people interacted with me, shared resources, and importantly, provided functional redundancy which allowed the project to continue despite the inevitable disturbances!

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Chapter 1

Introduction

1.1 Background and purpose of the study

The concept of resilience describes the ability of a system to persist and retain its identity through time by maintaining key components, functions and interactions (Holling, 1973; Gunderson, 2000; Cumming and Collier, 2005). Ecosystems often show a surprising ability to maintain important aspects of their functioning (whether good or bad), despite various natural and human–generated disturbances. This resilience underpins the ability of ecosystems to continue to provide essential 'goods and services' in the face of increasing human pressure and an uncertain future. Understanding how to preserve and nurture sources of resilience in ecosystems is therefore an important goal.

Biodiversity is widely held to enhance resilience by providing a source of options for responding to change and disturbance (Walker and Salt, 2006; Worm *et al.*, 2006; Chapin *et al.*, 2009a). Biodiversity potentially provides 'insurance' for maintaining current ecosystem functioning, as well as a source of novelty for creative reorganization. It can be equated with maintaining a set of possible 'answers' to 'questions' posed by the environment, and is therefore valuable during times of change (Norberg and Cumming, 2008). Despite the intuitive appeal of the idea that biodiversity enhances resilience in ecosystems, the mechanisms underlying this relationship are poorly understood. Part of the problem lies with the multifaceted, scale–dependent nature of both biodiversity and resilience, which has generated much debate and confusion over the past few decades (Hurlbert, 1971; Purvis and Hector, 2000; McCann, 2000; Ives and Carpenter, 2007).

One of the important ways biodiversity is thought to enhance resilience is through a property called redundancy. Redundancy refers to the replication of entities or pathways in a system, allowing functionally similar entities to fully or partly compensate for each other (Naeem and Li, 1997). Redundancy is generally thought to increase with the number of species present. While the importance of redundancy is well accepted in other fields, such as genetics and molecular biology (Thomas, 1993; Vavouri *et al.*, 2003), it has been a contentious concept in ecology.

Walker introduced the term redundancy to ecology to describe the presence in an assemblage of multiple species which function similarly *with respect to a particular function* (Walker, 1992, 1995). He recognised the possibility that species similar in one respect could differ in their environmental responses and tolerances, and in fact saw this as an essential part of resilience because it allows the function to be maintained over time through a wide range of conditions. Unfortunately the concept of redundancy has frequently been misunderstood by ecologists. The term has most often been assumed to mean that certain species are similar in *all aspects* of their functioning ('identical copies'), implying that 'redundant species' are dispensible and can be removed from an assemblage with no ill effects on its functioning. The suggestion that certain species are dispensible or less worthy of protection has been strongly criticized by ecologists and conservation biologists (Naeem, 1998; Fonseca and Ganade, 2001; Rosenfeld, 2002; Loreau, 2004; Gitay *et al.*, 1996; Jaksic *et al.*, 1996). Recent efforts have focused on providing evidence against this 'identical copies' type of redundancy. Many recent studies have shown that few or no species are dispensible when all the functions performed by an assemblage are considered over a long enough time period (Petchey and Gaston, 2002a; Micheli and Halpern, 2005; Hector and Bagchi, 2007; Gamfeldt *et al.*, 2008; Palumbi *et al.*, 2009; Isbell *et al.*, 2011). Many authors still imply that redundancy, if it were to exist, would somehow diminish the value of individual species for ecosystem functioning and the provision of ecosystem services. The above context has unfortunately diverted attention away from the positive aspects of redundancy and its value in providing resilience, and led to an unproductive discussion about whether or not assemblages contain functionally identical species. Walker's propositions about the value of redundancy for resilience have yet to be properly explored.

In this thesis, I show that Walker's concept of redundancy is a valid and useful way of examining resilience in ecosystems. I further develop his ideas about redundancy, deal with some methodological issues which have hampered their application, and apply these ideas and methods to real, species–rich riparian plant assemblages. The resilience literature is characterised by a strongly theoretical/conceptual approach and there is a dearth of empirical studies. A much stronger empirical foundation is needed to allow testing of existing theory and development of new ideas. This thesis is a contribution to that empirical foundation. It represents the first attempt to empirically test two proposals of Walker *et al.* (1999): that species in the tail of the abundance distribution provide redundancy for functions performed by the dominant species, and that sets of species with similar functions differ widely in their responses to disturbance, increasing the 'insurance value' of the redundancy. Walker *et al.* (1999) provided a test of their ideas using a limited dataset, but both this and a later attempt (Walker and Langridge, 2002) ran into methodological problems related to how to quantify disparity and redundancy. Recent research has produced improved methods for measuring functional diversity and has suggested some possible solutions to these problems. These are explored and developed here. This thesis extends the pioneering work of Walker *et al.* (1999) both methodologically and conceptually.

The strong and complex linkages between riparian zones and their catchments make them particularly difficult to manage. The needs and perspectives of a wide variety of stakeholders must be taken into account. Riparian ecosystems frequently display non–linear and multi–scale dynamics and rapid change in system drivers, which make heavy demands on our limited ecological understanding (Biggs and Rogers, 2003; Bennett *et al.*, 2005). Rather than using ecological prediction or forecasting to develop a single optimal management strategy, an alternative approach is to manage in a way that maintains or promotes the resilience of desirable system attributes (Walker and Langridge, 2002). Managing systems for resilience represents an 'ecosystem approach' rather than a 'species approach' to conservation management (Goldstein, 1999; Walker, 1999). In other words, management aims to maintain system functioning rather than particular species or populations.

An ecosystem approach to conservation is, however, difficult to translate into management policies and practices. Doing so requires that our concept of biodiversity moves beyond 'counting species', and that we begin to address how biodiversity relates to resilience. We do not yet understand what effects conservation or other management regimes have on resilience, either in savannas or in riparian zones within savannas. This is clearly an essential area to explore if the ecosystem approach to conservation is to be applied effectively. This thesis contributes to strengthening the empirical foundation of the ecosystem approach by investigating how certain land management practices affect riparian biodiversity, redundancy and resilience.

The Sand River catchment in Mpumalanga, South Africa, provides a suitable context in which to examine the effects of different land management practices on ecosystem resilience. Sections of river in close proximity to one another are exposed to three different management regimes: Kruger National Park, managed by the South African National Parks Board, the Sabi–Sand Wildtuin, a privately–owned conservation area, and communal grazing land with dense rural settlements. Riparian assemblages from these three areas were expected to differ in composition and/or diversity, providing an opportunity to find out how these differences translate into differences in functioning and resilience.

1.2 A conceptual framework linking biodiversity and resilience

This section introduces general concepts central to the thesis and develops the conceptual framework on which the thesis is based. Reviews of more specifically riparian literature and the effects of land management on riparian ecosystems are found in Chapters 3 and 4.

1.2.1 Biodiversity

Biodiversity or biological diversity in its broadest sense refers to the variety of life on earth; 'the totality of genes, species and ecosystems in a region' (World Resources Institute, 1992). This meaning has gained wide popular usage in recent years. However, in its scientific sense biodiversity is more than simply an umbrella term for 'life on earth'.

The study of biodiversity has a long history in ecology. Despite the huge volume of work on the subject, a universally agreed–upon definition is still lacking (Oksanen and Pietarinen, 2004). Many different definitions have been proposed — as many as 85 were reviewed by DeLong (1996)! These definitions range in their inclusiveness from local to global spatial scales and short to long temporal scales, and also in whether they include abiotic components and processes or not. The existence of such a multitude of definitions is not really surprising, given that biodiversity is an abstract concept applied to complex biological systems. Biodiversity is also a profoundly scale–dependent property (Crawley and Harral, 2001; Willis and Whittaker, 2002); patterns of biodiversity change with spatial and temporal grain and extent, as well as with the taxa or entities studied (Willig *et al.*, 2003). Magurran (1988, p1) put it as follows: 'Diversity is rather like an optical illusion: the more it is looked at, the less clearly defined it appears to be and viewing it from different angles can lead to different perceptions of what is involved'.

Much of the debate about the meaning of biodiversity can be interpreted as addressing what is encompassed by the prefix 'bio'. Early accounts mentioned only species (e.g. Pielou, 1975; Grassle *et al.*, 1979), while later work expanded the scope to other levels of organisation including genes, populations, assemblages, ecosystems, and also biotic structures and processes (see Table 1 in DeLong, 1996; Noss, 1990). DeLong (1996, p745) defined biodiversity as "a state or attribute of a site or area that specifically refers to the variety within and among living organisms, assemblages of living organisms, biotic communities, and biotic processes, whether naturally occurring or modified by humans". This definition gives a sense of the broad scope of biodiversity, but it tells us little about the meaning of the root word ('diversity') itself, except that it is an attribute related to the concept of variety.

Variety is defined as 'the quality or state of having different forms or types' (Merriam–Webster online dictionary, `www.merriam-webster.com`). Variety, and diversity, are attributes of any system whose elements may be divided into categories or types (Leonard and Jones, 1989). In ecology, diversity is most commonly understood in terms of two components: the number of different types present (e.g. the number of species), and the number of individuals of each type (e.g. species relative abundances) (Magurran, 2004). Counting the number of types is perhaps the most obvious way of measuring diversity, given the definitions above. It is often supplemented with information about the relative abundances of the types, however, because of our intuitive sense that a sample of 10 species should be considered more diverse if it has 10 individuals of each species than if it has 91 individuals of one species and only a single individual of each of the remaining nine species (Purvis and Hector, 2000; Maclaurin and Sterelny, 2008). Most ecological diversity indices therefore measure either the number of types (richness indices) or the distribution of abundance among types (evenness or dominance indices), or they combine these two quantities into various 'dual–concept' (Junge, 1994) diversity indices, such as the widely used Gini–Simpson and Shannon–Wiener indices (Magurran, 2004). The combination of species richness and species evenness is often referred to as 'species diversity'.

However, comparing ecological concepts of diversity to diversity concepts from other fields of study suggests that ecologists have been missing something. The concept of diversity in fact features prominently in many other disciplines, including chemistry, genetics, geography, urban planning, linguistics, communication, psychology, sociology, information science, economics and policy studies. Stirling (2007) presented a very useful conceptual framework based on a synthesis of the way diversity is conceptualised and used in a wide variety of different fields. This framework has up to now not been appreciated by ecologists, because the author is an economist and his ideas have not been published in ecological journals. He concluded that diversity refers to a remarkably similar and particular set of properties across all these different contexts, namely *variety* (how many types of thing?), *balance* (how many of each type?) and *disparity* (how different are the types from each other?) (Figure 1.1).

Variety, balance and disparity are each necessary but individually insufficient aspects of diversity. Only all three together fully capture the property of diversity (Stirling, 2006, 2007). Although each of these aspects can vary independently, they are linked at a deep conceptual level and affect each other in various ways. For example, variety can only be understood in the light of disparity and balance. The types to be counted are distinguished from each other in the first place on the basis of disparity, and the number of types counted is wholly dependent on the way they are distinguished. Balance has some important implications for how effectively the types can be sampled, and hence, what number is recorded for variety. Very rare types have a lower chance of being counted, so reasonable estimates of variety can only be obtained if sampling schemes account for the balance component.

If ecological concepts of diversity are compared with the above scheme it becomes obvious that the disparity component has generally been neglected. Although a few ecologists have recognised all three components (e.g. Clarke and Warwick, 1998; Purvis and Hector, 2000; Ricotta, 2007; Maclaurin and Sterelny, 2008), most authors dealing with the concept of diversity, including some influential ones, mention only variety and balance (e.g. Hubbell, 2001; Magurran, 2004; Moreno and Rodríguez, 2010; Tuomisto, 2010). Tuomisto (2010) recently suggested that the term 'true diversity' be reserved for the effective number of types, a measure which includes only the variety and balance components of diversity. I would argue that a concept of diversity that does not include disparity is fundamentally incomplete.

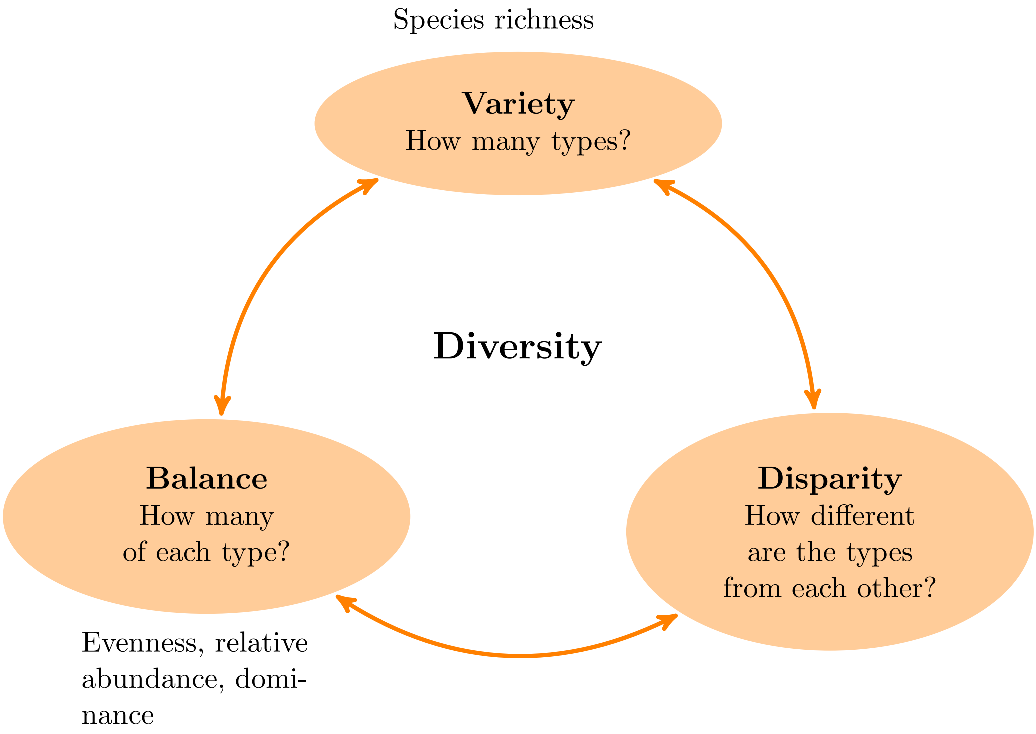


Figure 1.1: Three essential components of diversity identified by Stirling (2007).

A possible reason for the neglect of disparity as a component of biodiversity is that most studies of biodiversity deal with species as the types to be counted. The existence of a relatively uncontroversial taxonomic classification for species (Maclaurin and Sterelny, 2008) has not forced biodiversity scientists to think about issues of disparity, and has led to more focus on variety and balance. Fields of study in which there is no generally accepted classification scheme, such as geography or the social sciences, have paid far more attention to disparity (Stirling, 2006). However, disparity must be addressed in order to understand the link between biodiversity and resilience in ecosystems.

1.2.2 Disparity: the neglected component of diversity

Disparity describes the degree of difference between types. All types are, by definition, different in one or more ways. In fact, as pointed out by Wimsatt (1994), ecological entities such as organisms, species or assemblages have the potential to differ in an extremely large number of ways, because they occur at relatively high levels of biological organisation. For example, they may differ in many possible aspects of morphology, function, composition, size, lifespan, behaviour, spatial location, history or interaction with other entities. With so many possible dimensions of difference, it can be argued from basic principles of combinatorics that the probability of two entities being identical in all respects quickly becomes vanishingly small (Ulanowicz, 2009).

The central question to ask when dealing with disparity is therefore: ‘disparity in what?’. Recognising disparity as an essential component of diversity (Figure 1.1) is valuable precisely because it forces those seeking to describe diversity to think about which kinds of differences they are interested in. There is no single ‘right’ measure of disparity. The kind of disparity underpinning a particular study of diversity should therefore always be made explicit. For example, if phylogenetic differences are used we are studying ‘phylogenetic diversity’. If differences in morphology are the focus then it is ‘morphological diversity’, if differences in functional traits then we are dealing with ‘functional diversity’. Likewise we could describe ‘vegetation height diversity’, ‘nitrogen cycling diversity’, ‘cell growth diversity’, etc. The possibilities are almost endless. The differences chosen determine the ‘lens’ through which diversity is viewed, this view being one of many possible perspectives. Diversity can be described in a consistent way from each of these different perspectives, however, by identifying the variety, balance and disparity components of diversity, at any scale or level of organisation, for any of the compositional, structural or functional dimensions of systems (such as those described by Noss, 1990).

In some studies, the differences of interest are the same differences used to distinguish the types from each other in the first place. For example, a series of fossil specimens may have been classified using morphological features. A researcher may then be interested in determining whether the specimens from one site have greater morphological diversity than specimens from another site. There are many cases, however, where other sorts of differences may also be of interest, besides the ones used to distinguish the types. For example, a sociologist may have classified people on the basis of nationality, and may then wish to examine how the different nationalities differ in their food preferences. Or an ecologist may wish to study the functional differences between species classified according to morphological or phylogenetic criteria. Many possible types of differences among species may be of interest to ecologists, apart from those used to create the taxonomic classification (e.g. differences in various ecological functions, differences in genetic variability, morphology, value to humans, population dynamics etc.).

Ignoring the disparity component is equivalent to assuming that all types are equally different from each other — an assumption which is almost guaranteed never to be true, given the number of possible ways ecological entities can differ. Studies of so–called 'species diversity' that include only variety and balance, and ignore disparity, assume that the only differences between species that matter are the ones used to construct the taxonomic classification, and the differences in abundance between the species. These assumptions become especially problematic when dealing with questions about ecosystem functioning or resilience, because taxonomic differences between species do not always correlate well with functional differences (Naeem and Wright, 2003; Hooper *et al.*, 2005).

In light of the above, I would recommend that the term 'species diversity' not be used for the incomplete concept of diversity that excludes disparity. Calling this 'species diversity' suggests that there is only one possible way of looking at diversity among species. This type of diversity should rather be called 'taxonomic diversity'. If disparity is not specified explicitly, the differences being considered are, in fact, the differences that were used to construct the taxonomic classification.

Recognising the multitude of possible dimensions of disparity that can be measured for the same set of types (e.g. species) is the first step towards truly understanding the wealth associated with biodiversity. While variety and balance are relatively simple to measure, they cannot adequately represent the pervasive difference and heterogeneity that is the lifeblood of diversity. To do this it is essential to include disparity in our concept of diversity.

While disparity has been neglected as a component of biodiversity, it has been studied extensively in its own right in ecology, although not under the same name. Differences between species play a central role in a large body of ecological theory that addresses stable coexistence of species and ecological community assembly (MacArthur and Levins, 1967; Abrams, 1983; Tokeshi, 1999; Weiher and Keddy, 1999; Keddy, 2001; Tilman and Lehman, 2001). The theory of 'limiting similarity' states that there is a limit to how similar a set of species can be if they are to coexist stably (Abrams, 1983). In general, the more similar species are with respect to habitat and resource requirements, the more intense the competition between them will be, and this can be an important factor determining how ecological communities are assembled (Tokeshi, 1999; Keddy, 2001). On the other hand, strong environmental stresses or disturbances can increase similarity among species, because these environmental 'filters' place restrictions on the trait combinations that are feasible in a particular habitat (Poff, 1997). The debate around neutral theory in recent years has also centered around the extent to which similarities and differences in species characteristics influence community assembly and the maintenance of diversity (Hubbell, 2001; Chave, 2004; Adler *et al.*, 2007; Leibold, 2008). It is ironic that disparity has featured so prominently in theories explaining the maintenance of 'diversity' (species richness) in assemblages, yet it has seldom been included in the concept of diversity! Disparity has been seen as a stabilising mechanism (Adler *et al.*, 2007), as something that creates diversity, rather than as an expression of diversity itself.

Ecologists have long recognised the multidimensional nature of 'difference' between species; this is embodied in the concept of the niche. Grinnell (1917) and Hutchinson (1957) developed the concept of a species' niche as a hypervolume within a multidimensional space, where the axes of the space are biotic and/or abiotic variables (resources). The hypervolume indicates the combinations of resources needed by the species to maintain a viable population. This concept of the niche emphasises the multitude of different ways species may differ from each other in their responses to the biotic and abiotic environment.

Elton (1927) suggested a slightly different concept of the niche: a multidimensional space where the axes of the space reflect the impact of the species in its environment, particularly its position in a trophic network or food web. The Eltonian niche concept has recently been expanded into the concept of the functional niche, defined by the multiple different functional effects a species may have on its biotic or abiotic environment (Rosenfeld, 2002). This concept emphasises how species differ in their functional effects, i.e. in what they *do* rather than in what they *need* (Devictor *et al.*, 2010). Understanding the functional effects of species has become increasingly important to ecologists in recent years, in light of the need to predict the effects of human activities on biodiversity, ecosystem functioning and the provision of ecosystem services (Webb *et al.*, 2002; Hooper *et al.*, 2005; McGill *et al.*, 2006; de Bello *et al.*, 2010).

Species influence ecosystem functioning *via* their functional traits: morphological, phenological or ecophysiological characteristics that have known relationships to ecological functions (Violle *et al.*, 2007). Functional traits determine both species' responses to the environment and their effects on the environment (Lavorel and Garnier, 2002), and can therefore be used to characterise both Hutchinsonian and functional niches. Measuring how species differ from one another in various different functional traits is therefore a useful way of quantifying differences in functioning, or functional disparity, among species.

Several authors have recognised the potential of functional trait–based approaches to provide a 'common currency' for integrating phylogenetics, community ecology, ecosystem ecology and biodiversity, allowing ecologists to address questions about the effects of changes in biodiversity on the functioning of ecosystems (Díaz and Cabido, 2001; Webb *et al.*, 2002; McGill *et al.*, 2006; Webb *et al.*, 2010). A large amount of research in recent years has focused on understanding the ecological and evolutionary significance of plant functional traits and on developing standardised protocols for measuring them (e.g. Weiher *et al.*, 1999; Westoby *et al.*, 2002; Lavorel and Garnier, 2002; Cornelissen *et al.*, 2003; Reich *et al.*, 2003; Wright *et al.*, 2004, 2005; McGill *et al.*, 2006; Westoby and Wright, 2006). The term 'functional diversity' has become increasingly common in the ecological literature (Cadotte *et al.*, 2011). However, there is still much confusion about what functional diversity is and how it is related to biodiversity or to taxonomic diversity. There is an urgent need for a better integration of these concepts.

1.2.3 Functional diversity

Various definitions of functional diversity have been proposed. These include 'the value and range of functional traits present' (Díaz and Cabido, 2001), 'the amount of interspecific variation in functional traits in a community' (Poos *et al.*, 2009), and 'the distribution of functional units (e.g. species) in a multidimensional space' (Villéger *et al.*, 2008). It has also been used to refer to the complexity of food webs (Hulot *et al.*, 2000). The most common usage of the term, however, seems to be simply 'how functionally different different species are' (Schleuter *et al.*, 2010). In this sense functional diversity refers only to functional *disparity* in the variety–balance–disparity framework presented in the previous section (Figure 1.1). According to this framework, functional *diversity* includes the variety (richness), balance (evenness) and disparity of the species (or other entities of interest), where the disparity component describes differences in function. Functional diversity is one way of describing the multifacted concept of biodiversity. It would therefore be more appropriate to call functional diversity 'a type of biodiversity' rather than 'a component of biodiversity' (as in Petchey and Gaston, 2006, p753). Variety, balance and disparity are the fundamental components of functional diversity or any other type of biodiversity.

Mason *et al.* (2005) introduced a framework identifying three components of functional diversity: functional richness, functional evenness and functional divergence. On the surface, these appear to be conceptually equivalent to variety, balance and disparity (Figure 1.1), but closer examination reveals otherwise. Mason *et al.* (2005) define functional richness as 'the amount of niche space filled by species in a community'. It describes the range of trait values present in an assemblage and is therefore a measure of how different the component species are, i.e. a measure of disparity. Functional evenness is 'the evenness of abundance distribution in filled niche space', and functional divergence is 'the degree to which abundance distribution in niche space maximises divergence in functional characters within the community' (Mason *et al.*, 2005). Functional evenness and functional divergence both describe aspects of the dispersion or spread of species in a functional space, and are therefore also both measures of disparity. All three aspects of functional diversity proposed by Mason *et al.* (2005) are, therefore, measures of functional *disparity*. The conceptual framework and indices proposed by Mason *et al.* (2005) will be critiqued further in Chapter 2.

Recent work on 'functional diversity' shows that the missing disparity component of functional diversity is, therefore, starting to be integrated into the concept. Recognising that functional disparity is only one aspect of functional diversity is an important step towards better integrating concepts of functional diversity and taxonomic diversity, which are sometimes thought of as 'two very different concepts' (Mouillot *et al.*, 2005). The variety–balance–disparity framework (Figure 1.1) can be extremely useful in guiding work on functional diversity. As will be seen in Chapter 2, knowing which components of diversity are being measured by a particular functional diversity index allows users to think more carefully about what they are measuring and why. Many functional diversity indices have already been proposed, and there is potential for the situation to become even more confusing than it is for taxonomic diversity, because of the multidimensional nature of disparity.

Functional diversity studies to date have predominantly focused on functional *differences* between species and how these influence *ecosystem functioning at a particular point in time* (e.g. Tilman *et al.*, 1997; Díaz *et al.*, 2004, 2007; de Bello *et al.*, 2010; Villéger *et al.*, 2010; Vogt *et al.*, 2010; Díaz *et al.*, 2011). The relationship between disparity and resilience, the ability of a system to maintain its current functioning into the future, has hardly ever been explored. To do this, we need to turn disparity on its head somewhat, and consider *similarities* among species as well as differences, because it is these similarities that are thought to provide the functional redundancy that underlies the 'insurance value' of biodiversity.

1.2.4 Redundancy

Redundancy in a system refers to the existence of more than one means or set of resources to perform an activity or function, or the repetition of parts or subsystems (or whole systems) to provide a backup in case of primary system failure (`www.businessdictionary.com`). In biological systems it refers to the presence of multiple entities that can perform a particular function, or multiple different ways that a function may be performed (Walker, 1992, 1995; Naeem and Li, 1997; Thomas, 1993; Vavouri *et al.*, 2003). Before investigating why the concept has been so contentious in ecology (see §1.1), it is useful to take a broader look at the meaning of the term and its use in other contexts.

In general use the word redundancy has a negative connotation because it implies something excessive or unnecessary. A redundant entitity is 'surplus to requirements; unnecessary or superfluous' (`www.thefreedictionary.com/redundancy`). Redundancy also describes 'excessive wordiness or repetition in expression' (in linguistics), and 'a dismissal of an employee from work for being no longer necessary; a layoff' (in business). However, when associated with systems, redundancy is generally seen as a positive attribute which provides resilience or robustness (Low *et al.*, 2003).

Walker (1992) introduced the term redundancy to describe the presence in ecological assemblages of multiple species which function similarly with respect to a particular function, but which may differ in other respects, particularly in their environmental responses and tolerances. The concept was not intended to have a negative connotation or to suggest that certain species are superfluous or unnecessary, but rather to describe a positive attribute of ecological systems proposed to be important for resilience. The choice of the term was probably unfortunate, given the negative connotations associated with redundancy outside the systems context. Walker himself later regretted using it because of the negative reaction it evoked, and subsequently avoided it as much as possible (Brian Walker, pers. comm.).

The misunderstanding of Walker's concept of redundancy also stemmed from a failure by biodiversity scientists to fully appreciate the multidimensional nature of disparity. Biodiversity–ecosystem functioning studies in the late 1990's and early 2000's focused largely on single functions (usually productivity), because this was tractable for manipulative experiments (e.g. Naeem *et al.*, 1994; Tilman *et al.*, 1996; Hector *et al.*, 1999; Hooper *et al.*, 2005). This led to a tendency to consider only single functional roles for species, with the implicit assumption that species similar in one functional role are similar in other functional roles as well, like (functionally) identical copies or 'analogues'. If only one dimension of functioning is considered, certain species will appear dispensible or superfluous. As described in §1.1, this unidimensional view of redundancy caused conservation biologists to be alarmed by the concept, and the discussion about redundancy was unfortunately abandoned (a case of the 'baby' being thrown out with the 'bathwater').

However, species do not need to be identical in all respects for redundancy to be present in an ecosystem! If two or more species are similar with respect to a particular function, such that they are able to compensate for each other should one disappear, then redundancy is present in the system *with respect to that function.* It is highly unlikely that these species will be similar in all other aspects of their functioning, as has been argued on the basis of combinatorics in §1.2.2. So redundancy, like disparity, really only makes sense with reference to a particular function. It is not meaningful to talk about 'redundant species' in a general sense, just as it is not meaningful to talk about 'disparate species' in a general sense, without specifying in what way they differ or are similar. Considering redundancy on a per–function basis immediately makes the concept of redundancy much less controversial.

At this point it is useful to compare Walker's concept of redundancy with concepts from other fields of study. Probably the most comprehensive typology of redundancy in complex systems is that presented by Low *et al.* (2003). This incorporates ideas from genetics, engineering design and social sciences and identifies five types of redundancy which may be present in social–ecological systems, which I shall call types 1 to 5:

1. Multiple identical in–use copies
2. Multiple nonidentical in–use copies
3. Many rules, one outcome

4. Backup systems not currently in use
5. Redundant strength to reduce margins of error

The first three types differ from the last two in that they describe redundancy provided by 'in–use' copies of system elements. The last two types describe redundancy provided by 'backup' copies that do not contribute to functioning unless the primary components fail. Types 4 and 5 are common in information theory and engineering. Redundancy is a common feature of engineered systems, where duplication or repetition of elements provides alternative functional channels in case of failure. For example, redundant parts in electronic equipment can substitute for others that malfunction or fail, or augment output when demand for a particular output increases (type 4). In information theory, redundancy refers to the repetition of messages, which is important for reducing transmission errors (type 5) (Low *et al.*, 2003). These two types of redundancy are probably not important in biological systems, because redundancy in biological systems is not planned, and no entities have the provision of backup functioning as their only purpose — all components are 'in use'.

The first two types describe redundancy provided by multiple copies of 'in–use' entities, the difference between them being in whether the copies are identical to each other or not. Walker's concept of redundancy corresponds to type 2, but is often misunderstood to be type 1. In genetics, both type 1 and type 2 redundancy have been described. Geneticists usually refer to the presence of identical copies of genes as 'redundancy', and the presence of nonidentical (partially similar) copies as 'partial redundancy' or 'degeneracy' (Tononi *et al.*, 1999; Edelman and Gally, 2001), with a continuum of degrees of similarity possible (Pickett and Meeks-Wagner, 1995). Identical copies of genes, produced during gene duplication events, tend to diverge fairly rapidly as each copy acquires new functionality or mutations. The end result is that redundancy provided by identical gene copies (type 1) is relatively rare compared to redundancy provided by nonidentical copies (Thomas, 1993; Vavouri *et al.*, 2003). Type 1 redundancy is, however, important under certain specific conditions, such as when the function performed by a gene is extremely beneficial to the organism and can be enhanced by having many identical copies of the gene (e.g. genes that facilitate resistance to organophosphorus insecticides in mosquitoes) (Low *et al.*, 2003).

The third type of redundancy, 'many rules, one outcome', refers to the presence of redundant pathways in networks of interacting entities, such that removing one or more entities has no effect on the final or aggregate outcome. The entities in this case may even have no apparent similarities except that they contribute to the production of a particular function or end product. This type of redundancy has also been called 'distributed robustness' and has been shown to be important in maintaining metabolic pathways or developmental sequences even when key functional components are missing (Wagner, 2005).

For this work I chose to focus on similarities between species that are reflected in easily measurable functional traits, which allowed me to collect functional data for a large number of species. This is equivalent to assuming that only species with observable similarities are able to provide redundancy for a given function. This may underestimate the amount of redundancy present, because it excludes the possibility of type 3 redundancy. Assessing type 3 redundancy, however, requires data on species interactions, which are simply not available for the majority of species.

I chose to use the term 'redundancy' as originally intended by Walker (1992), to refer to functional similarity among *nonidentical* species, in order to locate the work within the context of the debate about redundancy in ecosystems. Suggestions for alternative terms will be made at the end of the thesis (Chapter 5). I also chose to study functional disparity and redundancy between taxonomically defined species, rather than deriving a new functionally–based classification of individuals for each function of interest. Using species provides a common currency for analysing the redundancy associated with different functions, a currency which is familiar to biodiversity scientists and conservation managers. Some more technical reasons for this choice will be discussed in Chapter 2.

Having redundancy in a system provides 'insurance' (Naeem and Li, 1997) which allows the system to continue functioning in the face of disturbances. However, before we can look more closely at how this works, we need a better understanding of resilience.

1.2.5 Resilience

The proposal that diversity promotes stability in ecosystems has a long history in ecology. Early field evidence suggested that more diverse ecosystems were more stable in terms of population fluctuations and resistance to invasions (MacArthur, 1955; Elton, 1958). Theoretical work using different types of models appeared to contradict these observations, however (Gardner and Ashby, 1970; May, 1972), and the period between 1950 and 1980 was characterised by a great deal of debate about this issue (e.g. Goodman, 1975; McNaughton, 1977).

The more recent drive to understand the role of biodiversity in ecosystem functioning has led to a revival of theoretical work on diversity–stability relationships (Loreau and Behera, 1999; Tilman and Lehman, 2001; Loreau *et al.*, 2002), adding to earlier work by King and Pimm (1983) and Pimm (1984). A range of empirical studies has also been published on various aspects of the diversity–stability relationship (reviewed in Schmid *et al.*, 2001).

It has become increasingly clear that stability, like diversity, is a complex and scale–dependent concept, and interpretation of any relationship between the two will depend on which aspects we choose to study. Not surprisingly, stability in ecosystems has been described or measured in a wide variety of different ways. Some consider stability under 'normal' conditions, while others consider it in relation to discrete disturbance events (Lepš, 2005). Under 'normal' conditions, stability may refer to low temporal variability in a population (MacArthur, 1955; Koenig and Haydock, 1999), low variability in aggregate ecosystem properties such as total biomass or net respiration (McGrady-Steed *et al.*, 1997; Naeem and Li, 1997), low susceptibility of a community to invasion (Elton, 1958; McGrady-Steed *et al.*, 1997), or a lack of directional changes in community composition (Lepš, 2005).

The concept of resilience was introduced by Holling (1973) to describe a particular notion of ecosystem stability. He suggested that ecologists should see stability less in terms of equilibrium states and more in terms of persistence of system components and interactions (Holling, 1973). Changes in the abundances or the spatial distributions of system components occur continuously, yet the character and functioning of a system may persist over long periods. This is well illustrated by work on spruce budworm pest outbreaks in Canadian forests, where wide fluctuations in the populations of budworm and balsam fir trees (extreme instability from an equilibrium point of view) have been shown to be important for the persistence of the budworm, its natural enemies, balsam fir, and other dominant tree species in the long term (Holling, 1973). Later work highlighted the role of periodic system reorganization (the 'adaptive cycle') in maintaining resilience, when disturbances cause resources accumulated within the system to be released and open the system up to the introduction of novelty, such as new species or interactions (Holling and Gunderson, 2002). An important contribution of Holling's work to the thinking about stability in ecosystems was his emphasis on change as the means by which stability is achieved, and the insight that change does not necessarily imply a lack of stability.

While measures of population fluctuations or changes in species composition reflect system behaviour around a local equilibrium, Holling's concept of resilience includes the possibility of multiple equilibria. Ecosystems are seen to occupy a 'stability landscape' with multiple possible equilibrium points or domains of attraction (Gunderson, 2000). Resilience is determined by the magnitude of disturbance a system can absorb before crossing a threshold into another domain of attraction (Gunderson, 2000). Resilience therefore describes a system's ability to persist in a particular self–organised state and to maintain the functioning associated with that state. This persistence is achieved through fluctuation and variability.

Some authors have defined resilience more narrowly, as the rate at which an ecosystem returns to its previous state after a disturbance event (e.g. Pimm, 1984; Tilman and Downing, 1994; Díaz and Cabido, 2001). This definition of resilience is widely used in the fields of engineering and physics to describe system behaviour around a single equilibrium, and has been called 'engineering resilience' by Holling (1996), to distinguish it from the ecological resilience described above. In this study I use the term resilience in the sense of Holling (1996), to refer to ecological rather than engineering resilience.

Resilience is sometimes also called 'robustness' (e.g. Wagner, 2005; Levin and Lubchenco, 2008; Whitacre and Bender, 2010), particularly in the fields of genetics and molecular biology. It is also conceptually related to the concept of sustainability, but implies something more active than either robustness or sustainability. As McMurry (2010, p1) put it:

> "Resilience implies action, as in 'building resilience'. To be resilient suggests an inner toughness: the strength, as its etymology tells us, to 'jump back' to a previous state. Sustainability, by contrast, suggests a defensive posture: a desire to stay the same, to resist change, without the attractive ability to push back against change and win out. Resilience also connotes a measure of risk, while sustainability suggests that systems are set: they simply need to be cared for and so carried forward. Resilience acknowledges that risk is a constant, and that systems are always in a struggle against dissipation. If the seas are always calm and the weather mild, you dont need to be resilient. But in this world, you must be resilient to survive."

The above quote suggests that resilience is always a positive or desirable system attribute. While it always has a positive effect on system 'survival', whether resilience is considered positive or negative from a human perspective depends on whether the functions being maintained are considered desirable or not. For example, resilience can be undesirable if it allows diseases or destructive patterns of overconsumption to persist (Levin and Lubchenco, 2008), or prevents restoration of desirable ecosystem services (Troell *et al.*, 2005).

Current theories see the following as important in generating resilience in ecosystems: (1) the system components—biotic and abiotic entities/agents, (2) the capacity for innovation in response to change, (3) the relationships and interactions that link components, including the nature of feedbacks, and (4) the ability to maintain continuity through space and time, through seed banks, biotic legacies and other forms of ecological memory (Carpenter *et al.*, 2001; Cumming *et al.*, 2005).

Biodiversity describes the system components: how many there are (variety), their relative abundances (balance), and the similarities and differences between them (disparity) (point 1 above). Biodiversity, and particularly functional diversity, has been proposed as one of the important factors that determines the capacity of ecosystems to respond to change (point 2), by determining the possibility for functional compensation. Interactions between species, and their spatial and temporal arrangement, are also important for resilience (points 3 and 4 above). However, the focus of this study is on points 1 and 2 above — the functional similarities and differences between species and the way these similarities and differences determine the potential for various functions to be maintained over time in species assemblages. The following section describes in more detail how this is proposed to work.

1.2.6 How functional diversity promotes resilience

The complementary roles of redundancy and response disparity

Functional diversity is thought to promote resilience by making functional compensation possible. Functional compensation occurs when substitution among functionally similar entities facilitates the maintenance of a particular function. One way such compensation can occur is through changes in the balance (abundance) of functionally similar species. If a species that performs a particular function declines, the function can be maintained if other, functionally similar species increase in abundance. For example, palatable grass species typically decrease in abundance due to heavy grazing in rangelands, while unpalatable species increase (Lavorel *et al.*, 1997). Although the unpalatable species do not provide fodder for livestock, increases in their abundance allow other functions performed by the palatable grasses to be maintained in the ecosystem, such as soil protection, nutrient cycling, and soil moisture retention. This kind of functional compensation has been described in many different species assemblages including among graminoid species in rangelands (McNaughton, 1977; Walker *et al.*, 1999), plankton in lakes (Frost *et al.*, 1995; Klug *et al.*, 2000), estuarine fish (Villéger *et al.*, 2010) and crustose algae in marine intertidal assemblages (Menge and Lubchenco, 1981).

The presence of redundancy in a system is essential for functional compensation to occur. The similarities among species determine the levels of redundancy associated with particular functions (§1.2.4). However, the differences among species are also important. Walker *et al.* (1999) and Elmqvist *et al.* (2003) have emphasised that species with similar functional effects are able to compensate for each other *not only because of their similarity, but also because they differ in their responses to disturbance or stress.* The term 'response diversity' has been used to describe differences in the response characteristics of species (Chapin *et al.*, 1997; Elmqvist *et al.*, 2003). Under the framework used here (Figure 1.4), a more appropriate term would, however, be *response disparity.*

The advantage of having response disparity amongst functionally similar entities is straightforward to see. The differences between entities will tend to confer upon them different weaknesses, so that a particular disturbance is unlikely to present the same risk to all the entities at once. This same reasoning lies behind portfolio theory in economics, ensemble approaches in machine learning and the use of diverse problem solvers in decision making (Whitacre and Bender, 2010). Response disparity can promote resilience by providing multiple distinct paths to a particular state.

The way redundancy works together with response disparity to provide functional compensation is best explained using examples. Peterson *et al.* (1998) described how in Ugandan forests, seed dispersal is performed by a range of different–sized mammals, from mice to chimpanzees. While the small mammals are negatively affected by localised disturbances, the larger, more mobile species are not, and can therefore maintain the seed dispersal function. This allows tree populations to persist through different sized disturbances. Differences in size, spatial scale of operation or lifespan often translate into differences in response traits, providing a 'cross–scale' dimension to resilience (Peterson *et al.*, 1998). In grasslands, differences in the responses of plant species to rainfall events allow green biomass production to be maintained during periods of variable rainfall. Species that increase their growth rate after a shower can produce green biomass quickly, but tend to dry out rapidly between showers. During dry periods, the biomass production function is maintained by other species which respond less rapidly to rainfall but which dry out more slowly between showers (McNaughton, 1977). Both of these examples show how function lost by the decline of certain species can be compensated for by other species that are less severely affected by a particular disturbance.

It is therefore not only the similarities between species that are important for resilience, but the way these similarities are combined with differences. The combination of redundancy and response disparity enhances the capacity of an assemblage to maintain its functioning by means of functional compensation.

The role of balance in resilience

The balance of an assemblage also has important implications for functional compensation. Species abundance distributions (SAD's) in biological assemblages are typically highly uneven, appearing as an exponentially decreasing 'hollow curve' on an arithmetic scale (Preston, 1948). This means that most of the individuals, biomass and cover in an assemblage are made up by only a few species. Most of the species present occur at low abundances in the tail of the distribution (Figure 1.2). Hurlbert (1977) appropriately called these tail species the 'great biocenotic proletariat'.

Consequently, the functional traits of the dominant species will largely determine the functioning of the assemblage at a given point in time (the 'biomass ratio hypothesis'; Grime, 1998). This is because they make up most of the individuals present, and their functional traits dominate the assemblage. Changes in the dominant species can have large impacts on ecosystem functioning if the new species are functionally dissimilar to the original species, as has been documented in many systems where invasive aliens have become dominant (Witkowski, 1991; Tabacchi and Planty-Tabacchi, 2003; Dwire and Kauffman, 2003; Dye and Jermain, 2004; Dukes and Mooney, 2004; Holmes *et al.*, 2005; Richardson *et al.*, 2007; Villéger *et al.*, 2010). If functioning is to be maintained through time, therefore, sufficient redundancy must be present for the functions performed by the dominant species.

Walker *et al.* (1999) predicted that because of the shape of the SAD, a large proportion of this redundancy will be provided by 'minor' species in the tail of the abundance distribution, and that the tail species are therefore important for resilience. They also predicted that response disparity will be high among groups of species providing redundancy for particular functions, so that functioning can be maintained in a wider variety of conditions. I have formalised these proposals as two hypotheses about the way functional diversity produces resilience in species assemblages (Box 1.3).

Walker *et al.* (1999) provided evidence of similarities in functional traits between dominant and minor species from a savanna rangeland, and showed how changes in grazing pressure could lead to functional compensation. However, they used a rather limited dataset, containing only 22 graminoid species, and five functional traits. Few other studies have explicitly examined functional similarities or differences between dominant/abundant species and those in the tail, for a number of reasons.

Firstly, few datasets are suitable for studying patterns of functional redundancy and disparity among tail species. Tail species are often removed from ecological community datasets, either because they are not considered functionally important, or because they are not considered 'permanent' members of the assemblage (Grime, 1998). Tail species are also often not thoroughly sampled in the first place because a large amount of effort is required to do so, due to the asymptotic shape of species accumulation curves (Colwell and Coddington, 1994). A dataset with a well sampled tail is required to test the hypotheses of Walker *et al.* (1999).

Secondly, a number of methodological problems were identified by Walker *et al.* (1999). Fortunately, recent research has produced improved methods for measuring functional disparity (Mason *et al.*, 2003; Botta-Dukát, 2005; Mason *et al.*, 2005; Mouillot *et al.*, 2005), as well as standardised protocols for measuring plant functional traits (Cornelissen *et al.*, 2003). However, there are no standardised methods for measuring redundancy. Addressing the conceptual and methodological difficulties involved in measuring redundancy and response disparity will therefore be an important component of this thesis.

1.2.7 Summary and conceptual model

The conceptual exploration of the relationship between biodiversity and resilience developed in this chapter is summarised in Figure 1.4. Biodiversity is seen as having three components, variety, balance and

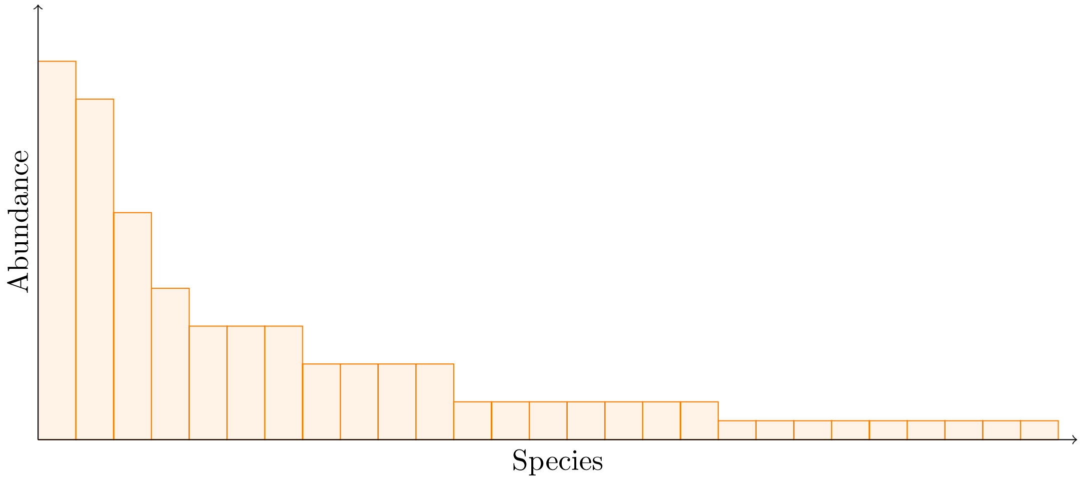


Figure 1.2: A generic representation of a typical species abundance distribution (SAD) on an arithmetic scale

1. Minor species in the tail of the abundance distribution provide redundancy for functions performed by the dominant species.
2. Groups of species that provide redundancy for each others' functioning differ in their response traits, thus providing response disparity.

Figure 1.3: Hypotheses of Walker *et al.* (1999) relating balance, redundancy and response disparity to resilience

disparity. The disparity component, describing differences among species, has generally been neglected by ecologists. Many different types of disparity may be considered, leading to many possible perspectives on biodiversity, such as phylogenetic diversity, taxonomic diversity, structural diversity or functional diversity. Functional diversity is increasingly being addressed in the quest to understand the relationships between biodiversity and ecosystem functioning in a changing world.

It is generally recognised that the functioning of an assemblage at a particular point in time is largely determined by the species that are dominant at that time (Grime, 1998). Less abundant species in the tail of the abundance distribution may contribute relatively little to functioning *at that point in time*, but these species have been proposed to be important in providing redundancy and response disparity which *enable functioning to be maintained over time* (Figure 1.4, Box 1.3).

The disparity component of functional diversity is of central importance in linking diversity and resilience (Figure 1.4). Disparity determines both redundancy (similarities among species) and response disparity (differences in species' responses to disturbance), which are proposed to work together to determine the system's capacity for functional compensation, and therefore its resilience. Other factors determining resilience, but not dealt with in this thesis, are indicated with dashed arrows.

Patterns of redundancy and response disparity may be different for each different ecological function performed by an assemblage, leading to a number of different perspectives on resilience. The overall resilience of an ecosystem is a function of the full set of functional perspectives, including possible interactions and tradeoffs between them.

1.3 Aims of this study

- To critically evaluate the proposition that biodiversity enhances resilience, by unpacking the concepts of biodiversity and resilience used by ecologists, and developing a conceptual framework linking biodiversity and resilience in assemblages of species.
- To contribute to resolving the conceptual and methodological difficulties experienced when measuring redundancy and response disparity.

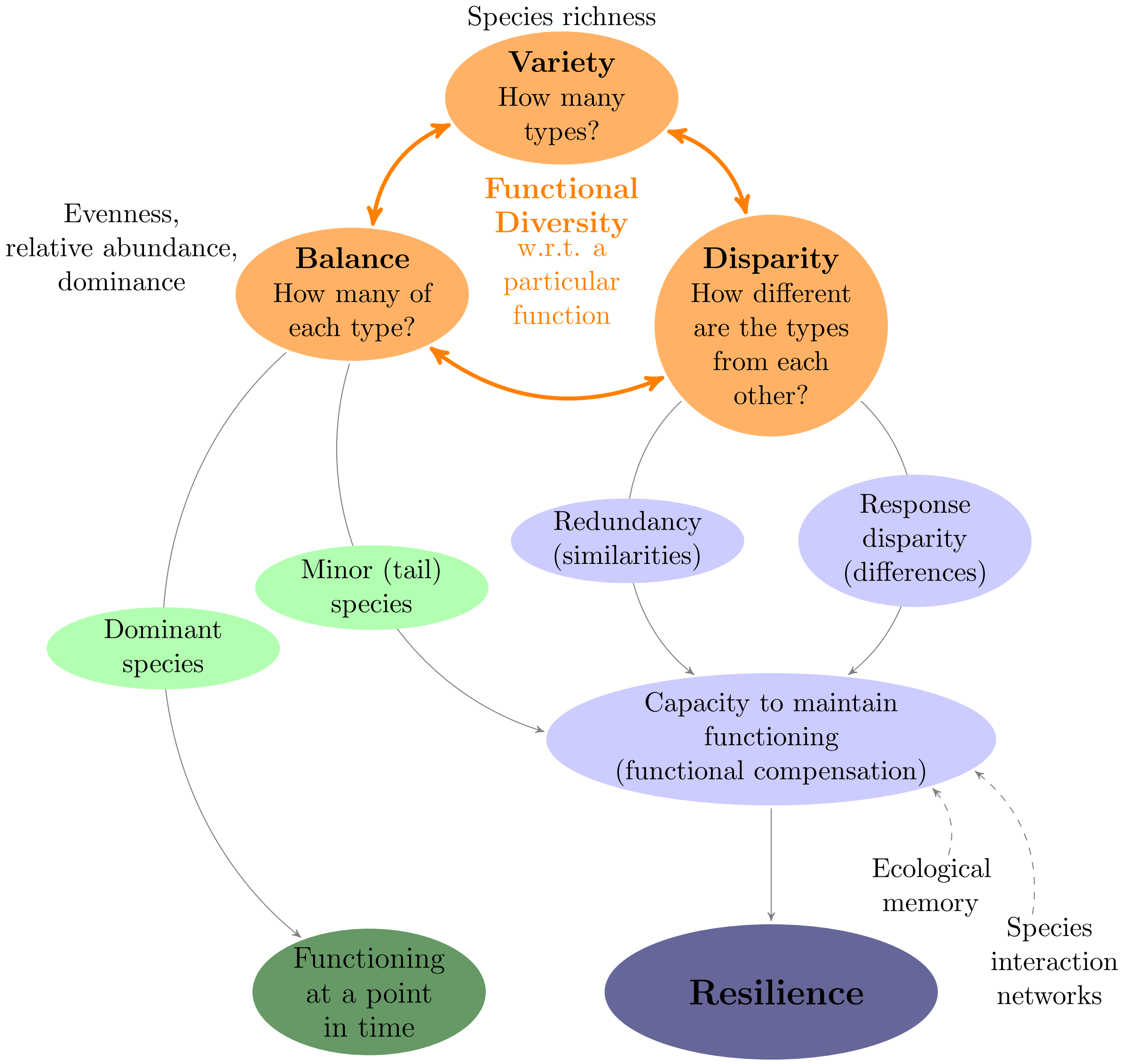


Figure 1.4: Conceptual framework linking biodiversity and resilience

- To test the hypotheses of Walker *et al.* (1999) about the role of redundancy and response disparity among minor species in providing resilience, using a larger number of species and functional traits than used by Walker *et al.* (1999), and for different functions separately.
- To investigate the relationships between redundancy and response disparity and commonly used measures of biodiversity often assumed to reflect resilience (species richness, species diversity).
- To evaluate the impact of three different land management regimes on the resilience of riparian plant assemblages.

1.4 Structure of the thesis

The first two chapters provide the conceptual and methodological foundation for the thesis. The first aim is addressed by the current chapter. Chapter 2 addresses the second aim by providing a critical analysis of current methods for measuring disparity and functional diversity. The usefulness of these methods for measuring redundancy is explored and a methodological approach with several novel features is presented.

The results of the empirical investigation of redundancy and response disparity in riparian plant assemblages are presented in Chapters 3 and 4. Chapter 3 primarily addresses the third aim, providing a much–needed empirical test of the hypotheses of Walker *et al.* (1999). In Chapter 4 I address the relationships between redundancy and response disparity and commonly used measures of biodiversity often assumed to reflect resilience (the fourth aim). I explore the implications of differences in species richness, composition and balance in the different management areas for resilience, as well as the implications of the results for land management and conservation. The last aim is addressed jointly by Chapters 3 and 4. Chapter 5 contains a broader synthesis of the implications of the results for our understanding of biodiversity, redundancy and resilience.

Chapter 2

Measuring disparity and redundancy: a critical review and development of methods

> "I say every dog looks like no other but that isn't true. Not entirely. Difference is slippery."
> — Mary Jo Bang.

2.1 Introduction

Given the proposed importance of redundancy in providing resilience in ecosystems, I have argued that it is time for ecologists to put redundancy back on the research agenda, and to re–evaluate and test the hypotheses of Walker *et al.* (1999) about redundancy and response disparity among dominant and minor species (Chapter 1).

One of the reasons these hypotheses have not been tested empirically is that it has been unclear how redundancy and response disparity should be measured. There are no well–established methods for measuring redundancy. Walker *et al.* (1999) encountered several problems with measuring functional similarities and differences between species. Since their paper was published many new methods for measuring 'functional diversity' (disparity) have been developed in this rapidly growing field (reviewed by Petchey and Gaston, 2002b; Cornelissen *et al.*, 2003; Petchey and Gaston, 2006; Mouchet *et al.*, 2010). However, no attempt has yet been made to investigate the potential of these methods for measuring redundancy, and few measures of response disparity have been proposed. This is in part due to the confusion around the concept of functional diversity and how it relates to disparity and redundancy, discussed in the previous chapter. In this chapter, I will critically evaluate some of the methods and approaches from the growing literature on functional diversity, with the conceptual framework presented in Chapter 1 as a guide, with the aim of finding and/or developing measures of these two aspects of disparity thought to be important for resilience.

Measuring functional redundancy is conceptually the same as measuring functional disparity, because similarities (redundancy) and differences (disparity) are two sides of the same coin (Figure 1.4). Two species that are 'very similar' could equally be described as being 'not very different'. Importantly, similarity (or difference) is a continuum rather than an either/or property, and a whole range of degrees of similarity or difference are possible (Petchey and Gaston, 2006). This is one reason why "difference is slippery". The other reason that difference is slippery is that it is multidimensional. Ecological entities affect and respond to their environment in a multitude of different ways (§1.2.2). Species can function very similarly in one respect yet very differently in another. For example, different species of aquatic macrophytes may all enhance water clarity, but have different effects on light penetration and oxygen concentrations, and different responses to flood disturbance (Takamura *et al.*, 2003). Patterns of similarity may be different for each different function studied. This dimensionality needs to be taken into account when measuring redundancy/disparity. It has already been shown (Chapter 1) that a failure to appreciate the multidimensionality of differences between species led to a misunderstanding of the concept of redundancy proposed by Walker (1992).

To test the hypotheses of Walker *et al.* (1999) (Box 1.3), it is necessary to:

1. measure species' functioning (because we need to know how species function before we can measure how functionally similar or different they are), in a way that takes the multidimensionality of functioning into account;
2. measure similarities among species (redundancy) for different functions separately (because redundancy is determined by similarity among species with respect to a particular function);
3. measure the differences in response to disturbances (response disparity) among subsets of species that perform a particular effect function similarly.

The first requirement is challenging at present, because our understanding of how species perform different functions is still fairly approximate (Díaz *et al.*, 2011). Requirements 2 and 3 involve measuring different aspects of disparity. However, disparity must be measured for different functions and different subsets of species separately in order to understand the interplay between redundancy and response disparity (Walker *et al.*, 1999).

The overall aim of this chapter is to find and/or develop methods that meet the above three requirements, to lay the foundation for testing the hypotheses of Walker *et al.* (1999) about the roles of redundancy and response disparity in the resilience of species assemblages. The above methodological requirements for testing the hypotheses of Walker *et al.* (1999) will now be discussed in more detail, together with a critical evaluation of existing approaches and methods, including those used by Walker *et al.* (1999). More detailed chapter aims will be specified at the end of this section (§2.1.4).

2.1.1 Requirement 1: measuring species' functioning

Ideally, species' functioning should be measured directly. This is routinely done in detailed autecological and ecophysiological studies, typically carried out at relatively small spatial scales (e.g. Knapp, 1985; Harrington *et al.*, 1989; Rood *et al.*, 2003; Kuzovkina and Volk, 2009; Myron, 2012; Takagi and Hioki, 2013). A few studies have directly measured species' contributions to a particular function at larger scales (e.g. Kremen *et al.*, 2002; Balvanera *et al.*, 2005). However, when seeking to quantify the functioning of several hundred species for several different functions at larger scales, such detailed studies are simply not practical.

Functional trait–based approaches have become increasingly popular for such purposes (Díaz and Cabido, 2001; Lavorel and Garnier, 2002; Díaz *et al.*, 2004; Garnier *et al.*, 2004; Westoby and Wright, 2006; Quétier *et al.*, 2007; Díaz *et al.*, 2007; Suding *et al.*, 2008; de Bello *et al.*, 2010). These approaches have become feasible thanks to the large amount of work that has been done on trait–function relationships in recent years, the availability of standardised protocols for measurement of traits, and the availability of electronic trait databases on the Internet (see §1.2.2). These developments address the concerns raised by Walker *et al.* (1999) about the need for ease of measurement and repeatability in studies of ecological functioning based on functional traits.

Functional traits are morphological, physiological and phenological traits which affect growth, reproduction and survival, the three components of individual performance (Violle *et al.*, 2007). In other words, they can be seen as surrogates of performance or functioning (Violle *et al.*, 2007). The link between functional traits and functions may be conceptualised as follows. Species possess many traits, and species perform many different functions (Figure 2.1). Each trait has a number of potential trait states (categories or values); for example the trait 'wood density' may be recorded as an ordinal trait, with trait states 'hard wood', 'medium wood' and 'soft wood', or as a continuous trait with measured values of wood density as the trait states. Trait states are combined in different ways in different species, and the combination determines the way in which a species will perform a particular function (Figure 2.1). Furthermore, if combined with information about the relative abundances of the species, functional traits can also provide information about the functioning of whole assemblages (because this is largely determined by the functioning of the most abundant species) (Villéger *et al.*, 2010; Díaz *et al.*, 2011).

It is widely recognised that different sets of traits underlie the various different functions performed by species (Cornelissen *et al.*, 2003). There is some overlap between these sets because each trait can be important for several functions. For example, the trait of spinescence is obviously important in plant anti–herbivore defence, but may also play a role in reducing heat or drought stress (Cornelissen *et al.*, 2003).

Species may contribute to functions in several different ways. Some functions are dependent on the traits of one particular species (e.g. pollination carried out by a host–specific fig wasp, products supplied by a particular species), while others are determined by a relatively small group of dominant species (e.g. provision of fodder by palatable grass species in rangelands, modification of the albedo effect by large

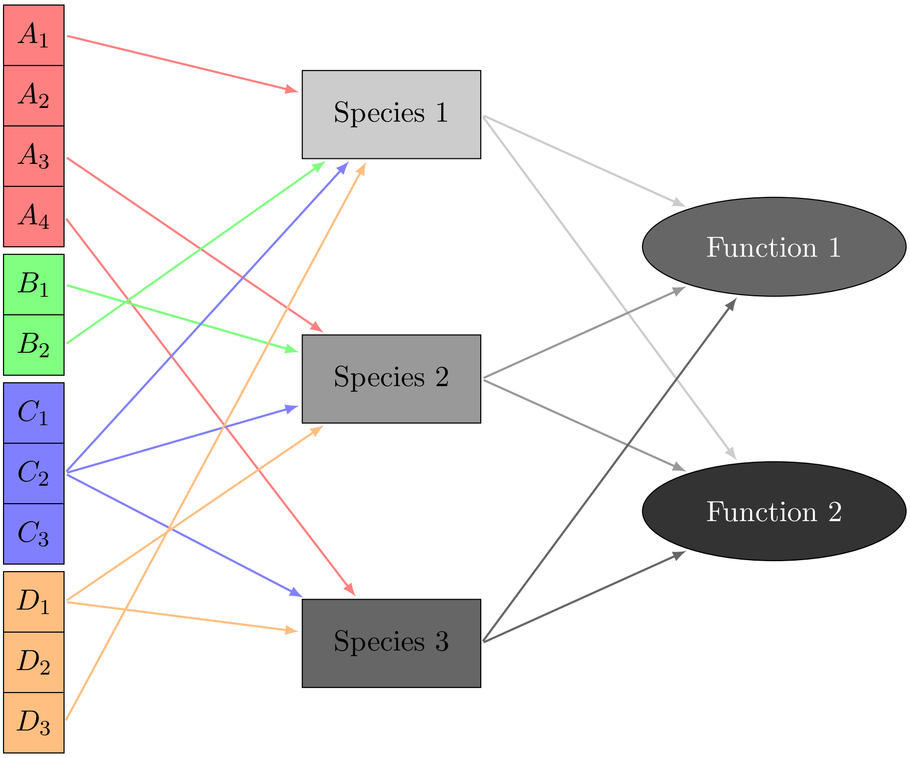


Figure 2.1: A conceptualisation of the way in which trait states and combinations of trait states affect species functioning. Four traits (A, B, C, D) are represented here, each with a number of possible trait states (categories or values, represented by subscripts). The trait states present and the way in which they are combined determine the way in which a species performs each of several functions. For example, traits A and B may be important in determining how species perform Function 1, while traits B, C and D may be important for Function 2. Species 1 differs from Species 2 and 3 in traits A and B, suggesting that Species 1 would perform Function 1 differently. Species 2 and 3 are, however, identical in traits B, C and D and would therefore be expected to perform Function 2 in a similar way.

deciduous shrub species that protrude above the snow). Yet other functions are performed by a large number of different species acting in concert (e.g. soil formation, nutrient cycling) (Díaz *et al.*, 2011).

Functional trait approaches to determining species' contributions to functioning assume that differences among species in traits relevant to a particular function translate into differences in the way the species perform that function. There are several reasons why this is not always a reasonable assumption.

Not all functions are determined solely by species and their traits; many involve physical processes and feedbacks between biotic and abiotic elements of the system as well. A good example is soil formation. Soil formation is affected by physical processes of weathering on a particular geological substrate and by the topography of the area, as well as by the actions of many different soil organisms, plants and animals which influence the rate of soil formation and the characteristics of the soil (Wardle, 2002). Another example is sedimentation in rivers, which is influenced by the traits of plants growing in or near the channel but also by physical factors such as channel shape, size, slope, geology, land use in the catchment, and the hydrological regime itself (Allen, 1982; Ellery *et al.*, 1993). Ecosystem services — ecological functions considered valuable by humans — additionally are influenced by human factors such as the socio–economic context and the values of the various social actors (Díaz *et al.*, 2011).

The link between species and functions is further complicated by the fact that the functioning of a species may vary depending on its context, for example its abiotic environment, its spatial location, or the identity of its neighbours or interaction partners (Power *et al.*, 1996; Wellnitz and Poff, 2001; Poff *et al.*, 2003). For example, a certain tree species may be an important food source for black rhino when elephant are present to push over trees, but not in the absence of elephant because rhino cannot reach the foliage. Such context–specific functioning is probably the rule rather than the exception, given the ubiquity of heterogeneity in ecological systems (Stewart *et al.*, 2000). Functions performed by mobile organisms, such as pollination and seed dispersal, require consideration not only of the local scale where the services are delivered, but also the distribution of resources at the landscape scale and the foraging ranges and dispersal movements of the mobile agents (Kremen *et al.*, 2007).

Furthermore, individuals of a species do not all have identical traits, and this intraspecific trait variation may have important influences on functioning (Pachepsky *et al.*, 2007). Functioning may also vary with the size, age or sex of the individual. For example, certain insects may function very differently at different life stages, or tree seedlings may function differently to adult canopy trees in a forest (Naeem and Wright, 2003).

Nevertheless, despite the above considerations, enough is known about the relationships between traits and functioning, particularly in plants, for functional traits to be used as a reasonable way of obtaining information about the functioning of large numbers of species (de Bello *et al.*, 2010; Díaz *et al.*, 2011). The rich and detailed literature about plant traits contains much information about the correlations among traits within species and the relationships between traits and functions. This literature includes observational studies of trait distribution across environmental gradients (e.g. Garnier *et al.*, 2004; Falster and Westoby, 2005b; Cornwell and Ackerly, 2009) and evolutionary lineages (e.g. Williams-Linera, 1997; Helmus *et al.*, 2010; Uriarte *et al.*, 2010), experimental studies of the effects of traits on ecological functioning (e.g. Kremen *et al.*, 2007) and theoretical models of trait distributions in communities and ecosystems (e.g. Bellingham and Sparrow, 2000; Silvertown, 2004). Synthesis of these studies has provided insight into important axes of trait variation among plant species (Shipley *et al.*, 2006; Chave *et al.*, 2009), and shortlists of important traits that influence species' functioning in predictable ways have been developed (Lavorel and Garnier, 2002; Cornelissen *et al.*, 2003).

Effect and response traits

Early functional trait work focused on classifying species into 'functional types' and identifying general 'plant strategies' (e.g. Grime, 1977; Noble and Gitay, 1996; Lavorel *et al.*, 1997; Westoby, 1998; Pausas, 1999; Pillar, 1999; Wilson, 1999). These classifications mostly described differences in the resource requirements and tolerances of species, including their responses to disturbance or stress — in other words, their Hutchinsonian niches (§1.2.2). The more recent focus on the effects of species on ecosystem functioning (i.e. species' functional niches) has prompted calls for the need to distinguish between response traits and effect traits when studying diversity–ecosystem function relationships (Díaz and Cabido, 2001; Lavorel and Garnier, 2002; Naeem and Wright, 2003; Hooper *et al.*, 2005; Suding *et al.*, 2008).

Response traits determine the response of a species to aspects of the biotic and abiotic environment, such as resource availability, climatic conditions or the disturbance regime. Effect traits determine the effect of a species on processes such as primary productivity, nutrient cycling, trophic transfers, and provision of non–food resources to other organisms (e.g. shade, building material, chemical compounds etc.) (Díaz and Cabido, 2001). Some traits act as response and effect traits simultaneously, for example, traits related to biogeochemical cycling. Plants growing in nutrient–rich environments tend to have traits that further contribute to nutrient–rich conditions at the site (Lavorel and Garnier, 2002).

Distinguishing between effect and response traits is crucial for testing the hypotheses of Walker *et al.* (1999), namely (1) that minor species in the tail of the abundance distribution provide redundancy for functions performed by the dominant species, and (2) that groups of species that provide redundancy for each others' functioning differ in their response traits, thus providing response disparity (Box 1.3). In order to test these hypotheses, redundancy in effect functions must be distinguished from disparity in responses to disturbance.

A potential danger in studies of ecological functioning based on functional traits is that insufficient thought may be given to which functions are actually being studied. This is a particular problem in functional diversity studies, where a large number of traits known to have some relevance to functioning are often lumped together to produce an overall measure of functional diversity (disparity) (Petchey and Gaston, 2002b). While such a combined measure of 'functioning' may be appropriate in some circumstances, the relation between such a measure and any particular function is usually unclear. If the aim of a study is to understand ecosystem functioning or resilience, the functions of interest should be clearly identified, and careful consideration given to which traits should be selected to best represent those functions, based on available knowledge about trait–function relationships (Petchey and Gaston, 2006). Redundancy and response disparity are properties that apply to functions and not to species (Chapter 1). It is therefore necessary to relate the measurement of redundancy to particular effect functions, and the measurement of response disparity to particular response functions.

2.1.2 Requirement 2: measuring redundancy

To assess the suitability of the many recently developed measures of disparity as measures of redundancy, it is necessary to first understand the different approaches to measuring disparity. It will then be possible to identify which, if any, are appropriate for testing the hypotheses of Walker *et al.* (1999) about the roles of redundancy and response disparity in providing resilience.

Assuming that functioning can be adequately represented by species' functional traits, studying patterns of redundancy requires, firstly, some way of measuring similarity (or dissimilarity) in functional traits among species, and secondly, it requires identifying which species perform a particular function similarly.

Similarity/dissimilarity measures

After collecting functional trait data for a set of species, an ecologist will typically have a matrix of trait values (columns) for each species in an assemblage (rows). The traits measured will often include several different types of variables (Table 2.1), which have different mathematical and statistical properties and which may be measured on very different scales. Combining these different variables into a measure of dissimilarity or disparity is one of the major challenges in functional diversity studies (Pavoine *et al.*, 2009).

All existing measures of disparity based on multiple traits use a 'dissimilarity metric' to calculate pairwise dissimilarities among entities (species). These dissimilarity values directly represent disparity — how different the species are for whichever characteristics you have chosen to measure. Dissimilarity is usually measured on a scale of 0–1, with identical species having a dissimilarity of zero and completely different species having a dissimilarity of one. Calculating pairwise dissimilarities for all possible pairs of species produces a matrix of dissimilarity values between each species and all others present in the assemblage.

The dissimilarity metric is therefore at the heart of all measures of functional disparity. Commonly used dissimilarity metrics include Euclidean distance, Manhattan, Gower and Bray–Curtis dissimilarities, as well as many usually referred to as 'similarity measures', such as the Jaccard and Sorenson indices (Legendre and Legendre, 1998). The problem with many of these metrics is that they can only be used with certain of the variable types listed in Table 2.1). For example, Euclidean distance can only be used with continuous data. Subtraction, multiplication and division operations are not meaningful for non–continuous variables, and these operations are required when calculating dissimilarities. These restrictions have been problematic for ecologists seeking to measure similarity or dissimilarity from multiple traits, because it is not always possible to measure all traits in the same way. For example, nominal traits such as growth form are difficult to measure as continuous variables, and in many cases the available information only allows traits to be measured as ordinal or binary (e.g. wood density categories or rooting depth categories) rather than as continuous. Walker *et al.* (1999) used only simple ordinal traits measured on

Table 2.1: Types of variables, with examples of functional traits belonging to each type. Different types of variables represent different levels of measurement, depending on how much information the numbers associated with the variable contain. For further details see Legendre and Legendre (1998) and Pavoine *et al.* (2009).

Variable type	**Description**	**Example**
Nominal	Categories which cannot be ordered.	Growth form (tree, shrub, climber etc.).
Ordinal	Categories which can be ordered or ranked.	Sprouting vigour (weak, moderate, strong).
Binary	Nominal variable with two categories or levels, usually coded as 0 and 1. Can be symmetrical (strictly two states, which state is assigned 0 is arbitrary, two species with zero values considered identical) or asymmetrical (category 1 represents presence, category 0 absence, of something, two species with zeroes not considered identical).	Symmetrical: woodiness (hard wood/soft wood), asymmetrical: nitrogen fixing ability (present/absent).
Nominal multichoice	Special type of binary variable with more than two categories.	Flower colour (red, blue, purple or yellow), each species is assigned a value of 1 for one of these colours and a value of 0 for the rest.
Fuzzy	Special type of nominal variable where entities may belong to more than one category (can be transformed to proportions).	Dispersal agent (wind, water, animal), where a species may be dispersed by two or more agents in varying proportions.
Continuous	Quantitative variables expressed in numerical form. Can be interval (arbitrary zero point, ratios between numbers not meaningful) or ratio variables (zero point and ratios both meaningful).	Plant height (ratio).
Circular	Special type of continuous variable related to time series.	Flowering start month (where December must be equally close to January and November).

the same scale (a scale of 1–5), which allowed them to treat the data as ranked continuous data and therefore to use Euclidean distance. Fortunately, recent extensions to the Gower metric (Podani, 1999; Pavoine *et al.*, 2009) have removed many of the restrictions on data type, making it possible to include a much wider range of functional traits than Walker *et al.* (1999) did, in a way that accounts for the unique statistical properties of each.

A pairwise dissimilarity matrix calculated from functional trait data contains information about the similarities and differences among the species in an assemblage. Pairwise dissimilarity matrices have been used in different ways to generate a large number of 'functional diversity' measures in the last decade (Table 2.2). These measures actually measure functional disparity, although some combine disparity with balance (Table 2.2). Three different approaches can be discerned:

1. The dissimilarity matrix is used to calculate a summary statistic such as the total or mean dissimilarity for the assemblage as a whole (FAD2, APWD, MFAD; Table 2.2).
2. The dissimilarity matrix is used as input to a clustering algorithm which produces a functional dendrogram. Disparity can then be measured as the number of species in each functional group (FGR) or the distance between species along the tree branches (FD, GFD; Table 2.2).
3. The dissimilarity matrix is used to place the species in a functional space using multivariate ordination methods, then the dispersion of species in this space is described (FRic, FEve, FDiv, multivariate dispersion, FDis, functional specialization; Table 2.2).

Unfortunately, the above approaches are generally applied in such a way that the wealth of information contained in the pairwise dissimilarity matrix is reduced to a single–number summary of disparity in the assemblage as a whole, and there is a strong emphasis on creating functional diversity *indices* (see Mouchet *et al.*, 2010; Schleuter *et al.*, 2010, for an overview). While these summaries have their place, they represent a substantial loss of the information contained in the original dissimilarity matrix.

Any of the 'pure' measures of disparity in Table 2.2 could easily be modified to provide an assemblage–level measure of redundancy (low disparity = high redundancy). Such a measure would describe the total, average or range of similarity present in the assemblage. However, this would not be very useful for testing the hypotheses of Walker *et al.* (1999). To test these hypotheses it is necessary to explore patterns of redundancy *within* the assemblage, to identify which species function most similarly to which other species and which species are functionally unusual. In other words, it is necessary to consider the different functional roles of each species individually, as well as the redundancy and response disparity associated with each of these roles. The three approaches outlined above provide suggestions as to how this might be done, but the focus needs to be shifted from calculating an assemblage–level summary measure to exploring the patterns of redundancy and response disparity within the assemblage.

Several authors have in fact recognised the value of being able to determine the contribution of individual species to the overall disparity of an assemblage, to answer questions about the conservation value of particular species (Vane-Wright *et al.*, 1991; Faith, 1992; Pavoine *et al.*, 2005; Mouillot *et al.*, 2008) and the possible impacts of species losses on ecosystem functioning (Petchey and Gaston, 2002a; Bellwood *et al.*, 2006; Mouillot *et al.*, 2008; Villéger *et al.*, 2010). Such measures may have potential to be modified to measure the amount of redundancy associated with each species.

Table 2.2: Existing indices for measuring functional diversity from multiple traits, with an indication of which of the three components of diversity, variety, balance and disparity, are being measured in each case. Indices designed to work with only one trait at a time (e.g. Mason *et al.*, 2003; Mouillot *et al.*, 2005) are not included.

Acronym	Name	Description	Aspect of diversity measured	Author(s)
FGR	Functional group richness	No. of functional groups derived by cluster analysis.	Disparity	Laliberté *et al.* (2010), etc.
FD	Functional diversity	Sum of dissimilarities among species within a community, calculated as branch lengths on a functional dendrogram.	Disparity	Petchey and Gaston (2002b)
GFD	Generalised functional diversity	Like FD but dendrogram includes all species in the (regional) species pool.	Disparity	(Mouchet *et al.*, 2008)
FAD1	–	No. of different attribute combinations, less than or equal to no. of species.	Variety	Walker *et al.* (1999)
FAD2	Functional attribute diversity	Sum of pairwise dissimilarities between species.	Disparity	Walker *et al.* (1999)
APWD	Average pairwise dissimilarity	Sum of pairwise dissimilarities between species divided by no. of pairwise comparisons.	Disparity	Heemsbergen *et al.* (2004); Petchey and Gaston (2006)
MFAD	Modified FAD2	Mean functional dissimilarity, mean pairwise dissimilarity between 'functional units' (species with identical traits combined into FU's).	Disparity	Schmera *et al.* (2009a)
FRic	Functional richness	Multivariate equivalent of range, convex hull volume occupied by species in functional space.	Disparity	Cornwell *et al.* (2006); Villéger *et al.* (2008)
FEve	Functional evenness	Regularity in the distribution of species abundances within the convex hull volume occupied by the assemblage in functional space; sum of MST branch length weighted by relative abundance.	Balance + disparity	Villéger *et al.* (2008)
FDiv	Functional divergence	Divergence of species abundances from the centre of gravity of the assemblage within the functional space; deviance from the mean distance to the centre of gravity.	Balance + disparity	Villéger *et al.* (2008)
–	Multivariate dispersion	Dispersion of species in functional space; multivariate equivalent of variance (MAD); mean distance of species from centroid or spatial median.	Disparity	Anderson *et al.* (2006)
–	Functional specialization	As for multivariate dispersion but calculated using all species in the species pool.	Disparity	Bellwood *et al.* (2006); Villéger *et al.* (2010)
FDis	Functional dispersion	Weighted dispersion of species in functional space, multivariate equivalent of weighted mean absolute deviation, multivariate dispersion weighted by species abundances, weighted mean distance of species from weighted centroid.	Balance + disparity	Laliberté and Legendre (2010)
Q (DIVC)	Rao's quadratic entropy	Weighted dispersion of species in functional space, mean pairwise dissimilarity between species, weighted by species abundances.	Balance + disparity	Rao (1982); Botta-Dukát (2005)

Measuring the amount of redundancy associated with each species in an assemblage

Measures of species contributions to disparity have been proposed using all three of the approaches mentioned in §2.1.2. Dendrogram–based measures (approach 2) of species uniqueness, based on the relative rarity, uniqueness or 'originality' of the features (trait states) possessed by a species, have been proposed by Vane-Wright *et al.* (1991), Faith (1992), Warwick and Clarke (1995), Petchey and Gaston (2002b) and Pavoine *et al.* (2005). These measures are calculated from the changes in branch length on a phylogenetic or functional dendrogram after a species is removed, or in the case of Pavoine *et al.* (2005), on the lengths of branches shared by pairs of species (which represents the expected number of features shared). However, these methods suffer from the problems shared by all dendrogram–based measures of disparity, namely that the results may vary substantially depending on the clustering technique used to produce the dendrogram, and it is not always clear which result is to be preferred (Podani and Schmera, 2007; Poos *et al.*, 2009; Schmera *et al.*, 2009b).

An ordination–based method of calculating species contributions to disparity (approach 3) was suggested by Bellwood *et al.* (2006). They used the distance of a species from the centroid (origin) in Principal Components (PCA) or Principal Coordinates Analysis (PCoA) as a measure of its 'functional specialisation' (Table 2.2). Species with large scores on important axes were considered to contribute more to the overall disparity (i.e. to be more functionally unusual) than species near the centroid. However, Schmera *et al.* (2009b) showed that this method is also problematic, because the species at the centroid do not necessarily have zero or close to zero contribution to the overall disparity.

Schmera *et al.* (2009b) suggested a different approach based on using the values in the dissimilarity matrix directly (most closely related to approach 1 above). They suggested calculating the contribution of individual species to the assemblage–level disparity using an additive decomposition of MFAD (Modified Functional Attribute Diversity; Table 2.2). MFAD is a modified form of the FAD2 measure used by Walker *et al.* (1999), standardised by the number of functionally unique species to reduce its dependence on the number of species present (Schmera *et al.*, 2009a). This method has the advantage that it is simple and involves the least transformation of the information in the dissimilarity matrix.

The contribution of a species to the total assemblage–level MFAD is calculated as the sum of the dissimilarity values between that species and all others in the assemblage (i.e. the sum of all the values in a particular row or column of the pairwise dissimilarity matrix, excluding the diagonal), divided by the number of 'functional species' (Schmera *et al.*, 2009b). Schmera *et al.* (2009b) called the contribution of a species to the overall MFAD its 'functional value' (fv). What this quantity actually represents is the total amount of dissimilarity associated with that species. If a species is very dissimilar to most of the other species present (i.e. alone in a particular region of the functional space), then it will have a high 'functional value' and will make a large contribution to the overall amount of disparity in the assemblage. If, on the other hand, a species is very similar to several other species, it will have a lower fv and make a smaller contribution to the overall disparity.

The fv measure of Schmera *et al.* (2009b) can be adapted as a measure of the amount of redundancy associated with a particular species (in the context of a particular assemblage), if one calculates $1 - fv$ instead of fv. This would give a measure of the *total amount of similarity associated with each species*, or the extent to which the rest of the assemblage is similar to that species, for a particular function. Species with many similar species in their particular region of functional space will have more redundancy associated with their functioning than species that are isolated.

However, calculating $1 - fv$ using the method of Schmera *et al.* (2009b) still does not provide an ideal measure of redundancy. Firstly, Schmera *et al.* (2009b) proposed that before the analysis is performed all species with identical values (trait states) for all the traits measured should be combined into a single 'functional species', as suggested by Ricotta (2005). They argue that such species should be considered a single functional entity because they function identically. However, combining functionally equivalent species is not appropriate when it comes to measuring redundancy, because replication of function contributes to redundancy, and it is precisely this replication of function which one is trying to measure. Species with identical trait states will each contribute seperately to the total amount of similarity (redundancy) present in the assemblage. Secondly, the similarities between a particular species and *all* other species in the assemblage are used to calculate $1 - fv$; even those species that are very dissimilar to the focal species will contribute a small amount of redundancy. It may be unrealistic to include very dissimilar species when calculating redundancy, because a certain minimum amount of similarity may be needed for species to actually be able to compensate for each other effectively. In other words, the $1 - fv$ measure may overestimate the amount of redundancy associated with the functioning of each species.

I therefore developed my own measure of the amount of redundancy associated with the functioning of a particular species, based on the approach of Walker *et al.* (1999), which involves identifying groups of functionally similar species. This new measure provides a 'species–eye view' of redundancy and will be described in detail in §2.2.2.

Identifying groups of functionally similar species

The most common approach to identifying patterns of similarity and dissimilarity within an assemblage is to divide the species into functional groups. Groups are either defined *a priori* (usually as broad groupings based on trophic level, morphology, size or growth form), or using clustering techniques (approach 2 above). Functional groups represent groups of species that function similarly, and the number of species in each group is therefore a measure of the redundancy associated with that particular function. This approach has been suggested by several authors as a useful way of measuring redundancy (Peterson *et al.*, 1998; Bellwood *et al.*, 2003; Allen *et al.*, 2005; Nyström, 2006; Nyström *et al.*, 2008), but it has only been applied in a handful of case studies (Forys and Allen, 2002; Fischer *et al.*, 2007; Laliberté *et al.*, 2010).

Deriving functional groups using clustering techniques is a non–trivial and potentially controversial task (Quinn and Keough, 2002). The results may vary substantially depending on the clustering technique used (Poos *et al.*, 2009), and it is not always clear which result is to be preferred. Mouchet *et al.* (2008) showed that no combination of dissimilarity metric and clustering method consistently outperforms the others when producing a functional dendrogram, because of the complexity of interactions between trait correlations, species richness, and the choice of dissimilarity metrics and clustering methods. It is therefore necessary to use several different options and seek consensus between them (Mouchet *et al.*, 2008), and/or use expert opinion to decide on the best classification (e.g Laliberté *et al.*, 2010). This can be very time–consuming if functional classifications must be derived for many different functions.

Functional groups derived from cluster analysis are usually mutually exclusive and have 'crisp' boundaries — a species can only belong to one group. Placing species into mutually exclusive groups assumes that species are either the same or different (in the same group or in a different group), and differences among members of a group are ignored. This does not reflect the continuous nature of disparity accurately (Petchey and Gaston, 2002b; Botta-Dukát, 2005). Fuzzy clustering methods provide a way of avoiding this problem, by allowing species to belong to more than one group and assigning each species a degree of 'belongingness' to each group (Legendre and Legendre, 1998). However, fuzzy clustering usually requires the number of groups to be specified beforehand, and this number is unknown when identifying groups of similar species.

The most commonly used clustering methods, agglomerative hierarchical methods, actually introduce rigidities into the grouping process because of the way the analysis is performed. These methods start with individual species, then add other species to form groups, and then join these groups to other groups successively until all species are linked (Quinn and Keough, 2002). A group formed early in the process cannot be broken later, so the method does not actually use all the pairwise dissimilarities (Quinn and Keough, 2002; Podani and Schmera, 2006). A species may therefore end up in a particular group because it is similar to one of the group members, while its similarities to members of other groups are ignored. Calculating redundancy as the number of species within functional groups formed in this way is therefore likely to underestimate the amount of redundancy present.

Walker *et al.* (1999) took a different approach, using the values in the pairwise dissimilarity matrix directly, and determining a threshold dissimilarity below which species were considered 'functionally similar'. For each dominant species, they identified which other species were most similar to it (i.e. had the smallest dissimilarities), thereby forming groups of functionally similar species around each dominant species. The greater the number of similar species associated with a particular dominant, the more redundancy the dominant species was considered to have. Identifying the amount of redundancy associated with the functioning of individual species is a much more flexible approach than dividing the assemblage into functional groups using clustering methods. Using the dissimilarities directly also has the advantage that decisions about which clustering method to use can be avoided. However, some problems remain with the method proposed by Walker *et al.* (1999).

Firstly, the groups formed by Walker *et al.* (1999) were also mutually exclusive: each species could only belong to one group, implying that each minor species could only provide redundancy for the functioning of one dominant species. Again, this will probably underestimate the amount of redundancy present. The amount of redundancy associated with the functioning of each species needs to be specified in a more flexible and continuous way.

Secondly, Walker *et al.* (1999) used apparent clusters in the pairwise dissimilarity data to define four categories of similarity: 'functionally similar', 'similar to average', 'average to dissimilar' and 'functionally dissimilar'. They used these categories to define how similar two species needed to be to provide redundancy for each other's functioning. They suggested these clusters may be natural groups which reflect self–organization and the operation of structuring processes across different scales, in the same way as the 'lumpy' distribution of animal body masses described by Holling (1992) and Allen *et al.* (2005). However, such claims must be made with great caution.

While biological processes can affect the distribution of dissimilarity values among species (MacArthur and Levins, 1967; Poff, 1997), this can also be highly influenced by the type of trait variables and the dissimilarity metric used (Pavoine *et al.*, 2009). Each type of variable (Table 2.1) affects the distribution of values in the dissimilarity matrix in different ways, leading to a specific shape of the cloud of species in multivariate space. For example, nominal and ordinal variables separate species into distinct groups, circular variables produce circles or arcs, and ratio–scale variables produce a continuous one–dimensional cloud of points (Pavoine *et al.*, 2009). The final distribution of the dissimilarities is produced by the combination of these different patterns, as well as the correlations between the variables (Pavoine *et al.*, 2009).

The clustering of dissimilarity values observed by Walker *et al.* (1999) could therefore have been produced by their exclusive use of ordinal traits (which produce clusters of dissimilarities), rather than by any biologically meaningful process. Before claims can be made about the meaning of patterns in the dissimilarity data, we need to have a good understanding of how the choice of traits and their coding (e.g. the number of categories specified for categorical traits) is influencing the patterns observed, as well as the effects of correlations between traits (Petchey and Gaston, 2002b). These factors are often not sufficiently appreciated in functional diversity studies.

The second hypothesis of Walker *et al.* (1999) stated that groups of similar species that provide redundancy for each others' functioning differ in their response traits, thus providing response disparity (Box 1.3). The combination of redundancy and response disparity was proposed to enhance resilience in species assemblages (§1.2.6). Although Walker *et al.* (1999) emphasised the importance of response disparity, they did not suggest a way of measuring it.

2.1.3 Requirement 3: measuring response disparity

In fact, few authors have suggested how response disparity may be measured. Peterson *et al.* (1998) and Elmqvist *et al.* (2003) suggested that body size or mass may be a useful indicator of the spatial and temporal scale at which animals operate. Organisms operating at different scales will be affected by disturbances differently, and this type of cross–scale resilience can be seen as a type of response disparity (see examples in §1.2.6). Allen *et al.* (2005) suggested that the number of functional groups (e.g. body size groups) within and between scales could be used as a measure of response disparity, although they did not use this term. Given the above discussion about the pitfalls involved in a arriving at a functional classification and the questions around the occurrence of 'natural' groups in dissimilarity data, I do not favour counting functional groups as a way of measuring response disparity.

A completely different approach was described by Winfree and Kremen (2009). To measure disparity in bee species' responses to land–use change, they used the bee species—native vegetation interaction term from a generalised linear model. The model described changes in bee abundance with native vegetation cover in the surrounding landscape. If different bee species responded differently to a particular pattern of land–use change, this was taken as a signal that response disparity was present. This is a much more direct approach, not relying on the relationship between traits and species responses. It can only be used where appropriate data are available, however, and the cost of obtaining such data make it more suitable for studies focused on a particular ecosystem function (e.g. pollination (Winfree and Kremen, 2009)) than for studies involving hundreds of species and many different functions.

If functional traits determining species' responses to particular disturbances can be identified (§2.1.1), then response disparity could in principle be measured using any of the three approaches identified in §2.1.2 and any of the measures of disparity in Table 2.2. It would, however, need to be measured for each set of species with similar functional effects separately, instead of for the assemblage as a whole, in order to provide a measure of the response disparity associated with each species.

Laliberté *et al.* (2010) measured response disparity within groups of functionally similar species (determined by clustering) using the FDis index (Table 2.2). FDis measures the mean dispersion of a group of species in a specified functional space. If the traits used to define this space are carefully chosen to reflect species' responses to disturbance, then FDis can be used as a measure of response disparity.

Combined measures of disparity and balance (i.e. disparity measures weighted by species abundances, such as FEve, FDiv, FDis and Rao's Q) should not be used if the aim is to investigate the role of rare 'tail' species in resilience, as weighted measures downplay the importance of these species. Weighted

Table 2.3: Summary of requirements for testing the hypotheses of Walker *et al.* (1999) about the roles of redundancy and response disparity in the resilience of species assemblages, together with existing approaches described in this section.

Requirement	Existing approaches
Measure species' functioning	Direct measurement (e.g. Kremen *et al.*, 2002; Balvanera *et al.*, 2005); Use functional traits as surrogates of function (e.g. de Bello *et al.*, 2010).
Measure redundancy associated with species' functioning	Group the species into mutually exclusive 'functional groups', then count the number of species per group (Laliberté *et al.*, 2010); Count the number of species that are functionally similar to each dominant species (Walker *et al.*, 1999).
Measure response disparity associated with species' functioning	Measure variation in the scale of operation of organisms within functional groups (Peterson *et al.*, 1998; Elmqvist *et al.*, 2003; Allen *et al.*, 2005); Measure the multivariate dispersion (FDis) within each functional group (Laliberté *et al.*, 2010).

measures can, however, be converted to unweighted ones by using them with presence/absence species data, as done by Laliberté *et al.* (2010).

2.1.4 Summary and chapter aims

The requirements for testing the hypotheses of Walker *et al.* (1999) about the roles of redundancy and response disparity in the resilience of species assemblages, and the existing approaches reviewed in this section, are summarised in Table 2.3. Several shortcomings in the existing approaches were identified.

Firstly, the link between traits and functioning is often made carelessly and needs to be more explicit, with careful consideration of which functions are being measured and which traits have an important influence on each. Furthermore, effect and response traits need to be distinguished because testing the hypotheses of Walker *et al.* (1999) requires measuring redundancy for particular effect functions, and response disparity for particular response functions. This requires a more thoughtful approach to the use of functional traits than simply combining many traits that influence functioning in some way.

Few measures of redundancy and response disparity have been proposed. The major problem with existing measures of redundancy is that they do not properly take into account the continuous and multidimensional nature of similarities and differences among species. Similarity or difference is defined in terms of mutually exclusive functional groups, where all species in a group are assumed to have a single, similar, functional role (Forys and Allen, 2002; Allen *et al.*, 2005; Fischer *et al.*, 2007; Laliberté *et al.*, 2010). This is unrealistic and is likely to underestimate redundancy, because the similarities between members of different functional groups are ignored. The approach of Walker *et al.* (1999) is better, because it focuses on identifying the total amount of redundancy associated with each (dominant) species, but it still uses rigid grouping methods to identify which species are most similar to each other. Likewise, proposed measures of response disparity also rely on imposing mutually exclusive grouping structures on the continuous similarity/dissimilarity values.

It was therefore necessary to develop new measures of functional redundancy and response disparity in this study, to allow testing of the hypotheses of Walker *et al.* (1999) about the roles of redundancy and response disparity in the resilience of species assemblages.

The detailed chapter aims are as follows:

- To develop a way of linking traits and functions that takes the continuous and multidimensional nature of disparity into account, and which distinguishes between effect and response functions. This forms the basis for measuring species' functioning and functional disparity (requirement 1).
- To develop a measure of redundancy which does not require the grouping of species into mutually exclusive functional groups, and which measures the redundancy associated with each aspect of the functioning of each species within an assemblage (requirement 2).
- To develop a measure of response disparity which is likewise not based on the formation of mutually exclusive groups, and which measures the differences in response to disturbance among species that perform a particular effect function similarly (requirement 3).

- To compare the performance of the methods developed here with existing methods for measuring redundancy and response disparity.

Aims 1–3 are addressed in the following section, while Aim 4 is addressed in §2.3.

2.2 Development of methods for this study

The methods described in this section were designed to address the three requirements identified as necessary for testing the hypotheses of Walker *et al.* (1999) about the roles of redundancy and response disparity in the resilience of species assemblages (§2.1). These three requirements are encapsulated in aims 1–3 above.

2.2.1 Requirement 1: measuring species' functioning

For the purposes of testing the hypotheses of Walker *et al.* (1999), it did not matter which particular functions were selected, as long as there was at least one effect function and at least one response function. However, because this study also aimed to compare the resilience of riparian plant assemblages under different land management regimes, functions were chosen to reflect the key differences between the three land management regimes in this study, namely fire, herbivory and human impact (see §3.1.1). The aim was not to include all possible aspects of functioning, but rather to choose a few relevant aspects which could be measured from functional traits, within the time and budget constraints of the study.

Only the plant component of riparian ecosystems was studied (a single trophic level). Plant species in the riparian zone create three–dimensional structure and are functionally important for many terrestrial and aquatic animal species, providing food in the dry season, nesting sites, cover, shade, litter inputs to soil and water, soil stabilization and many other important functions (Naiman *et al.*, 2005).

Selection of functions and traits to measure

Functions were defined broadly rather than narrowly. For example the function 'nutrient cycling' (Table 2.4) could have been broken down into more specific functions, such as carbon fixation, carbon storage, annual nitrogen releases from litter, nitrogen retention in plants, nitrogen fixation rate, etc. (Walker *et al.*, 1999). Using broadly defined functions allowed me to differentiate between different aspects of ecological functioning without making unrealistic demands on the available data. Function was interpreted purely as activity, with no implication of purpose or design, good or bad.

Functional traits were used as a surrogate measure of how each species performed each function. Dealing with each trait separately (e.g. Mayfield *et al.*, 2005; McGill *et al.*, 2006)) has limited usefulness for linking to ecosystem functioning, because most functions are not determined by a single trait (Figure 2.1). A measure of how each species performed each function was therefore obtained by using *sets of traits* known or hypothesised to influence each of the selected functions (Table 2.4). The traits used in each set were limited to those that were practical to measure for large numbers of species, had well–established correlations with the function, or that were considered good indicators of other, difficult to measure traits. They should not be considered the only traits that could have been included in each set. Within each set, all traits were considered to contribute equally to the function. Although some traits are probably more important than others, we do not yet know enough about the relationship between traits and functions to include such information. The methods used here do, however, allow for the possibility of including trait weightings as information on the relative importance of traits to different functions becomes available.

It can be difficult to distinguish effect traits from response traits, and some traits can act as both, depending on how they are combined with other traits (Suding *et al.*, 2008). Rather than classifying traits as either effect or response traits, I focused on distinguishing between effect and response *functions*, each determined by partially overlapping sets of traits (Table 2.4). Response 'functions' are not functions in the same sense as effect functions, but describe the responses of species to particular types of disturbance or change. These responses are determined by species traits, particularly (but not only) traits related to regenerative ability. For example, species with an ability to resprout will tend to have longer–lived individuals and to recover more rapidly from defoliation than species that lack this ability (Bond and Midgley, 2001).

The use of overlapping sets of traits to distinguish between different effect and response functions is a novel approach, as far as I am aware. It is a valuable approach because it allowed me to investigate

Table 2.4: Definition of functions and the traits used to represent them. Traits marked with * were measured for woody species only, while traits marked with $^+$ were measured for herbaceous species only.

Effect functions	
Nutrient cycling	Specific leaf area, leaf tensile strength, leaf phenology, N–fixing ability, potential height
Provision of food for animals	Leaf tensile strength, spinescence, growth form, leaf phenology, below-ground storage, flowering start, flowering period, fruiting start* fruiting period*
Provision of shade*	Growth form, leaf phenology, potential height
Provision of fuelwood*	Growth form, woodiness, potential height
Response functions	
Response to damage	Life form, lifespan, clonal spread, resprouting*/below-ground storage$^+$, specific leaf area
Response to water stress	Woodiness, succulent$^+$, potential height, riparian affinity, below–ground storage$^+$

the interplay between effect and response functions, which is critical for understanding resilience and ecosystem responses to environmental change (Walker *et al.*, 1999; Suding *et al.*, 2008), and made it possible to test the hypotheses of Walker *et al.* (1999).

The choice of trait sets for each of the functions (Table 2.4) is justified in the following sections.

Nutrient cycling

Ecosystem nutrient cycling depends strongly on the productivity of the species present and the decomposition rates of the litter they produce (Cornelissen *et al.*, 2001). A large amount of evidence indicates that the carbon economy of plant species can be described as a spectrum ranging from fast to slow return on investments of nutrients and dry mass in plant structures, determined by fundamental physiological constraints and tradeoffs (Grime, 1977; Chapin, 1980; Westoby, 1998; Díaz *et al.*, 2004; Wright *et al.*, 2004; Craine *et al.*, 2005). At one end of this spectrum, species have tough tissues, a high C:N ratio, relatively low tissue N and P concentrations, long–lived structures and slow growth rates, while species at the other end have fast growth rates, high tissue nutrient concentrations, and fast turnover of parts, with relatively little investment in structure. The position of a species on this spectrum is therefore an important descriptor of its nutrient cycling ‘strategy’.

Specific leaf area (SLA), or the amount of light–intercepting leaf area per unit of invested dry mass (Westoby, 1998), is a good correlate of potential relative growth rate, or mass–based maximum photosynthetic rate (Cornelissen *et al.*, 2003). It indicates how rapidly a plant is able to allocate resources to growth and is strongly correlated with leaf N and P concentrations across a broad range of species (Wright *et al.*, 2004). Plants with high SLA values have fast growth rates, while low SLA values indicate slow growth rates and greater investment in leaf structure, making SLA a good indicator of a species’ position on the resource economic spectrum.

Litter decomposition, an important aspect of nutrient cycling, is strongly influenced by the litter quality of different species (Pérez-Harguindeguy *et al.*, 2000). Litter quality has been shown to be strongly correlated with the quality of living leaves (which is determined by the relative investment in leaf structure), and both are strongly correlated with decomposition rate (Pérez-Harguindeguy *et al.*, 2000). Leaf tensile strength, a measure of the physical strength of leaves, is a good surrogate measure of litter quality because of its strong correlations with decomposition rate and C:N ratios across a broad range of species, and because it is quick and easy to measure for large numbers of species (Pérez-Harguindeguy *et al.*, 2000; Cornelissen *et al.*, 2003).

Leaf phenology also has a well documented effect on litter quality in perennials. Evergreen species have longer–lived leaves, grow more slowly, and generally produce less decomposable litter than deciduous species (Reich *et al.*, 1992; Cornelissen, 1996). Leaf phenology also determines the timing of litter inputs to the soil.

The mode and efficiency of nutrient (N and P) uptake is important not only for the growth of plants but also for nutrient concentrations in the soil. Species with the ability to fix nitrogen, through symbioses with nitrogen–fixing bacteria, are able to take up inorganic forms of soil nitrogen more efficiently than non–fixers (Cornelissen *et al.*, 2003). This represents an alternative way in which biomass can be produced in nitrogen–poor soils, besides slow growth and investment in long–lived tissues (Craine *et al.*, 2002). Nitrogen fixers differ from other species able to utilise nitrogen–poor soils by having higher tissue N concentrations and higher potential productivity (Ritchie *et al.*, 1998; Knops *et al.*, 2002). Nitrogen fixing ability was included here because published information was available. However, other nutrient uptake adaptations are also important in determining the rate and efficiency of uptake of N and P, such as associations with the various types of mycorrhizal fungi, and root parasitism. These have been shown to consistently coincide with variation in key carbon cycling traits (Cornelissen *et al.*, 2001, 2003). These other modes of nutrient uptake should have been included here, but this was not possible due to the lack of published information and the difficulty of determining nutrient uptake strategy in the field for large numbers of species.

Potential height is the maximum height that may potentially be attained by a species in a particular environment (not the actual height achieved) (Díaz *et al.*, 2004). It reflects the ability of a species to secure carbon profit through light capture (Falster and Westoby, 2005a), and is therefore relevant to nutrient cycling because it reflects the potential for carbon to be tied up in biomass.

Provision of food to animals

This broadly defined function includes provision of food from above– and below–ground plant parts, including flowers and fruit, to terrestrial or aquatic insect, bird and mammalian herbivores.

Leaf tensile strength is a good indication of the relative carbon investment in structural protection of the photosynthetic tissues, and is inversely proportional to palatability (Cornelissen *et al.*, 2003). The ratio of protein to fibre in a leaf has been established as a good predictor of leaf palatability to generalist chewing folivores, and this ratio shows a strong negative correlation with leaf toughness (Choong *et al.*, 1992). Tough leaves are less vulnerable to both vertebrate and invertebrate herbivory, and leaf toughness is often shown to be the most important, but not the only, factor controlling patterns of herbivory (Coley, 1983; Sanson, 2006; Clissold *et al.*, 2009).

Other traits important for defence against herbivores are spinescence and the presence of secondary metabolites for chemical defence (Cornelissen *et al.*, 2003). Spinescence (the types, sizes and densities of spines, thorns and prickles), contributes mainly to defence against large (mammalian) herbivores (Cooper and Owen-Smith, 1986), and spiny plants are common in ecosystems with many large herbivores (Grubb, 1992). Large herbivores including elephant, hippo, giraffe, buffalo, rhino, zebra, wildebeest and kudu have a long history of association with the vegetation in the study area, as do cattle and goats, and spiny species are common in the area (see §3.1.1). Spinescence is therefore an important trait determining the way in which plant species function in providing food to animals.

Like mechanical defences, chemical defences (mainly involving various phenolic compounds) are known to deter a wide range of vertebrate and invertebrate herbivores, with effects including toxicity and reduced digestibility (Read *et al.*, 2009). While leaf toughness and phenolics are sometimes positively correlated (Read *et al.*, 2009), there is often little correlation between the various different traits that confer physical and chemical defence against herbivores (Coley, 1983; Agrawal and Fishbein, 2006). Many different chemical compounds may play a role in chemical defence, and these vary in importance between plant organs and over the lifespan of the plant (Agrawal and Fishbein, 2006). However, despite the importance of chemical defence traits, it was not possible to include them in this study. A preliminary survey of published information on plant defence chemicals revealed that little quantitative information was available, and what information there was was highly scattered in the literature. Furthermore, the proportion of species for which no information could be found was unacceptably high (33% of 40 species in the preliminary survey). I decided that including information on chemical defences in a highly simplified form (e.g. phenolics present/absent) would not be useful, because almost all species would have some kind of phenolics present in some part of the plant, and the effort involved in collecting the information would not be well spent.

Growth form was included here because it affects the accessibility of the foliage (and other plant parts) to different sizes and types of herbivores. For example, smaller mammalian herbivores can access shrub canopies but not tall trees with aerial canopies. Forbs with prostrate and rosette growth forms are well known to be more resistant to grazing than erect leafy forbs (Landsberg *et al.*, 1999; Lavorel *et al.*, 1999). Growth forms with leaves that remain tightly folded or rolled during leaf expansion, such as palms, also experience significantly less attack by herbivores (Grubb *et al.*, 2008).

Below–ground storage organs such as bulbs, tubers and rhizomes are the primary source of food for a large and taxonomically diverse group of animals, including rodents, insects and nematodes (Andersen, 1987). Below–ground herbivory is often neglected, but is likely to be important because more than 50% of net primary production is commonly allocated to below–ground plant parts (Andersen, 1987).

Phenological traits (leaf phenology, flowering start, flowering period, fruiting start and fruiting period) were included because they determine the temporal availability of a plant as a food source for folivores, nectarivores and frugivores. Since most of the woody species in the study area lose their leaves in the dry season, those evergreen species that continue providing browse in winter may be particularly important (Bergström, 1992).

Provision of shade

Shade is a valuable resource for animals, whether wild or domestic, aquatic or terrestrial (Hynes, 1970; du Toit and Apps, 2000; Kotzen, 2003; Schütz *et al.*, 2009). Many animals modify their behaviour to make use of shade, especially in subtropical arid and semi–arid areas, contributing to accumulation of nutrients and seeds under shade trees which can have important consequences for ecosystem structure (Dean *et al.*, 1999). However, shade can also limit understorey plant growth, so when specifying the provision of shade as an effect function it is necessary to specify which part of the trophic network one is looking at.

Growth form, leaf phenology and potential height were considered to affect the ability of woody species to provide shade for other plant and animal species (Table 2.4). Growth form is important because trees can potentially provide a larger area of shade than shrubs, and the shade is more accessible to large animals because the canopy is elevated above the ground. Leaf phenology determines the temporal availability of shade. The use of potential height rather than actual height is not ideal because plants may not reach their maximum potential height due to herbivory, fire or flood damage, in which case they may in fact provide little shade. However, the potential for shade provision remains in the system, and this function should be seen as describing the *potential* of woody species to provide shade.

Provision of fuelwood

Rural communities in South Africa are highly dependent upon fuelwood as their primary energy source (Shackleton, 1993; Twine *et al.*, 2003; Madubansi and Shackleton, 2007). The potential of woody species to provide fuelwood was defined in this study by growth form, woodiness and potential height (Table 2.4). Growth form influences the suitability of woody species for fuelwood, with certain shrubby species being avoided by harvesters because the growth form does not allow collection of pieces of the preferred size (11–40 cm) (Shackleton, 1993). Woodiness (wood density) is also an important determinant of the value of a species for fuelwood. While the most preferred species vary between villages and regions, favoured species all have dense wood that burns well with little smoke (Tietema *et al.*, 1991; Tabuti *et al.*, 2003; Madubansi and Shackleton, 2007). Plant height is related to main stem and branch diameter and volume via various allometric equations, so plant height influences the size distribution of stems available for harvest (Salis *et al.*, 2006). It is a rather approximate measure, however, because the stem volume required to reach a given height may vary substantially between species (Kooyman and Westoby, 2009). The same caveat as above applies to the use of potential height rather than actual height.

Response to damage

Savanna plants are exposed to many potential sources of damage, including fires, herbivory and physical damage by humans and animals (trampling, pushing over of trees by elephant, human harvesting of fuelwood and other plant products, etc.) (Shackleton and Shackleton, 2000; Bond and Keeley, 2005; Midgley *et al.*, 2010). Plants in riparian zones additionally are susceptible to physical damage by flooding (Naiman *et al.*, 2005). Variations in how plants survive and respond to these various types of physical damage underpin vegetation dynamics in savannas (Midgley *et al.*, 2010) and are therefore key to understanding resilience in these systems.

Many savanna plants are able to recover from damage by resprouting (Bond and Midgley, 2001; Luoga *et al.*, 2004). Resprouting is the production of new vegetative parts after the destruction of living tissues, from buds on remaining above–ground parts, roots or below–ground storage organs (Bellingham and Sparrow, 2000). Resprouting has been most well studied as a response to fire, but it is in fact a widespread trait in woody angiosperms and also commonly occurs in response to other types of damage (Bond and Midgley, 2001; Vesk and Westoby, 2004). A study of resprouting responses to flood damage, in the same area as this study, showed that 91% of woody riparian individuals resprouted after damage by a large flood, with almost all species able to resprout, but varying in the strength and nature of the response (Kotschy, unpublished manuscript).

Resprouting responses are determined by the location and protection of buds, the nature of below–ground storage organs, and the growth rate of the plant (Clarke *et al.*, 2010). The life form classification of Raunkiaer (1934) is based on the position of the perennating tissue (buds) relative to the ground surface, reflecting the degree of protection of the buds from adverse climatic conditions. This information is also relevant to resprouting responses (del Tredici, 2001; Cornelissen *et al.*, 2003). It is, however, a rather coarse classification because it refers only to the position of the highest buds and does not describe the distribution of buds on the rest of the plant. Nevertheless, life form was included here as a trait relevant to species' responses to damage.

Resprouting is often dependent on resources stored below ground, particularly if the damage involves loss of large amounts of above–ground biomass (Iwasa and Kubo, 1997; Bellingham and Sparrow, 2000). Early allocation of carbohydrate to roots, the development of swollen rootstocks or lignotubers in woody saplings, and reproduction by root suckering are common features of savanna trees compared to forest trees, and these features have been linked to the high likelihood of fires occurring before saplings are tall enough to escape the flame zone (Bond and Keeley, 2005; Ratnam *et al.*, 2011). Below–ground storage organs are likewise important in facilitating resprouting in herbaceous species (Klimešová and Klimeš, 2003).

Growth rate is important because it determines the speed of recovery after damage (together with the productivity of the site; (Bellingham and Sparrow, 2000)). Fast growth rates allow tree seedlings and saplings to rapidly attain a size at which they are less susceptible to disturbance (Higgins *et al.*, 2000; Bond and Keeley, 2005). Many fast–growing species are tolerant of herbivory because lost biomass can be rapidly replaced (du Toit, 1990). Interspecific variations in growth rate were incorporated by including specific leaf area as a surrogate for growth rate (Table 2.4).

Clonality, the ability of a species to reproduce vegetatively by producing new aboveground units (ramets), is also dependent on below–ground storage (Cornelissen *et al.*, 2003). Clonality allows regrowth after disturbance in a similar way to resprouting, with the additional possibility that where the effects of damage are patchy, undisturbed ramets may subsidise the replacement of damaged ones (Marshall, 1990). Clonality also confers lateral mobility, allowing for spatial responses to damage (Hutchings and Mogie, 1990). Clonality is more common among herbaceous than among woody species in savannas, being particularly important in grasses.

Many species do not respond to damage by resprouting or producing new ramets, but rather by producing seed. It has been suggested that tradeoffs occur between resprouting and seed production, because resources stored below–ground must be diverted away from sexual reproduction (Chapin *et al.*, 1990; Iwasa and Kubo, 1997; Bellingham and Sparrow, 2000; Bond and Midgley, 2001). Studies of responses to fire damage have tended to classify species as either 'sprouters' or 'seeders', but if a broad range of disturbance types and severities are considered, this dichotomous classification appears too simplistic (Vesk and Westoby, 2004). Many species' responses to damage include both resprouting and seed production (Kotschy *et al.*, 2005).

I originally planned to include seed size (seed mass) as a measure of the sexual reproductive component of response to damage. Species with smaller seed mass can produce more seeds for a given reproductive effort, making seed mass a good predictor of seed output per unit of canopy cover (Westoby, 1998). It also provides a rough measure of the likelihood that a plant will disperse a propagule to an establishment opportunity (Westoby, 1998). However, it was not possible to obtain seed mass data for all the species within the time constraints of this study. Instead, I included life span to distinguish between annuals (mostly recover from damage by establishment of new individuals from seed, seeds often small and widely dispersed), short–lived perennials/biennials, and perennials (recover from damage by either resprouting, reseeding or both, a range of seed sizes possible).

Response to water stress

Species responses to changes in the amount and timing of water availability are highly relevant for understanding the composition and diversity of riparian vegetation, particularly when rainfall and streamflow are highly variable, as they are in the semi–arid Sand River catchment (§3.1.1). On top of the natural flow variability, reductions in water supply and modifications to the flow regime are expected in future as human pressure on water resources increases (Pollard, 2001). Under these conditions, the diversity of responses to water stress among species that perform similar functions is likely to be an important element of resilience.

Woodiness (wood density) is important in determining a plant's response to water stress because it influences hydraulic conductance, or the ability of a stem to transport water (Hacke *et al.*, 2000). Wood density is in fact a good predictor of a whole suite of characteristics, including stem water storage capacity, leaf water potential, total daily transpiration and the daily timing of sap flow, making it a good surrogate measure for water transport efficiency and storage capacity (Bucci *et al.*, 2004). Low wood density (soft wood) is associated with high hydraulic conductance, allowing for rapid uptake of water, but is also associated with an increased risk of cavitation (development of air bubbles in the xylem) during periods of water stress, which decreases the plant's ability to supply its leaves with water and is potentially lethal (Hacke *et al.*, 2001). Species with high wood density (hard wood) generally have less risk of cavitation due to the thicker cell walls and/or smaller diameter of their xylem vessels (Hacke *et al.*, 2000). Maintaining a 'safe' xylem is therefore costly both in terms of hydraulic efficiency and construction cost, and the evidence suggests that there are several other ways in which species may reduce their experience of physiological water stress (Hacke *et al.*, 2000; Ackerly, 2004; Chave *et al.*, 2009).

An important factor influencing the extent of water stress experienced by a plant is rooting depth (Hacke *et al.*, 2000). Since field measurement of root depth distributions was not possible for the large number of species included in this study, potential height was included because of its positive allometric relationship with rooting depth (Cornelissen *et al.*, 2003). Species with deep root systems are able to access deep soil water and maintain positive water potentials during the dry season, making investment in safe xylem less important than it is in shallow–rooted species (Hacke *et al.*, 2000). Storage of water in succulent plant parts or below–ground storage organs also reduces the amount of physiological water stress experienced.

Of course rooting depth needs to be interpreted in relation to the depth of the water table and its seasonal changes. In riparian environments, the depth of the saturated zone varies with elevation above the stream channel, and riparian plant species typically show preferences for particular elevations that are at least partly determined by their water requirements and responses to the stresses imposed by drought and flooding (Hupp and Osterkamp, 1985; Blom, 1999; van Coller *et al.*, 2000; Lenssen *et al.*, 2004; Henszey *et al.*, 2004; Lite *et al.*, 2005). I therefore included a measure of riparian affinity which reflects the frequency of occurrence of a species in riparian vs upland areas (see Table 2.5).

One aspect of response to water stress which has not been included here is the regeneration component of species life histories. Aquatic species from seasonally variable habitats often have a range of different regeneration pathways, facilitating persistence under different conditions of water supply (Rogers, 1984; Mitchell and Rogers, 1985; Combroux *et al.*, 2001; Combroux and Bornette, 2004; Hölzel and Otte, 2004). For example, species may persist through drought periods as seeds or vegetative propagules. As mentioned in the previous section, seed size is a reasonable 'soft' measure of regeneration strategy (Westoby, 1998; Cornelissen *et al.*, 2003), but was excluded here due to time constraints.

Trait data collection

Functional trait data were collected for all 350 herbaceous and 130 woody species recorded in riparian vegetation transects in the three different management areas (detail of methods in Chapter 3). Traits were measured according to the standardised protocols described in Cornelissen *et al.* (2003) and Díaz *et al.* (2004), where available (Table 2.5).

The traits measured for woody and herbaceous species differed slightly, partly because of inherent differences in trait variability between the two groups, and partly because of differences in data availability. Data on leaf and fruiting phenology in herbaceous species were difficult to obtain, so for herbaceous species I simply recorded whether plants are known to be green in winter, regardless of the lifespan of the species (Table 2.5). This is comparable to the way leaf phenology was recorded for the (perennial) woody species, but provides less detailed information. Fruiting phenology was not recorded for herbaceous species. Resprouting ability for herbaceous species could only be recorded as a binary trait (able to resprout or not). This trait was later excluded for the herbaceous species as it was strongly correlated with life span (perennials mostly have the potential to resprout, annuals do not). Below–ground storage was not recorded for woody species as very little information was available on the rooting systems of savanna trees and shrubs.

Functional trait information was collected from a variety of published sources, including field guides, checklists, taxonomic works, scientific papers and online databases. Details of these sources and how the information was extracted are given in Appendix A: Details of Methods. Several of these sources represent significant compilations of literature in their own right. Local sources (dealing with the study area) were given priority over sources from elsewhere in South Africa, and South African sources were given preference over those from other parts of the world. In some cases herbarium specimens and field observations were used to supplement the data obtained from published sources, particularly for flowering phenology and below–ground storage for herbaceous species.

Field sampling of leaves for measurement of leaf traits (SLA and TS) was done mainly within the Kruger National Park and leaves were processed at laboratory facilities in Skukuza. Species not present in the national park were sampled where they were encountered. As far as possible, leaf traits were measured on ten leaves per species (two leaves from each of five plants, equivalent to five statistical observations), as recommended by Cornelissen *et al.* (2003). These values were then combined to give a mean value for each species. It was not, however, possible to find five individuals of some of the rarer species, and some species recorded in the vegetation survey could not later be relocated for sampling of leaf traits. For species with unusually variable SLA or TS values, additional plants were sampled if possible (up to 10 plants and 20 leaves). Otherwise, intraspecific variation was not taken into account; individuals of a species were assumed to function more similarly than individuals of different species. Although interspecific variation may be important, this was a necessary assumption because of the large number of species involved.

Table 2.5: Variable types, units and categories for functional trait data used in this study. Units and categories follow Cornelissen *et al.* (2003) except for those marked *, for which no standardised protocols were available. Traits marked ^{woody} were only measured for woody species, while those marked ^{herb} were only measured for herbaceous species.

Plant trait	Variable type	Units/categories
Growth form	Categorical	23 categories
Life form	Categorical	7 categories
Life span	Ordinal	1 = annual; 2 = biennial; 3 = perennial
Leaf phenology^{woody}	Ordinal	1 = deciduous; 2 = evergreen
Wintergreen^{herb}	Binary	Yes/no
Flowering start, end	Circular	Month (1–12)
Fruiting start, end^{woody}	Circular	Month (1–12)
Flowering period	Continuous	Number of months
Fruiting period^{woody}	Continuous	Number of months
Succulence^{herb}	Binary	Yes/no
Woodiness*	Ordinal	0 = non–woody; 1 = semi–woody; 2 = soft–wooded ($<$0.6 mg.mm^{-3} or $<$750 kg.m^3 air–dry mass); 3 = dense–wooded ($>$0.6 mg.mm^{-3} or $>$750 kg.m^3)
Riparian affinity*	Ordinal	1 = obligate riparian (99% of individuals in riparian); 2 = facultative riparian (67–99% in riparian); 3 = riparian/upland (33–67% in riparian); 4 = facultative upland (67–99% upland); 5 = obligate upland (99% in upland)
Spinescence	Ordinal	5 categories reflecting increasing spine density and hardness
Resprouting ability^{woody}	Ordinal	1 = weak ($<$25% of severely damaged individuals resprout); 2 = moderate (25–50% resprout); 3 = strong (50–75% resprout); 4 = very strong ($>$75% resprout)
Clonal spread	Ordinal	0 = absent; 1 = limited; 2 = extensive
Below–ground storage^{herb}	Categorical	6 categories (none, taproot, rootstock, rhizome, bulb, tuber)
Nitrogen–fixing ability	Binary	Present/absent
Specific leaf area (SLA)	Continuous	mm^2 leaf area / mg leaf mass
Leaf tensile strength (TS)	Continuous	Newton mm / leaf width
Potential height	Continuous	m

Leaves were collected from robust, healthy, mature individuals growing in the sun as far as possible, to minimise plastic variation in leaf traits in response to light. Species only occurring in shade were taken from the least shady locations available (Cornelissen *et al.*, 2003). Young leaves that were not yet fully extended, senescent leaves and leaves with obvious signs of disease or herbivory were avoided. Where possible, plant fragments with multiple leaves, or whole plants for some herbaceous species, were collected. These were kept hydrated in sealed ziplock bags, refrigerated, and measured within two days of collection. Leaves were removed from the plant fragments just prior to measurement. If enough suitable leaves were available, leaves from the same fragments were used for measurement of SLA and TS. Further details of the methods and apparatus used are provided in Appendix A.

Specific leaf area measurements were made for 113 woody species (87% of the woody species present), and 290 herbaceous species (83% of the herbaceous species present). Values for the remaining species were estimated from the values obtained for species with similar leaf characteristics and/or from similar habitats. Since SLA is not particularly strongly conserved within genera (Hoffmann *et al.*, 2005; Anderson *et al.*, 2011), the fact that these estimates were sometimes made from species in other genera was not considered problematic. Leaf tensile strength measurements were made for 110 woody species (85%) and 289 herbaceous species (83%), the remaining values being estimated as above.

2.2.2 Requirement 2: measuring redundancy

Measuring redundancy and response disparity both require calculation of dissimilarities (or similarities) in functioning between species.

Calculation of inter–species dissimilarities

Functional disparity (dissimilarity in function) among species was calculated from the functional trait data collected for each species. For each combination of traits representing a different effect or response function, pairwise dissimilarity matrices were calculated, as described in §2.1.2. These dissimilarity matrices contain the dissimilarities between each pair of species with respect to a particular function.

Woody and herbaceous species were kept separate when calculating dissimilarity matrices, both to accommodate the differences in the traits collected for the two groups (Table 2.5) and to account for the possibility that the mapping between traits and functions is likely to be different for woody and herbaceous species Walker and Langridge (2002).

Prior to calculating the dissimilarity matrix, the trait data were transformed if necessary to improve normality. Of the woody traits, flowering period, fruiting period and potential height were log transformed, SLA was square–root transformed and leaf tensile strength was eighth–root transformed. Of the herbaceous traits, potential height and leaf tensile strength were log transformed and SLA was square–root transformed. Trait data were then standardised by the range to remove the effects of different scales of measurement (Gower, 1971; Laliberté and Shipley, 2010).

Correlations between traits were checked. This was important because using traits that are highly correlated with each other, either positively or negatively, duplicates information and gives the correlated traits a greater influence on the dissimilarity values (Botta-Dukát, 2005). If a pair of traits were highly correlated, one was removed, so that each trait included in the dissimilarity calculation represented a meaningfully different aspect of ecological functioning.

For the woody species, there were several relatively high correlations among traits relating to flowering and fruiting times (flowering end and flowering period: $r = 0.46$, flowering start and flowering end: $r = 0.33$, flowering start and fruiting start: $r = 0.32$, flowering end and fruiting start: $r = 0.24$). I therefore excluded flowering end and fruiting end from the analysis. For the herbaeous species, lifespan and resprouting were highly correlated ($r = 0.66$). I excluded resprouting, rather than lifespan, because the resprouting data were of a lower quality. After removal of these traits, the correlations among trait variables were generally low (Figure 2.2), suggesting that each represented a different aspect of species' functioning.

The Gower dissimilarity metric was then used to calculate the pairwise species dissimilarity matrices (Gower, 1971). The Gower metric is a mathematical formula for calculating dissimilarities between pairs of entities. Unlike other metrics, the Gower metric was developed for use with trait variables of mixed types (continuous, binary and nominal) and has recently been extended to include ordinal (Podani, 1999) and circular (Pavoine *et al.*, 2009) variables. Since the functional trait data in this study included variables of all these different types (Table 2.5), the Gower metric was the only appropriate choice.

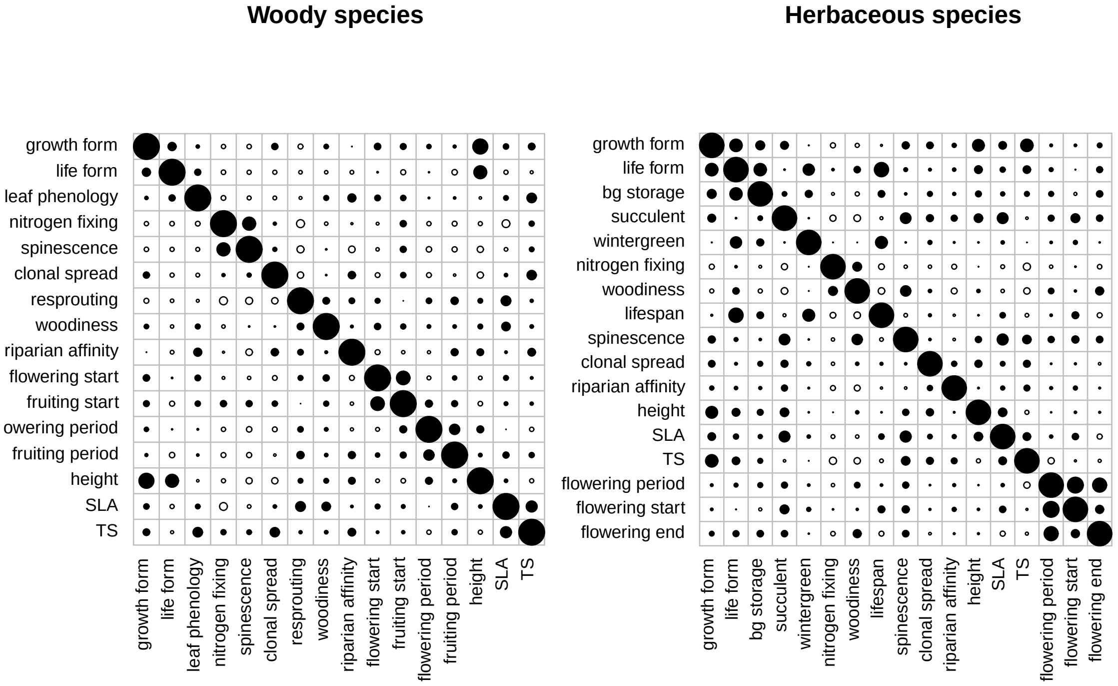


Figure 2.2: Graphical representation of Pearson correlations among traits for woody and herbaceous species. Size of circle indicates strength of correlation, where circles on the diagonal represent perfect correlation ($r = 1$). Black circles indicate positive correlation, white circles negative correlation.

Dissimilarity clearly cannot be calculated in the same way for different types of variables. For example, dissimilarity for binary and nominal variables can be calculated using a simple matching coefficient (dissimilarity of 0 if two species have the same value and 1 if they have different values), while continuous variables require a more complex measure and may produce a whole range of dissimilarity values. The Gower metric applies an appropriate dissimilarity measure to each different type of data and then combines the results (Legendre and Legendre, 1998).

Gower (1971) defined the similarity between two objects (species) j and k as:

$$G_{jk} = \frac{\sum_{i=1}^{n} W_{ijk} S_{ijk}}{\sum_{i=1}^{n} W_{ijk}}$$

Where G_{jk} is the similarity between objects j and k; W_{ijk} is the weight of variable i for the jk pair; and S_{ijk} is the partial similarity of the jk pair for variable i. This varies according to variable type.

The function `gowdis` in the R (R Development Core Team, 2005) package `FD` (Functional Diversity) was used to calculate the dissimilarity matrices using the Gower metric (Laliberté and Shipley, 2010). The `gowdis` function includes the extensions proposed by Podani (1999) for ordinal variables, but not the extensions proposed by Pavoine *et al.* (2009) for circular variables. To allow for correct handling of the circular trait variables in this analysis (leaf, flower and fruit phenology), I extended the code for `gowdis` to be able to handle circular variables, based on R code by Pavoine in her implementation of the Gower dissimilarity measure (function `dist.ktab` in the package `ade4`). I also corrected a mistake in her treatment of circular variables and made it more general (see Appendix B: R Code). These improvements will be submitted for inclusion in future versions of the `FD` R package.

Pairwise dissimilarities were calculated using the full set of species for which abundance was recorded, so that species dissimilarity values were standardised across the entire range of functional traits present in the species pool. This did not affect the pairwise dissimilarity calculations, only the scaling, because the dissimilarities were divided by a bigger range than they would have been if a dissimilarity matrix had been calculated for each assemblage separately. This global dissimilarity matrix was then subsetted to obtain dissimilarity matrices for each of the different assemblages (including only the species present in each). This allowed dissimilarity matrices for different assemblages (but for the same function) to be validly compared with each other.

Weighting of traits to account for differences in variable type

It has already been argued that the effects of different types of trait variables (Table 2.1) on the distribution of dissimilarities needs to be taken into account (§2.1.2). If certain types of traits have a greater influence on the final dissimilarity values than others, this amounts to a form of unintentional trait weighting. While there may be good biological reasons why some traits have a greater influence on a particular function than others (see Figure 2.1 and §2.1.1), the influence of a trait on the outcome of the analysis should *not* be determined by an artificial factor like the variable type chosen by the researcher to measure the trait (e.g. whether it is measured as ordinal or continuous).

I therefore carefully explored the effects of variable type on the final dissimilarities. To do this, I used graphical displays showing how each (non–continuous) trait variable divided up the cloud of species points in the functional space (function `s.class` in the package `ade4`). I also calculated the contribution of each trait to the overall dissimilarities (ie. the dissimilarities obtained using all the traits) using the function `kdist.cor` in `ade4`. This analysis showed that different types of trait did indeed have different effects: nominal, binary and ordinal traits tended to have greater effects on the overall dissimilarity value than continuous or circular traits.

I therefore developed a method for ensuring that each trait contributes equally to the overall dissimilarity, by differentially weighting the traits to remove the effects of variable type (details of code and method in Appendix B). This required developing a new method for assessing trait contributions to the overall dissimilarity, one that could also assess the effects of trait weighting. This new method calculates trait contributions by measuring the effect on the overall dissimilarity of removing each trait in turn, and is conceptually similar to the approach suggested by Petchey and Gaston (2002a) for calculating the contribution of species to the disparity of a whole assemblage (Appendix B).

In Gower's (1971) formulation, the weighting factor W_{ijk} was included to allow handling of missing values. It takes a value of 0 if species j and k cannot be compared because information is missing for one of the species, and a value of 1 when information is present for both species (Legendre and Legendre, 1998). In other words, no comparison is computed for variables where information is missing for one of the species. Legendre and Legendre (1998) suggested that this approach could easily be extended to allow weighting of traits, by assigning to W_i a value between 0 and 1 corresponding to the weight one wishes each trait to have in the analysis. Traits with weights close to 0 would contribute little to the final similarity value whereas traits with higher weights (closer to 1) would contribute more. Giving a weight of 0 to a trait is equivalent to removing it from the analysis.

The facility for weighting the contributions of traits to the overall dissimilarity, as suggested by Legendre and Legendre (1998), has been implemented in R by Laliberté and Shipley (2010). I assigned weights to traits using this facility, but for the sole purpose of *equalising* the contributions of traits to the overall dissimilarity, so as to eliminate any effects of differences in variable type (Appendix B). I have called this type of weighting ‘corrective weighting’. The reasoning behind the corrective weighting is that in the absence of biological information about the relative contributions of traits to a function, all traits should contribute equally. I did not weight the contributions of traits to each function here, because our understanding of the relative contributions of traits to functions is not yet sufficient to provide a solid basis for applying these kind of weightings. However, this can easily be accommodated in future as understanding improves, using the method described in Appendix B for assessing trait contributions to the overall dissimilarity.

The effect of equalising the contributions of the different traits can be clearly seen in Figures 2.3 to 2.7. Where the traits defining a function were mostly nominal or ordinal variables, the dissimilarity matrix contained clear clusters of values (e.g. for shade provision in Figure 2.4 or response to damage in Figure 2.7). Continuous variables (e.g. height, SLA and TS) made much lower contributions to the overall disparity than any of the categorical–type variables (e.g. height in Figure 2.4). Weighting the traits so that all made equal contributions produced a more continuous distribution of dissimilarities.

Using appropriate trait weightings, pairwise dissimilarity matrices were then calculated for each function of interest. These matrices were used to calculate the measures of redundancy and response disparity, and also to graphically display the species in a multidimensional space representing each function. Species close together in each functional space can be assumed to perform that function similarly. For example, species close together in the nutrient cycling space will cycle nutrients similarly, because they have similar traits (e.g. similar litter breakdown rates, or carbon storage capacities). Species close together in the functional space can therefore be seen as providing redundancy for the functioning associated with that particular region of the space.

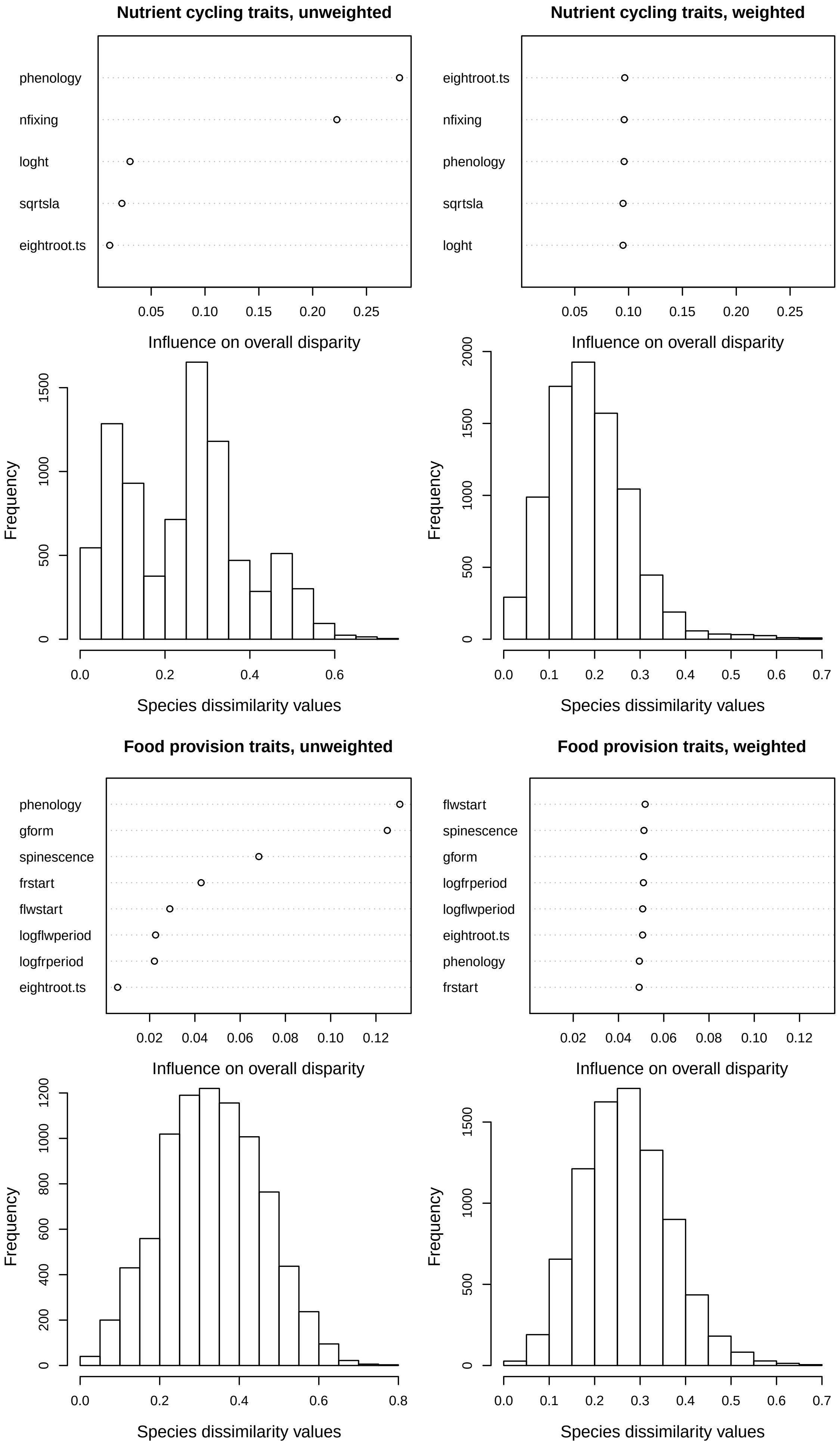


Figure 2.3: Contributions of trait variables to the overall disparity showing how trait weighting can be used to equalise the contributions of the different traits: nutrient cycling and food provision functions, woody species.

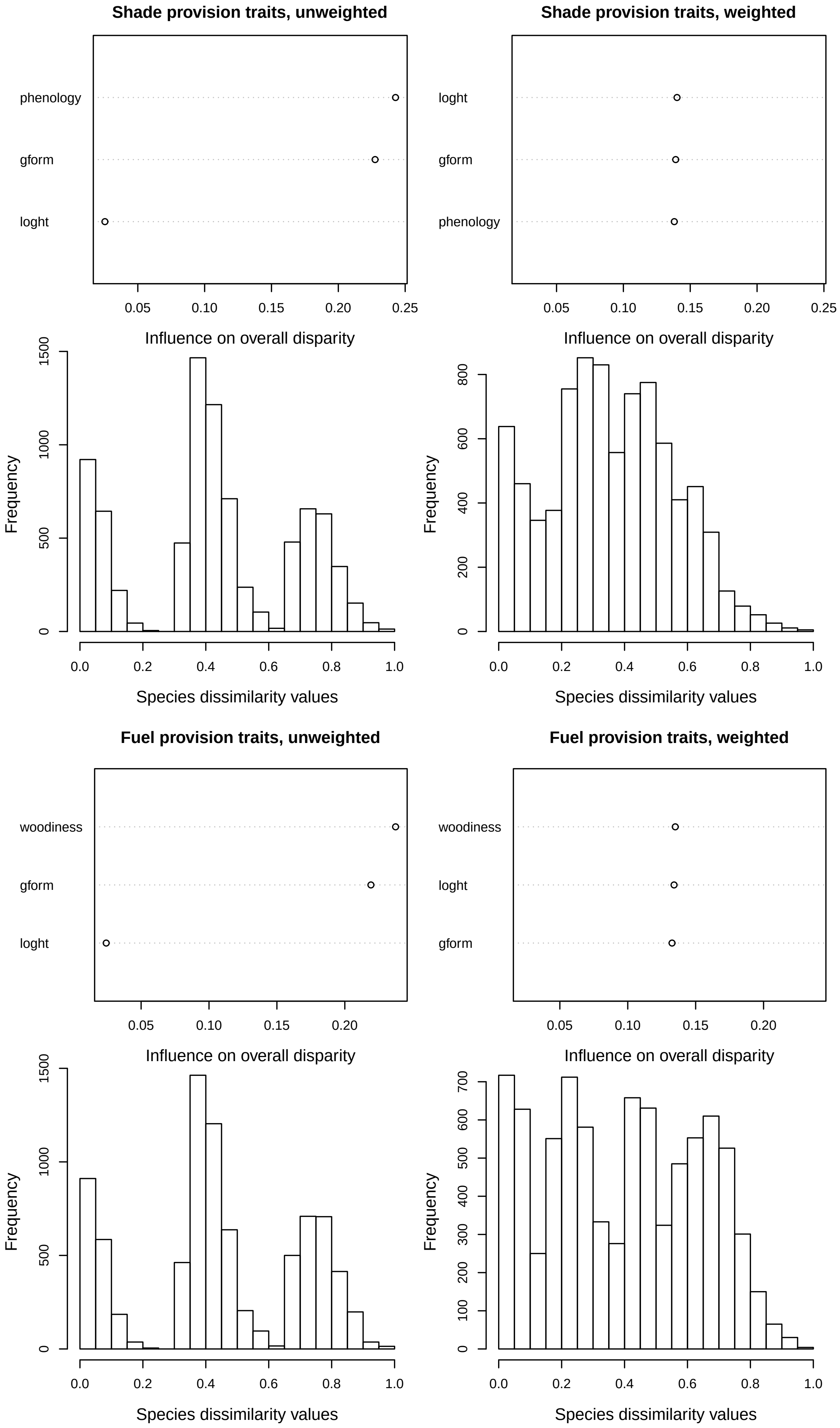


Figure 2.4: Contributions of trait variables to the overall disparity showing how trait weighting can be used to equalise the contributions of the different traits: shade and fuelwood provision functions, woody species.

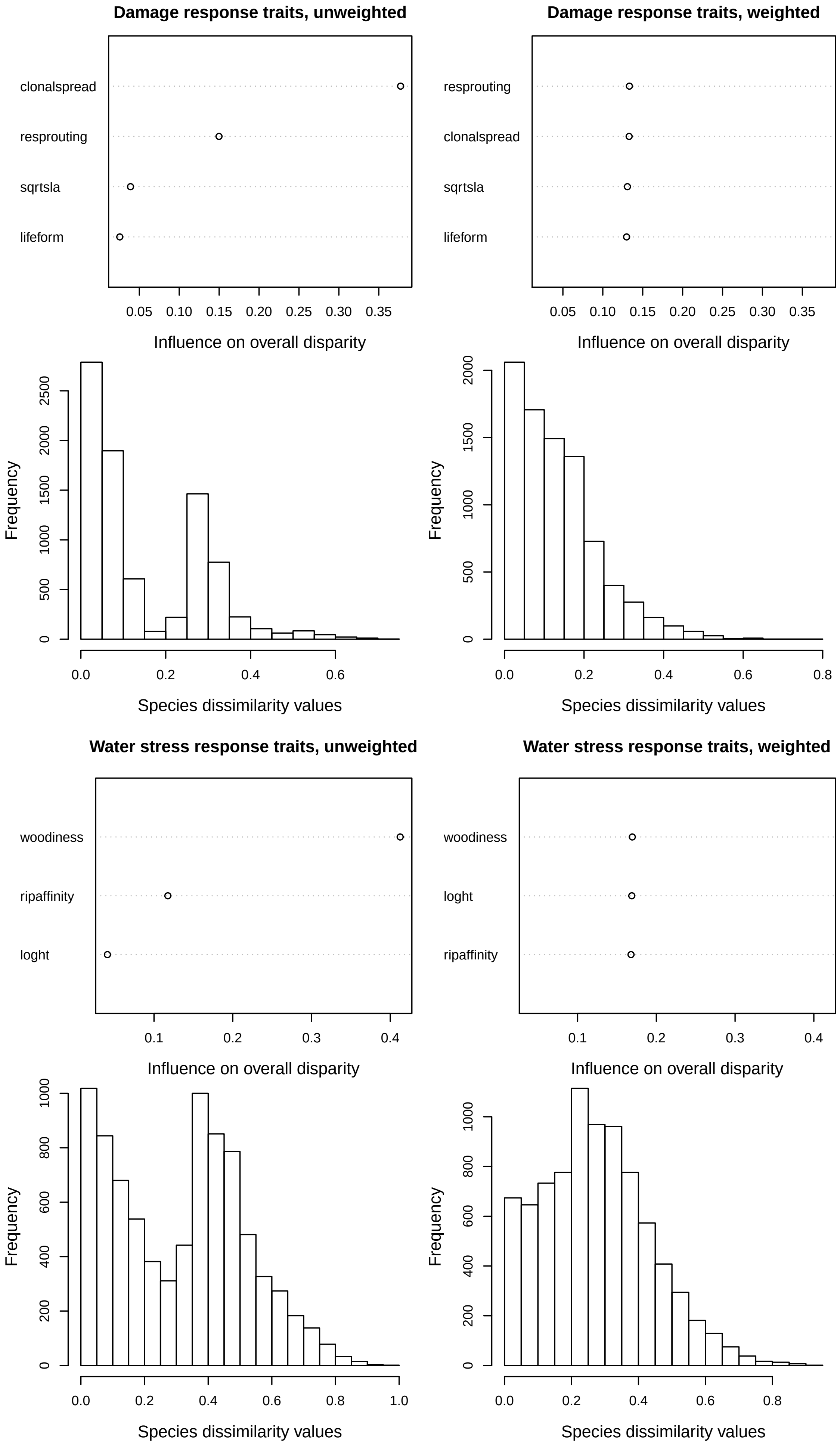


Figure 2.5: Contributions of trait variables to the overall disparity showing how trait weighting can be used to equalise the contributions of the different traits: response to damage and response to water stress, woody species.

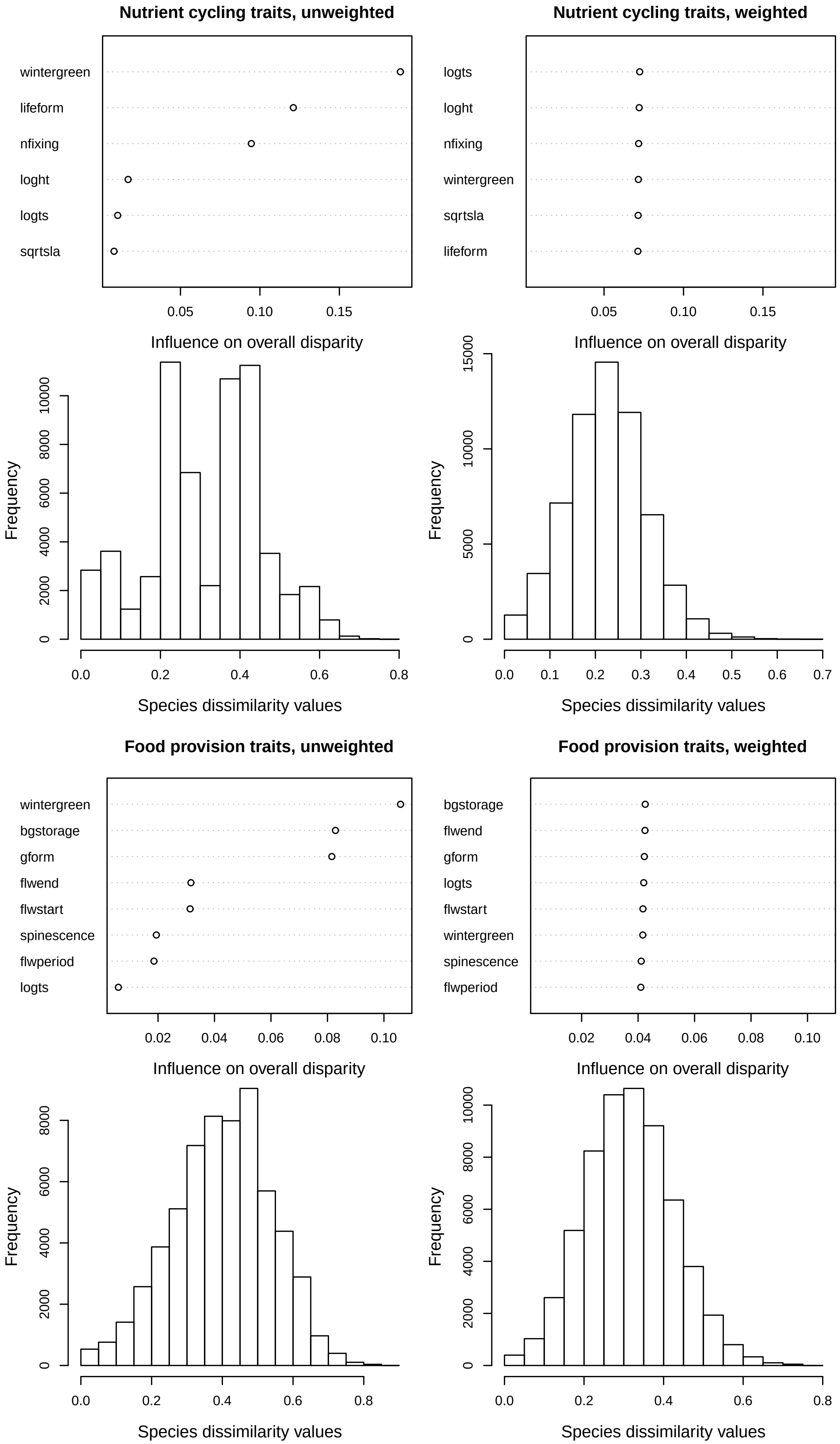


Figure 2.6: Contributions of trait variables to the overall disparity showing how trait weighting can be used to equalise the contributions of the different traits: nutrient cycling and food provision functions, herbaceous species.

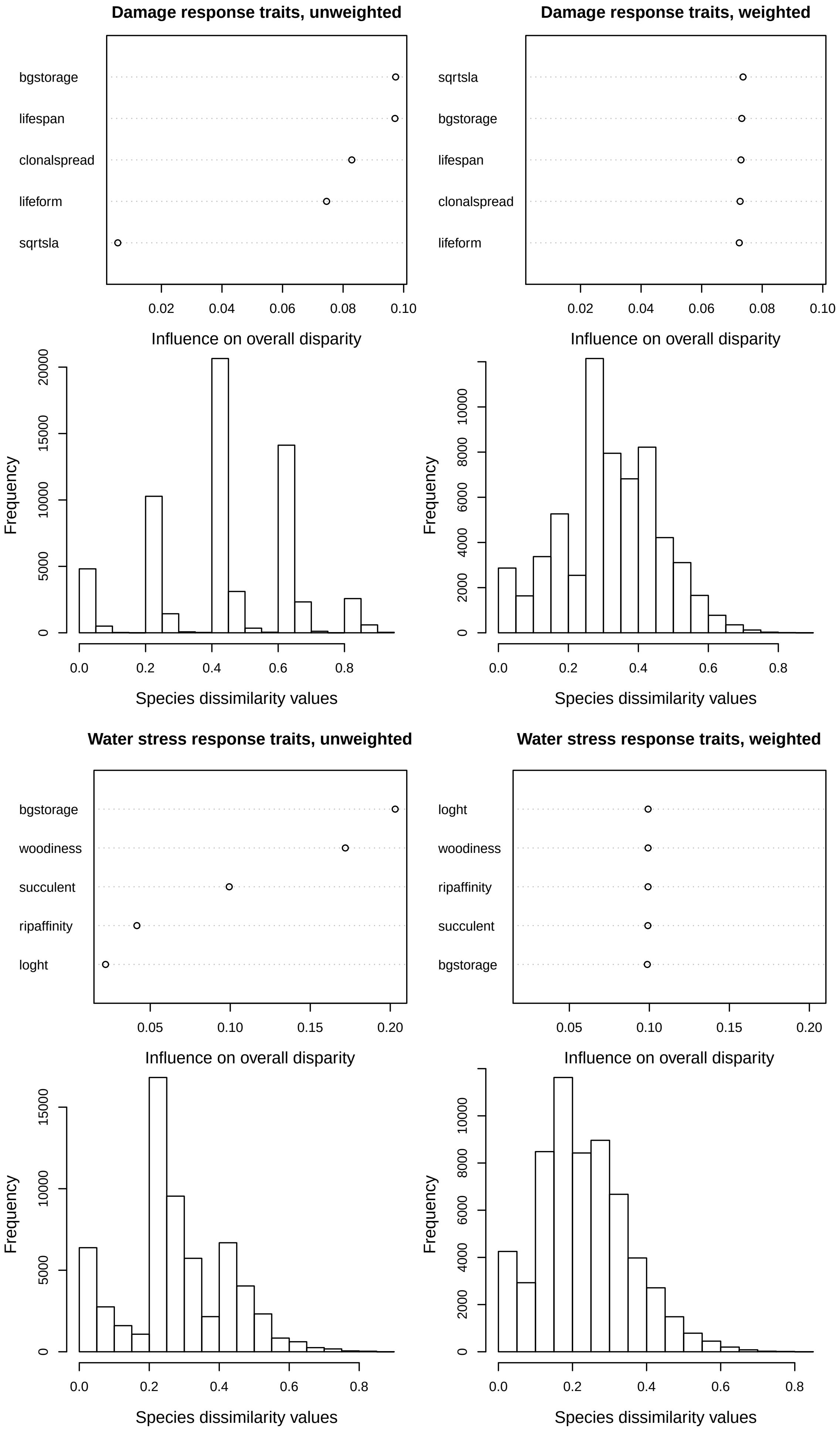


Figure 2.7: Contributions of trait variables to the overall disparity showing how trait weighting can be used to equalise the contributions of the different traits: response to damage and response to water stress, herbaceous species.

A species–level measure of redundancy

None of the existing measures of redundancy or response disparity reviewed in this chapter are compatible with the species–centric view of functioning described above. I therefore developed my own species–level measures of the amount of redundancy and response disparity associated with *each aspect of the functioning* of *each species*. This was necessary because, as argued in §2.1.2, assemblage–level measures of redundancy and response disparity are not useful for testing the hypotheses of Walker *et al.* (1999) about the functional roles of individual species (see Fig. 1.3). Assemblage–level measures describe the total, average or range of similarity present in an entire assemblage. However, to test Walker's hypotheses it is necessary to explore patterns of redundancy *within* the assemblage, to identify which species function most similarly to which other species and which species are functionally unusual. In other words, it is necessary to consider the different functional roles of each species individually, and the redundancy and response disparity associated with each of these roles.

I developed a species–level measure of redundancy which measures, for a particular focal species, the *redundancy provided by all other species which are very similar to the focal species.* This measure is calculated from the dissimilarity matrix directly. I defined 'very similar' as similarity greater than or equal to 0.9 (90% similarity, or 10% dissimilarity). This choice of threshold value was essentially arbitrary, but it was intended to represent a relatively strict criterion for redundancy.

The redundancy measure was obtained by first computing a species × species Gower dissimilarity matrix from a species × traits data table containing the traits considered important for a particular effect function (Figure 2.8(a, b), §2.2.1). This dissimilarity matrix determines the distribution of the species in the functional space pertaining to that effect function (Figure 2.8(c)).

For each species, 'nearest neighbour functional groups' (nngroups) were then identified (Figure 2.8(d)). These groups contained all species that had similarities to the focal species greater than or equal to 0.9. In other words, the nngroup for a particular focal species contained its nearest neighbours in functional space. The number of species in the nngroup was then used as a measure of the amount of redundancy available for that particular aspect of functioning of the focal species.

$$\text{Redund}_{sp} = \text{No. of species in nngroup}$$

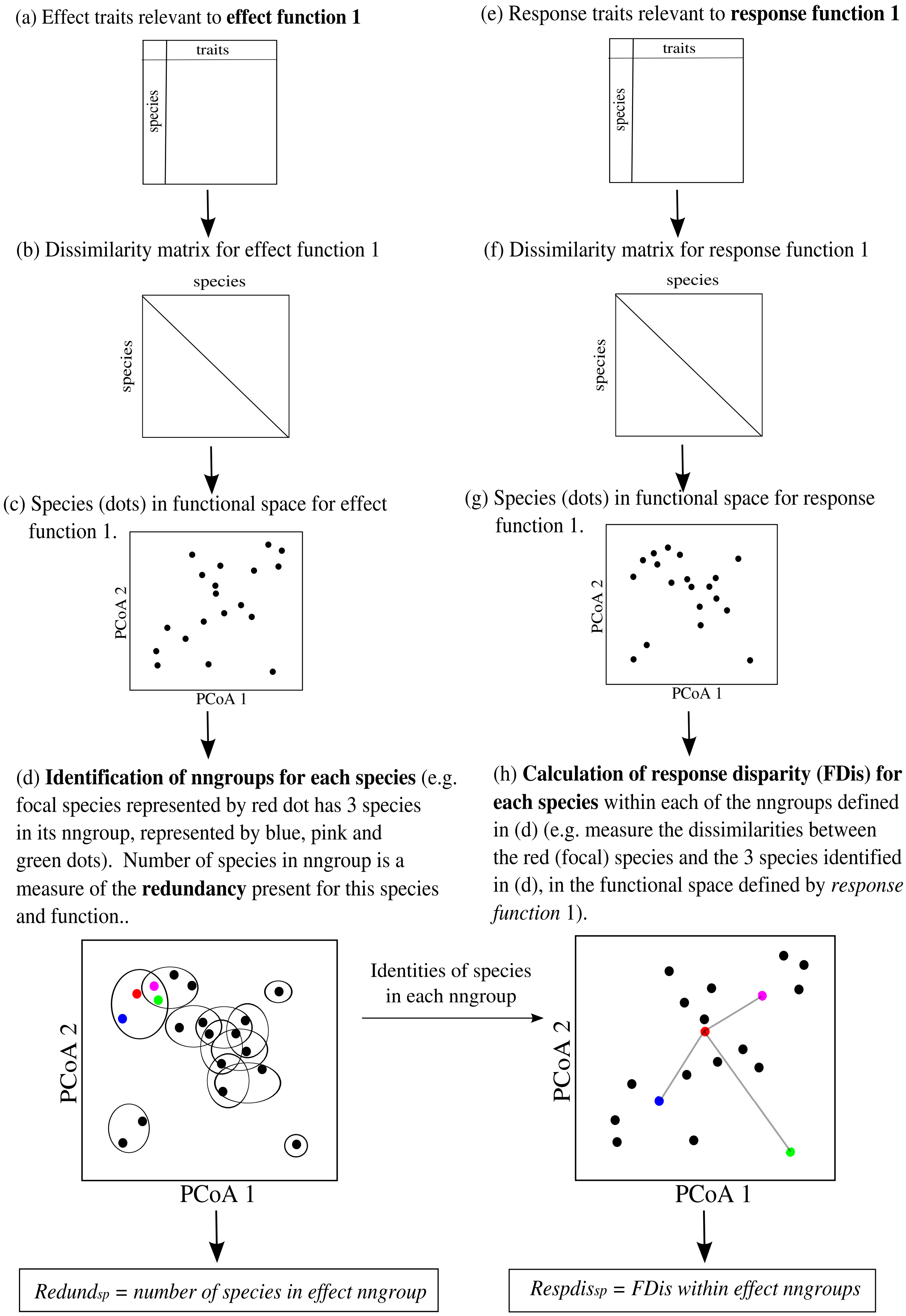
R code for the calculation of this measure is provided in Appendix B.

Unlike the groups used by Walker *et al.* (1999) and those usually obtained from clustering, the nearest neighbour functional groups were not mutually exclusive and could overlap, i.e. a species could be a member of more than one group. This allowed me to avoid problems that arise when there are ties in the dissimilarity matrix, e.g. if species A is equally similar to species B and species C, should it be considered to provide redundancy for the functioning of B or C?. Since the groups could overlap, species A could be recognised as providing redundancy for both species B and C.

Using overlapping groups also better recognises the continuum of functional similarity in an ecological assemblage (e.g. a species near the outskirts of a particular functional group may be almost as similar to species in another functional group as it is to the species in its own group). This approach to identifying groups of similar species was appropriate in this context, where the purpose was not to find the best functional classification of a set of species, but rather to identify which species were involved in providing redundancy for the functioning of which other species. It provides a 'species-eye view' of redundancy which is flexible and useful, as will be seen in the following chapter. Measuring redundancy in terms of the number of species which are similar enough to potentially compensate for the loss of a particular species is also intuitively easy to understand.

2.2.3 Requirement 3: measuring response disparity

Response disparity is the extent to which species that perform a given effect function similarly, differ in their responses to disturbance. For example, a group of species may function similarly with respect to nutrient cycling (the effect function). Response disparity measures how different these same species are in their responses to a particular disturbance (response function). High response disparity contributes to resilience by increasing the range of conditions under which a particular function can be performed, because some of the species performing that function will respond positively to disturbance while others respond negatively.



(a) Effect traits relevant to **effect function 1**

(b) Dissimilarity matrix for effect function 1

(c) Species (dots) in functional space for effect function 1.

(d) **Identification of nngroups for each species** (e.g. focal species represented by red dot has 3 species in its nngroup, represented by blue, pink and green dots). Number of species in nngroup is a measure of the **redundancy** present for this species and function..

(e) Response traits relevant to **response function 1**

(f) Dissimilarity matrix for response function 1

(g) Species (dots) in functional space for response function 1.

(h) **Calculation of response disparity (FDis) for each species** within each of the nngroups defined in (d) (e.g. measure the dissimilarities between the red (focal) species and the 3 species identified in (d), in the functional space defined by *response function* 1).

Identities of species in each nngroup

$Redund_{sp}$ = *number of species in effect nngroup*

$Respdiss_{sp}$ = *FDis within effect nngroups*

Figure 2.8: Schematic representation of the procedure followed to calculate redundancy and response disparity for each species and function.

A species–level measure of response disparity

To calculate response disparity, I first created a Gower dissimilarity matrix for each response function, based on the selected response traits (§2.2.1), (Figure 2.8(e, f)). The distribution of dissimilarity values in these response matrices determines the distribution of species in the corresponding response functional space (Figure 2.8(g)). I then calculated response disparity as the multivariate dispersion within each species' nearest neighbour functional group, for each effect function separately (Figure 2.8(h)). The species in an nngroup by definition perform a particular effect function similarly. Because each species in the assemblage had its own nngroup, and these groups were different for each of the effect functions, application of this measure produced a set of response disparity values for each species, for each combination of effect and response functions (e.g. disparity in response to damage for nutrient cycling nngroups, disparity in response to damage for food provision nngroups, disparity in response to water stress for nutrient cycling nngroups, etc.). These species–level response disparity values indicate the amount of response disparity associated with the functioning of a species, i.e. how much its group of potential compensating species differ in their responses to disturbance.

$$\text{Respdis}_{sp} = \text{multivariate dispersion of response dissimilarities within effect nngroup}$$

Following Laliberté *et al.* (2010), I calculated multivariate dispersion using the FDis index (Table 2.2) unweighted by species abundances. FDis, in its unweighted form, is a measure of the average disparity among a group of species, or the average distance of the species from the group centroid. The fact that it is an average makes it less strongly influenced by the number of species in the group than some other measures of disparity (e.g. FRic and FAD2 in Table 2.2). This is a desirable feature because it reduces the dependency of the response disparity measure on the redundancy measure (Laliberté *et al.*, 2010).

While the use of FDis to measure response disparity is not novel, calculating FDis within the nearest neighbour groups (nngroups) associated with each species is a novel approach. My approach differs from that of Laliberté *et al.* (2010) in that FDis was calculated within each nngroup (and each species had its own nngroup), rather than within each of the functional groups into which the assemblage was divided (see previous section). Because the nngroups were defined by the similarities between the focal species and its nearest neighbours in functional space, the focal species is near the group centroid, and the FDis value therefore provides a good measure of the response disparity associated with the functioning of that species (i.e. the mean response disparity of its nearest neighbours; Figure 2.8(h)). If FDis is calculated within functional groups such as those used by Laliberté *et al.* (2010), the group centroid may be far from a particular focal species, especially if the group is large. The FDis value obtained for the group may therefore not be a good measure of the response disparity associated with that particular species.

2.2.4 Graphical display of results

Applying the redundancy and response disparity measures described above generated a large amount of information. It was therefore important to be able to display this information in a concise and easily understandable manner. I used Principal Coordinates plots to display the distribution of species in each functional space, with enhancements suggested by Villéger *et al.* (2010).

The Principal Coordinates Analysis for these plots was performed using the R function `betadisper` in the package `vegan`, which corrects for negative eigenvalues resulting from the non–Euclidean dissimilarity matrices (Anderson *et al.*, 2006). Negative eigenvalues arise from the use of the Gower dissimilarity metric (as well as other semi–metric or non–metric measures), and are problematic because they do not allow the dissimilarities among species to be fully represented in a Euclidean space (Gower, 1982).

In these plots, the size of the species points is scaled by their abundance in the assemblage, making it easy to see at a glance which are the dominant and which are the rare species (Figure 2.9). Species redundancy (or response disparity) values can be indicated using colours, e.g. green for high redundancy, red for low redundancy, or species with particular traits can be highlighted. The convex hull, or smallest convex envelope containing all the species, is also shown. This is the equivalent of the multivariate range of the dissimilarity values in a particular functional space, or the volume of functional space occupied, which has been used as a measure of functional richness (FRic, see Table 2.2). Species on the convex hull form the vertices — the points defining the shape of the convex hull (Figure 2.9). These species have the most extreme values for one or more traits, in other words they are more unusual in the traits used to define the space than species near the centre. It is useful to be able to identify vertex species, because loss of these species, particularly those which significantly enlarge the volume of the convex hull, will decrease the amount of functional space occupied by the assemblage. Vertex species which

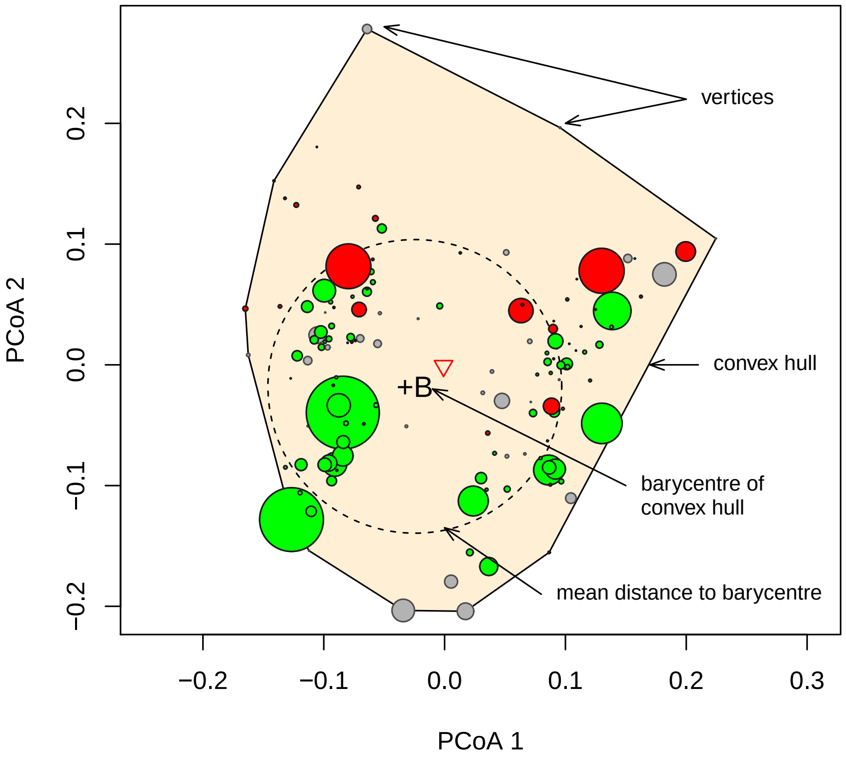


Figure 2.9: Example of Principal Coordinates plots used to display species redundancy, response disparity and abundance information. The axes represent the first two dimensions of the multivariate functional space. Species are represented by circles, with the diameter of the circle scaled by the abundance of the species. Species with high redundancy are coloured green, intermediate redundancy orange, and low redundancy red.

are relatively abundant but which have low redundancy and/or response disparity, represent potential keystone species. The mean distance to the barycentre (central point) of the convex hull is shown as a dashed circle (Figure 2.9). This makes it easy to see if a particular species is more or less similar than the average for its assemblage. Species near the edges of the space may be interpreted as being functionally specialized, with generalist species occurring closer to the centre (Villéger *et al.*, 2010; Devictor *et al.*, 2010).

2.2.5 Novelty of proposed methods

The methods developed in this section are compared with existing approaches to measuring species' functioning, redundancy and response disparity in Table 2.6 (this table is an extension of Table 2.3).

The methods used and developed here have improved on and extended previously proposed methods in the following ways:

- The use of different trait sets to represent different effect and response functions (rather than just a single set of traits, as used by Walker *et al.* (1999)) allowed me to compare the patterns of redundancy among species for the different functions, and to quantify the amount of response disparity among species with similar functional effects. The separation of effect and response functions was essential for testing the hypotheses of Walker *et al.* (1999).
- The use of the recently extended Gower dissimilarity measure (Pavoine *et al.*, 2009) to calculate the dissimilarity matrix, rather than Euclidean distance, allowed me to include a wider range of types of trait variables than Walker *et al.* (1999), because the Gower measure allows inclusion of different variable types in the same analysis.

Table 2.6: Comparison between existing approaches and my approach to measuring species' functioning, redundancy and response disparity (extension of Table 2.3).

Requirement	Existing approaches	My approach
Measure species' functioning	Direct measurement (e.g. Kremen *et al.*, 2002; Balvanera *et al.*, 2005); Use functional traits as surrogates of function (e.g. de Bello *et al.*, 2010).	Use carefully chosen sets of traits to represent different functions, and distinguish between effect and response functions.
Measure redundancy associated with species' functioning	Group the species into mutually exclusive 'functional groups', then count the number of species per group (Laliberté *et al.*, 2010); Count the number of species that are functionally similar to each dominant species (Walker *et al.*, 1999).	Count the number of species that are functionally similar to each species in the assemblage, but allow species to belong to more than one group (overlapping nngroups), giving a measure of the redundancy associated with each of the functions performed by each species.
Measure response disparity associated with species' functioning	Measure variation in the scale of operation of organisms within functional groups (Peterson *et al.*, 1998; Elmqvist *et al.*, 2003; Allen *et al.*, 2005); Measure the multivariate dispersion (FDis) within each functional group (Laliberté *et al.*, 2010).	Measure the multivariate dispersion (FDis) within each nngroup, giving a measure of the amount of response disparity associated with each of the functions performed by each species.

- I used a novel 'corrective weighting' approach to remove artificial differences in the contribution of the various traits caused by differences in variable type. This allowed me to ensure that all the trait variables really contributed equally to each function.
- The approach to measuring redundancy presented here is similar to that suggested by Walker *et al.* (1999). As they did, I identified the species providing redundancy for the functioning of each dominant species, but I applied my 'species–level' measure of redundancy to all the species in the assemblage, not just the dominant ones. I identified functionally similar species in a different way, using 'nearest neighbour functional groups' (nngroups). These groups contained the species most similar to the focal species, or its nearest neighbours in functional disparity space. Unlike the groups used by Walker *et al.* (1999) and those usually obtained from clustering, the nngroups were not mutually exclusive and could overlap, better reflecting the continuous nature of similarity and dissimilarity among species.
- I measured response disparity using multivariate dispersion of the response dissimilarities in a similar manner to Laliberté *et al.* (2010). However, I measured the multivariate dispersion within the nngroups used in the calculation of redundancy. My response disparity measure therefore also took the continuous nature of disparity into account, something not achieved by any existing measures of response disparity.

The overall effect of these innovations is to produce measures of the amount of redundancy and response disparity associated with each aspect of functioning of each species in the assemblage, in a way that takes into account the continuous, multidimensional nature of disparity better than existing measures do.

2.3 Evaluation of performance of methods

The differences between my methods and previously published methods for measuring redundancy and response disparity were assessed by comparing the results of the different methods applied to the same dataset. Such comparisons are important because they provide a standardised means of comparing different methods, and help to develop understanding about how the choice of methodology may affect the results obtained and the conclusions drawn.

To assess the effect of using overlapping 'nearest neighbour groups' rather than mutually exclusive functional groups, I first compared these two approaches using the small dataset published by Walker *et al.* (1999). I then extended this comparison to the much larger dataset collected during this study, comparing my methods for measuring both redundancy and response disparity with those used by Laliberté *et al.* (2010).

2.3.1 Mutually exclusive groups vs nngroups: a comparison using data from Walker *et al.* (1999)

Walker *et al.* (1999) used species abundance data from a study examining the effects of artificial water supplies on rangeland biodiversity (Landsberg *et al.*, 1997), which included five sites along a grazing gradient, from very heavy grazing near a water point to very light grazing around 6 km from water. Five functional effect traits were collected for 22 graminoid species (21 grasses and one sedge), and the pairwise species dissimilarity matrix was calculated using squared Euclidean distance. Species with dissimilarity values ≤ 6 were considered 'very similar'. The advantage of using this dataset is that it is small and simple, and all steps in the analysis were published in Walker *et al.* (1999), including the dissimilarity matrix (Table 2.8).

I replicated their dissimilarity matrix using the function `vegdist` in the R package `vegan`, using squared Euclidean distance as the dissimilarity metric. I then generated nngroups for each of the 22 species, using a cutoff dissimilarity of 6, and compared these to the groups presented by Walker *et al.* (1999). This provides a direct test of the effects of using nngroups rather than mutually exclusive functional groups when measuring the amount of redundancy associated with the functioning of each species (measured as the number of species within the group in each case). The dissimilarity matrix and the threshold below which species were considered very similar were identical in both cases; only the way in which the groups were identified was different.

The identities of the species in the two sets of groups were similar, but my nngroups typically contained more species than the groups of Walker *et al.* (1999) (Table 2.7). A couple of mistakes were detected in the allocation of species to groups in Figure 3 in Walker *et al.* (1999); these have been corrected in Table 2.7 so that they do not cloud the comparison of the two methods. Firstly, they identified *Thyridolepis mitchelliana* as being very similar to *Enneapogon polyphyllus*, but this does not match the dissimilarities provided in their Table 4 (Table 2.8). *Enneapogon polyphyllus* and *T. mitchelliana* have a dissimilarity of 10, above the cutoff value of 6. The species most similar to *E. polyphyllus* is actually *Eragrostis dielsii* (4), and this species should be the only species providing redundancy to *E. polyphyllus*, as shown with my method (Table 2.7). Also, *Eragrostis xerophila* should have been included in the group containing *Aristida contorta*, *Aristida latifolia* and *Eragrostis microcarpa*, as it has a dissimilarity of 4 to *A. contorta* (Table 2.8). These corrections are shown in bold in Table 2.7.

However, there were also some differences between the methods which nicely illustrate the problems caused by using mutually exclusive groups, and the benefits of my approach. The groups of Walker *et al.* (1999) were formed by taking each dominant species in turn and identifying which other species were very similar to it (dissimilarity ≤ 6). However, once a species was allocated to a group it was not considered for inclusion in any other groups. For example, *Aristida latifolia*, *Eragrostis microcarpa* and *Eragrostis xerophila* were identified as being very similar to *Aristida contorta* (Table 2.7). This then constrained the latter three species to be associated only with each other and *A. contorta*, and did not allow for the fact that each of these may have had other species to which they were actually more similar. Using nngroups as I have suggested removes these constraints — my nngroups for *A. latifolia*, *E. microcarpa* and *E. xerophila* contained more and/or different species (Table 2.7). Similarly, the group for *Themeda triandra* included both *A. latifolia* and *E. xerophila* with my method, whereas with their method these species were excluded because they had already been allocated to another group. The constraints imposed by the grouping process of Walker *et al.* (1999) also sometimes caused species to be included in a group even though their dissimilarities to the focal species were greater than 6 (e.g. *Eragrostis microcarpa* in the groups of *Aristida latifolia* and *Eragrostis xerophila*, dissimilarity of 9 in both cases).

Furthermore, with the method of Walker *et al.* (1999), the order in which the focal species are considered affects the outcome. The first species considered will have no restrictions on which other species can belong to its group, but as the process proceeds, progressively fewer species will be available for inclusion in the groups. If one begins with the dominant species, as done by Walker *et al.* (1999), the least common species end up with much lower redundancy than with my nngroup method, because many of the species to which they are similar have already been allocated to other groups (see groups for *Eragrostis dielsii*, *Amphipogon caricinus*, *Thyridolepis mitchelliana* and *Eragrostis xerophila* in Table 2.7).

The use of overlapping nngroups is therefore preferred to the use of mutually exclusive, non–overlapping groups, because it avoids the problem of species allocations to groups being constrained by the grouping structure and the order in which the groups are formed. Using overlapping nngroups provides a more accurate measure of the amount of redundancy associated with the functioning of a particular focal species, because all species that are sufficiently similar to that focal species are free to be included in its nngroup, regardless of which other nngroups they may belong to. As predicted in §2.1.2, using mutually exclusive groups tends to underestimate the amount of redundancy present.

Table 2.7: Comparison between the mutually exclusive groups of similar species used by Walker *et al.* (1999) and my ‘nearest neighbour groups’ or nngroups, for the ten most frequent graminoid species in the dataset of Walker *et al.* (1999). Dissimilarities calculated as squared Euclidean distance, with dissimilarities ≤ 6 taken to indicate high similarity between species. Bold text indicates corrections made to the groups of Walker *et al.* (1999) based on the dissimilarities provided in their Table 4. They only provided groups for the top ten species, the rest were calculated by me from the dissimilarities provided. Species are displayed in order of their frequency in the plots surveyed.

Focal species	**Similar species providing redundancy**	
	(Walker *et al.*, 1999)	Kotschy (nngroups)
Aristida contorta	*Aristida latifolia* *Eragrostis microcarpa* ***Eragrostis xerophila***	*Aristida latifolia* *Eragrostis microcarpa* *Eragrostis xerophila*
Tripogon loliiformis	—	—
Enneapogon polyphyllus	***Eragrostis dielsii***	*Eragrostis dielsii*
Fimbristylis dichotoma	—	—
Aristida latifolia	*Aristida contorta* ***Eragrostis xerophila*** *Eragrostis microcarpa*	*Aristida contorta* *Eragrostis xerophila* *Themeda triandra* *Amphipogon caricinus*
Themeda triandra	*Amphipogon caricinus*	*Amphipogon caricinus* *Aristida latifolia* *Eragrostis xerophila*
Digitaria brownii	*Digitaria ammophila* *Austrochloris dicanthioides*	*Digitaria ammophila* *Austrochloris dicanthioides*
Chloris pectinata	—	—
Eragrostis microcarpa	*Aristida contorta* *Aristida latifolia* ***Eragrostis xerophila***	*Aristida contorta* *Panicum effusum* *Sporobolus actinocladus*
Eriachne pulchella	*Eragrostis basedownii*	*Eragrostis basedownii* *Eragrostis dielsii*
Panicum effusum	*Sporobolus actinocladus*	*Sporobolus actinocladus* *Eragrostis microcarpa* *Eragrostis dielsii*
Sporobolus actinocladus	*Panicum effusum*	*Panicum effusum* *Eragrostis microcarpa* *Eragrostis dielsii*
Digitaria ammophila	*Digitaria brownii* *Austrochloris dicanthioides*	*Digitaria brownii* *Austrochloris dicanthioides*
Dichanthium sericeum	—	*Austrochloris dicanthioides*
Austrochloris dicanthioides	*Digitaris brownii* *Digitaria ammophila*	*Digitaria brownii* *Digitaria ammophila* *Dichanthium sericeum* *Monachather paradoxa* *Amphipogon caricinus* *Thyridolepis mitchelliana*
Tragus australiensis	—	—
Eragrostis basedownii	*Eriachne pulchella*	*Eriachne pulchella* *Eragrostis dielsii*
Monachather paradoxa	*Thyridolepis mitchelliana*	*Thyridolepis mitchelliana* *Austrochloris dicanthioides*
Eragrostis dielsii	*Enneapogon polyphyllus*	*Enneapogon polyphyllus* *Eriachne pulchella* *Panicum effusum* *Sporobolus actinocladus* *Eragrostis basedownii* *Thyridolepis mitchelliana*
Amphipogon caricinus	*Themeda triandra*	*Themeda triandra* *Austrochloris dicanthioides* *Aristida latifolia* *Eragrostis xerophila*
Thyridolepis mitchelliana	*Monachather paradoxa*	*Monachather paradoxa* *Austrochloris dicanthioides* *Eragrostis dielsii*
Eragrostis xerophila	*Aristida contorta* *Aristida latifolia* *Eragrostis microcarpa*	*Aristida contorta* *Aristida latifolia* *Themeda triandra* *Amphipogon caricinus*

Table 2.8: Dissimilarity matrix of Walker *et al.* (1999). Values are squared Euclidean distances.

A. contorta	*Ac*																				
T. loliiformis	34	*Tl*																			
E. polyphyllus	33	13	*Ep*																		
F. dichotoma	42	12	21	*Fd*																	
A. latifolia	4	30	37	38	*Al*																
T. triandra	9	21	26	41	5	*Tt*															
D. brownii	22	24	25	20	18	21	*Db*														
C. pectinata	18	8	13	12	22	21	24	*Cp*													
E. microcarpa	5	25	20	25	9	14	21	9	*Em*												
E. pulchella	25	29	8	29	37	34	33	13	12	*Ep*											
P. effusum	10	16	9	28	14	9	24	8	5	9	*Pe*										
S. actinocladus	10	16	9	28	14	9	24	8	5	9	0	*Sa*									
D. ammophila	27	21	22	21	23	22	1	25	26	34	25	25	*Da*								
D. sericeum	10	24	13	28	14	13	8	16	9	13	8	8	9	*Ds*							
A. dicanthioide	14	20	17	24	10	9	4	20	13	25	12	12	5	4	*Ad*						
T. australianus	26	36	37	24	38	49	36	12	17	21	28	28	41	28	40	*Ta*					
E. basedownii	29	25	10	21	41	40	33	9	14	2	13	13	34	17	29	13	*Eb*				
M. paradoxa	14	8	13	12	10	9	8	8	9	21	8	8	9	8	4	28	21	*Mp*			
E. dielsii	21	17	4	17	25	22	21	9	8	4	5	5	22	9	13	25	6	9	*Ed*		
A. caricinus	7	29	34	37	3	6	9	25	14	38	17	17	12	9	5	41	42	9	26	*Ac*	
T. mitchelliana	25	17	10	13	21	20	9	17	14	18	13	13	10	9	5	37	20	5	6	18	*Tm*
E. xerophila	4	30	37	38	0	5	18	22	9	37	14	14	23	14	10	38	41	10	25	3	21

It was not possible to measure response disparity using the dataset of Walker *et al.* (1999), because the five traits they recorded were all effect traits rather than response traits (height, SLA, longevity, cover, leaf coarseness). A more comprehensive analysis of the effects of using the two different approaches to grouping species was therefore performed, including the effects on response disparity, using the data collected in this study (§2.2).

2.3.2 A comparison using riparian vegetation data

My riparian vegetation dataset contained many more species and functional traits than that of Walker *et al.* (1999) (480 species and 20 traits). Using this dataset and the Gower dissimilarity matrices described in §2.2 and Figure 2.8, I compared the redundancy and response disparity values obtained using my approach with those obtained using the similar approach published recently by Laliberté *et al.* (2010), where redundancy and response disparity were calculated from mutually exclusive groups derived from cluster analysis. This provides a test of how the different grouping methods affect the values of redundancy and response disparity obtained.

Laliberté *et al.* (2010) used Ward's minimum variance clustering to divide species into functional effect groups. This clustering method tends to form hyperspherical clusters with similar numbers of species per cluster if species are evenly distributed in trait space (Legendre and Legendre, 1998). The (mutually exclusive) groups derived from clustering were then ratified by experts with a knowledge of the flora. Redundancy was measured as the number of species within each group, and response disparity as the multivariate dispersion of response dissimilarities within each effect group. For purposes of comparison with my species–level redundancy, I converted the redundancy values obtained for each functional effect group into values associated with each species by assigning each species in a group a redundancy value equal to the number of species in the group minus one.

Redundancy

The correlations between the redundancy values obtained using the two different grouping approaches are shown in Figure 2.10. Redundancy values were positively correlated for all the effect functions measured. The correlations ranged from 0.15 to 0.86, and varied by function. The differences between the functions arose from differences in the types of trait variables used. Functions defined mostly by categorical traits, such as shade and fuelwood provision, tended to have stronger structure on the dendrograms (distinct groups at low heights). For these functions, the redundancy values calculated using the method of Laliberté *et al.* (2010) tended to be more strongly correlated with the values calculated using my method.

When identifying clusters from a dendrogram, it is necessary to specify at which height the dendrogram should be 'cut' to produce the groups. This is equivalent to specifying a cutoff dissimilarity below which

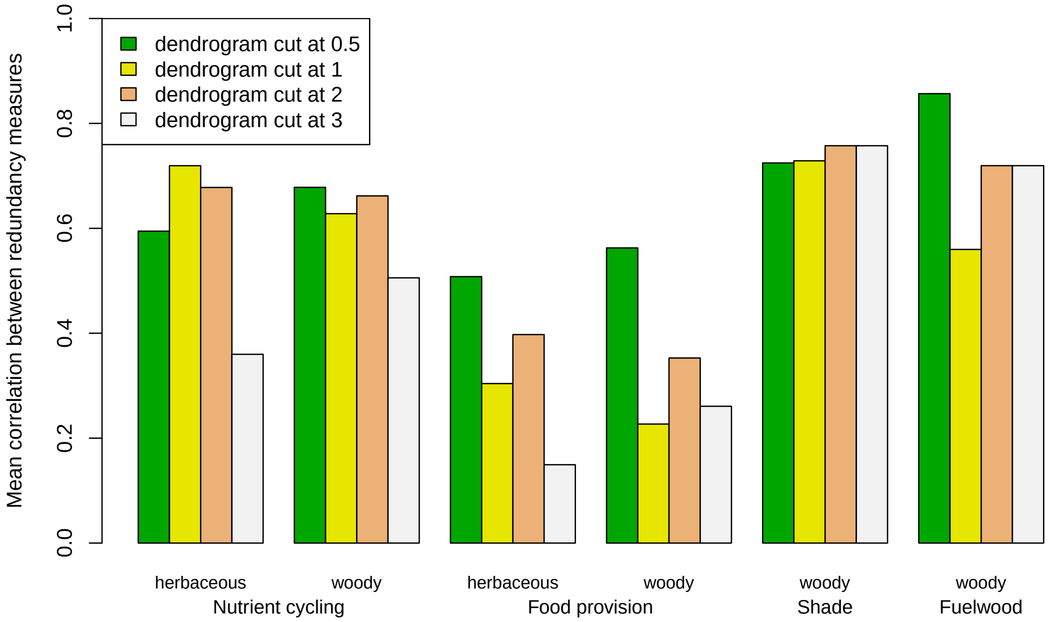


Figure 2.10: Mean correlation between my species–level redundancy measure and the measure used by Laliberté *et al.* (2010). Means were calculated across six sites. Correlations varied by function and were also influenced by the height at which the functional dendrogram was 'cut' to form the functional groups. Cutting the dendrogram at a height of 0.5 usually produced the strongest correlations (green bars), suggesting that this dendrogram cutoff value represented a similar threshold dissimilarity to the one used in my method.

species are considered similar enough to be placed in the same group (e.g. 0.1 was specified as the cutoff value for my nngroups). Since the correlations between the two sets of redundancy values depend on how closely aligned the cutoff values are, I explored the effects of cutting the dendrogram at different heights (Figure 2.10). Cutting the dendrogram at a height of 0.5 generally produced the strongest correlations with my redundancy values, so I used a cutoff of 0.5 for all subsequent comparisons. This ensured that the differences detected were due to the different approaches to forming the groups rather than to differences in the dissimilarity cutoff value.

The method of Laliberté *et al.* (2010), based on mutually exclusive groups, produced a smaller range of redundancy values than my method based on nngroups (Figure 2.11). While the minimum and the median values were similar with the two methods, my method consistently produced more large values (i.e. more species with high redundancy). This is consistent with the findings in the previous section, suggesting once again that using mutually exclusive groups generally underestimates redundancy.

The redundancy values obtained using the two methods are directly comparable because they have the same units (number of species in the group). They can therefore be plotted against one another (Figure 2.12 shows one example of the 36 possible combinations of functions and assemblages). The tendency for species to have higher redundancy values with my method can be clearly seen in Figure 2.12, because more points fall above the equality line than below it. Also, the redundancy values of Laliberté *et al.* (2010) were constrained to not be greater than the size of the largest group, which in this particular case was 16. The species in this group were almost all allocated higher redundancy values with my method, providing another example of the constraining effects of using mutually exclusive groups.

It is not only the size of a group that is important, but also the identities of the species in the group. If the two methods produce groups containing very different species, this will affect the measurement of response disparity within the groups, and will have implications for the expected patterns of functional compensation and vegetation dynamics. The large number of species involved makes it impractical to present all the differences in group memberships in the same way as was done in Table 2.7 for the dataset of Walker *et al.* (1999). The differences observed will therefore be described using a few representative examples.

In most cases, the groups of similar species produced using my method were larger than the groups produced using the method of Laliberté *et al.* (2010). The groups obtained with the two methods generally contained similar species, but differed in size (Table 2.9). Where one (usually my group) was larger, the smaller group was usually a subset of the larger one. In other words, the smaller group did not contain any species that were not present in the larger group. However, the groups formed by Laliberté's method did not always contain the species with the highest similarity to the focal species; some species that should have been included in a particular group were excluded simply because they were already part of another group (see groups for *Barleria elegans* and *Achyranthes aspera* in Table 2.9). The nngroups created using my method, however, by definition always contained only the species most similar to the focal species (dissimilarities ≤ 0.1, or similarity ≥ 0.9). Where their groups were larger than my groups, the additional species were always less similar to the focal species than the species in my group (see groups for *Panicum maximum* and *Phyllanthus asperulatus* in Table 2.9).

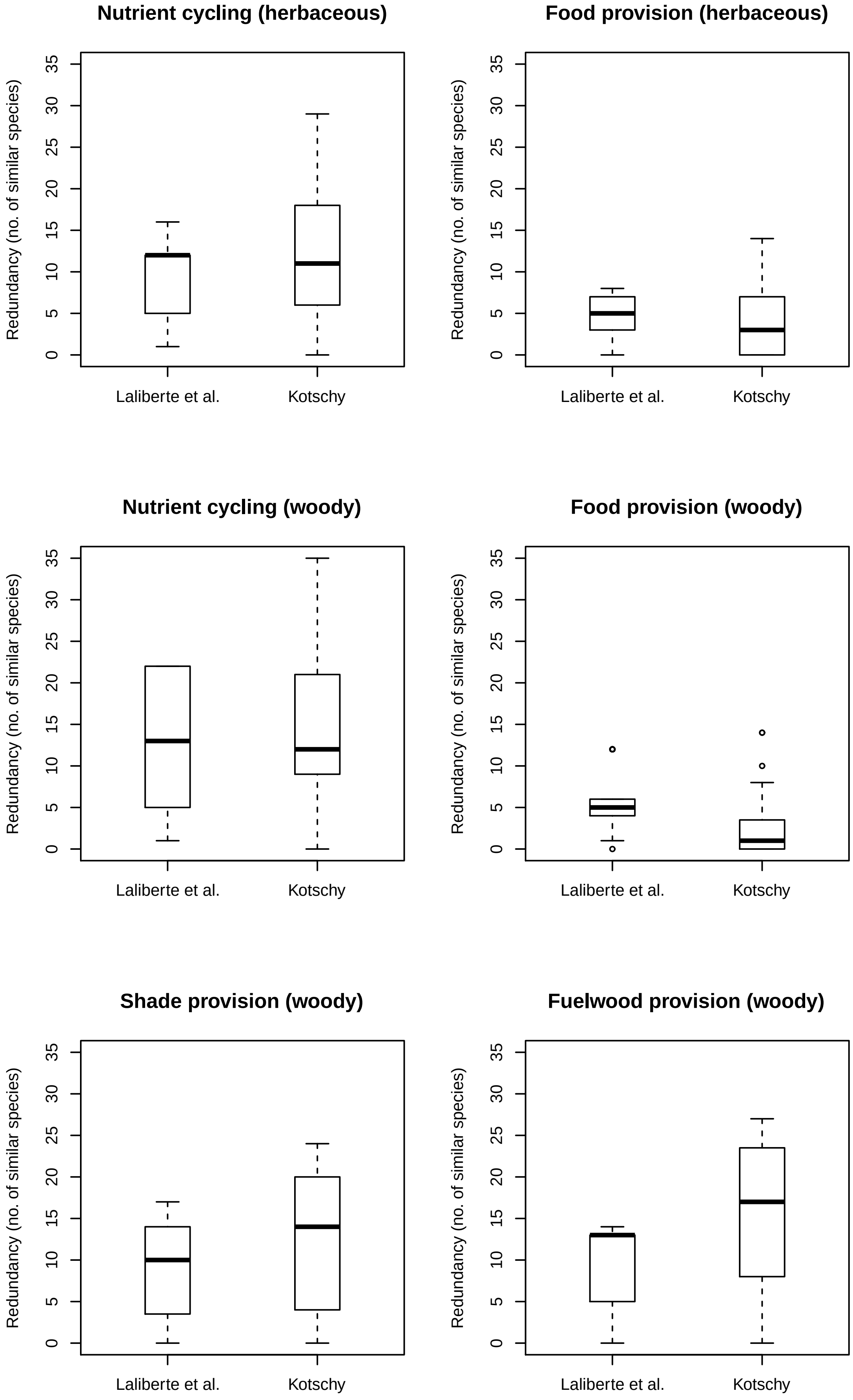
Using a clustering algorithm, as done by Laliberté *et al.* (2010), is better than the simple sequential grouping process used by Walker *et al.* (1999), because it removes the constraints related to the order in which the groups are formed. However, the mutually exclusive nature of the groups still appears to cause redundancy to be underestimated. I would therefore argue that using nngroups provides a better measure of the amount of redundancy associated with each aspect of the functioning of a species.

Response disparity

Unlike for redundancy, the overall distributions of response disparity values obtained with the two methods were very similar (Figure 2.13). However, the values obtained for particular species were very different, as evidenced by the low correlation between the values produced by the two methods (Figure 2.14).

The grouping structure once again constrained the values obtained with the clustering method, because each species in a particular group was assigned the same response disparity (FDis) value. When the response disparity values from the two methods are plotted against each other, it can be seen that species in the same clustering group, which therefore had the same response disparity, had different values with my method (points spread out along the y axis in Figure 2.15).

The differences in size and species composition between my nngroups and the groups derived using the method of Laliberté *et al.* (2010) therefore did influence the values obtained for response disparity. Neither method produced consistently higher or lower response disparity values. Rather, the results



Nutrient cycling (herbaceous)

Food provision (herbaceous)

Nutrient cycling (woody)

Food provision (woody)

Shade provision (woody)

Fuelwood provision (woody)

Figure 2.11: Boxplots showing the distribution of species redundancy values obtained using my method and the method of Laliberté *et al.* (2010), for different assemblages and different effect functions.

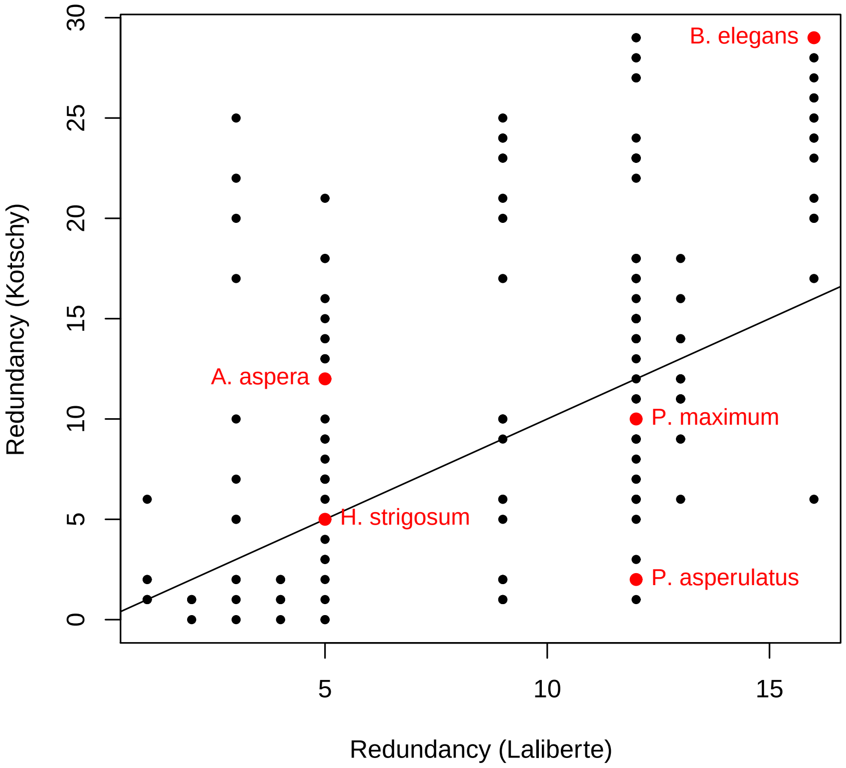


Figure 2.12: Scatterplot comparing species–level redundancy values obtained using two different methods, for a single function (nutrient cycling) and assemblage (herbaceous assemblage from small streams in the Communal area). Each point represents the redundancy associated with a single species. The x axis shows the value obtained using the measure of Laliberté *et al.* (2010), based on a clustering approach. The y axis shows the value obtained using my nngroup method. The line represents equality of the two measures (identical redundancy values). Points falling above this line represent species for which redundancy was higher with my method, while those below the line had higher values with the method of Laliberté *et al.* (2010).

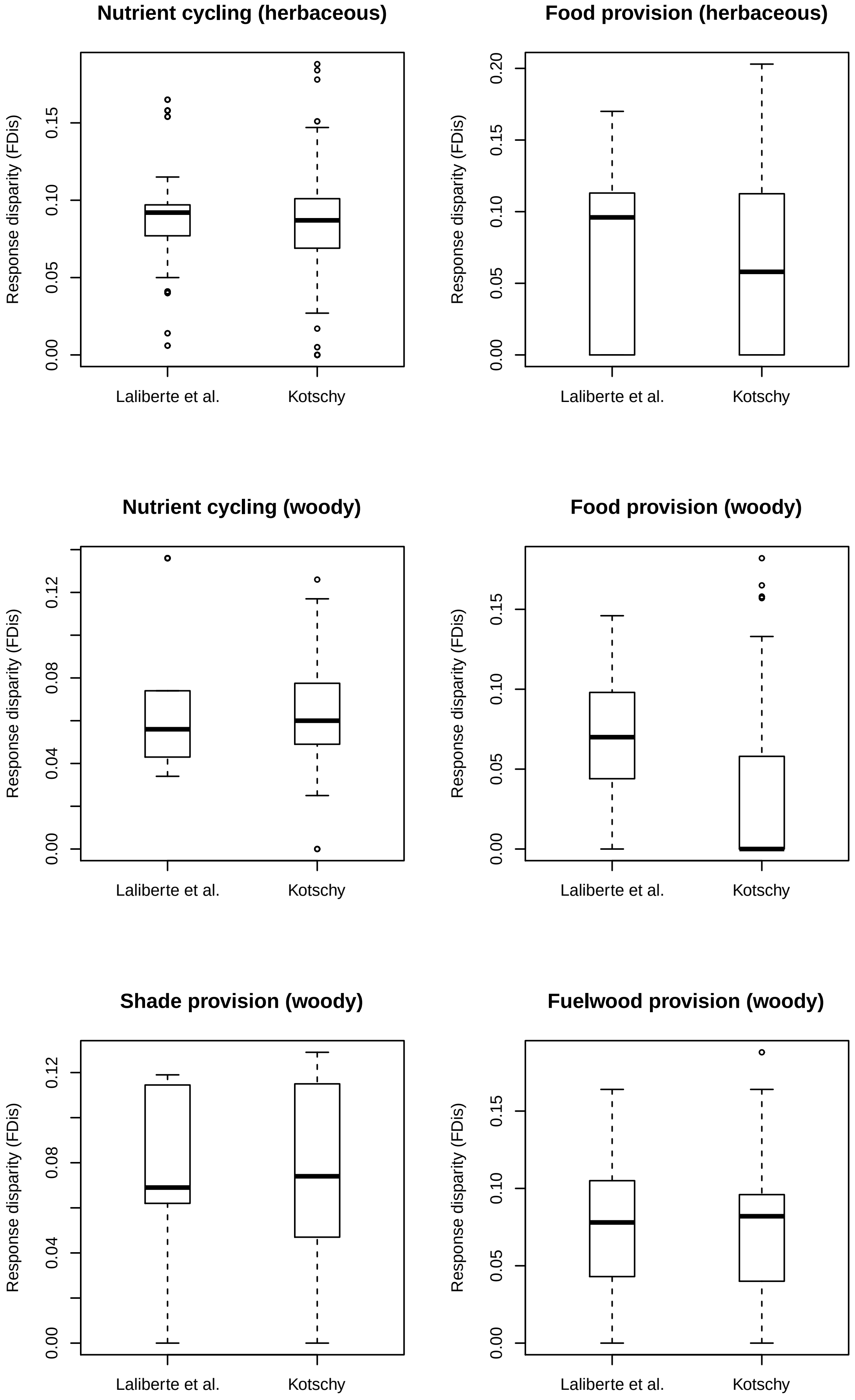


Figure 2.13: Boxplots showing the distribution of species' response disparity values (response to damage) obtained using my method and the method of Laliberté *et al.* (2010), for different effect functions.

Table 2.9: Comparison between the mutually exclusive groups of similar species used by Laliberté *et al.* (2010) and my 'nearest neighbour groups' or nngroups, for representative examples from the riparian vegetation dataset and for the nutrient cycling function (species shown in red in Figure 2.12). Group members are listed in decreasing order of similarity to the focal species. Species common to both groups are shown in bold. Full species names are given in Appendix A.

Focal species	**Similar species providing redundancy**	
	Laliberté *et al.* (2010)	Kotschy (nngroups)
Barleria elegans	***litga, hypfo, jusbe, sidac, thune, acavi, agabo, prico, walin, melpr, kalla, abuau, melfo, phyma, lepsc, kalbr***	***litga, hypfo, jusbe, sidac, thune***, *comer2*, ***acavi***, *achle*, ***agabo***, *comaf1*, ***prico***, *rueco*, ***walin***, *ociam*, ***melpr, kalla, abuau***, *leugl, vahca*, ***melfo***, *achas, ruepa, comec, chabu*, ***phyma***, *ortsu*, ***lepsc, kalbr***, *teppo*
Achyranthes aspera	***barox, phyin, leune, hibpu, helst***	***barox, phyin***, *barel*, ***leune***, *litga, hypfo*, ***hibpu***, *sidac, thune, jusbe, siddr*, ***helst***
Heliotropium strigosum	***barox, phyin, leune, hibpu, achas***	***barox, phyin, leune, hibpu, achas***
Panicum maximum	***botin, thetr, pande, setsp2, trimo, hetco, uromo, erasu, spofi, erime***, *eracu, diger*	***botin, thetr, pande, setsp2, trimo, hetco, uromo, erasu, spofi, erime***
Phyllanthus asperulatus	***ortsu, ruepa***, *leugl, ociam, comec, rueco, clete, comer2, comaf1, achle, chabu, vahca*	***ortsu, ruepa***

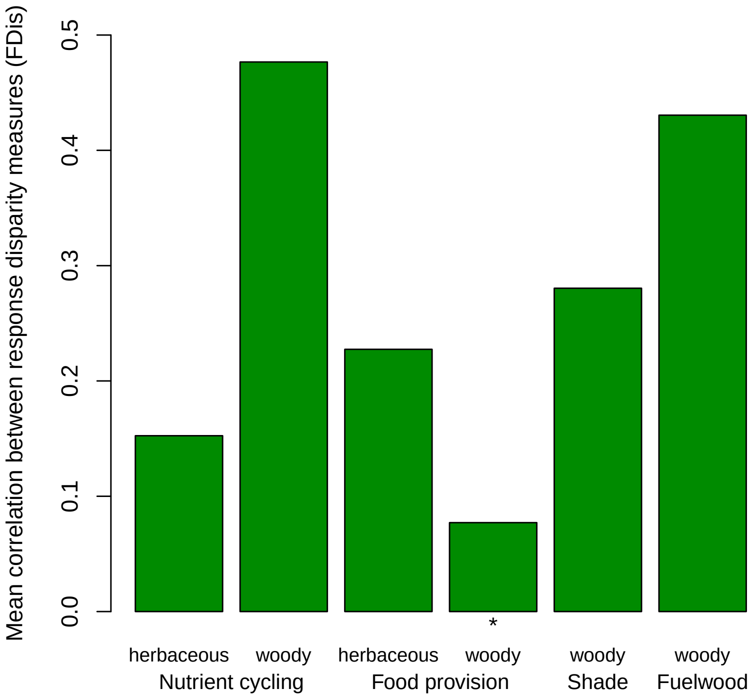


Figure 2.14: Mean correlation between species–level response disparity values calculated within nngroups and values calculated within groups derived from clustering. ∗ Indicates a negative correlation. Response disparity (disparity in responses to physical damage) was calculated as multivariate dispersion (FDis) unweighted by species abundances. Means were calculated across six sites.

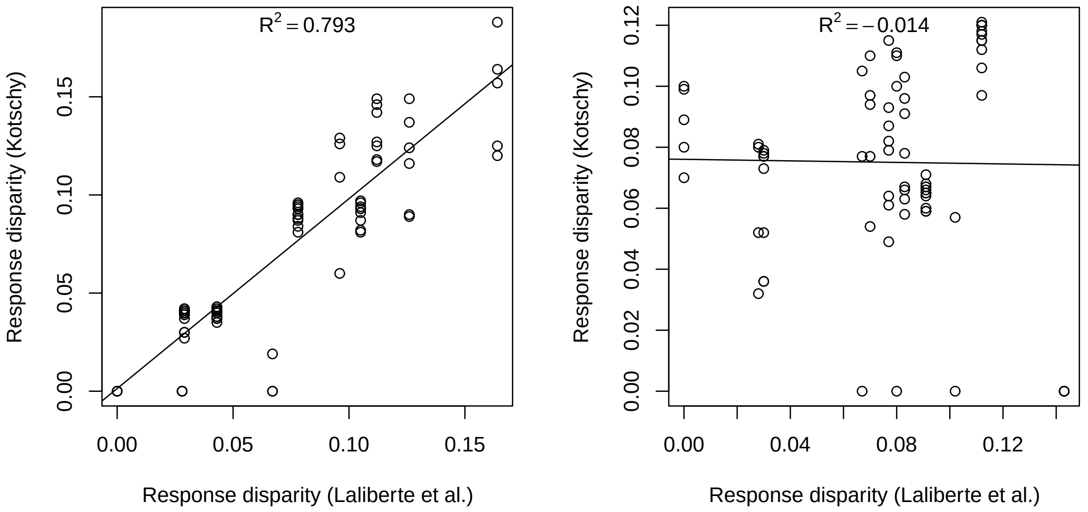


Figure 2.15: Scatterplots of the relationship between response disparity values obtained using my method and the method of Laliberté *et al.* (2010). Two examples are shown out of the 36 possible site–function combinations, representing the highest and the lowest correlations. Response disparity (disparity in responses to damage) was calculated as multivariate dispersion (FDis), unweighted by species abundances.

varied idiosyncratically depending on which species were present in a group and whether these species happened to be similar or dissimilar to the focal species in their response traits.

In conclusion therefore, using mutually exclusive functional groups in general underestimates the amount of redundancy associated with the functioning of each species. While species with low redundancy appear to be adequately detected using mutually exclusive groups, the amount of redundancy associated with the majority of species is under–represented when such groups are used. Measuring redundancy as the number of similar neighbours within overlapping nngroups, and response disparity as the dispersion of response traits within nngroups, as suggested here, removes the constraints imposed by the discrete grouping structure and produces measures of redundancy and response disparity which better reflect the continuous and multidimensional nature of similarity and dissimilarity among species.

2.4 Discussion

The approach to measuring redundancy and response disparity presented here takes into account the two reasons why ‘difference is slippery’ identified at the beginning of this chapter, namely its continuous nature and its multidimensionality. The multidimensional nature of difference/similarity is addressed by using different sets of traits to describe species’ contributions to different functions. Considering the patterns of similarity and difference associated with each of these functions separately recognises that species have multiple functional roles. It forces the researcher to specify which functions are being considered, and helps to avoid the pitfall of assuming that species that perform one function similarly are necessarily similar in all respects. Measuring redundancy for different functions separately can help to avoid pointless debates about whether or not species are dispensible, because when several functions are considered, few if any species will appear functionally identical (and therefore superfluous or dispensible). A multidimensional view of redundancy is therefore useful in advancing our understanding of the role of redundancy in providing resilience. Furthermore, response disparity cannot be measured without distinguishing between effect and response functions. The distinction between different functions is therefore a key component of my approach.

The continuous nature of difference/similarity is addressed by using overlapping nearest neighbour groups (nngroups) to identify which species are most similar to each other, rather than the mutually exclusive groups that are usually used in functional group classifications. It has been shown here that taking the continuous nature of similarity into account in this way allows more genuinely occurring redundancy to be detected than with mutually exclusive groups.

I have chosen to measure the amount of redundancy and response disparity associated with the functioning of *each species* within the context of a particular assemblage, rather than the amount of redundancy and response disparity associated with the whole assemblage. Each species is seen as performing a given function (e.g. nutrient cycling, shade provision) in a particular way, and all other species present that are sufficiently similar are seen as providing redundancy for this functioning. This provides what I have called a 'species–eye view' of redundancy, describing how much redundancy is present from the 'perspective' of a particular species, in the context of a particular assemblage. Likewise the response disparity measure provides a species–eye view of response disparity. This is very different to the approach used in most of the functional diversity literature, where the goal is to produce indices describing the amount of disparity or diversity present in the assemblage as a whole. While assemblage–level measures of redundancy may be useful for certain purposes, when it comes to testing the hypotheses of Walker *et al.* (1999) about the different roles of species in providing redundancy and response disparity, it is necessary to be able to deal with species individually. I have argued that the measures described here provide a simple way of doing this which obviates the need for clustering methods, but which is able to take the continuous and multidimensional nature of disparity into account (§2.2.2, §2.2.3).

There are, however, several ways in which the methods developed here could be improved. In any study based on functional traits, the number of traits measured and the degree of accuracy with which they are measured are constrained by the time and resources available. The following traits were considered relevant to the functions defined here, but were not included because they were too difficult or time–consuming to measure: nutrient uptake strategy (for the nutrient cycling function), plant chemical defenses and plant use by animals and people (for food provision), and root depth distribution (for response to water stress). Each of these could constitute a future project in its own right. The method developed here for determining the contribution of each trait to the overall dissimilarity, and the facility for weighting of traits, makes it easy to include new information on trait–function relationships as it becomes available.

The trait–based approach used to determine species' contributions to different functions depends heavily on our understanding of the association between traits and functions. While I believe enough information is available to make this approach feasible, there is substantial room for improvement. What is needed is more experimental and observational studies that directly measure various ecosystem functions and relate these to species and traits, such as the studies by Kremen *et al.* (2002), Balvanera *et al.* (2005) and Spehn *et al.* (2005). A promising approach was suggested by Ricotta and Moretti (2010) for constructing 'tailored' or 'supervised' dissimilarity matrices, as pioneered by researchers in molecular biology and biochemistry (Gute, 2002; Pollard and van der Laan, 2008). This involves first selecting the traits relevant to a particular function using stepwise regression, then replacing the values of each of these traits with the residuals before calculating the dissimilarity matrix. In this way the dissimilarity matrix is tailored to provide the best possible representation of species dissimilarities with respect to the function of interest (Ricotta and Moretti, 2010). This provides a way of formalising the choice of traits contributing to each function (§2.2.1).

Work on the relationships between traits and functions must increasingly take into account the role of intraspecific variability (Cianciaruso *et al.*, 2009; de Bello *et al.*, 2011), and the phenomenon of context–dependent functioning (Wellnitz and Poff, 2001). Furthermore, when dealing with ecosystem services considered valuable to humans, the human dimension needs to be included, using tools from the social sciences such as social actor strategies (Díaz *et al.*, 2011), social network analysis (Borgatti *et al.*, 2009) and ecological economics (Kremen, 2005; Perry, 2010). As our understanding of the interplay between the different species, processes and actors involved in controlling different ecological functions improves, it may become possible to tailor measures of redundancy and disparity to suit the particular situation. For example, the resilience of certain functions may depend more strongly on the redundancy and response disparity within human institutions (e.g. resource management agencies, law enforcement agencies) than on redundancy and response disparity among species.

The measures described in this chapter do not take into account differences in the spatial scales at which different species function, or the spatial scales at which different functions are performed. However, several authors have suggested that there is an important cross-scale component to resilience, where replication of function (redundancy) at different spatial scales allows for more flexible responses to disturbance (Holling, 1992; Peterson *et al.*, 1998; Allen *et al.*, 2005). This is an intriguing suggestion that deserves further study. Much of the work on cross–scale resilience has focused on body mass (in animals) as a surrogate measure of a species' scale of influence (Forys and Allen, 2002; Allen *et al.*, 2005; Fischer *et al.*, 2007; Wardwell *et al.*, 2008). Body mass (or body size) is correlated with several aspects of the functioning of animals, including growth rate, energy use, heat loss, home range size and nutrient cycling rates (Woodward *et al.*, 2005). Larger animals perceive and respond to environmental heterogeneity differently to smaller animals (Forman and Godron, 1986; Wiens and Milne, 1989). Animals of different sizes may therefore respond differently to a disturbance with a particular spatial imprint, thus providing response disparity (Peterson *et al.*, 1998; Elmqvist *et al.*, 2003).

While ecological studies have less often considered the role of body size in the functioning of plants, plants are subject to the same metabolic constraints as animals, and body size is expected to have similar correlates with functioning in plants as in animals (Niklas and Enquist, 2001). For example, plant size is related to a plant's 'zone of influence', the area over which the plant takes up resources, interacts with its neighbours, establishes ramets, casts shade or drops its litter (Casper *et al.*, 2000). Plant size is also related to reproductive traits, as larger plants are able to produce larger floral displays for pollinators and have greater lifetime reproductive outputs than smaller plants (Rees *et al.*, 2000; Falster and Westoby, 2005b). As with animals, plants of different sizes respond to environmental heterogeneity at different scales (Sutherland, 1990; Fahrig *et al.*, 1994; Higgins *et al.*, 2000; Wilson, 2000).

However, body size is not the only possible measure of an organism's scale of influence or the scale of its response to environmental heterogeneity. Sometimes organisms have effects disproportionate to their size, such as the effects of highly specialised pollinators or seed dispersers on plant populations (Bascompte *et al.*, 2003) or the effects of toxic phytoplankton that produce 'red tides'. Red tides can cause fish and shellfish kills over large areas of ocean, but the phenomenon is dependent on the toxin concentrations and population sizes rather than on the body sizes of the (tiny) algal species (Anderson, 1994). These algae are also much more mobile than their size would suggest. They are able to move over spatial scales of hundreds of kilometers with ocean currents and storms, thereby increasing their scale of influence still further (Anderson, 1994). There are many other examples among parasites and disease vectors where the ecological effects of species occur at much larger scales than their physical size would suggest (Ings *et al.*, 2009). In such cases, different measures of the species' scale of influence must be found.

Although my redundancy and response disparity measures are focused at the level of species, they can also be used to assess cross-scale redundancy and response disparity if the set of species used in the analysis covers a range of body sizes (or any other measure of an organism's scale of influence). Cross–scale redundancy can be measured by examining the spread of 'scale of influence characteristics' within each nngroup. If the species within a particular nngroup perform the same function but at different scales, cross–scale redundancy is present. Cross–scale response disparity can be measured by generating nngroups for response functions, as for effect functions, and assessing the spread of 'scale of influence characteristics' within these groups of species, which by definition have similar responses to disturbance.

Recent work on 'functional diversity' has produced several measures of disparity (although these are usually wrongly called diversity measures, and are sometimes combined measures of balance and disparity; see Table 2.2). None of these published measures could be directly adapted as a measure of redundancy to test the two hypotheses of Walker *et al.* (1999), that species in the tail of the abundance distribution provide redundancy for the functioning of the dominant species, and that species with similar functional effects have different responses to disturbance (response disparity).

I have outlined in this chapter an approach to measuring the redundancy and response disparity associated with the functioning of individual species within a particular context (the other species with which they co–occur in an assemblage). Species' functional roles for various effect and response functions were determined on the basis of carefully chosen sets of functional traits. Dissimilarity matrices were produced for each function using the Gower metric. A novel 'corrective weighting' method was used to remove unintentional trait weightings caused by differences in variable type, ensuring that all traits contributed equally to the overall dissimilarity. While differences in variable type are known to affect the dissimilarity values, and hence any measure of disparity or redundancy based on the dissimilarity matrix, this is seldom taken into account when disparity is measured from functional traits. The corrective weighting procedure makes it easy to determine the contribution of a particular trait to the overall dissimilarity values, both before and after the traits are weighted, so that any spurious effects of variable type can be removed.

The redundancy and response disparity measures developed in this chapter use elements of all three approaches to using dissimilarity matrices described in Section 2.1.2. The dissimilarity values were used directly (approach 1) to identify, for each species, all other species more similar than an arbitrarily chosen cutoff value. This produced groups of similar species (approach 2), but did so without requiring clustering methods. Unlike all other suggested measures of redundancy based on functional groups, these groups were not mutually exclusive. I have shown in §2.3 that removing the requirement for groups to be mutually exclusive resulted in a greater amount of redundancy being recorded per species, and the response disparity values obtained for each species were also different to those obtained using groups derived from clustering. The response disparity measure was calculated using ordination (approach 3), and ordination (Principal Coordinates) plots were used as the basis for useful graphical displays of the results.

The novelty of the methods developed in this chapter lies mainly in the use of different sets of traits to identify separate functions (effect and response), and in the use of overlapping 'nearest neighbour groups' or nngroups rather than mutually exclusive groups. Walker *et al.* (1999), like most functional trait studies, used only a single set of traits. The explicit identification of effect and response functions was essential to allow me to test the hypotheses of Walker *et al.* (1999), and also to measure response disparity. The use of nngroups accounts for the continuous and multidimensional nature of disparity better than mutually exclusive functional groups, however these are derived.

The redundancy and response disparity measures developed in this chapter will now be used to test the hypotheses of Walker *et al.* (1999) and to assess the effects of different land management regimes on the resilience of riparian vegetation assemblages.

Chapter 3

Resilience of riparian plant assemblages

3.1 Introduction

The insurance value of redundancy and response disparity is particularly relevant to riparian ecosystems. Riparian plant assemblages provide multiple goods and services to humans and other organisms, including filtering of contaminants, erosion control, nutrient inputs to instream habitats, flood attenuation, aesthetic value, and provision of habitat to a large number of animal species (Naiman *et al.*, 2005). The ability of riparian ecosystems to continue performing these beneficial functions is determined by their resilience.

Many factors have the potential to cause regime shifts in riparian ecosystems. Riparian plant assemblages, and the rivers with which they are associated, are affected by a multitude of direct and indirect influences operating over a range of scales, from the entire catchment to the adjacent hillslope (Allan, 2004). The arrangement of different types of land cover in river catchments and the way humans use or manage the land and its resources both have pervasive impacts on riparian ecosystems because of the position of rivers as topographic sinks in the landscape (Nilsson *et al.*, 2003; Naiman *et al.*, 2005). Land use changes in river catchments affect the hydrological regime by causing changes in runoff, groundwater movement and/or sediment supply (Allan, 2004), and these changes affect the supply of water to, and the nature of disturbance experienced by, riparian plants. In addition, riparian vegetation is often directly affected by clearing for agriculture or development, pollution, construction of dams and the introduction of alien species (Naiman *et al.*, 2005). With growing human demand for freshwater resources and ever increasing human modification of the earth's surface, these impacts are predicted to increase substantially in future (Vitousek *et al.*, 1997; Abell, 2002; Balmford *et al.*, 2005).

Regime shifts may occur if the components, interactions and feedbacks within a riparian assemblage change sufficiently to move it into an alternative stability domain (§1.2.5). Such regime shifts can be rapid and catastrophic (Scheffer *et al.*, 2001) or can take several years to unfold (Robinson and Uehlinger, 2008). Whether they are considered desirable or undesirable depends on whether functions considered valuable by human society at the time are impacted. The ability of an ecosystem to remain within a particular stability domain is determined by its ecological resilience, and any impacts that reduce this resilience will make regime shifts more likely to occur. An understanding of how land management practices affect the resilience of riparian assemblages would be valuable in preventing undesirable losses of resilience which may jeopardize valuable ecosystem services, and can also guide attempts to restore degraded ecosystems which are in undesirable but resilient states (Suding *et al.*, 2004).

Riparian plant assemblages generally exhibit a large amount of taxonomic and structural diversity (Gregory *et al.*, 1991), although biodiversity inventories are often very incomplete (Nilsson *et al.*, 2003). Functional diversity has seldom been assessed, and is even more poorly understood than for the terrestrial parts of the landscape. This situation has justly been called 'the freshwater biodiversity crisis' (Abell, 2002). In South Africa the situation is similar, with riparian biodiversity far more threatened and less well understood than terrestrial biodiversity (Nel *et al.*, 2004).

Changes in species composition (the identities of the species present and their relative abundances) are common in riparian assemblages in response to changes in land use or management (Kauffman and Krueger, 1984; Stromberg *et al.*, 1993; Busch and Smith, 1995; Knapp and Matthews, 1996; Patten, 1998; Jansson *et al.*, 2000; Opperman and Merenlender, 2000; Robertson and Rowling, 2000; An *et al.*, 2002;

Dwire and Kauffman, 2003). Changes in species composition may have a large impact on functioning, particularly if the dominant species are replaced by new species that are functionally different, as shown by studies of the impact of invasive alien species on riparian assemblages (Dukes and Mooney, 2004; Holmes *et al.*, 2005). For example, invasive species may precipitate changes in nutrient cycling (Witkowski, 1991; Yelenik *et al.*, 2004), water balance (LeMaitre *et al.*, 2000; Dye and Jermain, 2004), trophic dynamics (Lecerf *et al.*, 2005), sediment stability (Birken and Cooper, 2006), fire regimes (Dwire and Kauffman, 2003; Brooks *et al.*, 2004) and production of large woody debris (Tabacchi and Planty-Tabacchi, 2003).

However, little is known about the effects of changes in species composition and abundance on resilience. On the one hand, compositional changes can reflect functional compensation, where declines in certain species are compensated for by increases in the abundance of other, functionally similar, species (§1.2.6). Functional compensation can enhance resilience by allowing important functions to be maintained despite changes in species composition. On the other hand, changes in species composition can also indicate a shift to an alternative stability domain, or a loss of resilience (§1.2.5).

A few empirical studies have shown that land use or management practices can affect resilience. Laliberté *et al.* (2010) showed how land–use intensification, including forest conversion to pasture, rangeland development, and logging regimes of different intensity or frequency, reduced both redundancy and response disparity in plant assemblages, although the specific effects varied considerably among the different land–use gradients. Fischer *et al.* (2007) reported a decline in redundancy in bird assemblages in agricultural areas compared with areas of natural vegetation. Forys and Allen (2002), on the other hand, found no change in cross–scale redundancy among vertebrates in the Everglades, despite large changes in species composition which accompanied severe habitat transformation and invasion by non–native species. They concluded that in this case the changes in species composition did not affect the overall resilience of the system, although certain changes in functioning were predicted (Forys and Allen, 2002).

In this chapter, the measures of redundancy and response disparity developed in Chapter 2 will be applied to riparian plant assemblages in a semi–arid savanna in South Africa. The aims are:

- To build a stronger empirical foundation for the concept of resilience, which at present is very theoretical, by describing general patterns of redundancy and response disparity in riparian plant assemblages.
- To provide an empirical test of the two hypotheses of Walker *et al.* (1999) about the roles of redundancy and response disparity in resilience, namely that (1) minor species in the tail of the abundance distribution provide redundancy for functions involving the dominant species, and that (2) species providing redundancy for a particular function tend to differ in their responses to disturbance (response disparity) (Box 1.3).
- To compare patterns of redundancy and response disparity in assemblages from three areas with different land management regimes, and explore the implications of differences between areas for resilience.
- To assess the extent to which differences in species abundances between assemblages provide evidence of functional compensation.

Resilience was assessed in riparian assemblages from three areas with contrasting land management regimes, because of the potential of management regimes to affect both biodiversity and resilience.

3.1.1 The study area

The Sand River catchment in Mpumalanga Province, South Africa, provides a suitable context in which to examine the effects of different land management practices on the diversity and resilience of riparian assemblages. Parts of the catchment in close proximity to one another are exposed to three different management regimes: Kruger National Park, a large 'flagship' conservation area managed by the South African National Parks Board, the Sabi–Sand Game Reserve, a privately–owned conservation area made up of several smaller properties, and an area of dense rural settlements surrounded by communal grazing land and subsistence agriculture (Figure 3.1). Severe water shortages during a drought in 1992 prompted local concerns that ecological integrity and resilience in the Sand River catchment had been severely compromised, and led to the initiation of the Save the Sand Programme, a national pilot project for Integrated Catchment Management and Land Care (Pollard, 2001).

The Sand River catchment falls within the Sabie River catchment, which in turn is part of the Inkomati system, in the north–east of South Africa (Figure 3.1). The Sand River has its source in the Drakensberg escarpment, about 1500 m asl. It flows eastwards and then southwards, joining the Sabie River inside the Kruger National Park. The Sabie River then flows eastward through Mozambique to the Indian Ocean.

Mean annual precipitation in the catchment is around 2000 mm in the mountainous west, but drops rapidly to around 550 mm in the low–lying flat areas in the east. The catchment shows the typically high variability associated with semi–arid regions in terms of surface water availability, both within and between years (Smits *et al.*, 2004). Extensive commercial forestry plantations of exotic pines and eucalypts are present in the upper catchment, while commercial agriculture, mainly irrigated subtropical fruit, is the main land use in the middle reaches. Downstream of this, the catchment is semi–arid and drought–prone. Poor rural communities practice subsistence agriculture and raise livestock on very densely populated, communally–owned land, a legacy of the Apartheid government's resettlement policies (Pollard, 2001). The water resources are heavily utilised, and the lower portion of the Sand River now frequently experiences no–flow conditions (Pollard and Walker, 2000). There is concern about the ecological impacts of these flow reductions on the conservation areas downstream (Weeks *et al.*, 1996; Pollard, 2001).

The three areas chosen for study all occur within the semi–arid 'lowveld' part of the catchment (the local name for the low–lying area between the footslopes of the Drakensberg escarpment in the west and the Mozambique coastal plain in the east, Venter *et al.* (2003)). The areas are very similar in geology and vegetation type. The terrain is flat to undulating. Soils are shallow and sandy, derived from nutrient–poor granitic rocks, with deeper duplex (sodic) soils on the footslopes and coarse alluvial sediments in the valley bottoms (Venter *et al.*, 2003). Smaller streams are ephemeral and erosional in character, with little accumulation of alluvium, while the larger channels are often depositional and have well developed footslopes (Venter *et al.*, 2003). The main stem Sand River, like all the major rivers in the area, has incised into bedrock following uplift of the land surface in the recent geological past (Partridge and Maud, 1987). This has produced a channel–within–channel morphology. The incised channel has been termed the 'macro–channel' to differentiate it from the smaller perennial active channel(s) that flow within it. The macro–channel floor is 200–600 m wide and a typical floodplain is not present (Rogers, 2003).

The vegetation is closed to open woodland or savanna. Crest and midslope areas are associated with moderately dense woodland dominated by deciduous, broad–leaved, spineless trees and relatively unpalatable grasses. Footslope areas are associated with more open shrubland dominated by deciduous, fine–leaved, thorny species and palatable grasses (Venter *et al.*, 2003). Grass cover varies from sparse to dense depending on rainfall. Riparian vegetation along the main stem Sand River is dense riverine bushveld, woodland or gallery forest (Venter *et al.*, 2003, Figure 3.2). Smaller streams have narrower and less well–defined riparian zones, but trees tend to be taller along the channel (Figure 3.2). Differences between the three study areas include a rainfall gradient from 675 mm per year in the communal area to 550 mm in Kruger National Park. However, evaporation rates are considerably in excess of rainfall throughout the catchment (ranging from 1850 mm in the west to 2200 mm in the east), resulting in a deficit in the water balance (Pollard and van der Laan, 2008). This reduces the impact of the differences in rainfall. The main differences between the three areas therefore relate to differences in land use and management.

Conservation management in the two protected areas generally aims to conserve biodiversity, but there are several important differences in management practices. The Kruger National Park has an overarching vision to 'maintain biodiversity in all its facets and fluxes' (Rogers, 2003). Ecosystems are recognised as being inherently variable and heterogeneous, and there is an implicit assumption that healthy ecosystems can only be maintained in the long term by nurturing properties such as biodiversity and resilience. The private properties comprising the Sabi–Sand Wildtuin generally embrace the basic philosophies of the KNP management approach and have similar general objectives. However, they are subject to more intensive management (Peel *et al.*, 1998). Since the 1990's efforts have been made to improve the coordination of management practices and policies in these private reserves with those in the KNP. These efforts have included the removal of fences and the production of coordinated vegetation maps for the area (Peel *et al.*, 2007). However, some important differences remain. The Sabi–Sand Wildtuin, in keeping with its greater focus on ecotourism, has significantly higher animal densities. It also has a denser road network and a much higher density of artificial water points, making animals less dependent on the river. 'Bush clearing' is practiced in these reserves to prevent encroachment by woody species and create the open parkland thought to be more suitable for certain ungulates (Ben-Shahar, 1992, Figure 3.3). Neither of the two reserves allows direct human use of riparian vegetation (e.g. fuelwood collection), but the abovementioned differences in management have the potential to affect riparian vegetation diversity and resilience indirectly.

Rural communities in the adjacent communal lands depend heavily on natural resources obtained from the surrounding ecosystem, including fuelwood, fruits, construction materials, wood for carving and medicinal plants (Shackleton and Shackleton, 2000). Some riparian vegetation in the communal area

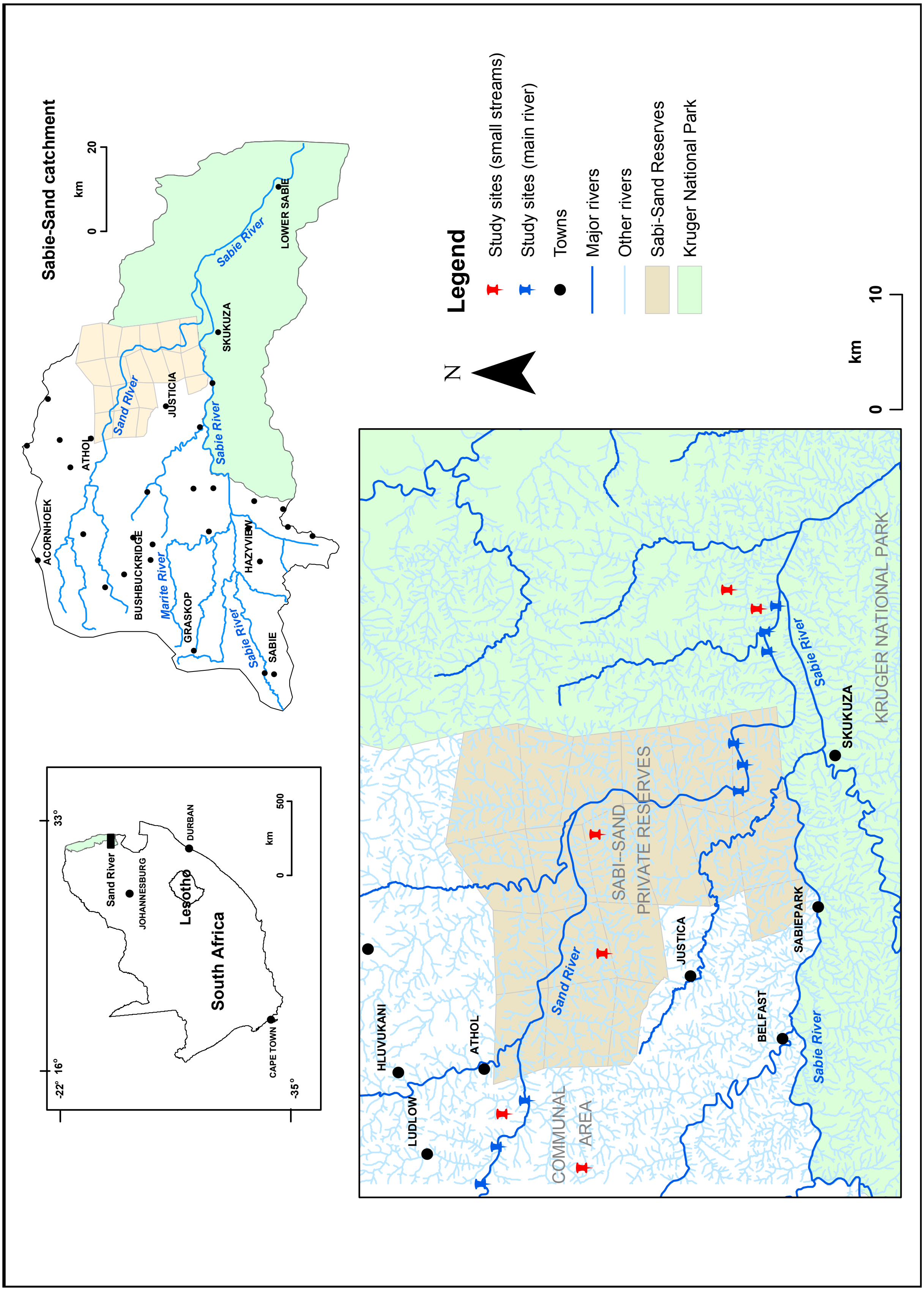


Figure 3.1: Map of the Sand River catchment showing the regional context, and the location of the study sites within the three different management areas (communal area, Sabi–Sand Game Reserve and the Kruger National Park).

Figure 3.2: Riparian vegetation along the main Sand River (top row) consists of extensive reedbeds together with various disturbance–tolerant woody and herbaceous species on large exposed sand bars (A), with a riparian fringe forest consisting of tall trees, woody and herbaceous climbers, and many clonal shrubs (B), and a herbaceous understory of grasses and forbs which varies greatly in composition and biomass with season (C). Along the ephemeral first order streams (bottom row) there is no surface water for most of the year, but sedges and other hydrophilic species colonise the alluvial sand (E). The riparian fringe is less clearly defined than along the main river, but trees are generally taller and greener than in the surrounding landscape (E, F). The understory is grassy with abundant forbs, and highly variable with season.

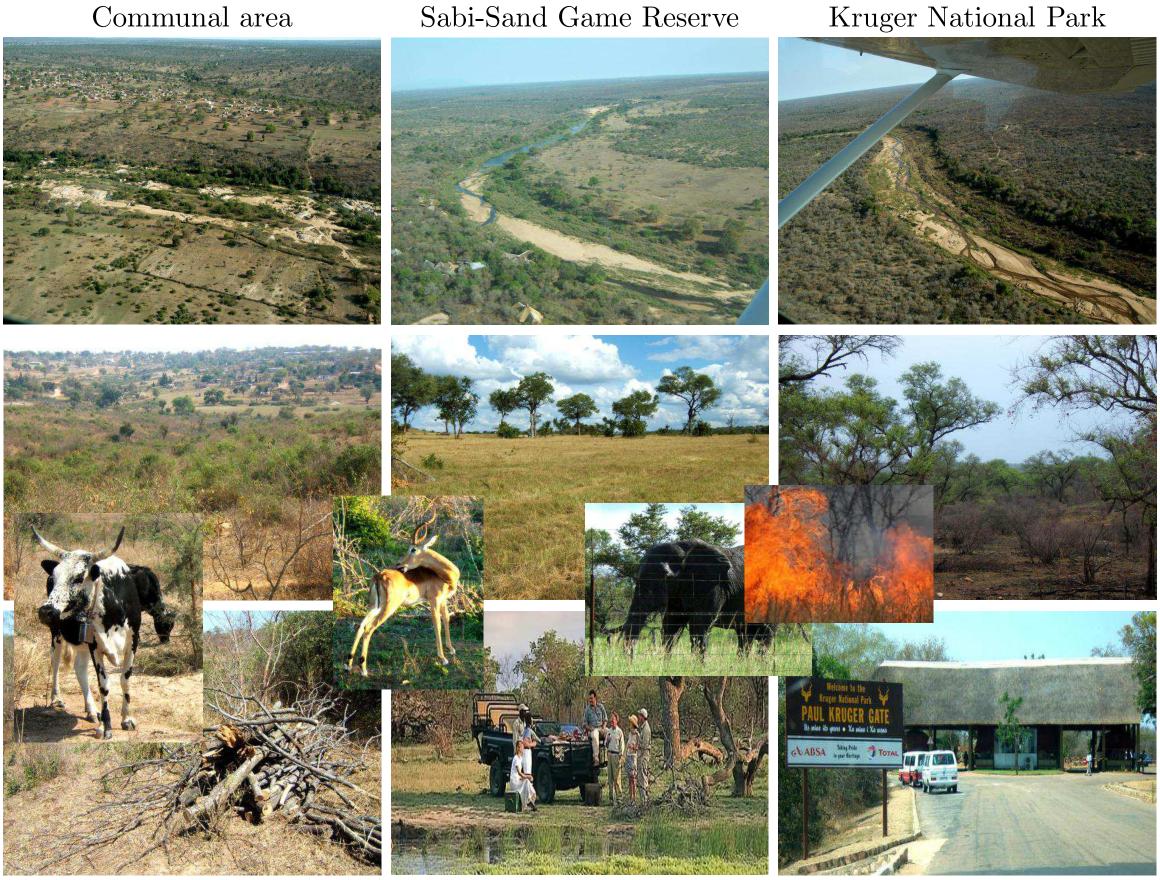


Figure 3.3: Photographs illustrating some of the differences between the three management areas. The catchment is most highly modified by people in the communally managed area (left column), with dense rural settlements and agricultural fields often adjoining the riparian zone. Riparian vegetation is harvested for fuelwood and other uses, and riparian areas are used for grazing of livestock (mainly cattle). In the Sabi–Sand Game Reserve (centre column), riparian areas are important for ecotourism, and several luxury game lodges have been built along the Sand River. Bush clearing is practised in this part of the catchment to reduce woody cover. Riparian vegetation provides browse and grazing for a wide range of indigenous herbivores, including a range of mammals from small antelope to elephant. The portion of the catchment in the Kruger National Park (right column) is the least modified by humans. While this area also supports ecotourism, the density of roads and camps is lower than in the Sabi–Sand Game Reserve. Fire is an important driver of vegetation dynamics in all three areas, but fires are hotter in the Kruger National Park and the Sabi–Sand Game Reserve due to higher fuel loads.

has been cleared to make way for agriculture or human settlements, and riparian species are extensively harvested (Figure 3.3). Population pressure and other factors have led to a breakdown of the traditional regulation of natural resource use in recent years (Pollard *et al.*, 1998). Livestock (mainly cattle and goats) are kept at high stocking rates (Parsons *et al.*, 1997). Changes in land cover in adjacent upland areas, such as increased proportions of bare ground, fields and settlements may also affect riparian vegetation indirectly (Shackleton, 2000, Figure 3.3). Fires occur frequently, but are of lower intensity than fires within the protected areas, because of the much lower fuel load (Shackleton, 2000). While these areas have lost many bird and mammal species, the impacts of communal land management practices on other aspects of biodiversity have seldom been studied, and the impacts on ecosystem resilience are unknown. The fact that all the major rivers in the area flow through or from the communal area into the reserves means that the condition of riparian zones in the communal area is of direct interest to managers in the reserves.

The state of the riparian vegetation outside the protected areas is generally considered undesirable by conservation managers. An assessment of riparian vegetation condition undertaken as part of the national River Health Programme, classified riparian vegetation in the communal lands as ‘poor’ in places, and ‘fair’ or ‘good’ in others. Inside the protected areas it was classified as ‘natural’ (the lowest level of impact) (Ballance *et al.*, 2001). The Riparian Vegetation Index used for that assessment was based on the extent of vegetation cover, its structural intactness, the relative cover of indigenous vs alien species, and whether regeneration of indigenous species was occurring (Kemper, 2001). The results of the River Health Programme assessment suggest that these characteristics of riparian vegetation may be altered by management practices, but the effects on resilience or ecosystem functioning are unknown. My study will contribute to a better understanding of the impacts of management practices on the resilience of riparian assemblages, and hence on their ability to continue functioning and providing important ecosystem services. The implications of the results for the management of riparian zones will be addressed in Chapter 4.

3.2 Methods

The collection of the functional trait data used to assess species’ functional roles, redundancy and response disparity was described in Chapter 2. Functional trait data were collected from field measurements and from the literature, and redundancy and response disparity were assessed using the species–level measures developed in Chapter 2. Different sets of traits were used to represent various different effect functions (nutrient cycling, provision of food to herbivores, shade provision, fuelwood provision) and response functions (responses to damage and water stress).

The functions chosen could all potentially be affected by the different management regimes in the three areas. Nutrient cycling, food provision and response to damage will be influenced by differences in fire regimes. Fire affects nutrient cycling through direct losses of nutrients to the atmosphere, alterations to soil microbial populations, changes in species composition, and changes in tree:grass ratios (Hobbs *et al.*, 1991; Wan *et al.*, 2001; Coetsee *et al.*, 2010). Vegetation regrowth after fires is highly palatable and attracts herbivores, which in turn influence nutrient cycling via dung and urine inputs (Naiman *et al.*, 2003; Archibald *et al.*, 2005). The amount of fuel biomass present (which is influenced by management practices), together with the timing of fires, influences the severity of damage to above–ground plant parts and therefore the nature of plant responses to fire (Turner *et al.*, 1999; Bond and Midgley, 2003; Gurvich *et al.*, 2005).

The differences in the identity and numbers of large herbivore species present in the three areas will also affect the provision of food to smaller animals, as well as shade provision and response to damage. For example, elephants, present in the reserves but not in the communal area, strip bark and branches and push over riparian trees. This makes fodder available to other species, simultaneously affecting vegetation structure and susceptibility to fire (Scholes *et al.*, 2003). Sustained heavy grazing, such as the grazing by cattle in the communal area, is known to promote rapid nutrient cycling and the retention of nutrients close to the soil surface (McNaughton *et al.*, 1988).

Harvesting of wood will have implications for the provision of shade as well as future supplies of fuelwood. Tall shade trees are functionally important in riparian assemblages because they lower soil and water temperatures and reduce evaporative losses (Naiman *et al.*, 2005). Loss of shade trees may therefore increase the extent to which other species experience water stress. Species’ responses to water stress are of interest in all three management areas in light of the concerns about increasing water use in the Sand River catchment (§3.1.1).

Species abundance information was needed to allow me to test the hypotheses of Walker *et al.* (1999), namely that minor species in the tail of the abundance distribution provide redundancy for functions involving the dominant species, and that species providing redundancy for a particular function tend to differ in their responses to disturbance (response disparity) (Box 1.3). Riparian vegetation was therefore sampled to obtain species composition (which species), variety (how many species) and balance (how many of each species) data for assemblages in the different management areas, so that the relationship between the abundances of species and their roles in providing redundancy and response disparity could be assessed.

3.2.1 Choice of sites for vegetation sampling

Assemblages from both small and large streams were sampled in each management area. Different sized streams within drainage networks have different patterns of heterogeneity in the underlying physical template, including differences in sediment and water distribution, valley form and slope (Wiens, 2002), and these differences have been shown to be associated with different patterns of riparian plant species distribution and diversity (Kalliola and Puhakka, 1988; van Coller *et al.*, 1997; Bendix and Hupp, 2000; Scott *et al.*, 2003; Lite *et al.*, 2005; Tye, 2011). In large rivers, heterogeneity is present in the longitudinal (along the length of the stream), lateral (perpendicular to the stream) and vertical (elevation) dimensions, leading to highly patchy and complex species distribution patterns (van Coller *et al.*, 2000; Bendix and Hupp, 2000). In small streams, however, longitudinal variation is more prominent than lateral or vertical variation (Bendix and Hupp, 2000).

Streams of different sizes are also expected to differ in their responses to land management practices in the catchment. Small streams, with their smaller catchments, are more directly influenced by local management practices on the adjacent hillslopes than larger streams. Assemblages along large streams are expected to have more complex interactions with activities in the catchment, because of the larger space and time scales involved and the connected nature of stream networks (Allan *et al.*, 1997; Strayer *et al.*, 2003; Allan, 2004).

Two small streams were chosen in each of the three management areas (Figure 3.1). These streams were all first order streams according to the stream ordering method of Strahler (1952), namely streams that joined with other first order streams to form a second order stream, rather than first order streams that flowed directly into the main river or a higher order stream. They were selected to be of similar length and elevation, and to be far enough away from the main river to reflect conditions in their own local catchments rather than the influence of the main river (Figure 3.1). In areas of similar geology and landscape dissection, like the three management areas in this study, stream order provides a useful approximation of catchment area (Hughes *et al.*, 2011). The first order catchments selected for this study all had areas of approximately 0.7 km^2.

A further criterion for the choice of small streams was the extent to which the stream was affected by the management practices of interest in each area. This was appropriate here because the aim was not to provide an assessment of the biodiversity or resilience of each management area as a whole, but rather to explore the potential of the different management practices to influence biodiversity and resilience in the different assemblages. First order streams in the communal area were chosen to reflect the response to harvesting of wood and other plant resources as well as livestock browsing/grazing. The sites chosen were therefore close to villages and accessible to people and livestock, but not directly cleared for agriculture or housing development. In the Sabi–Sand reserve, streams were selected in catchments impacted by bush clearing. The streams in the Kruger National Park supposedly represent the most ‘natural’ situation in that they had the least human activity in their catchments. In all three areas, streams directly modified by roads, bridges, camps, settlements or other structures (e.g. through clearing of vegetation or bank stabilisation) were not considered. Catchments with unusual geology (e.g. gabbro outcrops) were also avoided, as these have different soils and vegetation patterns (Venter *et al.*, 2003). The use of small catchments directly affected by particular land management practices made it possible to isolate these effects to some extent from the wide range of influences affecting the main river catchment.

The main stem Sand River is a 6th order stream within the study area. Three sites were chosen within each of the three management areas (Figure 3.1); the comparison in this case was between sites along the same river, in the same catchment, rather than between different catchments. Since all the sites were affected by the same catchment conditions upstream of the study area, this comparison primarily indicates the extent to which land use and management within a particular management area can influence the biodiversity and resilience of the riparian vegetation. As with the small streams, sites directly modified by roads, bridges, camps, settlements etc. were avoided.

3.2.2 Vegetation sampling

The sampling strategy was designed to include as many of the species in the tail of the abundance distribution as possible (§1.2.6). Obtaining a dataset with a well–sampled tail was essential for this study, to allow investigation of the functional roles of the tail species and their role in providing redundancy for the dominant species. Effective sampling of the tail was achieved in the following ways:

- Sampling effort was large. Data were collected by a full–time field technician over a 16–month period, with assistance from myself and several part–time technicians. The total number of plants counted was 114 605, from 130 woody species and 350 herbaceous species.
- Sites and transects were chosen so as to include heterogeneity rather than avoid it. Environmental heterogeneity is known to influence species accumulation curves, and including different types of patches increases the chances of recording rare species with restricted spatial distributions (Colwell and Coddington, 1994). At each main river site three transects were located in different types of river sections (wide rocky, wide sandy, and narrow sandy) to account for longitudinal variation in channel form. Each of these transects covered the elevation gradient from the centre of the macro–channel floor to the top of the macro–channel banks, to include as much lateral and vertical heterogeneity as possible. Along the small streams, transects were spread out longitudinally to increase the chance of including a variety of physical features (rock outcrops, river bends, sodic patches etc.), because in these streams there was more longitudinal than lateral variation.
- The smaller quadrats for sampling herbaceous vegetation were placed in a stratified random manner within the larger woody plots (see Appendix A for details). This sampling design allowed me to capture the lateral and vertical heterogeneity as well as accounting for small–scale variation/patchiness in environmental factors (Pettit and Naiman, 2005; Parsons *et al.*, 2005). Linear sampling generally fails to capture herbaceous diversity adequately when micro–scale heterogeneity is high, because it captures a lot of redundant information (due to spatial autocorrelation) while missing non–linear variation in the surrounding area, such as that due to animal disturbance, micro–scale soil differences and topographic features (Stohlgren *et al.*, 1998).
- An extra search in a wider area was performed for herbaceous species not recorded in the quadrats; this multiscale approach is similar to that used in the modified Whittaker plot design, which has been shown to improve the chance of observing rare species (Stohlgren *et al.*, 1998; Goslee, 2006).
- Sampling was spread across different seasons and times of year to account for differences in species' phenology and life cycles.

Woody vegetation was sampled between September 2007 and February 2008, in 30 m wide belt transects formed by stacking rows of three 10 × 10 m plots (see Appendix A for details). The number of rows of plots used varied with the width of the riparian zone at each site. The abundance and total percentage (aerial) cover of each woody species was recorded within each 10 x 10 m plot. All live individuals of each species were counted, including identifiable seedlings. GPS coordinates were taken to facilitate relocation of the plots during subsequent sampling sessions.

Along the small streams a larger number of shorter transects were placed at intervals along the length of the stream, making the sampling effort approximately equal to that for the main river. At all small stream sites, eight 30 x 30 m transects (three rows of plots) were placed between 50 and 60 m apart, extending from the channel perpendicularly up the adjacent hillslope. Along these small streams, the boundary between riparian and upland vegetation is diffuse and difficult to identify in the field. The width of the riparian zone can vary considerably with small–scale topographical features, such as rock outcrops and gullies draining into the main channel. The 30 m long transects were considered long enough to include all the riparian species (but do necessarily also include some species with stronger upland affinities; these were not excluded from the data).

Herbaceous vegetation was sampled between February 2008 and January 2009 (excluding August and September as it was too dry). From May to July, only the lower elevation portions of the main river transects were surveyed, as the herbaceous vegetation remained green in these plots. Due to time constraints, only two of the three transects at each main river site were sampled: one from a wide rocky section of river and one from a narrow sandy section, to maximise the range of habitats sampled. The fact that one of the transects used in the woody survey was not sampled for herbaceous species at each site did not have any implications for replication as the data from the transects were pooled in any case. Herbaceous species were sampled in 1 × 1 m quadrats placed within the 10 × 10 m plots used to sample the woody vegetation (Figure A.3, Appendix A). Species abundances and total percentage aerial cover were recorded within each quadrat. For tufted graminoid species, abundance was measured by counting

Table 3.1: Spearman rank correlation coefficients for species relative abundance vs relative cover

	Woody	**Herbaceous**
Small streams		
Communal	0.81	0.89
Kruger	0.84	0.94
Sabi–Sand	0.89	0.9
Main river		
Communal	0.73	0.87
Kruger	0.76	0.87
Sabi–Sand	0.85	0.88

individual tufts, while for creeping graminoids and clonal forbs an estimate of the number of separate tillers/ramets was made (however, cover is a more appropriate measure than abundance for such species). Herbaceous riparian species in this area were relatively unknown and undersampled prior to this study, particularly the non–graminoid (forb) species. Particular attention was therefore paid to the sampling and identification of these species.

Species identifications were made in the field where possible, with the help of published field guides (see Appendix A) and a field herbarium made up of pressed specimens and photographs collected by me and other researchers. The field herbarium was particularly useful for the herbaceous species. Specimens that could not be identified or that needed verification were pressed and identified in the herbarium at Skukuza (SKU) or the C. E. Moss Herbarium at the University of the Witwatersrand (J). Difficult cases were identified with help from the staff at the National Herbarium in Pretoria (PRE). Voucher specimens are lodged at J or SKU (SKU only contains specimens collected within the Kruger National Park). Germishuizen *et al.* (2006) was used as the authority for names and authors of taxa.

Data were recorded in the field directly onto a Palm Z22 handheld device running EcoNab (free software designed and maintained by the Stohlgren research group at the Natural Resource Ecology Lab, Colorado State University and distributed by the National Institute for Invasive Species Science, `www.niiss.org/cwis438/gather/EcoNab/EcoNabDownload.php`). EcoNab is designed to facilitate collection of ecological survey data on handheld (Palm) devices. It provides customizable, structured data entry screens with a facility for pre–loading species lists and plot designs, built–in error checking and a facility to transfer field data directly to an Microsoft Access database tailored for ecological studies, called VegSurvey. Both EcoNab and VegSurvey allow for sophisticated handling of ‘unknowns’ (specimens which cannot be identified in the field) and future species name changes. All vegetation survey data were stored in a VegSurvey database.

For the purposes of this study, plot data were pooled for each management area and stream order combination, giving a single dataset for each of the following six assemblages: communal small streams, Kruger small streams, Sabi–Sand small streams, communal main river, Kruger main river, and Sabi–Sand main river. These datasets each contained abundance, cover and frequency values for each species present. Aggregating the data in this way was appropriate because the focus was on comparing assemblages from areas with different land management regimes, and not on the smaller–scale variations in diversity associated with particular sites, elevations or geomorphic features. Aggregated assemblages reflect the integrated response of the riparian vegetation to the various management practices in the catchment. No attempt was made here to develop direct causal links between particular management practices and vegetation characteristics (this is very difficult; (Allan, 2004)). Rather, I wanted to compare the diversity, functioning and resilience of assemblages from the different areas, assuming that observed differences would reflect the direct or indirect impacts of the different land management practices.

3.2.3 Data analysis

Species cover and abundance values were both recorded during the vegetation survey, cover being a more appropriate measure for clonal species such as creeping graminoids (van der Maarel, 2005). Since cover and abundance values were found to be strongly positively correlated for woody and herbaceous species (Table 3.1), I used cover throughout the rest of the analysis to maintain consistency. Most of the functions considered here were in any case determined more by the cover (size) of the species than by the number of individuals present (food, shade and fuelwood provision and response to water stress; however this was not necessarily the case for nutrient cycling and response to damage).

Species cover (and abundance) distributions were all typical exponentially decreasing ‘hollow curves’ (§1.2.6), with only a few species making up the majority of the cover and most species making up the tail of the distribution (see Figures 4.6 to 4.9 in the following chapter). For the purpose of addressing the role of tail species in providing redundancy, I defined 'tail species' as those species making up the bottom 25% of the total cover in each assemblage, and termed the species making up the top 75% of cover 'core species'. This choice of cutoff value was considered reasonable because it allowed all individually abundant species (cover greater than 2%) to be classified as core species, while the majority of species (75–100%) in the tail species group had cover values of less than 1%. Tail species made up only 25% of the total cover in each assemblage, but 75–86% of the total species present in the woody assemblages, and 87–95% of the total species present in the herbaceous assemblages. The use of a proportional cutoff value made it possible to compare the cores and tails of assemblages with different numbers of species.

The methods used to calculate the redundancy and response disparity associated with different aspects of the functioning of each species were described in detail in Chapter 2. In summary, species' functioning was described by their position in each of a number of different functional spaces, representing several different effect and response functions. The redundancy associated with a particular species was measured as the number of species with high similarity (≥ 0.9) to the focal species (the number of species in its nearest neighbour group or 'nngroup'), for each function separately. The identities of the species providing the redundancy in each case were retained. The response disparity associated with a particular species was measured as the multivariate dispersion ($FDis$) of the species in its nngroup (species similar in a particular effect function) in each response functional space (see Figure 2.8).

Permutational multivariate analysis of variance (perMANOVA) using distance matrices (function `adonis` in the R package `vegan`) was used to compare redundancy and response disparity values between assemblages from the different management areas and stream sizes. This method is also known as non–parametric MANOVA (Anderson, 2001), and is analogous to redundancy analysis (Legendre and Anderson, 1999). It is a robust alternative to both parametric MANOVA and to ordination methods for describing how variation is attributed to different experimental treatments (Oksanen *et al.*, 2011). If Euclidean distance is used as the dissimilarity metric, perMANOVA is equivalent to MANOVA, except for the fact that permutations are used to generate the p–values. The use of permutations relaxes the need to impose distributional assumptions on the variables.

I used perMANOVA to test whether the distributions of redundancy and response disparity values among species (for multiple functions together) were more different between assemblages than they were within assemblages. I used Euclidean distance as the dissimilarity metric, and I used 999 permutations to generate the p–values. This method allowed the full distribution of redundancy and response disparity values within the different assemblages to be taken into account, thereby providing a more meaningful comparison than one based on single (e.g. mean) assemblage–level measures of redundancy or response disparity.

To assess the evidence for functional compensation in the riparian assemblages, I used the following procedure. For all species which were abundant ($\geq$2% cover) in one or more management areas *and* which differed markedly in abundance between areas, I categorised the differences in abundance into one of the following patterns:

1. Clear compensation (when dominant species decreases, similar minor species increase)
2. Limited compensation (as above but not evident in all management areas)
3. Pattern unclear (some minor species increase but others decrease, net effect uncertain)
4. No compensation (decrease or no change in minor species, or no redundancy present).

Chi–squared goodness–of–fit tests were then used to test whether there were significantly more cases of compensation than of non–compensation, for each assemblage and function. To account for the small sample sizes, categories 1 and 2, and 2 and 3 were combined, and P values were determined by Monte Carlo simulation rather than from the χ^2 distribution directly (random sampling from a uniform distribution, each sample size equal to the sum of x, with 2000 replicates).

3.3 Results

The results presented in this chapter represent the application of the resilience measures developed in the previous chapter to a real–world situation, that of riparian plant assemblages under different management regimes, as well as a much–needed empirical test of the hypotheses of Walker *et al.* (1999) about the roles of redundancy and response disparity in resilience. The aims of this chapter were, firstly, to describe general patterns of redundancy and response disparity in the riparian assemblages and compare these

Table 3.2: Mean nngroup sizes of the core species in each assemblage (mean number of species per group).

	Small streams			**Main river**		
Functions	**Communal**	**Kruger**	**Sabi–Sand**	**Communal**	**Kruger**	**Sabi–Sand**
Woody species						
Nutrient cycling	12	16	12	8	11	11
Food provision	3	3	2	1	2	2
Shade provision	13	13	12	9	9	15
Fuelwood provision	18	17	15	11	15	18
Herbaceous species						
Nutrient cycling	12	16	12	11	10	11
Food provision	5	6	4	3	5	6

with the patterns predicted by Walker *et al.* (1999), and secondly, to compare redundancy and response disparity (and therefore resilience) in the three different management areas. The results for redundancy and response disparity will be presented separately, with analysis of general patterns in each case followed by a comparison across management areas.

3.3.1 Redundancy in riparian plant assemblages

General patterns

The first hypothesis of Walker *et al.* (1999) states that redundancy for the functions performed by the core species is provided by the less abundant species in the tail of the abundance distribution. This hypothesis would be supported by the presence, for each function, of tail species that are able to function similarly to the core species (thus providing redundancy).

The amount of redundancy associated with the functioning of a particular core species was measured as the size of its 'nearest neighbour group' (nngroup), which indicates how many other species were similar to that core species in a particular function. Core species' nngroup sizes ranged from 0 to 29, with most (7–100%, mean of 67%) of the core species having five or more similar species providing redundancy for each function (Figure 3.4). The mean nngroup size was above 10 for most functions (Table 3.2). These results suggest that redundancy was both present and relatively common in the riparian assemblages. The implications of the large variability in nngroup sizes will be discussed later in this section.

Differences between functions in the amount of redundancy present (e.g. the lower redundancy for the food provision function) should not be considered particularly important. These differences are somewhat artificial because they are related to the number of traits used to represent each function (Chapter 2). Comparisons should therefore rather be made between assemblages for the same function than between different functions.

As predicted by Walker *et al.* (1999), most (53–100%, mean of 82%) of the redundancy for the functioning of the core species was provided by species from the tail of the abundance distribution (Table 3.3). The species providing redundancy typically had a wide range of abundances and were spread across the abundance profile of the assemblage, as illustrated by the distribution of coloured squares in Figure 3.5. This was true regardless of whether the number of species providing redundancy for a particular function was large or small (Figure 3.5). In some cases, core species provided redundancy for other core species (e.g. in Figure 3.5 (a)). However, the fact that so many tail species were functionally similar to the more abundant core species is significant. It means that the tail was an important reservoir of 'reserve' or 'backup' functional capacity, and that many of the species in the tail at least had the potential to compensate for losses of functioning caused by decline of the core species.

The patterns of redundancy described above were not, in fact, restricted to core species. Tail species had similarly high average levels of redundancy (mean nngroup sizes ranged from 9–15, except for the food provision function), but the levels of redundancy were also highly variable across species for all the functions studied (Figure 3.6). All assemblages contained species with no redundancy (no species able to perform that function similarly), as well as species with high redundancy (up to 35 species able to perform that function similarly). This variability is important. It means that even in assemblages with high overall redundancy, particular aspects of functioning can still be vulnerable to being lost, if they are performed by species with low redundancy for that function. It is therefore critically important that we consider the *variation* in redundancy and not only the mean, because this variation has important implications for resilience.

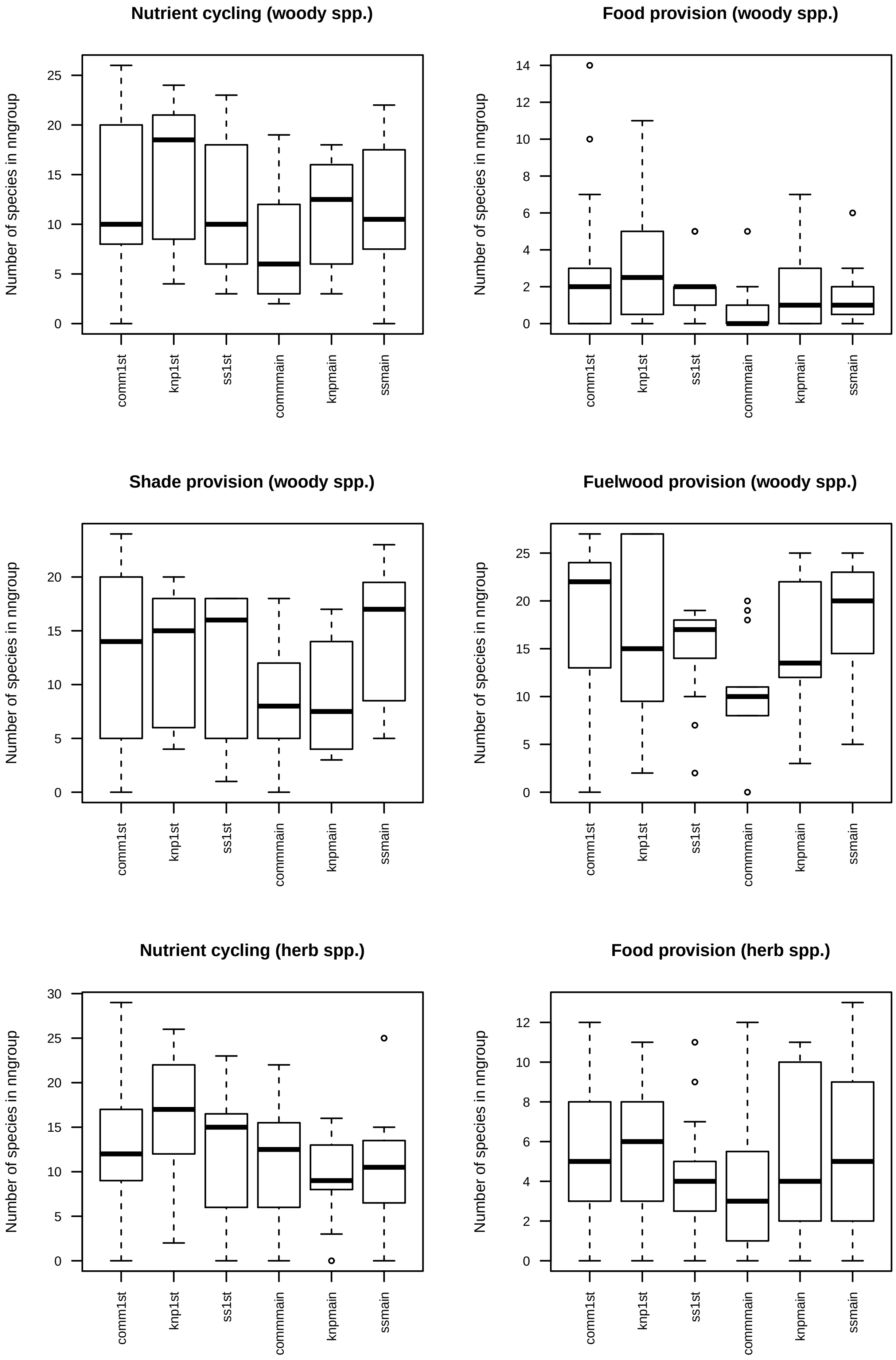


Figure 3.4: Boxplots showing the distribution of nngroup sizes (a measure of the amount of redundancy associated with a particular species) of the **core species** in each assemblage, for different functions.

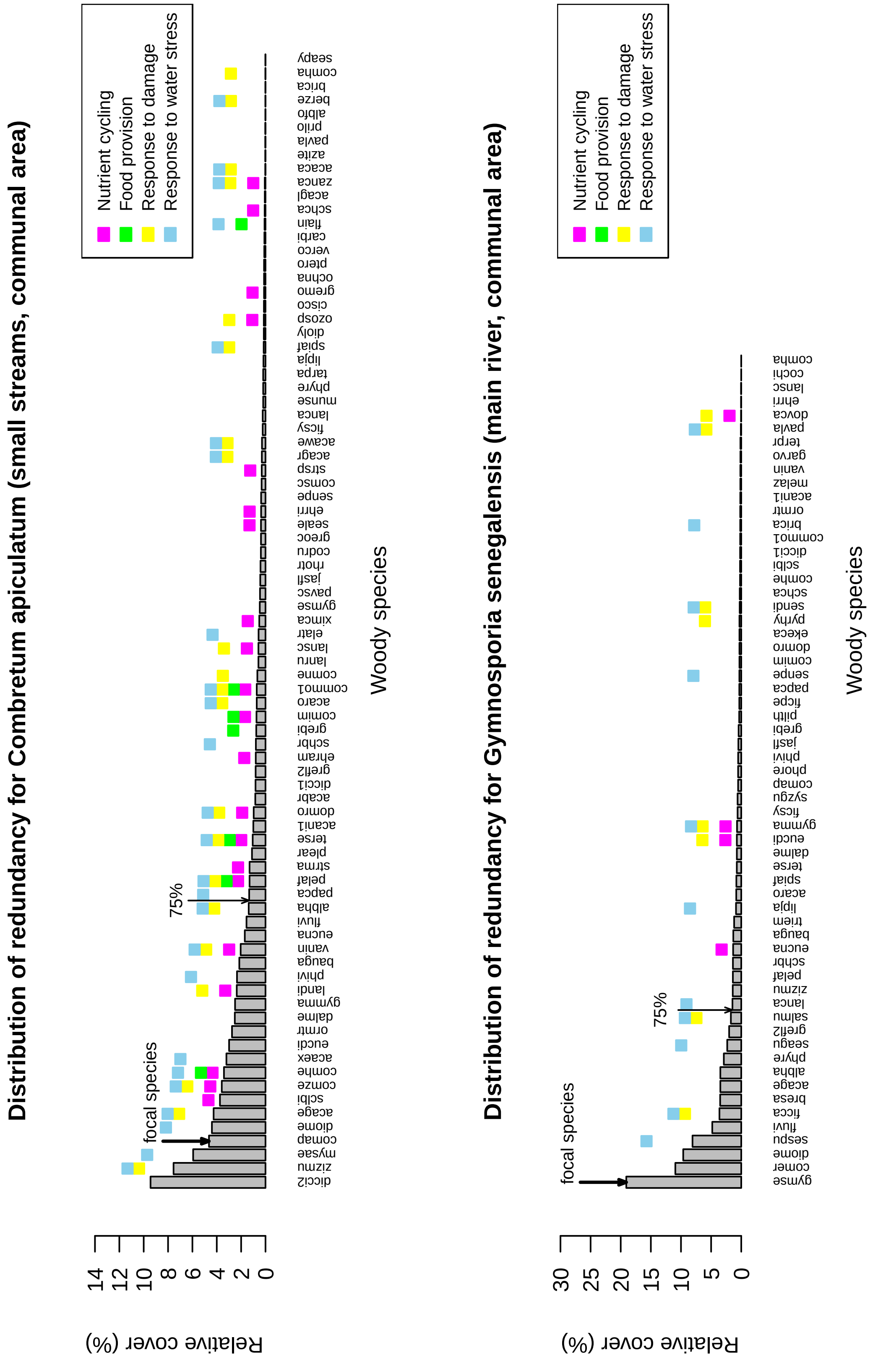


Figure 3.5: Example showing the distribution of redundancy for two core species with high and low redundancy respectively, (a) *Combretum apiculatum* in small streams and (b) *Gymnosporia senegalensis* in the main river, in the communal area. The bold arrow indicates the focal species for which redundancy is being shown. The different coloured squares indicate the species providing this redundancy (the members of the focal species' nngroup) for different functions. For example, pink squares indicate which species function similarly to the focal species in nutrient cycling. The arrow labelled '75%' indicates division of species into core (making up 75% of cover) and tail (making up 25% of cover). Full species names are given in Appendix A.

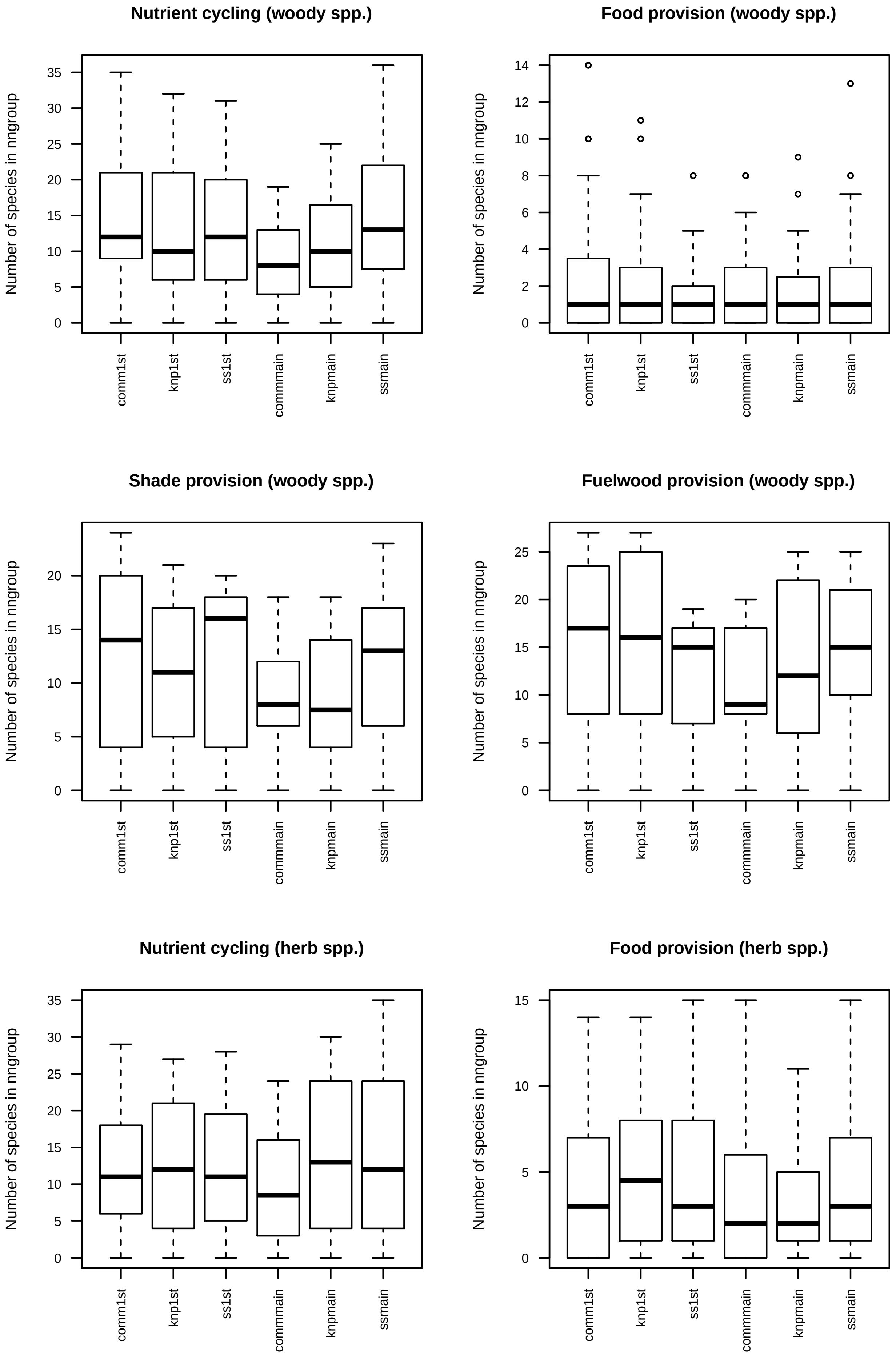


Figure 3.6: Boxplots showing the distribution of nngroup sizes (a measure of the amount of redundancy associated with a particular species) of **all the species** in each assemblage, for different functions.

Table 3.3: Proportion (%) of the total redundancy provided to the core species by species from the tail.

	Small streams			**Main river**		
Functions	**Communal**	**Kruger**	**Sabi–Sand**	**Communal**	**Kruger**	**Sabi–Sand**
Woody species						
Nutrient cycling	75	83	74	81	81	89
Food provision	68	64	53	100	85	89
Shade provision	73	88	73	80	81	85
Fuelwood provision	75	85	71	80	78	85
Herbaceous species						
Nutrient cycling	90	85	88	80	89	92
Food provision	83	74	89	86	89	95

Table 3.4: Proportion (%) of the total number of species in each assemblage with no redundancy (empty nngroups) for the various effect functions.

	Small streams			**Main river**		
Functions	**Communal**	**Kruger**	**Sabi–Sand**	**Communal**	**Kruger**	**Sabi–Sand**
Woody species						
Nutrient cycling	3.6	2.6	1.6	4.9	4.2	2.3
Food provision	33.7	32.9	36.1	37.7	38.9	35.6
Shade provision	3.6	2.6	8.2	4.9	2.8	1.1
Fuelwood provision	2.4	5.3	6.6	4.9	4.2	2.3
Herbaceous species						
Nutrient cycling	3.1	5.7	5.6	7.7	5.8	4.5
Food provision	26.4	20	17.5	31.5	21.7	20

As with the core species, the species providing redundancy for the various functions performed by each tail species were spread right across the abundance distribution (Figure 3.7). There was no relationship between the abundance or cover of a species and the amount of redundancy associated with its functioning. The correlation between (rank) cover abundance and (rank) nngroup size was weak to very weak, for all functions and assemblages. Eighty–three percent of the Pearson's correlation coefficients were below 0.2, the highest being 0.28. This means that there was no systematic difference in the levels of redundancy associated with core and tail species. The functioning of the core species was therefore not necessarily better 'insured' (with higher redundancy) than the functioning of the tail species.

The amount of redundancy associated with each species was also not related to its position in functional space. Species with very high or very low redundancy were distributed throughout the various functional spaces (Figure 3.8). While low–redundancy species by definition occurred within sparsely populated parts of the functional space, they were not necessarily restricted to particular parts of the space, e.g. the centre or the outer edges. Both high– and low–redundancy species were mixed throughout each of the spaces, and there was no clear relationship between particular trait combinations and the amount of redundancy associated with a species. This, together with the lack of relationship between species abundances and redundancy described above, suggests that the amount of redundancy associated with a particular species is idiosyncratic and cannot be systematically predicted. In other words, the amount of redundancy associated with a species for a particular function depends on the traits that species happens to possess as well as on the traits present in the rest of the assemblage.

Species with no redundancy: impacts on resilience

For all the effect functions except food provision, 1–8% of species in each assemblage had no redundancy (Table 3.4). For food provision, 20–40% of species had no redundancy, but this was largely due to the fact that more traits were used to define a species' contribution to food provision. It was therefore less likely that two species would be similar in all traits, leading to lower levels of redundancy for this function overall. The possibility that the number of traits used to define a function may affect the amount of redundancy measured is potentially problematic and requires further investigation.

Core species have a large influence on the functional profile of an assemblage because of their high abundance. Core species with low redundancy lack similar species that can compensate for their important contributions to functioning should they decline or be lost, so loss of core species could potentially lead to large changes in functioning. Core species with no redundancy may therefore represent 'weak points' in the resilience of an assemblage, and these species may function as keystone species. A number of riparian core species were identified as potential keystone species in the different assemblages (Table 3.5). Examples of how such information can be used to address particular management questions will be given

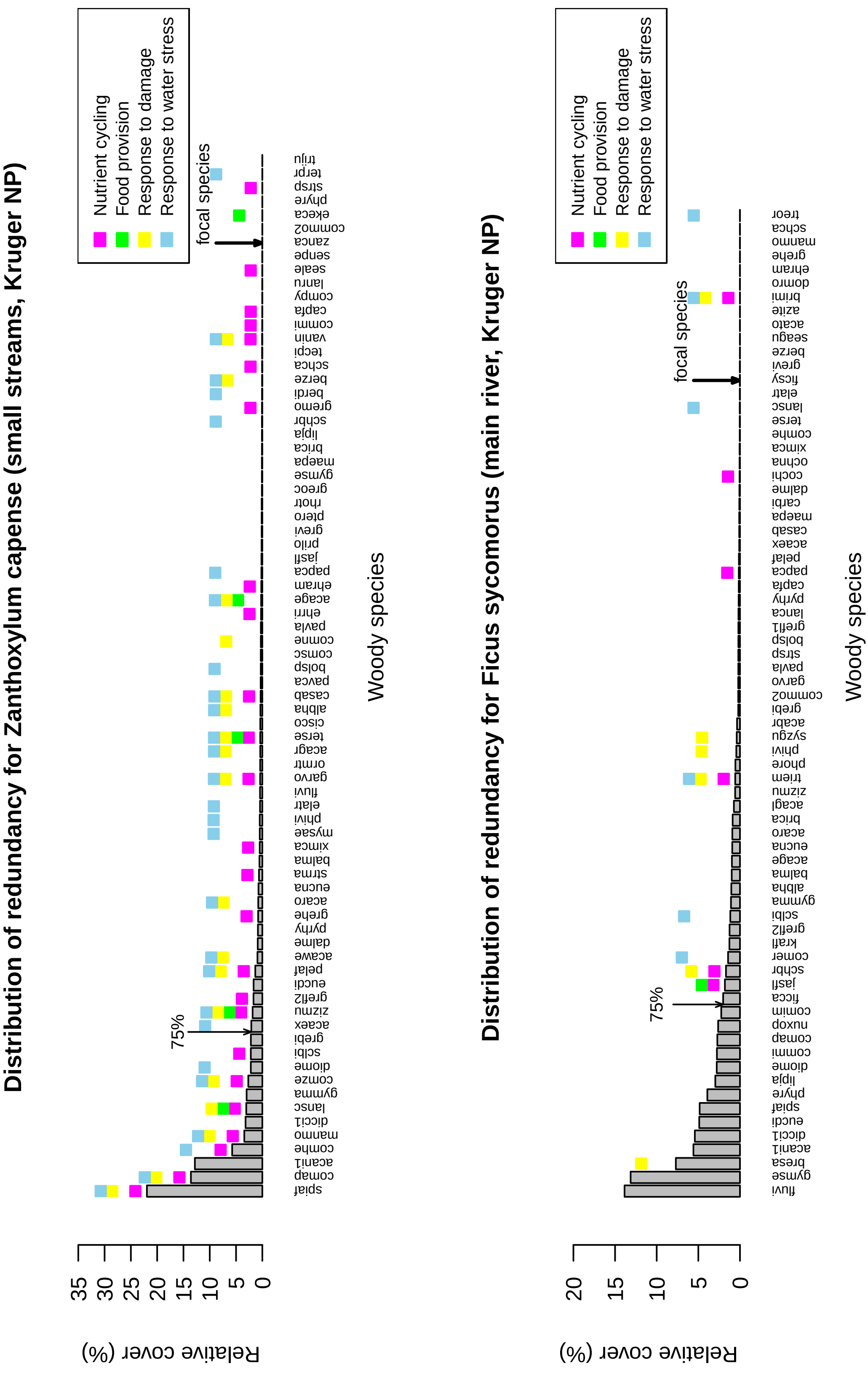
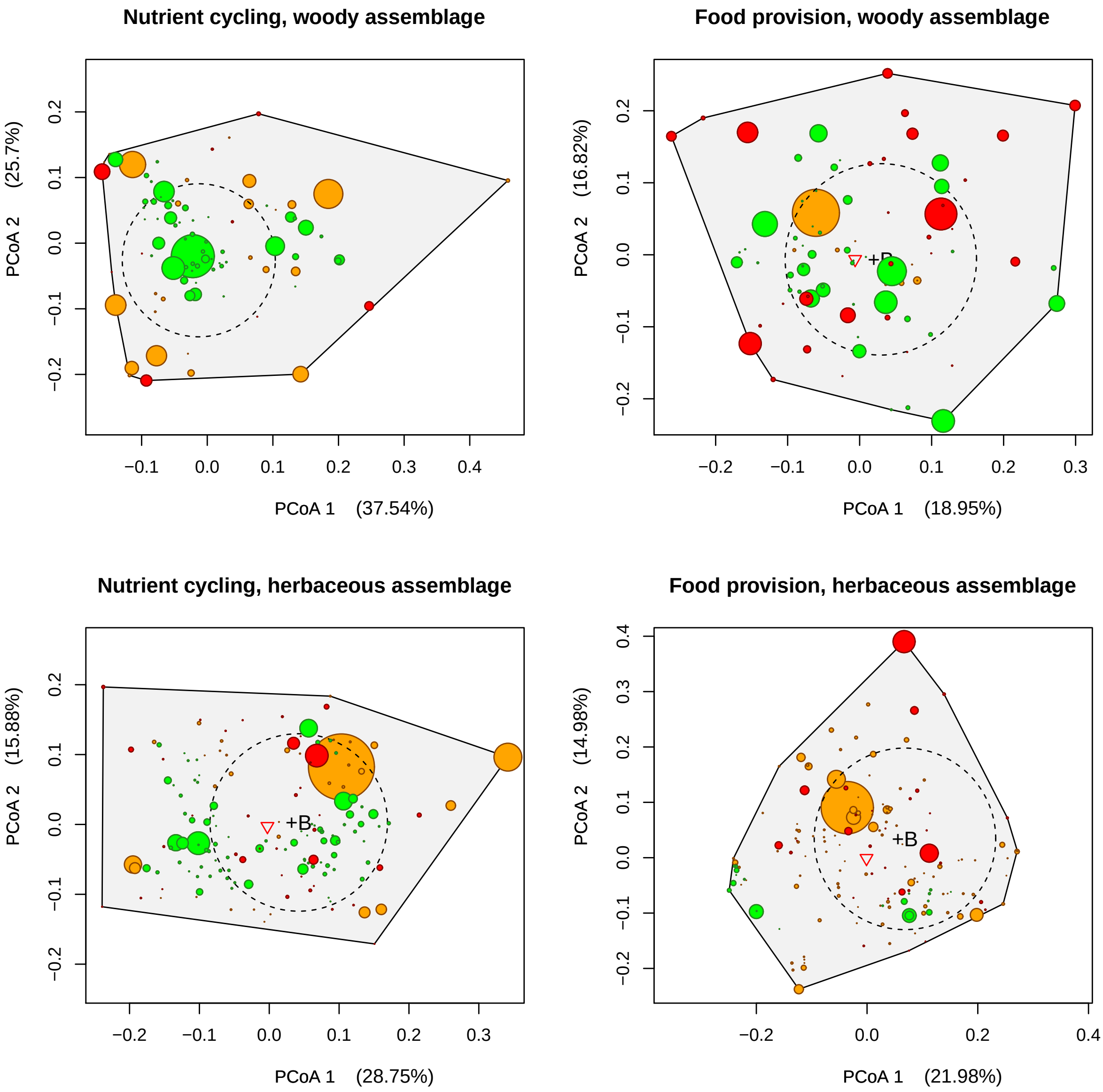


Figure 3.7: Example showing the distribution of redundancy for two tail species with high and low redundancy respectively, (a) *Zanthoxylum capense* in small streams and (b) *Ficus sycomorus* in the main river, in the Kruger National Park). The bold arrow indicates the focal species for which redundancy is being shown. The different coloured squares indicate the species providing this redundancy (the members of the focal species' nngroup) for different functions. For example, pink squares indicate which species function similarly to the focal species in nutrient cycling. The arrow labelled '75%' indicates division of species into core (making up 75% of cover) and tail (making up 25% of cover). Full species names are given in Appendix A.


Nutrient cycling, woody assemblage

Food provision, woody assemblage

Nutrient cycling, herbaceous assemblage

Food provision, herbaceous assemblage

Figure 3.8: Distribution of high and low redundancy species in the multivariate functional spaces for different effect functions, for the Sabi–Sand main river assemblage. Species are represented by circles scaled by their abundance. High redundancy species (green circles) have nngroups containing more than 10 species, low redundancy species (red circles) have nngroups containing fewer than 5 species. Species with intermediate redundancy are shown in orange. Refer to §2.2.4 and Fig. 2.9 in Chapter 2 for further details about these plots.

Table 3.5: Core species with no redundancy (empty nngroups) in each assemblage. The functions for which each species had low redundancy are indicated in brackets (nut = nutrient cycling, food = food provision, shade = shade provision, fuel = fuelwood provision, damage = response to damage, water = response to water stress). Response functions were included here because loss of a core species with unique response traits will cause that particular response to be lost from the assemblage, in the same way that particular effect functioning can be lost. These species represent potential keystone species.

	Small streams	
Communal	Kruger	Sabi–Sand
Philenoptera violacea (nut)	*Dichrostachys cinerea* (food)	*Euclea divinorum* (food)
Dichrostachys cinerea (food)	*Gymnosporia maranguensis* (food)	*Euclea natalensis* (food)
Mystroxylon aethiopicum (food)	*Diospyros mespiliformis* (food)	*Acacia nigrescens* (water)
Diospyros mespiliformis (food)	*Acacia nigrescens* (water)	*Xerophyta retinervis* (nut, food)
Euclea divinorum (food)	*Aristida adscensionis* (food)	
Dalbergia melanoxylon (food)		
Gymnosporia maranguensis (food)		
Bauhinia galpinii (food, shade, fuel)		
Euclea natalensis (food)		
Indigofera laxeracemosa (nut)		
Aloe marlothii (food, damage)		
Achyranthes aspera (food)		
	Main river	
Communal	Kruger	Sabi–Sand
Gymnosporia senegalensis (food)	*Flueggea virosa* (food)	*Philenoptera violacea* (nut)
Diospyros mespiliformis (food)	*Gymnosporia senegalensis* (food)	*Gymnosporia senegalensis* (food)
Breonadia salicina (food)	*Breonadia salicina* (food)	*Acacia welwitschii* (food)
Albizia harveyi (food)	*Acacia nigrescens* (food)	*Diospyros mespiliformis* (food)
Phyllanthus reticulatus (food)	*Diospyros mespiliformis* (food)	*Acalypha glabrata* (damage)
Grewia flavescens (food, shade, fuel)	*Acacia nigrescens* (water)	*Phragmites mauritianus* (nut, food)
Salix mucronata (food)	*Phragmites mauritianus* (nut, food)	*Brachiaria deflexa* (food)
Phragmites mauritianus (nut, food)		
Tephrosia purpurea (nut)		
Triumfetta pentandra (food)		
Digitaria eriantha (food)		

in Chapter 4.

Many tail species also had little or no redundancy. In fact, most of the species with no redundancy in each assemblage were tail species, simply because most of the species in the assemblage were tail species. What impact might these low–redundancy tail species have on resilience?

Many of the species at the edges of the cloud of species points in each functional space were tail species, suggesting that tail species were often themselves functionally unusual in one or more functions. Tail species were therefore important in defining the volume of functional space occupied by an assemblage, which is a measure of the range of functioning present (Table 3.6). On average, 84% of the convex hull vertices were tail species, and in several cases this value was 100% (Table 3.6; see Figure 2.9 for explanation of convex hull vertices). Up to 57% of the species on the convex hull were tail species with no redundancy, although this value varied between assemblages and functions (the mean was 21%) (Table 3.6). Tail species by definition have low abundances, making them more vulnerable to local extinction. If the range of functioning present within an assemblage is defined largely by low–abundance tail species, and if many of these tail species lack redundancy, this suggests that the volume of functional space occupied by an assemblage probably undergoes frequent change as the identity of the rare and/or low–redundancy vertex species changes.

In some cases, unusual tail species with little or no redundancy greatly enlarged the volume of functional space occupied by an assemblage (Figure 3.9). Loss of these species would result in a substantial decrease in the range of possible functioning, as illustrated in Figure 3.9. Of course it is unlikely that all unusual low–redundancy species would be lost simultaneously. However, the range of functioning present in the assemblage is less likely to be maintained over time if many of the species defining the volume of occupied space have low redundancy. Reductions in the range of functioning present are detrimental to resilience, because they reduce the number of functional 'options' available and the range of possible responses to disturbance.

In summary, the following general patterns were observed in all the riparian assemblages:

Table 3.6: Contribution of tail species to defining the volume of functional space occupied by each assemblage. Numbers are proportions (%) of convex hull vertex species which are part of the tail of the abundance distribution. Numbers in brackets indicate what proportion (%) of the vertex species are tail species with no redundancy.

	Small streams			**Main river**		
Function	Communal	Kruger	Sabi–Sand	Communal	Kruger	Sabi–Sand
Woody species						
Nutrient cycling	60 (10)	100 (11)	78 (11)	88 (12)	78 (22)	70 (10)
Food provision	56 (22)	73 (27)	86 (57)	83 (33)	67 (33)	67 (56)
Shade provision	100 (20)	86 (29)	86 (57)	80 (0)	67 (17)	100 (0)
Fuelwood provision	100 (17)	80 (40)	60 (20)	80 (0)	83 (17)	100 (0)
Herbaceous species						
Nutrient cycling	82 (9)	80 (10)	82 (36)	78 (33)	88 (25)	80 (20)
Food provision	100 (44)	80 (30)	100 (36)	80 (40)	91 (9)	91 (27)

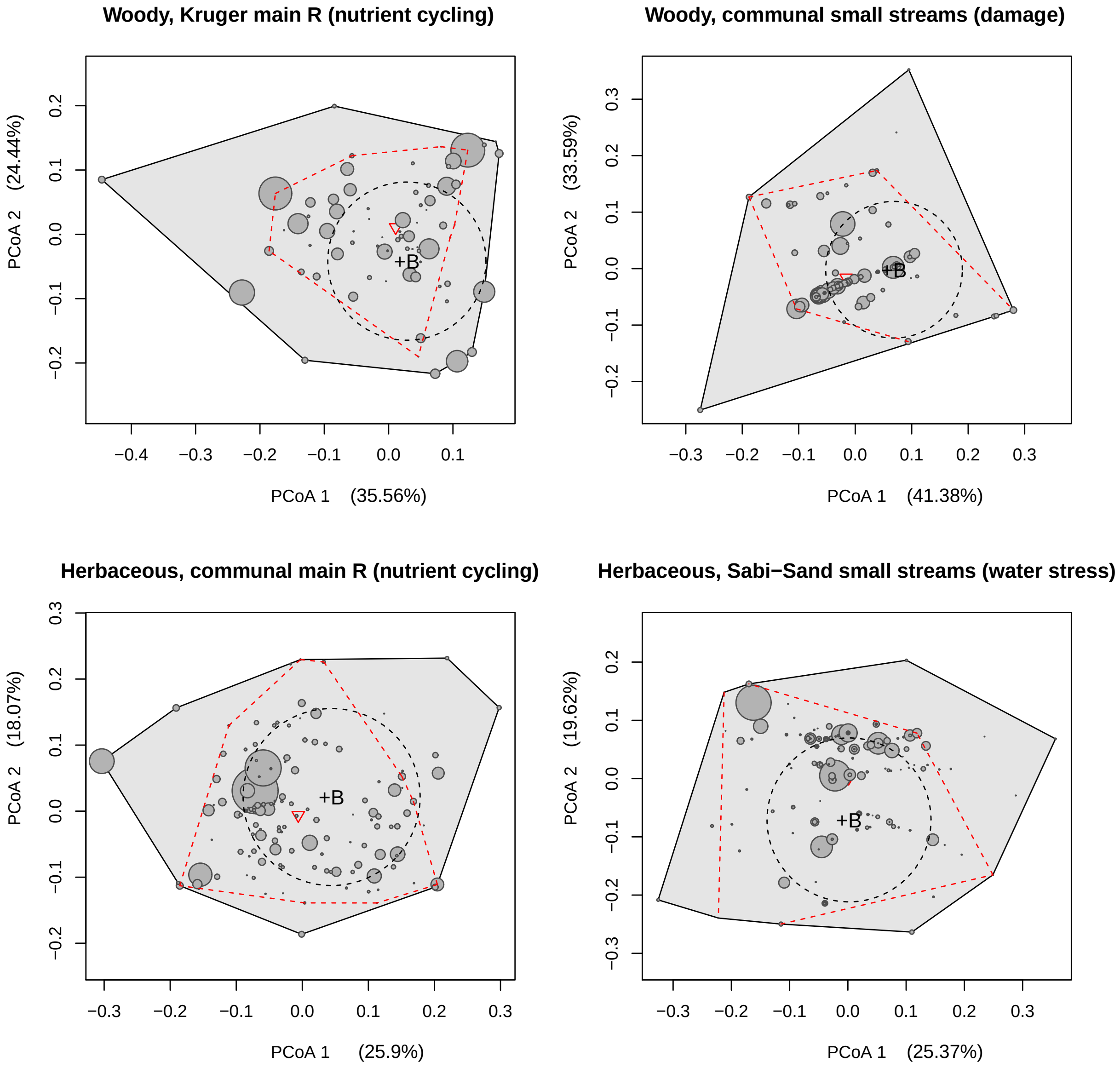


Figure 3.9: Principal coordinates plots showing the reduction in the volume of the convex hull (red dashed line) if all outer species with low redundancy (species with less than 5 species in their nngroups) are removed. Circles represent species and are scaled according to the abundance of the species in the assemblage. Refer to §2.2.4 and Fig. 2.9 in Chapter 2 for further details about these plots.

- Redundancy was on average high, but variable, for both core and tail species. The amount of redundancy associated with a particular aspect of functioning of a particular species did not depend on the abundance or cover of the species.
- Tail species were important in providing redundancy for the functioning of all species, since they make up the bulk of the species in an assemblage. The first hypothesis of Walker *et al.* (1999) was therefore supported, that species in the tail of the abundance distribution provide redundancy for the functioning of the core (abundant) species. However, tail species were also important providers of redundancy for other tail species.
- Species with low or no redundancy occurred in all assemblages.

However, differences were also evident between the three management areas.

Differences in redundancy between management areas

Permutational MANOVA revealed significant differences in redundancy between management areas for both woody and herbaceous assemblages, and significant differences between small streams and the main river for woody assemblages (Tables 3.7 and 3.8). There was also a significant interaction between management area and stream size for both woody and herbaceous assemblages (Tables 3.7 and 3.8). I therefore analysed the differences between management areas for small streams and for the main river separately.

Main river

The differences in redundancy between the management areas were strongest in assemblages from the main river (Table 3.9). Both woody and herbaceous assemblages in the communal area had less redundancy than assemblages inside the two nature reserves. The communal area assemblages had the least redundancy per core species (Table 3.2, Figure 3.4), the most species with no or low redundancy, and the fewest species with high redundancy, for most functions (Table 3.4, Table 3.5, Figure 3.6). While species with high levels of redundancy still occurred in the communal area, these assemblages appeared to have lost a certain amount of capacity to maintain their current functioning, compared to the assemblages inside the reserves. The assemblages in the Sabi–Sand reserve had the highest redundancy per species, the fewest species with low redundancy and the most species with high redundancy, while the Kruger National Park assemblages were intermediate (Figure 3.6, Table 3.4).

The differences in redundancy between assemblages from the main river with the most (Sabi–Sand) and least (communal area) redundancy are nicely illustrated by the example in Figure 3.10.

Small streams

The differences in redundancy between management areas were less clear for assemblages from the small streams. Herbaceous assemblages had similar redundancy in all three areas (Table 3.9). Among woody assemblages, the assemblage from Sabi–Sand generally had the lowest redundancy: the lowest redundancy per core species (Table 3.2), the most species with low redundancy (Table 3.4) and the fewest species with high redundancy (Figure 3.6). The lower redundancy in the Sabi–Sand assemblage was more evident for some functions than for others; it was particularly evident for the food provision and fuelwood provision functions (Figure 3.6). The assemblage from the communal area generally had the highest redundancy, with the highest maximum redundancy values for most functions (Figure 3.6). However, the assemblage from the communal area also had the most core species with no redundancy (Table 3.5, Figure 3.4) and the most species with no redundancy for nutrient cycling (Table 3.4). Redundancy within the woody assemblage from the Kruger National Park was intermediate between the low redundancy in Sabi–Sand and the higher redundancy in the communal area.

The picture that has emerged so far is one of highly distributed redundancy within each assemblage, meaning that the functioning of each species was ‘backed up’ by a number of other species with a range of different abundances. Most species had 5–20 other species in the assemblage that could perform a particular function similarly to them, the majority of these being part of the tail. The first hypothesis of Walker *et al.* (1999), that minor species in the tail of the abundance distribution provide redundancy for functions performed by the dominant species (Box 1.3), was therefore strongly supported. However, the amount of redundancy associated with each species for each function was highly variable, and species with low redundancy occurred in all assemblages.

I shall now turn my attention to addressing the second hypothesis of Walker *et al.* (1999), namely that response disparity is high within the groups of species providing redundancy for a particular effect function.

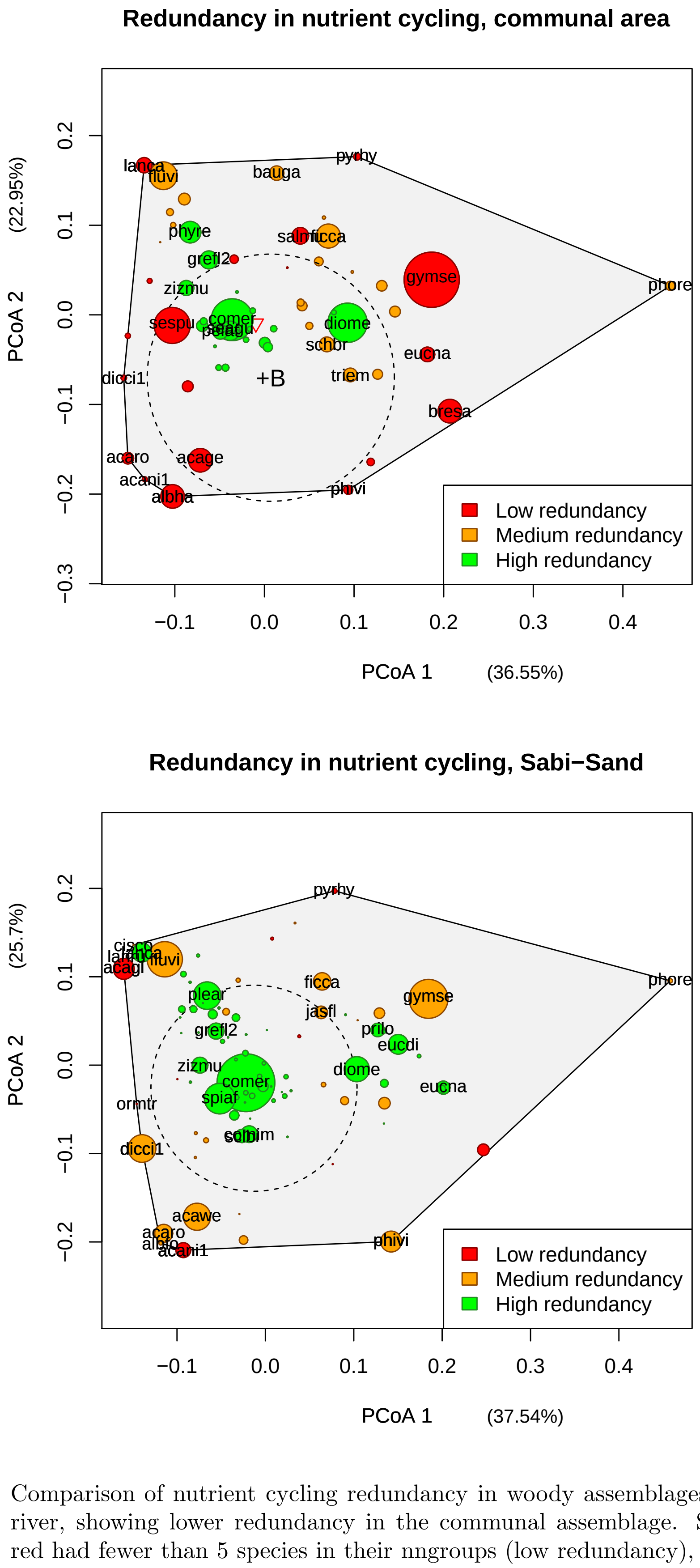


Figure 3.10: Comparison of nutrient cycling redundancy in woody assemblages from the main river, showing lower redundancy in the communal assemblage. Species coloured red had fewer than 5 species in their nngroups (low redundancy), species coloured orange had 5–10 species in their nngroups (medium redundancy), while species coloured green had more than 10 species in their nngroups (high redundancy). Refer to §2.2.4 and Fig. 2.9 in Chapter 2 for further details about these plots.

Table 3.7: Results of perMANOVA showing the effects of management area and stream size and their interaction on the distribution of redundancy values among species in woody assemblages (each function treated as a separate variable; functions included were nutrient cycling, food provision, shade provision and fuelwood provision).

	Df	SS	MeanSq	F.Model	R^2	$Pr(>F)$
ManagementArea	2	717	358.46	2.0582	0.009	0.08 .
StreamSize	1	1168	1167.53	6.7038	0.015	0.002 **
ManagementArea:StreamSize	2	2257	1128.44	6.4793	0.028	0.001 ***
Residuals	434	75586	174.16		0.948	
Total	439	79727			1	

Table 3.8: Results of perMANOVA showing the effects of management area and stream size and their interaction on the distribution of redundancy values among species in herbaceous assemblages (each function treated as a separate variable; functions included were nutrient cycling and food provision).

	Df	SS	MeanSq	F.Model	R^2	$Pr(>F)$
ManagementArea	2	725	362.27	3.9088	0.009	0.012 *
StreamSize	1	78	77.76	0.839	0.001	0.419
ManagementArea:StreamSize	2	781	390.57	4.2141	0.01	0.012 *
Residuals	859	79613	92.68		0.98	
Total	864	81197			1	

Table 3.9: Results of perMANOVA showing the effects of management area only on the distribution of redundancy values among species in the different assemblages (each function treated as a separate variable).

	Df	SS	MeanSq	F.Model	R^2	$Pr(>F)$
Woody species, small streams						
ManagementArea	2	723	361.7	1.8347	0.017	0.125
Residuals	217	42780	197.14		0.983	
Total	219	43503			1	
Woody species, main river						
ManagementArea	2	2413	1206.66	7.9816	0.069	0.001 ***
Residuals	217	32806	151.18		0.931	
Total	219	35219			1	
Herbaceous species, small streams						
ManagementArea	2	48	24.2	0.2869	0.001	0.841
Residuals	439	37030	84.35		0.999	
Total	441	37078			1	
Herbaceous species, main river						
ManagementArea	2	1465	732.67	7.2263	0.033	0.001 ***
Residuals	420	42584	101.39		0.967	
Total	422	44049			1	

Table 3.10: Mantel correlations between effect and response functions in the different assemblages.

	Small streams			Main river		
Functions	Communal	Kruger	Sabi–Sand	Communal	Kruger	Sabi–Sand
Woody species						
Nutrient cycling + damage response	0.31	0.28	0.2	0.37	0.41	0.36
Nutrient cycling + water stress response	0.36	0.35	0.34	0.24	0.29	0.31
Food provision + damage response	0.07	0.01	0.06	0.23	0.18	0.15
Food provision + water stress response	0.19	0.15	0.2	0.14	0.15	0.15
Shade provision + damage response	0.14	-0.03	-0.03	0.11	0.06	0.03
Shade provision + water stress response	0.45	0.49	0.48	0.4	0.49	0.46
Fuelwood provision + damage response	0.23	0.16	0.14	0.15	0.16	0.08
Fuelwood provision + water stress response	0.77	0.79	0.78	0.73	0.76	0.78
Herbaceous species						
Nutrient cycling + damage response	0.58	0.58	0.56	0.55	0.65	0.63
Nutrient cycling + water stress response	0.38	0.32	0.33	0.39	0.34	0.36
Food provision + damage response	0.41	0.38	0.37	0.37	0.41	0.39
Food provision + water stress response	0.42	0.35	0.33	0.38	0.32	0.35

3.3.2 Response disparity in riparian plant assemblages

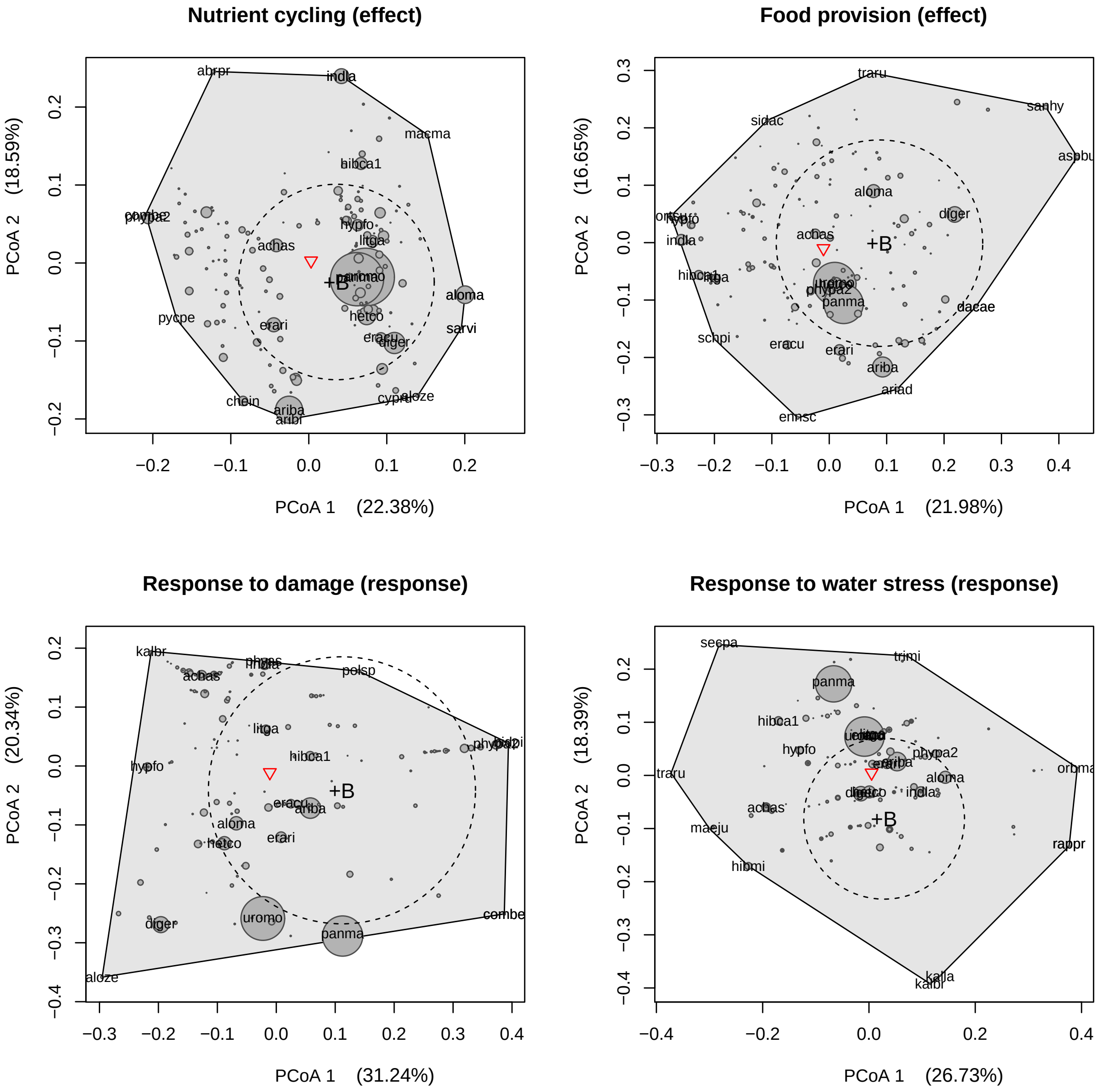
General patterns

Walker *et al.* (1999) proposed that the species providing redundancy for a particular effect function will differ in their responses to disturbance, thus providing response disparity (Box 1.3). Response disparity enhances resilience by increasing the range of conditions under which a particular effect function can continue to be performed. If response disparity is present in an assemblage, we would expect there to be little correlation between the dissimilarity matrices for effect and response functions, because species that are similar to each other in the way they perform a particular effect function would be dissimilar to each other in the way they respond to disturbances.

Correlations between the pairwise dissimilarity matrices for the various effect and response functions were indeed generally low (less than 0.4) in all the assemblages studied (Table 3.10). An exception to this was the strong relationship between fuelwood provision and response to water stress in woody species (0.73–0.79; Table 3.10). These two functions were probably correlated because the traits that make species good for fuelwood (dense wood) also confer resistance to water stress. Therefore, species that were similar with respect to fuelwood provision were also similar in their responses to water stress. However, these species still varied widely in their responses to physical damage (Table 3.10), indicating that response disparity was still present. Correlations between nutrient cycling and response to damage were also moderately high for herbaceous species (0.55–0.65; Table 3.10). This was related to life span. The short life span of annuals constrained both their nutrient cycling strategy and their responses to damage, while perennials had a bigger range of possible responses. Species similar in nutrient cycling were, however, more different from each other in their responses to water stress (Table 3.10).

In addition to the weak correlations between inter–species dissimilarities for effect and response functions (Table 3.10), the dissimilarities for the various effect functions were also only moderately correlated with each other (correlation coefficients between 0.22 and 0.58, mean correlation 0.42). This means that species providing redundancy for a particular aspect of functioning were likely to differ not only in their responses to disturbance or stress, but also in their contributions to other effect functions.

The generally low correlations between the various dissimilarity matrices can also be seen by comparing the distribution of a given set of species in different effect and response functional spaces (Figure 3.11).



Nutrient cycling (effect)

Food provision (effect)

Response to damage (response)

Response to water stress (response)

Figure 3.11: Principal coordinates plots showing the differences in distribution of herbaceous species within two effect and two response multivariate functional spaces, for the assemblage from small streams in the communal area. Refer to §2.2.4 and Fig. 2.9 in Chapter 2 for further details about these plots.

The same set of species was distributed very differently in the different functional spaces, indicating that species similar in one function were not necessarily similar in other effect or response functions.

The low correlation between effect and response functions has two very important consequences. Firstly, the second hypothesis of Walker *et al.* (1999) is supported, because sets of species providing redundancy for one of the effect functions had a wide range of responses to damage or water stress, thus providing response disparity. Secondly, few species were simultaneously similar in all the functions considered in this study. Rather, species overlapped only partially, being similar in some functions but not in others. Redundancy for each function was therefore provided by multiple *non–identical* species rather than by multiple identical species or 'analogues' as is often assumed by critics of the concept of redundancy (§1.2.4).

Many species in these riparian assemblages had no functional analogues (61–71% of woody species and 42–53% of herbaceous species per assemblage). Only 4–7% of woody species had two or more analogues. More herbaceous species had two or more analogues, particularly in the small streams (20–25% of species per assemblage). Although this shows that herbaceous assemblages from the small streams had a number of very similar species, the occurrence of functional analogues is really an artefact resulting from the fact that only a limited number of functions were considered in this study. The number of analogues recorded decreased as the number of functions considered increased (Figure 3.12), suggesting that if even

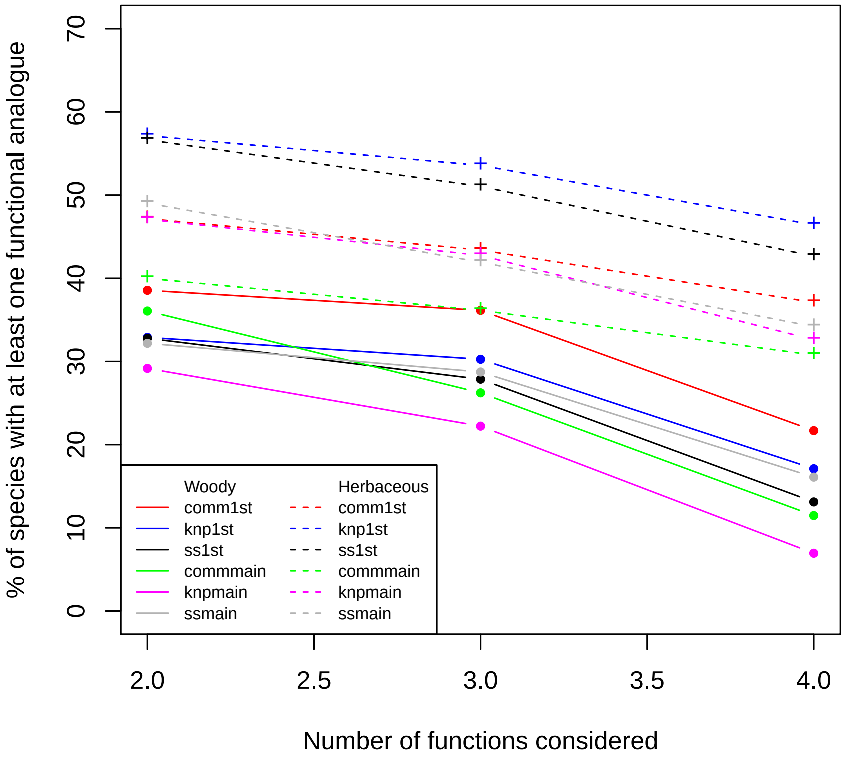


Figure 3.12: Change in the number of functional analogues recorded with the number of functions considered.

more functions were included the number of analogues would continue to decrease until every species was essentially unique in its functional profile. The relationship between the number of functions considered and the number of functional analogues recorded requires further study.

I measured the response disparity associated with each aspect of a species' functioning as the multivariate dispersion of the response dissimilarity values present within that species' nngroups (Chapter 2, Figure 2.8). Multivariate dispersion is a measure of disparity, or the degree of difference among entities. The members of a species' nngroup are, by definition, those species most similar to it for a given function. If, for example, a particular species' nngroup for an effect function contained ten species, response disparity would be measured as the degree of difference among these ten species in their responses to disturbance.

Species in the same nngroup for a particular effect function all had dissimilarities below 0.1, because the nngroups were formed by selecting only species with similarities ≥ 0.9 (or dissimilarities ≤ 0.1) with respect to that particular effect function (Chapter 2). Dissimilarities within nngroups for the *response functions* were, however, mostly greater than 0.1 (average range of 0.2). In other words, the species in the group were more dissimilar (less similar) in their responses to disturbance.

The relationship between redundancy and response disparity within nngroups

Response disparity within nngroups increased monotonically with nngroup size. Response disparity therefore increased with the amount of redundancy present (which is determined by the number of species in the nngroup), for all combinations of effect and response functions and in all assemblages (Table 3.11, Table 3.12). The relationship was approximately linear for nngroups containing more than about 5 species, after log transformation of the predictor variable (nngroup size). Theoretically the regression line should pass through the origin, because if there are no species in an nngroup, response disparity must also be zero. However, the intercept terms in Tables 3.11 and 3.12 were all positive and significant. The fact that the regression lines did not pass through the origin indicates that the relationship between species–level redundancy and response disparity was nonlinear for small nngroup sizes (Quinn and Keough, 2002). In other words, when nngroups were very small, each new species added caused response disparity to increase rapidly, but once there were about five species present it increased as shown in Table 3.11 and Table 3.12.

Intercepts ranged from 0.01 to 0.07, with a mean of 0.03 for both the woody and herbaceous assemblages (Tables 3.11 and 3.12). The mean slope was also 0.03 for woody and herbaceous assemblages. Coefficients of determination (R^2 values) ranged from 0 to 0.75, with a mean of 0.4 for the woody assemblages and 0.5 for the herbaceous assemblages, indicating that the relationship was stronger among herbaceous than among woody species. In all cases there was scatter about the regression line. The relationship was weakest for the combination of fuelwood provision and response to damage, indicating that for these functions the size of the nngroup was not a good predictor of the amount of response disparity present. However, for all other combinations of functions, the relationship between redundancy and response disparity had a significant positive slope.

This phenomenon can be explained as an example of the ‘sampling effect’: as more species are sampled, the chance of including some with unusual traits increases, assuming that the species are chosen randomly and are sufficiently dissimilar to each other. The more redundancy is present for a particular aspect of functioning, therefore, the more different responses to disturbance will be present, and the greater the chance will be that at least one species in the nngroup will be able to maintain that function through any particular disturbance.

Differences in response disparity between management areas

Woody and herbaceous assemblages from the different management areas had similar distributions of species–level response disparity (Figure 3.13). There were no significant effects of management area or stream size (Tables 3.13 and 3.14), except that woody assemblages from the main river had more disparity in responses to water stress. This was probably because species with high riparian affinities were present in the main river but not in the small ephemeral streams, giving assemblages from the main river a wider range of different responses to water stress.

The differences in redundancy between assemblages did not, therefore, translate into differences in response disparity, despite the positive relationship between species–level redundancy and response disparity described in the previous section. Assemblages with more high–redundancy species (species with large nngroups) were expected to have more large response disparity values, but this was not the case (Figure 3.13, Tables 3.13 and 3.14). The relationship between the redundancy and response disparity associated with each species was simply not strong enough to allow differences in redundancy to impact on the distribution of response disparity values in the assemblage as a whole. The amount of scatter about the regression lines (Tables 3.11 and 3.12) indicates that changes in redundancy (e.g. through loss or gain of species in a particular nngroup) had a variable effect on the amount of response disparity present. While the relationship was generally positive, in many cases an increase in redundancy resulted in a loss of response disparity, or a loss of redundancy resulted in an increase in response disparity. The relationship between species–level redundancy and response disparity therefore had low predictive power (Tables 3.11 and 3.12), and the exact effect of changes in redundancy on response disparity was determined to a large extent by the characteristics of the particular species involved.

A few examples serve to illustrate this point. In woody assemblages from the small streams in the communal area, six species provided redundancy for the food provision functioning of the tree *Sclerocarya birrea* (Marula). These six species (*Ozoroa sphaerocarpa*, *Combretum hereroense*, *Combretum molle*, *Spirostachys africana*, *Acacia caffra* and *Vangueria infausta*) therefore made up the food provision nngroup of Marula. In the Sabi–Sand reserve, only two species provided redundancy for this function (*Combretum hereroense* and *Spirostachys africana*). Marula therefore had lower redundancy for this aspect of its functioning in the Sabi–Sand assemblage than in the communal assemblage. However, despite the lower redundancy in Sabi–Sand, the response disparity for response to damage was higher in Sabi–Sand than in the communal area (FDis = 0.103 vs 0.044). This was because the four extra species present in the nngroup in the communal area were all very similar to *Sclerocarya birrea* in their responses to damage (pairwise dissimilarities of 0.042, 0.024, 0.036 and 0.025). The absence of these species in the Sabi–Sand assemblage caused response disparity to increase, because the two remaining species were less similar to *Sclerocarya birrea* in their responses to damage (dissimilarities of 0.171 and 0.035).

In a similar way, the addition of species with similar response traits to a particular nngroup sometimes caused the response disparity of the group to decrease. For example, in assemblages from the main river, the grass *Sporobolus africanus* had more redundancy for nutrient cycling in the communal area than in Sabi–Sand (six species vs three), but less disparity in response to damage (FDis = 0.137 vs 0.08). This was because the extra redundancy in the communal assemblage was provided by species that were all similar to *Sporobolus africanus* in their responses to damage.

Table 3.11: Ordinary linear regression coefficients for the relationship between log redundancy and response disparity within nngroups, for various combinations of effect and response functions (woody species). Regression equations are of the form $y = a + b\log(x)$. All intercepts and slopes were significant ($P \leq$ 0.05) unless otherwise indicated (NS=not significant).

	Intercept	**Slope**	**R^2**	**F(df)**	**p-value**
Communal, small streams					
Nutrient cycling + damage response	0.02	0.02	0.39	52.52 (1,81)	2.24e-10
Nutrient cycling + water stress response	0.04	0.03	0.48	76.81	2.33e-13
Food provision + damage response	0.02	0.03	0.42	60.68	1.95e-11
Food provision + water stress response	0.02	0.05	0.61	131.47	<2e-16
Shade provision + damage response	0.01	0.03	0.45	69.19	1.77e-12
Shade provision + water stress response	0.05	0.03	0.35	45.24	2.27e-09
Fuelwood provision + damage response	0.05	0.01 ^{NS}	0.02	2.52	0.116
Fuelwood provision + water stress response	0.02	0.02	0.39	53.85	1.49e-10
Kruger, small streams					
Nutrient cycling + damage response	0.02	0.02	0.36	43.2 (1,74)	6.09e-09
Nutrient cycling + water stress response	0.06	0.03	0.32	37.05	4.69e-08
Food provision + damage response	0.01	0.03	0.47	67.38	5.22e-12
Food provision + water stress response	0.02	0.05	0.53	85.44	5.78e-14
Shade provision + damage response	0.02	0.03	0.34	38.92	2.49e-08
Shade provision + water stress response	0.04	0.03	0.27	29.43	7e-07
Fuelwood provision + damage response	0.05	0.01	0.04	3.85	0.0536
Fuelwood provision + water stress response	0.03	0.02	0.44	59.17	4.94e-11
Sabi–Sand, small streams					
Nutrient cycling + damage response	0.04	0.01	0.11	8.21 (1,59)	0.00578
Nutrient cycling + water stress response	0.07	0.03	0.21	17.24	0.000107
Food provision + damage response	0.01	0.03	0.46	52.41	1.06e-09
Food provision + water stress response	0.02	0.05	0.49	59.13	1.83e-10
Shade provision + damage response	0.03	0.02	0.44	48.25	3.33e-09
Shade provision + water stress response	0.06	0.02	0.3	26.4	3.29e-06
Fuelwood provision + damage response	0.06	0.01 ^{NS}	0.01	1.71	0.196
Fuelwood provision + water stress response	0.02	0.02	0.53	69.34	1.53e-11
Communal, main river					
Nutrient cycling + damage response	0.02	0.02	0.34	32.01 (1,59)	4.75e-07
Nutrient cycling + water stress response	0.05	0.05	0.54	72.42	7.56e-12
Food provision + damage response	0.02	0.03	0.5	60.56	1.28e-10
Food provision + water stress response	0.03	0.07	0.67	123.08	4.56e-16
Shade provision + damage response	0.03	0.02	0.32	29.44	1.13e-06
Shade provision + water stress response	0.04	0.05	0.58	83.97	6.11e-13
Fuelwood provision + damage response	0.06	0.01 ^{NS}	0	0.95	0.333
Fuelwood provision + water stress response	0.01	0.04	0.48	56.73	3.39e-10
Kruger, main river					
Nutrient cycling + damage response	0.02	0.02	0.4	48.65 (1,70)	1.39e-09
Nutrient cycling + water stress response	0.04	0.04	0.63	119.99	<2e-16
Food provision + damage response	0.01	0.03	0.53	81.33	2.45e-13
Food provision + water stress response	0.03	0.06	0.58	97.22	7.15e-15
Shade provision + damage response	0.03	0.02	0.28	27.96	1.34e-06
Shade provision + water stress response	0.03	0.04	0.49	70	3.86e-12
Fuelwood provision + damage response	0.06	0.01	0.03	3.07	0.0842
Fuelwood provision + water stress response	0.01	0.03	0.71	173.12	<2e-16
Sabi–Sand, main river					
Nutrient cycling + damage response	0.03	0.01	0.31	39.16 (1,85)	1.52e-08
Nutrient cycling + water stress response	0.06	0.03	0.46	73.39	4.07e-13
Food provision + damage response	0.01	0.03	0.4	58.66	2.74e-11
Food provision + water stress response	0.02	0.06	0.65	159.92	<2e-16
Shade provision + damage response	0.02	0.02	0.39	56.79	4.82e-11
Shade provision + water stress response	0.05	0.03	0.34	45.83	1.57e-09
Fuelwood provision + damage response	0.04	0.01	0.1	10.78	0.00149
Fuelwood provision + water stress response	0.03	0.02	0.34	45.09	2e-09

Table 3.12: Ordinary linear regression coefficients for regressions of response disparity on log redundancy, for various combinations of effect and response functions (herbaceous species). Regression equations are of the form $y = a + b\log(x)$. All intercepts and slopes were significant ($P \leq 0.05$).

	Intercept	**Slope**	**R^2**	**F(df)**	**p-value**
Communal, small streams					
Nutrient cycling + damage response	0.03	0.02	0.36	90.15 (1,157)	<2e-16
Nutrient cycling + water stress response	0.03	0.03	0.44	125.05	<2e-16
Food provision + damage response	0.02	0.04	0.63	265.76	<2e-16
Food provision + water stress response	0.02	0.03	0.53	178.79	<2e-16
Kruger, small streams					
Nutrient cycling + damage response	0.04	0.02	0.19	33.85 (1,138)	3.97e-08
Nutrient cycling + water stress response	0.03	0.02	0.54	165.14	<2e-16
Food provision + damage response	0.02	0.04	0.67	277.23	<2e-16
Food provision + water stress response	0.02	0.03	0.51	145.52	<2e-16
Sabi–Sand, small streams					
Nutrient cycling + damage response	0.03	0.02	0.47	127.77 (1,141)	<2e-16
Nutrient cycling + water stress response	0.04	0.02	0.39	92.77	<2e-16
Food provision + damage response	0.02	0.04	0.51	149.91	<2e-16
Food provision + water stress response	0.01	0.03	0.46	123.51	<2e-16
Communal, main river					
Nutrient cycling + damage response	0.04	0.02	0.29	53.82 (1,128)	2.23e-11
Nutrient cycling + water stress response	0.04	0.03	0.44	102.85	<2e-16
Food provision + damage response	0.02	0.05	0.75	394.76	<2e-16
Food provision + water stress response	0.01	0.04	0.75	388.78	<2e-16
Kruger, main river					
Nutrient cycling + damage response	0.03	0.02	0.34	70.97 (1,136)	4.57e-14
Nutrient cycling + water stress response	0.03	0.03	0.58	192.6	<2e-16
Food provision + damage response	0.02	0.05	0.65	261.08	<2e-16
Food provision + water stress response	0.01	0.04	0.61	216.38	<2e-16
Sabi–Sand, main river					
Nutrient cycling + damage response	0.04	0.02	0.21	41.98 (1,153)	1.2e-09
Nutrient cycling + water stress response	0.04	0.03	0.43	115.36	<2e-16
Food provision + damage response	0.02	0.05	0.66	294.38	<2e-16
Food provision + water stress response	0.01	0.03	0.63	265.46	<2e-16

Table 3.13: Results of perMANOVA showing the effects of management area and stream size and their interaction on the distribution of response disparity values among species in woody assemblages (each function treated as a separate variable; functions included were nutrient cycling, food provision, shade provision and fuelwood provision).

	Df	SS	MeanSq	F.Model	R^2	Pr($> F$)
ManagementArea	2	0	0.02	1.2153	0.005	0.261
StreamSize	1	0	0.07	4.1374	0.009	0.006 **
ManagementArea:StreamSize	2	0	0.01	0.6971	0.003	0.725
Residuals	434	7	0.02		0.982	
Total	439	7			1	

Table 3.14: Results of perMANOVA showing the effects of management area and stream size and their interaction on the distribution of response disparity values among species in herbaceous assemblages (each function treated as a separate variable; functions included were nutrient cycling and food provision).

	Df	SS	MeanSq	F.Model	R^2	Pr($> F$)
ManagementArea	2	0	0.01	1.2352	0.003	0.258
StreamSize	1	0	0.01	1.2667	0.001	0.269
ManagementArea:StreamSize	2	0	0.01	0.8741	0.002	0.485
Residuals	859	8	0.01		0.994	
Total	864	8			1	

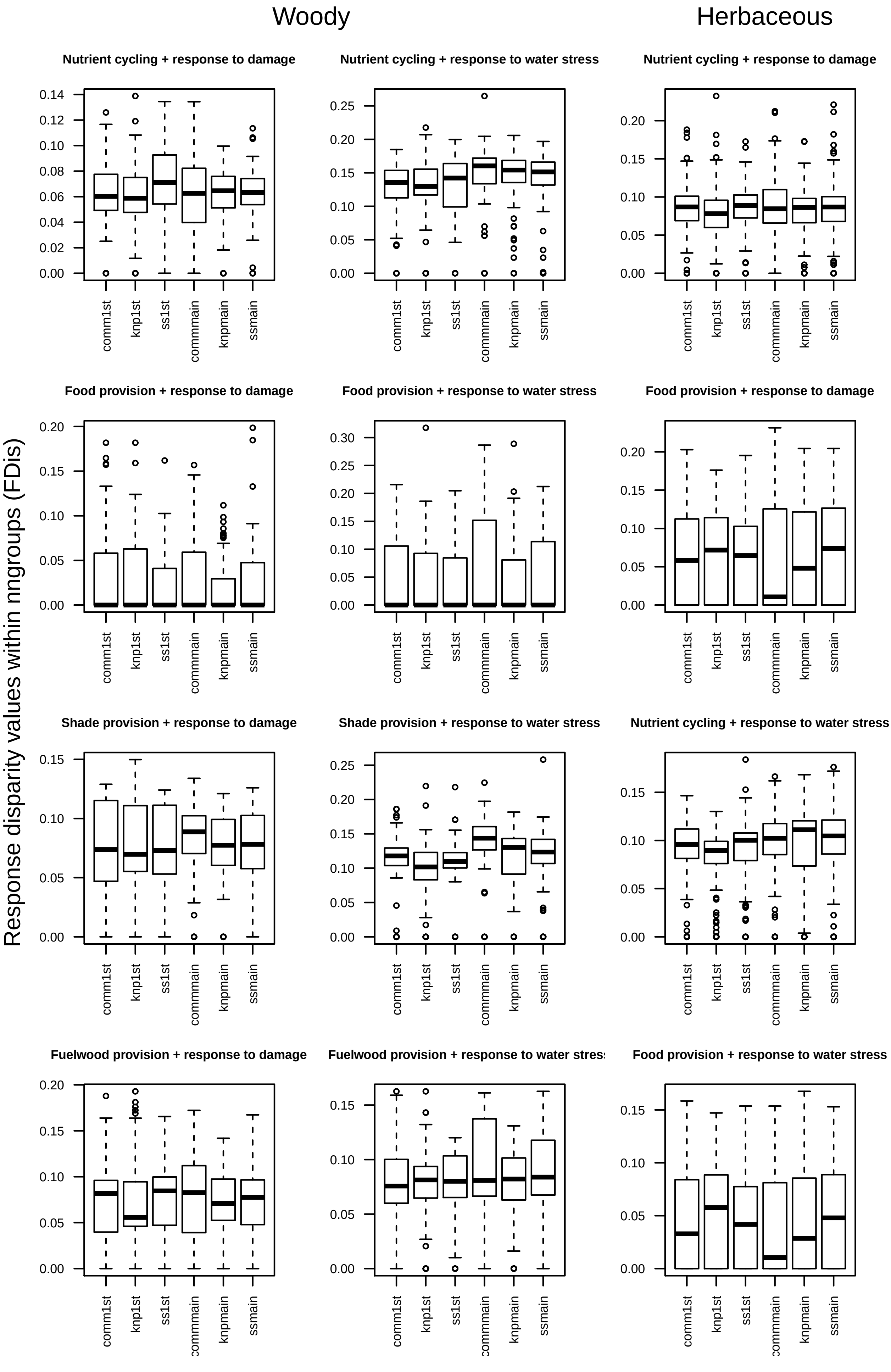


Figure 3.13: Boxplots showing the distribution of response disparity values within the nngroups for various effect functions, in assemblages from the different management areas. For example, the top left plot shows the distribution of response disparity values within groups of species with similar nutrient cycling traits.

Table 3.15: Frequency with which differences in abundance between management areas were either consistent with or not consistent with functional compensation, together with the results of χ^2 goodness–of–fit tests (H_0 = no difference in frequency between cases showing evidence of compensation and cases showing no evidence of compensation). Sample sizes were n = 21 species for woody assemblages from the small streams, n = 25 for woody assemblages from the main river, n = 16 for herbaceous assemblages from the small streams and n = 14 for herbaceous assemblages from the main river.

	Woody assemblages		**Herbaceous assemblages**	
Small streams				
Nutrient cycling	Comp: 11 cases	$\chi^2 = 0.2$	Comp: 7 cases	$\chi^2 = 0.25$
	No comp: 9 cases	$p = 0.83$	No comp: 9 cases	$p = 0.8$
Food provision	Comp: 7 cases	$\chi^2 = 2.33$	Comp: 6 cases	$\chi^2 = 1.47$
	No comp: 14 cases	$p = 0.2$	No comp: 11 cases	$p = 0.33$
Shade provision	Comp: 11 cases	$\chi^2 = 0.05$	–	–
	No comp: 10 cases	$p = 1$	–	–
Fuelwood provision	Comp: 10 cases	$\chi^2 = 0$	–	–
	No comp: 10 cases	$p = 1$	–	–
Main river				
Nutrient cycling	Comp: 11 cases	$\chi^2 = 0.36$	Comp: 4 cases	$\chi^2 = 1.92$
	No comp: 14 cases	$p = 0.69$	No comp: 9 cases	$p = 0.27$
Food provision	Comp: 8 cases	$\chi^2 = 3.24$	Comp: 7 cases	$\chi^2 = 0$
	No comp: 17 cases	$p = 0.1$	No comp: 7 cases	$p = 1$
Shade provision	Comp: 14 cases	$\chi^2 = 0.36$	–	–
	No comp: 11 cases	$p = 0.69$	–	–
Fuelwood provision	Comp: 8 cases	$\chi^2 = 3.24$	–	–
	No comp: 17 cases	$p = 0.12$	–	–

Redundancy and response disparity do not determine the level of functioning currently performed by an assemblage, but rather the potential to *maintain* whatever functioning is present; in other words, the resilience of the assemblage (Figure 1.4). Functional compensation was identified as one of the important ways in which redundancy and response disparity lead to resilience (§1.2.6). Functional compensation occurs when one or more species are able to continue performing a particular function, if the species originally performing that function are no longer able to do so. This can be achieved through changes in the balance of the assemblage, for example when tail species increase in abundance to compensate for a decrease in the abundance of a dominant species (§1.2.6).

The fact that both redundancy and response disparity were present in the riparian assemblages studied here, for most species and functions, means that the kind of functional compensation described by Walker *et al.* (1999) is certainly possible in these assemblages. In the following section, I will evaluate the evidence for such compensatory changes in abundance.

3.3.3 Evidence of functional compensation in riparian assemblages

Direct evidence for functional compensation can only be obtained by recording changes in species abundances, and functioning, over time. This was not done here. Indirect evidence for functional compensation can be obtained by comparing species abundances in assemblages from different areas. Where a dominant species in one assemblage is much less abundant in another assemblage, an increase in functionally similar minor species in the second assemblage provides indirect evidence that functional compensation has occurred.

A number of core species showed large differences in abundance between the three different management areas (21 woody and 16 herbaceous species from assemblages along the small streams, and 25 woody and 14 herbaceous species from assemblages along the main river). For each of these 76 core species, I sought evidence of compensation by comparing the abundances of the species providing redundancy for these core species in the different assemblages.

Differences in abundance consistent with compensation occurred in about 50% of cases (Table 3.15). In the other 50%, the differences were either difficult to interpret (some species increased but others decreased, making the net effect unclear) or were not consistent with compensation (similar species decreased or showed no change, or no similar species were present). Chi–squared goodness–of–fit tests indicated that compensation–like and non–compensation–like patterns occurred with approximately equal frequency for all functions (Table 3.15).

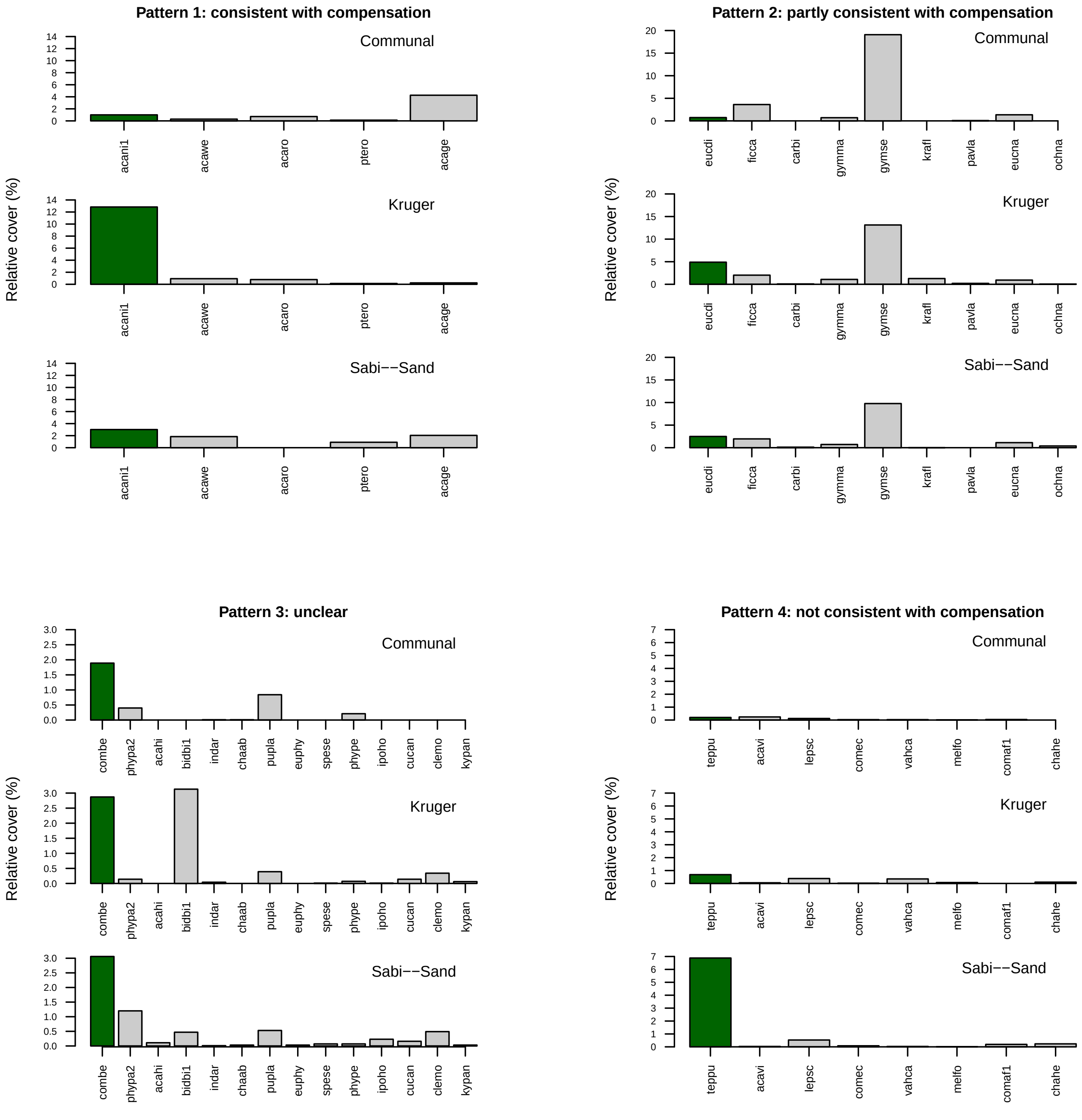


Figure 3.14: Representative examples of the four patterns of abundance differences between management areas, showing differences consistent with the occurrence of compensation (pattern 1), differences partly consistent with compensation (pattern 2), differences where the pattern is unclear (pattern 3), and differences not consistent with compensation (pattern 4). For the Chi–squared tests in Table 3.15, patterns 1 and 2 were combined to form a group generally showing compensation, and patterns 3 and 4 were combined to form a group generally not showing compensation. The core species and functions involved in the examples shown are as follows. Pattern 1: *Acacia nigrescens*, small streams, nutrient cycling; pattern 2: *Euclea divinorum*, main river, shade provision; pattern 3: *Commelina benghalensis*, main river, food provision; pattern 4: *Tephrosia purpurea*, small streams, food provision. The core species in each case is indicated in green, the species providing redundancy for the core species' functioning in grey.

Representative examples of the different patterns are shown in Figure 3.14. *Acacia nigrescens* in assemblages from the small streams showed a pattern consistent with compensation (pattern 1). This species was a dominant nitrogen–fixing tree along small streams in the Kruger National Park, with a relative cover of 12.8%, but had much lower cover values in Sabi–Sand and the communal area (3% and 1% respectively). In the latter two areas, the similar species *Acacia gerrardii* and *Acacia welwitschii* were more abundant than they were in Kruger (cover of *A. gerrardii* nine times higher in Sabi–Sand and 19 times higher in the communal area, where it was a core species), suggesting that these species may have been compensating for the reduced cover of *A. nigrescens* (Figure 3.14).

In some cases the differences in abundance were consistent with compensation in one management area but not in another (pattern 2). In the example in Figure 3.14, *Euclea divinorum* had a higher abundance in the Kruger National Park than in Sabi–Sand or the communal area. In the communal area, *Gymnosporia senegalensis* and *Ficus capreifolia* showed increased abundances, suggesting compensation. In Sabi–Sand, however, both *Gymnosporia senegalensis* and *Ficus capreifolia* were less abundant than they were in the Kruger National Park, suggesting that compensation did not occur.

Commelina benghalensis in the main river assemblages was an example of an unclear pattern (pattern 3). This annual forb species was more abundant in the reserves (relative cover of 3.1% in Sabi–Sand and 2.9% in Kruger) than in the communal area (1.9%). A number of other species had similar food provision characteristics to *Commelina benghalensis* and hence provided redundancy for this function. Two of these species had increased abundances in the communal area (*Phyllanthus pentandrus* and *Pupalia lappacea*), while another was less abundant (*Phyllanthus parvulus*). In Kruger, one species (*Bidens bipinnata*) had seven times greater cover than in Sabi–Sand, but the rest of the similar species showed reduced cover (Figure 3.14). In cases like this it is difficult to decide whether the differences were suggestive of compensation or not.

Finally, there were many cases where the differences in abundance were clearly not consistent with functional compensation (pattern 4). *Tephrosia purpurea* in assemblages from the small streams provided an example of this pattern. The much lower cover of this forb species in the Kruger and communal assemblages was not accompanied by increases in cover of any of the species that performed the food provision function similarly (Figure 3.14).

The fact that species similar in a particular effect function may be quite different in other functions, including response functions (§3.3.2), has important consequences for functional compensation. The species that provide redundancy for each species' functioning are seldom functional analogues and therefore do not simply act as 'drop–in replacements'. Functional compensation via changes in the balance of an assemblage will therefore usually be associated with many 'knock–on' effects, as the compensating species bring a new mix of traits to the fore. Compensation for one function may lead to many distributed changes in other functions, as well as to changes in the contributions of species to redundancy and changes in interspecific interactions.

For example, all the species providing redundancy for the food provision functioning of *Commelina benghalensis* (Figure 3.14) were rather different in their responses to damage (none were able to spread clonally from fragments, unlike *Commelina benghalensis*). Several also differed in their responses to water stress and their contributions to nutrient cycling. For example, *Indigofera arrecta* was very dissimilar to *Commelina benghalensis* in damage response, water stress response and nutrient cycling (pairwise dissimilarities of 0.5, 0.25 and 0.35 respectively), and *Pupalia lappacea* had a dissimilarity to *Commelina benghalensis* of 0.25 for damage response and 0.16 for nutrient cycling. This means that if any of the species similar to *Commelina benghalensis* in food provision were to increase in abundance as compensation for a decline in *Commelina benghalensis*, this would cause the response profile of the assemblage to change and possibly lead to changes in other functions.

The species able to compensate for the nutrient cycling functioning of *Acacia nigrescens* (Figure 3.14) were generally quite similar, because several of them were members of the same genus. However, *Acacia robusta* and *Albizia forbesii* had stronger riparian affinities than *Acacia nigrescens* and were therefore less tolerant of water stress. *Pterocarpus rotundifolius* differed from *Acacia nigrescens* in response to damage, response to water stress and also in food provision, being a spineless broad–leaved shrub rather than a fine–leaved spiny tree (pairwise dissimilarities of 0.15, 0.12 and 0.2 respectively). Decreases in the abundance of *Acacia nigrescens* and compensatory increases in the abundance of these other species would therefore be expected to lead to various changes in the response characteristics and the food provision characteristics of these assemblages. Further examples of how differences in species composition and balance among management areas can affect redundancy and compensation potential will be given in Chapter 4.

It is important to note that there are many reasons why species abundances may vary in space and in time, and not all differences in abundance are evidence of functional compensation. However, the results of this study do show that where sufficient redundancy exists for a particular function, compensation is indeed possible. Indirect evidence for compensation was found in about half the cases examined. The fact that species similar in one function were generally not similar in other functions suggests that compensation does not involve simple substitution of one species for another, and compensatory changes in abundance which allow one function to be maintained may lead to distributed changes in several other functions.

3.4 Discussion

This study has produced some of the first empirical evidence for the existence of both functional redundancy and response disparity in real, species–rich plant assemblages. Redundancy was present in the form originally proposed by Walker (1992, 1995), as backup or excess functional capacity provided by a number of *non–identical* species, most of which made up the tail of the abundance distribution. Different sets of species provided redundancy for the different functions performed by each member of the assemblage. The amount of redundancy measured (Figure 3.6) was lower than that reported by Laliberté *et al.* (2010) for plant assemblages (8.7–63 species per functional group, with a mean of 31.1 across 18 different studies). These authors measured redundancy as the mean number of species within the functional groups present in an assemblage, rather than as the number of species similar to each species individually. I have shown in Chapter 2 that using functional groups in fact underestimates the amount of redundancy associated with each species, suggesting that the species–level redundancy values in the assemblages described by Laliberté *et al.* (2010) would in fact be even higher. However, the use of functional groups to measure redundancy has several problems, including the difficulties involved in deciding how the groups should be formed (Chapter 2). It is therefore not possible to make direct comparisons with these results.

Species providing redundancy for a particular function differed in their response traits, as well as in many effect traits, and functional analogues (species identical in all measured traits) were relatively rare. This has important implications for ecosystem ‘multifunctionality’, or the ability of an assemblage to perform multiple functions simultaneously (Gamfeldt *et al.*, 2008). If redundancy occurred in the form of identical analogue species, the number of functions performed by an assemblage would increase with the number of species, but it would be a saturating function because the analogues would not add any new functionality. Few studies of multifunctionality in real ecosystems have been published, but some very recent studies have shown that the relationship between multifunctionality and the number of species does not saturate, because each species contributes a unique set of functions (Gamfeldt *et al.*, 2008; Isbell *et al.*, 2011; Mouillot *et al.*, 2011). Species may be similar to other species in some aspects of their functioning, but if all traits are considered together, each species contributes something unique. Each species therefore contributes simultaneously to redundancy and disparity in the assemblage.

The partial functional overlap among species, where species were similar in some functions but different in others, also has important implications for understanding change and resilience in species assemblages. The presence of redundancy makes functional compensation possible, and some evidence of functional compensation was found in the riparian assemblages. However, the non–identical nature of the species involved means that any compensatory increases in species abundances will have many ‘knock–on’ effects, because the new species will differ in their responses to disturbance as well as many other aspects of functioning. Compensatory changes in species abundances are therefore likely to involve many species, and to be complex and difficult to detect, especially at larger spatial scales when many species are involved (as found by Walker and Langridge, 2002; Winfree and Kremen, 2009, and in many succession experiments).

It is therefore important for an assemblage to have a sufficient variety of ‘options’ (species and their traits), to accommodate all the necessary adjustments involved in functional compensation. The idea that a certain amount of variety is necessary to allow a system to maintain particular desirable outcomes (e.g. maintenance of important functions) when faced with various disturbances, is encapsulated in the law of requisite variety from the field of cybernetics (Ashby, 1958). This law states that the number of different responses available must at least be greater than the number of different disturbances experienced by the system. The response disparity among species providing redundancy for a particular function increases the number of possible responses to a particular disturbance.

The relationship between redundancy and response disparity was shown to be positive in this study for individual species, although the relationship had low predictive power and was not reflected at the assemblage level. Laliberté *et al.* (2010) also found a positive association between redundancy and response disparity in 14 of the 18 studies they considered in their meta–analysis. The positive relationship between these two aspects of resilience shows that redundancy does not necessarily occur at the expense of disparity in species assemblages, because when redundancy increases, disparity tends to increase, and vice versa. Redundancy should not therefore be seen as an undesirable property that reduces the amount of disparity present (see Chapter 1).

The nature of the relationship between redundancy and response disparity suggests that sampling effects are important, as was also suggested by Laliberté *et al.* (2010). As the number of similar species (redundancy) increases, the chance of including some with unusual traits also increases, assuming that the species are chosen randomly and are sufficiently dissimilar to each other (Huston, 1997). Sampling effects have been much discussed in relation to the construction of artificial assemblages for experimental studies of the relationship between biodiversity and ecosystem functioning (Aarssen, 1997; Wardle, 1999; Lepš *et al.*, 2001), but their importance in resilience has not previously been recognised. The relationship between redundancy and disparity will be discussed further in Chapter 5 in the context of complex systems.

The low predictive power of the relationship between redundancy and response disparity also suggests strong idiosyncratic effects, where changes in the the number of species present and their abundances can have different effects depending on the identities of the species involved. This makes response disparity a difficult property to summarise adequately. The measure I have used here, multivariate dispersion within groups of species with similar effect traits, is essentially a measure of variance, which is more appropriate than a measure of central tendency (Chapter 2). However, response disparity is only valuable in an assemblage if one or more species with the 'right' response traits for a particular situation are present. Having a large number of species from which to 'choose' (redundancy) helps, as does having a large variety of different response traits (response disparity), but there is no guarantee that functioning will be maintained even with high redundancy and response disparity.

There are some interesting parallels between the patterns of redundancy, response disparity and compensation described in this study and those observed in genetic and molecular biological systems. Genetic redundancy, the existence of multiple copies of genes that can perform a particular function similarly, is common in many different organisms. The genomes of many organisms contain multiple duplicate genes, which arise from recombination, DNA–repair processes or whole–genome duplication events (Pickett and Meeks-Wagner, 1995). These duplicates are, however, seldom identical. They may start out as identical but over time tend to diverge as the copies acquire new functions (Edelman and Gally, 2001; Wagner, 2005; Crow and Wagner, 2006; Vavouri *et al.*, 2003). While identical duplicates tend to be lost, duplicates that acquire new functions while still maintaining partial similarity with the original gene are retained stably over long periods (Vavouri *et al.*, 2003). Interestingly, many of the new functions acquired by duplicate genes involve specialisations in their substrate preferences, localisation or mode of expression (Vavouri *et al.*, 2003). These specialisations result in differences in the environmental preferences/tolerances or in the timing of the functioning of duplicate genes, which is analogous to response disparity in species assemblages.

Functional compensation has been more extensively studied in genetics and molecular biology than in ecology, because of the possibility of experimentally silencing particular genes and observing the effects on functioning. Several gene deletion studies have provided evidence for compensation by partially similar duplicate genes (Pickett and Meeks-Wagner, 1995; Gu *et al.*, 2003; Conant and Wagner, 2003). When genes with redundancy are deleted, the effect is less likely to be lethal than when single–copy genes with no redundancy are deleted. Also, genes with redundancy are more likely to have no effect on functioning when removed. The more similar two duplicates are, the less severe the effect is of silencing one of them, suggesting that compensation by the remaining gene mitigates the effect of the deletion (Gu *et al.*, 2003; Conant and Wagner, 2003).

Other evidence suggests that genes with more redundancy (larger number of duplicates) evolve faster, implying that they can tolerate more mutations (Conant and Wagner, 2002), and the functions they perform are more resilient. Polyploidy (which increases the amount of redundancy in a genome) often enhances the ability of plant populations to survive in variable environments or to extend their ecological range (Taylor and Raes, 2004). Gene products that must interact with the external environment tend to have more redundancy than those that are localised in intracellular compartments, again suggesting that redundancy and response disparity are important in allowing the system to 'handle' variability (Liang and Li, 2007).

Genetic networks and species assemblages therefore have in common highly distributed functioning (many entities able to perform the same function similarly) and partial functional overlap (entities similar in some functions but not others; this is known as 'degeneracy' in genetics). Redundancy and response disparity appear to act in similar ways in these different systems to make functional compensation possible and allow functioning to be maintained despite disturbance. It is possible that this is a very general pattern common to self–organized complex systems (to be discussed further in Chapter 5).

The riparian assemblages studied here also have another feature in common with molecular/genetic systems: the presence of a number of entities that lack redundancy (Wagner, 2005; Liang and Li, 2007). Some of these entities may be important for the identity and/or functioning of the system, and targeted removal of these 'weak points' can cause dramatic changes in system functioning, possibly leading to regime shifts as has already been discussed (Hughes, 1994; Brose *et al.*, 2005; Nyström, 2006; Douek *et al.*, 2002). However, this is not always the case. Often even entities with no redundancy can be removed from a system with no apparent effect on functioning. Thousands of genes whose deletion has no detectable effect are single-copy genes with no duplicates in the genome (Wagner, 2005). Functional compensation of the type described so far, namely the full or partial replacement of one entity by a similar entity, is not possible in these instances. This suggests that there are other mechanisms by which functional compensation can be achieved in complex systems.

Researchers working on molecular networks and ecological interaction networks such as food webs have suggested that even if none of the individual components of a network (genes, molecules, species etc.) are functionally similar, redundancy may still be present in the form of alternative network pathways by which the same function may be performed (Wagner, 2005). A simple example is the switching of predators between alternative prey species in food webs (Pimm, 2002). In the metabolic network responsible for respiration, removal of enzymes important for the production of NADPH can be compensated for by systemic reorganisations of metabolic flow in the network, allowing NADPH to be produced by a different route (Wagner, 2005). This type of redundancy has been called 'distributed robustness' (Wagner, 2005). The hallmark of distributed robustness is a systemic adjustment of network properties to compensate for a perturbed network part. It is equivalent to the 'many rules, one outcome' type of redundancy in the typology of Low *et al.* (2003) (§1.2.4).

Whitacre and Bender (2010) have recently highlighted another important dimension to distributed robustness: the ability of the entities in a network to modify their functional roles or the amount or rate of their functioning, depending on the context (functional plasticity). Context here includes the internal states of the entity and the demands or constraints placed on it by its environment and by other entities. Whitacre and Bender (2010) show that functional plasticity, together with partial functional overlap between entities such as that described between the species in my study, make the number of potential reconfiguration options in a network very large. Their concept of 'networked buffering' explains how redundancy ('excess resources') for one type of function can indirectly support many unrelated functions, via a series of partial functional overlaps. The loss of a particular network component can be compensated for via a number of different pathways, in a highly distributed manner, through many (often small) context–induced changes in functioning. Context–specific functioning indeed seems ubiquitous in ecological systems (Mills *et al.*, 1993), but its implications for resilience have as yet been little explored by ecologists (but see Wellnitz and Poff, 2001; Poff *et al.*, 2003).

In this study, function was assumed to be 'fixed' for a given species. Adding functional plasticity to the patterns of redundancy and response disparity described here would simply increase even further the number of possible ways functions may be apportioned among the species. The members of the nngroups for each function would vary with context, creating even more possible sources of redundancy and therefore, possible ways for compensation to be achieved. In other words, the fact that the functioning of species almost certainly can vary with context does not detract from the results of this study. The distributed type of functional compensation described as 'distributed robustness' or 'networked buffering' arise from the same patterns of distributed functioning and partial functional overlap that give rise to the more direct type of compensation described in this study. This more distributed type of resilience is not yet well understood, but provides an intriguing direction for future research.

Interestingly, some of the important species with low redundancy for particular functions in this study are known to have high developmental or functional plasticity or to have flexible life histories that promote persistence. For example, *Phragmites* reeds have a high physiological tolerance for waterlogging, anoxia and burial, and the extensive rhizome system and clonal growth form makes them tolerant of physical damage, browsing, fire and mowing (Armstrong and Armstrong, 1990; Gries *et al.*, 1990; Pagter *et al.*, 2005; Kotschy and Rogers, 2008), to the point that *Phragmites* species can be very difficult to eradicate (Chambers *et al.*, 1999; Gusewell *et al.*, 2000). Species such as *Gymnosporia senegalensis*, *Phoenix reclinata*, *Diospyros mespiliformis*, *Breonadia salicina* and *Grewia flavescens* all have good resprouting abilities which help them to persist after various types of damage such as fire, herbivory, harvesting and flood damage (Kotschy et al., in prep.). These kinds of life history factors represent another means of achieving functional compensation; where the compensation is due to changes in the behaviour or functioning of the species affected by the disturbance and does not involve other species.

A third way in which compensation can be achieved, besides through distributed robustness and flexible life histories, is through spatial heterogeneity. Spatial heterogeneity can prevent regime shifts (van Nes and Scheffer, 2005), for example when patches unaffected by a particular disturbance serve as sources of ‘ecological memory’, facilitating recovery of nearby affected patches (Turner *et al.*, 1999; Nyström and Folke, 2001; Parsons *et al.*, 2005). Spatial resilience refers to the ways in which spatial heterogeneity in relevant variables influences system resilience across multiple spatial and temporal scales (Cumming, 2011). It therefore represents another way that resilience can arise in ecosystems besides via redundancy and features of the biota.

On the whole the riparian assemblages in the Sand River catchment were resilient, in the sense that many similar species were present that could potentially compensate should any of the core species decline or be lost. Response disparity was also present in all the assemblages and for all the functions considered. However, some effects of land management practices on resilience were detected.

Assemblages in the different management areas differed in redundancy but not in response disparity. Along the main river, riparian assemblages were less resilient in the communal rangeland adjacent to the conservation areas than in the conservation areas themselves. This finding was in keeping with expectations and with the current River Health Programme classification (Ballance *et al.*, 2001). Since the main river sites in the three management areas were all on the same river, the differences in resilience cannot be explained by impacts occurring upstream of the study sites (forestry, commercial agriculture and urban development; see Figure 3.1). If impacts from these activities were merely lessened with distance downstream, assemblages in the Kruger National Park should have the highest resilience, whereas in fact assemblages from Sabi–Sand had the highest resilience. The most likely cause of differences between areas is the management practices in each area that directly impact the riparian vegetation along the main river. In the communal area these include the practice of clearing land adjacent to the riparian zone for agriculture, and the harvesting of riparian species for fuelwood or medicine. Both these practices may reduce the potential for regeneration of riparian species and cause species losses. It was, however, beyond the scope of this study to develop statistical relationships between particular management practices and resilience.

The fact that resilience in assemblages from the main river was lowest in the area most impacted by human activities (the communal rangeland area) supports the findings of Fischer *et al.* (2007) and Laliberté *et al.* (2010), who both found a negative relationship between land use ‘intensification’ (human modification of the landscape) and measures of resilience. However, as in my study, there was a large amount of scatter about the regression lines, and redundancy and/or response disparity sometimes increased in response to land–use intensification (Laliberté *et al.*, 2010).

The complexity of the relationship between land use or land management practices and resilience is well illustrated by the differences between the plant assemblages from the main river and the small streams in this study. Contrary to the negative impact of human activity on assemblages from the main river, assemblages from the small catchments in the communal area (with the most intense human impacts) did not have less resilience than the presumably more ‘natural’ assemblages in the reserves. This was not expected. Possibly the larger–scale and more varied impacts in the main Sand River catchment had a more severe impact on resilience than the more local impacts experienced in the small catchments. These findings indicate that changes in land cover, land use and management practices cannot universally be assumed to have a negative impact on resilience.

So how should empirical findings about resilience, such as those described in this chapter, be used to inform conservation and land management policies and practices? This will be the subject of the following chapter.

Chapter 4

Using resilience measures to inform conservation and land management

4.1 Introduction

Resilience is not only of theoretical interest; it is of critical interest to those tasked with conserving and managing ecosystems and ecosystem services. The accelerating worldwide loss of biodiversity (Dirzo and Raven, 2003) and the growing recognition of the inadequacy of species–centric approaches to conservation (Moss, 2000; Scott *et al.*, 2005) have led to the emergence of ecosystem–based approaches to conservation and land management in the last two decades (Walker, 1992; Grumbine, 1994; Walker, 1995; Christensen *et al.*, 1996; Arkema *et al.*, 2006; Chapin *et al.*, 2009a; Hopkins *et al.*, 2011). Ecosystem–based management (EBM), also known as ecosystem stewardship or 'the ecosystem approach', emphasises the protection of key ecological structures, functions and processes rather than particular species, and as such represents a fundamental departure from species–centric approaches to conservation. The concept of resilience is of central importance in EBM (Fischer *et al.*, 2006; Walker and Salt, 2006; Chapin *et al.*, 2009a), because resilience underpins the ability of ecosystems to maintain components, functions and interactions over time, allowing continued provision of ecosystem services in the face of increasing human pressure and an uncertain future (Cumming and Collier, 2005). EBM focuses on maintaining or promoting the resilience of desirable system attributes rather than developing a single 'optimal' management strategy (Walker and Salt, 2006). This is seen to be more appropriate in complex systems, where reductionist scientific methods are not always useful in solving complex environmental problems or making predictions for the future (Cilliers, 1998; Levin, 1999; Norberg and Cumming, 2008; Ulanowicz *et al.*, 2009).

Despite the theoretical appeal of the EBM approach, there are significant difficulties with its implementation (Arkema *et al.*, 2006; Tallis and Polasky, 2009). Many of these are related to social, economic and institutional issues that influence how humans interact with ecological systems (Ostrom, 1990; Folke *et al.*, 2005; Roux and Foxcroft, 2011; Biggs *et al.*, 2012). For example, the existence of multiple stakeholders with different perceptions, values and expectations often makes it difficult to reach consensus on what a system should look like or how it should function (Rogers and Biggs, 1999; Davis and Slobodkin, 2004; Venter *et al.*, 2008). Frameworks for ecosystem management increasingly recognise that defining what is considered 'healthy' for an ecosystem is inherently a subjective process informed by human needs, wants and perceptions, and such frameworks include consensus–building and 'visioning' processes involving the stakeholders who use and manage the system, to make these preferences explicit (Rogers and Biggs, 1999; Waltner-Toews and Kay, 2005; Venter *et al.*, 2008; Hopkins *et al.*, 2011). On the basis of the identified preferences, 'desired states' or desired ranges of variation or functioning can be identified, within which system change is considered acceptable (Rogers and Biggs, 1999).

Apart from these more socially–based issues, there are also significant difficulties with relating features of ecosystems observed 'on the ground' to the goal of EBM, namely to produce or maintain 'healthy' ecosystems that perform the required functions sustainably. Ecosystem managers are faced with a dilemma: they need to be able to judge whether a system is functioning 'healthily' or is 'sufficiently' resilient, and whether observed changes are cause for concern or not, yet it is unclear what should be measured to inform such decisions (Figure 4.1).

The difficulties in knowing what to measure are, ironically, caused by the same complexity that made an ecosystem–based approach to management necessary in the first place. The large number of entities (e.g. species) and interactions present in even the simplest ecosystem makes the number of possible

Figure 4.1: The ecosystem manager's dilemma.

configurations or states in which the system can exist, and the number of possible ways the system can change, almost infinite (Ulanowicz *et al.*, 2009). Implementing EBM requires scientists and managers to have some way of judging which of these states and which of these changes are relevant to the desired states or functions and their resilience. However, in complex systems, causal relationships are difficult to determine. Non–linear interactions and feedbacks between components give the system a degree of unpredictability, and the presence of many simultaneous non–linear interactions makes it practically impossible to keep track of all the causal relationships between components (Levin, 1999; Cilliers, 2005). Something that appears unimportant now, may turn out to be vitally important later (Stirzaker *et al.*, 2010). In addition, present and future states are determined to some extent by the history of the system (Cilliers, 1998; Walker and Salt, 2006), further complicating attempts to understand causality. It is therefore extremely challenging, in a complex system, to find something to measure or monitor that is both relatively simple and practical to measure, and that provides information useful to managers seeking to evaluate the success of EBM programs.

A huge amount of attention has been focused on the manager's dilemma in the conservation and applied ecological literature, where the problem has mostly been phrased as 'how can one measure the health (integrity, condition) of ecosystems?' (Costanza *et al.*, 1992; Norris and Thoms, 1999; Karr, 1999). I will use the term 'integrity' rather than 'health' to avoid implying that ecosystems have a defined, evolved equilibrium state in the same way that individual organisms do. In contrast to organisms, ecosystems are much more open, loosely defined collections of entities with weaker evolutionary interactions, and as such have no objective state of 'health' (De Leo and Levin, 1997). 'Integrity' is a more pragmatic term, a measure of the intactness of particular processes or functions which have been deemed important or useful by humans (De Leo and Levin, 1997).

In the following section I will first critically review existing approaches to solving the manager's dilemma, before presenting a new approach which allows the resilience measures developed in this thesis to be integrated into assessments of ecosystem integrity. The value of this new approach will then be demonstrated using data from the riparian ecosystems described in the previous chapter.

4.1.1 Addressing the manager's dilemma

To solve the manager's dilemma, it is necessary to find a way of relating measurable features of the ecosystem to the 'integrity' of the ecosystem (in other words, to bridge the gap between left and right in Figure 4.1). As discussed above, this is difficult to achieve because of the complexity of both social and ecological systems, and the large number of different criteria which may be used to measure the integrity of ecosystems. Attempts to bridge this gap tend to become very complicated and technical, with the drawback that the results become increasingly difficult to communicate effectively to the managers who must use them to make decisions. Interestingly, similar problems are faced in the insurance/financial services sector, where management decisions and strategies rely heavily on highly technical data such as those generated by risk analysis models (International Association of Insurance Supervisors, 2012). Even if the risk analysis models generate valid data, a failure to communicate these data effectively to decision–makers can cause a company to mismanage its risk, thereby compromising its resilience (Stulz, 2009).

In seeking solutions to the manager's dilemma in complex ecosystems, scientists need to find the appropriate balance between simplicity and detail to maximise the usefulness of their work to managers (Stirzaker *et al.*, 2010). The most common approach to finding the required simplicity has been to devise *indices*, which are perceived as a useful way of encapsulating the results of a set of detailed analyses (Reynoldson *et al.*, 1997; Boulton, 1999). These include taxonomic and functional diversity indices, and many different indices of ecosystem health or integrity (e.g. Karr, 1991; Costanza *et al.*, 1992; Mageau *et al.*, 1995; Meyer, 1997; Deegan *et al.*, 1997; Bunn *et al.*, 1999; Karr, 1999; Norris and Thoms, 1999, see

Figure 4.2). Indices usually provide output in the form of single numbers, which can easily be communicated to managers and other stakeholders. However, as I will show below, there are several problems with using indices to address the manager's dilemma.

Problems with using indices to measure ecosystem integrity

Most indices used as measures of ecosystem integrity require as input some kind of biodiversity data, under the assumption that diversity is important for ecosystem integrity (Chapter 1). As shown in Chapters 1 and 2, a large number of taxonomic and functional diversity indices have been proposed, based mostly on the variety and balance components of diversity. These indices, while relatively easy to calculate, are difficult to relate to the desired states or functions of the ecosystem in question (assuming that these have been defined), and are therefore limited in their usefulness to managers (Figure 4.2). For example, if a manager were to be presented with a set of numbers showing that the taxonomic (e.g. Shannon) diversity of a particular ecosystem had declined, he/she would have no basis for judging how this might affect the desired functioning defined for that system, short of simply assuming that a decrease in diversity is 'bad'. This lack of information would make it very difficult to plan appropriate management actions.

Many ecosystem integrity indices attempt to strengthen the link between what is measured and the desired functioning by including direct or indirect measures of ecological functioning (e.g. total respiration, functional composition) and also environmental variables (Allan, 2004). Multivariate or 'multimetric' indices combine many different aspects of diversity and ecological functioning, with the aim of providing a more holistic and/or useful measure of integrity (Karr and Chu, 1997; Roux, 1999). The South African River Health Programme uses several multimetric indices, including the Riparian Vegetation Index (RVI), Fish Assemblage Integrity Index (FAII) and Index of Habitat Integrity (IHI), which are then combined into an overall river health score (Roux, 1999; Kemper, 2001). The well–known SASS (South African Scoring System) index is another example of this type of index, based on the presence and abundance of selected invertebrate indicator taxa (Dickens and Graham, 2002). Similar indices used elsewhere in the world include the Index of Biotic Integrity (IBI Karr, 1991), RIVPACS (Wright, 1995) and AUSRIVAS (Norris and Hawkins, 2000).

I agree with the proponents of multimetric indices that including functional data is a good idea, because functional traits can often be related directly to the desired states or functions (Díaz *et al.*, 2007; de Bello *et al.*, 2010; Díaz *et al.*, 2011), as long as the functions are clearly specified and the traits used to represent those functions are carefully selected (§1.2.2). Using functional data can therefore strengthen the ability of managers to relate the results of monitoring programs to the goal of EBM (Figure 4.2). I also agree that measuring many different aspects of integrity is a good idea, because ecosystem integrity, like human health, can be seen from multiple different perspectives which may not be correlated with each other. For example, a person may have a healthy circulatory system yet be mentally ill. Similarly, an ecosystem may recycle nutrients efficiently but have little capacity to support livestock, or it may be resilient to one type of disturbance but not to another.

However, the practice of combining all these different perspectives or pieces of information into a single number (index) is problematic. The structure of an index, as a fixed formula into which data must be inserted, is not an ideal way to find the simplicity required to guide management actions in a complex system. The structure of an index suggests that there is only one way to combine the various aspects considered important, and specifies the scale and level of detail at which each component must be measured. As a result, a particular index may be a good indicator of the integrity of a system in the context for which it was developed, but it is not very flexible. If the context changes (for example, if what is considered desirable changes, or a completely unforeseen event occurs), the index may need to be reformulated because it may be difficult to 'go back' and ask new questions of the data. For example, the new situation may require the collection of different data, at a different scale or level of detail, and/or the relative weightings of the data used to calculate the index may need to be changed. Indices developed for a particular context are often not transferable to other contexts, which has led to a proliferation of indices tailor–made for particular types of ecosystems, regions or taxonomic groups (as is the case with river health indices based on the abundances of sensitive or indicator species of macroinvertebrates; Reynoldson *et al.*, 1997; Norris and Thoms, 1999). The inflexibility associated with indices is undesirable. We need to build as much flexibility as possible into the way we monitor and assess ecosystems, to accommodate the inevitable unpredictability associated with complex systems (Roux and Foxcroft, 2011).

The fact that the details involved in the calculation of indices are hidden behind a single number also makes it easy for indices to be used without sufficient consideration of how appropriate they are in a particular situation (Boulton, 1999), or to be presented as 'the answer' to questions about the relative integrity or condition of a set of assemblages, when in reality there is no single answer. No single index can claim to represent the definitive measure of ecosystem integrity. A particular index represents only one perspective on the integrity of a system, based on the aspects of diversity or function the authors have chosen to include and the relative weightings of each (Boulton, 1999).

Furthermore, reducing a large amount of information to a single number necessarily involves a large amount of data summarisation. Much of the information present in the original data is not used. For example, information on variance is often discarded in favour of means, causing some trends to be eclipsed by others (Suter, 1993; Andreasen *et al.*, 2001). Discarding information on variance seems particularly inappropriate in studies of diversity, given the close relationship between the concepts of diversity and variance. Similarly, species identities are often discarded in favour of abstract assemblage–level properties such as diversity (a practice decried by Goldstein, 1999). Diversity indices do not provide any information about *which* species are present, although the species names are usually present in the original data. Given the resource constraints usually associated with the collection of data for ecosystem monitoring and assessment (Lindenmayer and Likens, 2010), this loss of information seems wasteful.

While the need for simplicity is a reality, it is also important to retain the ability to deal with the specifics of a particular system and context, and also the flexibility to allow new questions to be answered as they arise. The results of the previous chapter have shown that when it comes to resilience, the particularities of which species are associated with which other species can be important. Retaining the ability to consider the particular is, however, not possible with an index–based approach.

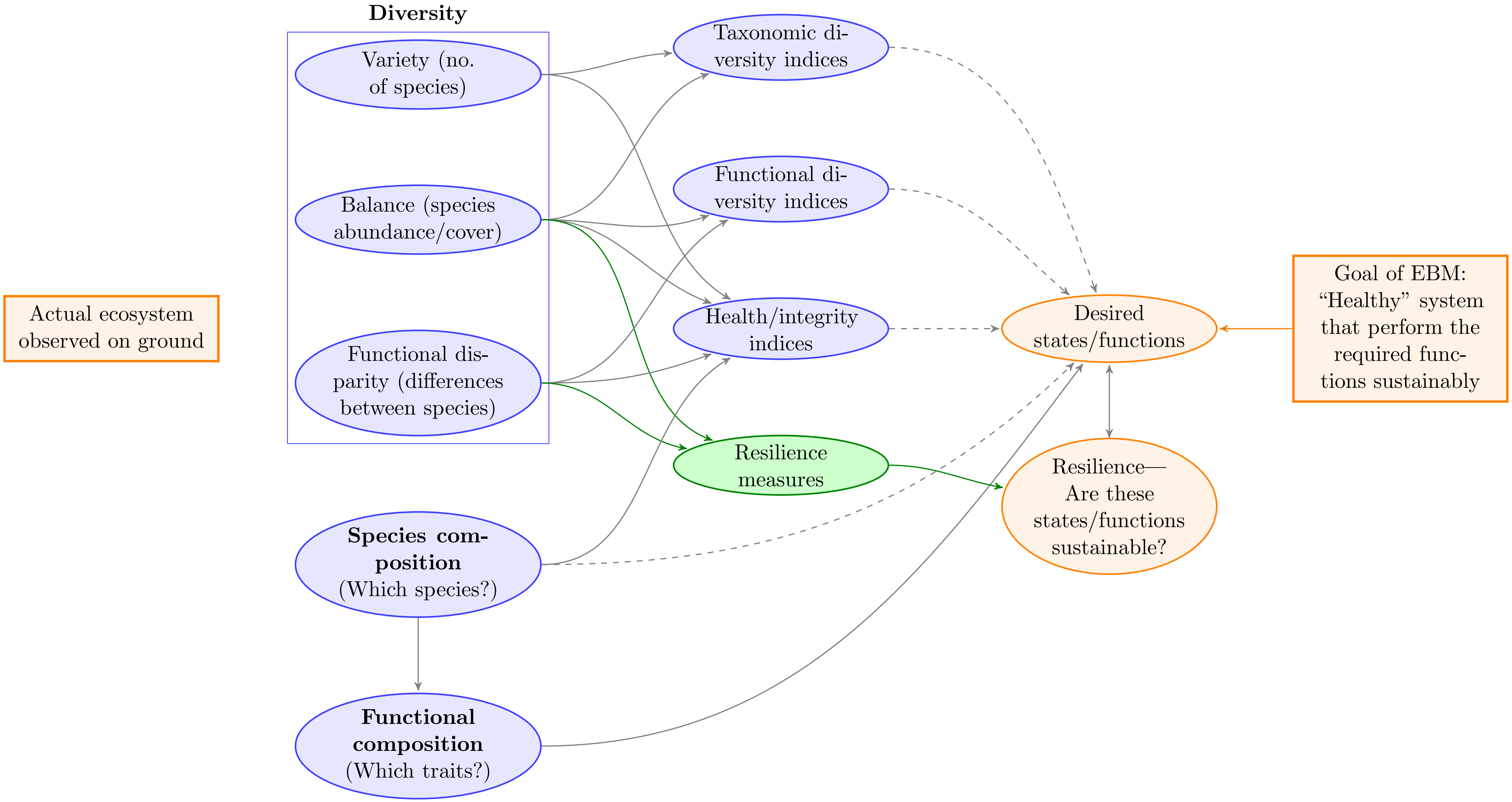


Figure 4.2: Approaches to solving the ecosystem manager's dilemma. Translating the goal of EBM into measurable endpoints requires specification of desired states and/or functions for the system (orange ellipse). The achievement of these states/functions is usually measured using various indices of diversity or functional integrity derived from species diversity, species composition and functional composition data (blue ellipses). However, the links between these indices and the desired functioning are often rather obscure (dotted arrows). An important aspect of integrity often missing from ecosystem assessments is resilience. The measures of redundancy and response disparity developed in this study (green ellipse) make it possible to include resilience in assessments of ecosystem integrity.

Including resilience in ecosystem integrity

Resilience is an important part of ecosystem integrity (Costanza and Mageau, 1999). However, this is often not recognised, or only recognised implicitly (Rapport *et al.*, 1998), because the emphasis with ecosystem integrity is on the desirability of the current configuration rather than on the potential for desirable configurations to persist. Resilience is therefore seldom included in ecosystem health indices. The difficulties involved in measuring resilience (Chapter 2) have also contributed to the neglect of the resilience component of ecosystem integrity (see Figure 4.2).

In the previous chapter I showed how the relative resilience of species assemblages can be compared using the measures of redundancy and response disparity developed in Chapter 2. However, it is not my intention that these measures of redundancy and response disparity simply be added to the collection of ecosystem integrity indices that have already been proposed, or that they be used as part of an index–based approach. Given the problems with indices discussed above, there is a clear need for a new approach.

A new approach to solving the manager's dilemma

So what alternatives do we have, besides indices, for finding the requisite simplicity needed by managers? One way of reducing the amount of detail that needs to be considered is to seek useful generalisations by establishing predictive relationships between variables, a strategy foundational to science (Carnap, 1995). Elucidating such relationships increases our understanding of causal mechanisms and can allow prediction in new situations. However, the growing understanding of the complex nature of ecosystems has led many authors to caution against the use of generalisations in ecology (e.g. Kay *et al.*, 1999; Ulanowicz *et al.*, 2009). The existence of multiple non–linearities, feedback loops and context–dependency in complex systems (see above) severely limit the scope and predictive power of the generalisations that can be made (Kay *et al.*, 1999). Nevertheless, regularities do occur in complex systems, and describing these in terms of general relationships remains a useful strategy as long as their scope is suitably qualified, and as long as they are not treated as 'universal laws' (Wimsatt, 1994).

Ecosystem integrity indices are often based on empirically–derived relationships between variables (e.g. abundance of species x decreases with increasing concentration of pollutant y). These relationships provide the generalisations necessary to make the index useful as a monitoring tool. Any limitations on the scope of the generalisations will equally limit the scope of the index. However, as argued above, the practice of combining many different pieces of information also makes indices inflexible. It may therefore be better to use these generalisations in a different way.

Díaz *et al.* (2007) suggested an approach to 'reducing uncertainty in the prediction of ecosystem services' (as opposed to 'predicting' them) which involves first making use of generalisations (relationships between ecosystem services and abiotic factors/assemblage–level properties) to reduce the amount of unexplained variance, and only then focusing on the particular (idiosyncratic species effects). The advantage of this approach is that the generalisations can guide the formulation of questions about how, when and where the particular matters.

In this chapter, I outline an approach that contributes towards assessing the integrity of ecosystems. I believe this approach is more flexible and powerful than the usual approach using indices. This approach involves using generalisations to help identify variables to measure or monitor, while retaining as much flexibility as possible to allow exploration of different scenarios and consideration of particular situations. This flexibility is achieved by viewing assemblages from different perspectives or points of view, while retaining the species–level information. These perspectives include a functional perspective, a compositional perspective, and a resilience perspective. The use of species–level measures of functioning and resilience provides a way of shifting flexibly between these different perspectives.

Information about the functioning of species and assemblages (the functional perspective) is of critical importance when assessing ecosystem integrity for EBM, because of the priority placed on maintaining key processes and functions. The compositional perspective (which species are present and their relative abundances) is also important, however. Certain functions can only be performed by certain species with particular (unique) combinations of traits (Díaz *et al.*, 2011), e.g. pollination of fig trees by particular species of wasps, tourism centred around particular species such as mountain gorillas or 'the big five'. Maintenance of these functions therefore obviously requires the persistence of the species that provide them. Secondly, ecosystem management agencies often also have a conservation mandate which requires them to prevent species losses and to protect rare and endangered species, regardless of their functional importance (Noss, 1990). There is therefore a certain amount of tension between the functional and compositional perspectives when it comes to implementing EBM (Goldstein, 1999; Walker, 1999; Perry, 2010). I believe this tension can best be resolved by viewing ecosystems from both compositional and functional perspectives.

Species composition (presence and abundance) data are often collected during monitoring programmes, where repeat surveys are used to track changes in species composition over time (Lindenmayer and Likens, 2010). While these data are intended to provide managers with useful information about change, in reality they can be difficult to interpret. Species composition data from different time periods are seldom identical, due to the complex, dynamic and non–equilibrial nature of ecosystems (Wallington *et al.*, 2005). But which of these changes matter? For example, how does one assess compositional changes that do not involve the dominant species? Can they simply be ignored (a common practice)? Understanding the implications of changes in species composition for ecosystem integrity is very difficult if one does not have a way of relating the observed changes to both ecological functioning and resilience (Figure 4.2).

The measures of redundancy and response disparity developed and used in this thesis (Chapters 2 and 3) are valuable because they provide a new perspective, a resilience perspective, which has generally been missing from assessments of ecosystem integrity. The resilience perspective does not supercede the other perspectives, however. I aim to show that the resilience perspective is most useful when combined with compositional and functional perspectives, and when all of these different perspectives are strongly linked to the desired states or functions identified for the system being managed.

The approach will be illustrated using data from the riparian assemblages in the Sand River catchment, introduced in Chapter 3. This will require the presentation of additional data, which will be used to develop the additional perspectives needed to complement the resilience perspective developed in Chapter 3. The value of the approach will be demonstrated with the aid of examples showing how it can be used to address particular management questions, and how the understanding gained can sometimes challenge existing ideas about the conservation and management of particular systems.

The aims of this chapter are, therefore:

- To investigate possible useful generalisations in the relationship between diversity and resilience, particularly to investigate the relationship between species richness (variety) and resilience, because species richness data are relatively easy and cost–effective for managers to obtain.
- To illustrate the value of using the proposed composition–function–resilience approach in the context of EBM, using data from the riparian assemblages in the Sand River catchment.
- To demonstrate, with the aid of examples, how this approach can be used to address particular management questions. The examples aim to address the following three issues commonly faced by managers when evaluating ecosystem integrity for EBM:
    - The effects of species losses on ecological functioning and resilience
    - The effects of invasive alien species on functioning and resilience
    - The effects of changes in species abundances on functioning and resilience

4.2 Methods

4.2.1 Useful generalisations in the relationship between diversity and resilience

As shown in Chapter 1, diversity consists of three interrelated components, variety, balance and disparity, and many different types of disparity may be described (e.g. genetic disparity, morphological disparity, functional disparity). In Chapters 1 to 3 I have focused on the roles of functional disparity and its complement, functional redundancy, as well as balance or evenness, in generating resilience. However, the relationship between variety (species richness) and resilience is also of great interest to managers because species richness data are often the only data available, and they are by far the easiest and most cost–effective to obtain (Maclaurin and Sterelny, 2008). Conservation management agencies typically have a strong reliance on species richness as a surrogate for other aspects of biodiversity and for ecosystem functioning (Mayfield *et al.*, 2010), and species richness data are often collected during monitoring programmes aimed at assessing the effectiveness of management policies (Magurran, 2004). The relationship between variety and resilience, ignored up till now (see Figure 1.4), will therefore be explored further in this chapter to determine to what extent species richness can act as a useful surrogate measure of resilience. The strength of this relationship in the riparian plant assemblages will determine the extent to which it is necessary to monitor other aspects of diversity such as balance and functional disparity (which are harder to obtain), when assessing resilience.

Species richness data for the riparian assemblages were collected in the course of the vegetation surveys described in Chapter 3. Because sample sizes were different for the main river in the three management areas (due to differences in the width of the macro–channel), I used rarefaction techniques to find the expected number of species present in samples of equal area (Gotelli and Colwell, 2001, R function `specaccum` in the package `vegan`).

To relate species richness to redundancy and response disparity, it was necessary to aggregate the species–level measures of redundancy and response disparity up to the level of assemblage. I chose to do this by calculating the mean values across all the species present in each assemblage. Weighted least squares regression (function `lm` in the `stats` package) was used to describe the relationships between species richness and redundancy, and species richness and response disparity, for each function separately. Weighted least squares regression is appropriate in cases where a regression line is to be fitted to a small number of points (here three), but where each point is a mean (R Development Core Team, 2005). The means for each assemblage are weighted by the inverse of the variance, allowing differences in variance between assemblages to be taken into account.

As has been shown in Chapter 3, the variation in redundancy and response disparity among the species in these assemblages was substantial and had important implications for understanding the responses of assemblages and species to particular disturbances or management practices. I outline below how the approach of developing different perspectives was applied to the riparian vegetation assemblages, and the development of tools for translating between these different perspectives.

4.2.2 A composition–function–resilience approach to guide riparian vegetation assessment for EBM

The compositional perspective

This perspective describes assemblages in terms of which species are present and their relative abundances (the balance component of diversity).

Differences in species composition between the assemblages from the different management areas were represented on ordination plots using Principal Coordinates Analysis and the Jaccard dissimilarity metric. This metric is rank–order similar to the Bray–Curtis metric usually used for species composition data, but is preferred because it is metric rather than semi–metric (Oksanen *et al.*, 2011). To explore the differences in composition of the more abundant ‘core’ and less abundant ‘tail’ parts of the assemblages, I plotted the between–assemblage dissimilarities for the cores and tails separately (see §3.2.3 for explanation of how cores and tails were defined). The species composition of the core will have more of an influence on the net functioning of an assemblage than the species composition of the tail, because the traits of the core species dominate (Grime, 1998). Assemblages with similar core species are therefore likely to function similarly, even if the species composition of the tail is very different. Assemblages with different tail species compositions may differ in redundancy and/or response disparity, depending on the distribution of the species within each particular functional space.

The functional perspective

The functioning of a species in each of its different functional roles was measured in this study as the position of the species in various different functional spaces determined by sets of carefully chosen functional traits (Chapter 2). The similarities and differences in functioning among species were then used to calculate measures of redundancy and response disparity associated with each species, for each function (Chapter 2).

The value of functional trait approaches as a practical means of obtaining information on functioning (and their disadvantages) were discussed extensively in Chapter 2. In order to close the gap between what is measured and the goal of EBM (Figure 4.1), it is not sufficient to simply measure any traits and calculate an index of functional diversity. The traits must be carefully chosen and must be related to the states or functions identified as desirable or important for the particular system. For example, if an area is being managed as commercial rangeland, food provision will be an important function of the vegetation, and the traits that determine the suitability of species as fodder will be important (e.g. palatability, lifespan).

However, the functional importance of a particular species is often strongly modulated by its abundance (Grime, 1998). More abundant species contribute more to functioning because their traits are more abundant in the assemblage. I did not include abundance when measuring functional disparity among the species (Chapter 2), because I wanted to explore the relationship between disparity and abundance separately, to test the hypotheses of Walker *et al.* (1999). To take the effect of abundance on functioning into account for the present purposes, I calculated the functional composition of the riparian assemblages (R function `functcomp` in the package `FD`).

Functional composition is the balance or relative representation of *trait values*, rather than species, in an assemblage (Table 2.2). It is increasingly being recognised as a useful indicator of the functioning of assemblages (Díaz *et al.*, 2007; Lavorel *et al.*, 2008; Mouillot *et al.*, 2011). Functional composition is calculated from species composition data (species × sites) combined with functional trait data (traits × species), for each trait separately. For non–continuous traits, the proportional abundance of each category or level of the trait is calculated (with option `CWM.type = "all"`), while for continuous traits, a mean trait value is calculated, weighted by the species abundances (Laliberté and Shipley, 2010).

To provide a holistic picture of functional composition including all the traits measured, I performed a Principal Components Analysis (PCA) on the functional composition data. I used a modified version of PCA able to handle mixed continuous and non–continuous variables (R function `dudi.mix` in the package `ade4`; Hill and Smith, 1976; Kiers, 1994). For continuous variables only, this is equivalent to a normed PCA, while for categorical variables only it is equivalent to a multiple correspondence analysis. The principal components are centered and normed vectors maximising the sum of the squared correlation coefficients for quantitative variables, the squared multiple correlation coefficients for ordinal variables, and the correlation ratios for factors (Dray and Dufour, 2007).

This provided a functional perspective on the differences between the riparian assemblages. The functional composition data described how they differed in functioning overall, for various functions, while the location of the species within the various functional spaces (see Chapter 2) indicated the contributions of individual species to the various functions.

Functional composition is determined by species composition in the sense that the mix of traits present is determined by which species are present and their relative abundances. Two assemblages with the same species composition will have the same functional composition. Differences in species composition, on the other hand, may or may not lead to differences in functional composition.

The resilience perspective

The species–level measures of resilience (redundancy and response disparity) described in Chapter 2 allow differences between assemblages to be described from a resilience perspective. The way these resilience measures were calculated makes it possible to describe the redundancy and response disparity associated with different aspects of the functioning of each species, and also to identify which other species are involved in providing this redundancy and response disparity. This perspective has already been described in previous chapters, so it will not be discussed further here.

Aids to shifting flexibly between perspectives

The major benefit of the approach followed here is that species–level information is available for each of the three perspectives described above. Species can be described in terms of their abundance (a compositional perspective), their functional effects and responses for various different functions (a functional perspective), and also in terms of the redundancy and response disparity associated with these different aspects of their functioning (a resilience perspective). While this species–level information can be aggregated up to the level of the assemblage, for example in measures of evenness or functional composition, having species–level information greatly increases the range of questions that can be addressed. Besides comparing the composition, function and resilience of whole assemblages, it allows us to ask questions like ‘what are the functional implications of a particular change in species composition?’, ‘what new functions does a particular invasive species add?’, ‘how do losses of particular species affect the resilience of particular functions?’, ‘which species are responsible for an observed change in functional composition?’, and ‘which species are important for maintaining the resilience of a particular function?’. Examples of how the different perspectives were used to address such questions in the riparian assemblages will be presented in the following section.

The Principal Coordinates Plots described in §2.2.4 provide a useful way of combining the different perspectives and shifting between them, because information on species abundances, species functional roles and the resilience associated with these functional roles can all be displayed simultaneously (Figure 2.9). Species abundances are shown by the size of the species points (scaled by abundance), making it easy to distinguish 'core' and 'tail' species. Functioning can be inferred by a species' position within a particular functional space, while resilience values can be shown using colours. It is also possible to highlight species with particular traits of interest, e.g. tall trees, geophytes, evergreen species etc. This makes for a powerful and flexible framework for data exploration.

4.3 Results

4.3.1 Useful generalisations in the relationship between diversity and resilience

The riparian assemblages in this study were all relatively species–rich, containing 61–84 woody species and 130–154 herbaceous species (Table 4.1). Woody and herbaceous species richness were strongly positively correlated with each other in assemblages from the main river, but less so in assemblages from the small streams (Pearson correlation coefficients 0.99 and 0.58 respectively, woody and herbaceous species rarefied to the same number of plots).

Woody assemblages from the small streams had the highest species richness in the communal area (84 spp.), followed by Kruger (79 spp.) and Sabi–Sand (61 spp.), while along the main river this pattern was reversed, with highest richness in Sabi–Sand (84 spp.), followed by Kruger (73 spp.) and then the communal area (62 spp.) (Figure 4.3, Table 4.1). Few woody alien species were recorded in any of the assemblages (Table 4.1).

Assemblages in the three management areas were more similar in herbaceous species richness than they were in woody species richness, particularly along the main river. Small streams in the communal area, however, had more herbaceous species (154) than small streams in either of the two reserves (136 and 138 spp.; Figure 4.3). The greater species richness in the small streams in the communal area was not due to the presence of a large number of alien species (Table 4.1).

The patterns of species richness in the different management areas matched the patterns for redundancy described in Chapter 3, suggesting a relationship between species richness and redundancy. This would make sense because the more species are present in an assemblage, the more species should be available to provide redundancy for each others' functioning.

Table 4.1: Summary of differences in diversity, density and cover between riparian assemblages from different management areas.

	Small streams			**Main river**		
	Communal	**Kruger**	**Sabi–Sand**	**Communal**	**Kruger**	**Sabi–Sand**
Woody species						
Rarefied species richness	84	79	61	62	73	84
Rarefied species density	84	79	61	62	69	80
% of tot sp. richness in tail	75	84	79	79	81	86
% Unique species	23	20	5	21	11	30
Density (individuals per m^2)	0.6	0.4	0.4	0.4	0.5	0.4
Cover (mean % per plot)	30	30	17	46	46	33
% Alien species cover	0.2	0	0	10	0.2	2.4
No. of alien species	1	0	1	4	1	3
Evenness (Pielou's J)	0.42	0.35	0.38	0.38	0.38	0.35
Simpson diversity	0.96	0.91	0.93	0.92	0.94	0.92
Shannon diversity	1.84	1.5	1.57	1.57	1.61	1.55
Herbaceous species						
Rarefied species richness	154	136	138	130	136	146
Rarefied species density	150	134	134	130	132	137
% of tot sp. richness in tail	92	87	90	88	93	95
% Unique species	25	17	20	26	19	19
Density (individuals per m^2)	24	20	37	22	25	28
Cover (mean % per quadrat)	19	22	24	19	19	22
Grass cover (mean % per quadrat)	14	16	14	12	14	15
% Alien species cover	1.5	0.1	1	4.9	5	4.6
No. of alien species	7	3	5	11	14	18
Evenness (Pielou's J)	0.29	0.33	0.33	0.34	0.29	0.26
Simpson diversity	0.86	0.89	0.93	0.9	0.84	0.78
Shannon diversity	1.49	1.62	1.66	1.64	1.41	1.31

Table 4.2: Results of weighted least squares regressions of the mean redundancy per assemblage on species richness, for woody and herbaceous assemblages from the small streams and the main river separately. Regression equations are of the form $y = a + bx$. Degrees of freedom = (1,1) in all cases.

	Intercept	**Slope**	**R^2**	**F**	**p-value**
Woody, small streams					
Nutrient cycling	9.48	0.06	0.81	9.79	0.197
Food provision	-0.72	0.04	0.9	19.44	0.142
Shade provision	9.92	0.03	-0.87	0.07	0.833
Fuel provision	2.44	0.16	0.93	28.56	0.118
Woody, main river					
Nutrient cycling	-6.22	0.24	0.99	288.22	0.0375
Food provision	1.54	0	-0.98	0.01	0.938
Shade provision	2.41	0.1	0.63	4.37	0.284
Fuel provision	2.18	0.14	0.95	41.66	0.0979
Herbaceous, small streams					
Nutrient cycling	12.01	0	-0.7	0.18	0.746
Food provision	10.03	-0.04	1	1187.41	0.0185
Herbaceous, main river					
Nutrient cycling	-9.92	0.16	0.36	2.14	0.382
Food provision	-2.88	0.05	0.98	103.21	0.0625

The mean redundancy per assemblage was indeed positively related to species richness for the majority of functions studied (Figure 4.4, Table 4.2). This means that redundancy generally increased when more species were present. The slope of the relationship varied between functions, however (Table 4.2), indicating that the amount of redundancy increased with the number of species at different rates for different functions. The relationship was weakest for shade provision by woody species ($P = 0.83$, $P = 0.28$ in small streams and main river respectively), food provision by woody species in the main river ($P = 0.94$), and nutrient cycling by herbaceous species ($P = 0.75$ and $P = 0.38$). In these few cases, the mean amount of redundancy present in the assemblage was not strongly correlated with species richness, and increasing the number of species present would not necessarily enhance the redundancy associated with these functions. Redundancy was negatively correlated with species richness in one case only (food provision in herbaceous assemblages from small streams; Table 4.2), meaning that the amount of redundancy in food provision actually decreased as the number of species increased in these assemblages.

These results indicate that, although in general a positive relationship between species richness and redundancy was present, there were variations in this relationship between assemblages as well as between the different functions considered. These variations should not be ignored when using the generalisation for informing EBM decisions, because they may have important consequences for the decisions that are made. For example, in woody assemblages from the main river, increasing species richness from 61 to 87 species increases the mean redundancy in nutrient cycling by around 65%, but the same increase in species richness in the small stream assemblages only increases nutrient cycling redundancy by around 8% (Figure 4.4a, pink lines). This may have implications for restoration programmes, as managers would need to take these differences into account when designing revegetation programmes in different sized streams, for example. Similarly, increasing the number of species would benefit the redundancy associated with some functions more than others.

Mean response disparity per assemblage was generally not, however, correlated with species richness (Figure 4.4, Table 4.3). Of the 24 regressions for the various combinations of functions in the different assemblages, only five had p–values below 0.2, and all slopes were less than 0.005 (Table 4.3). Having a larger number of species present in an assemblage did not, therefore, particularly enhance response disparity.

4.3.2 A compositional perspective on riparian assemblages from different management areas

Riparian assemblages in the Sand River catchment all differed in terms of the species present. Around 33% of the species pool occurred in all three management areas, while 40% of the species pool was recorded in only one area (Fig. 4.5). Assemblages from the small streams had higher proportions of shared species than assemblages from the main river (Fig. 4.5). Importantly, assemblages with lower species richness did not simply contain a subset of the species present in the more species–rich assemblages (with the

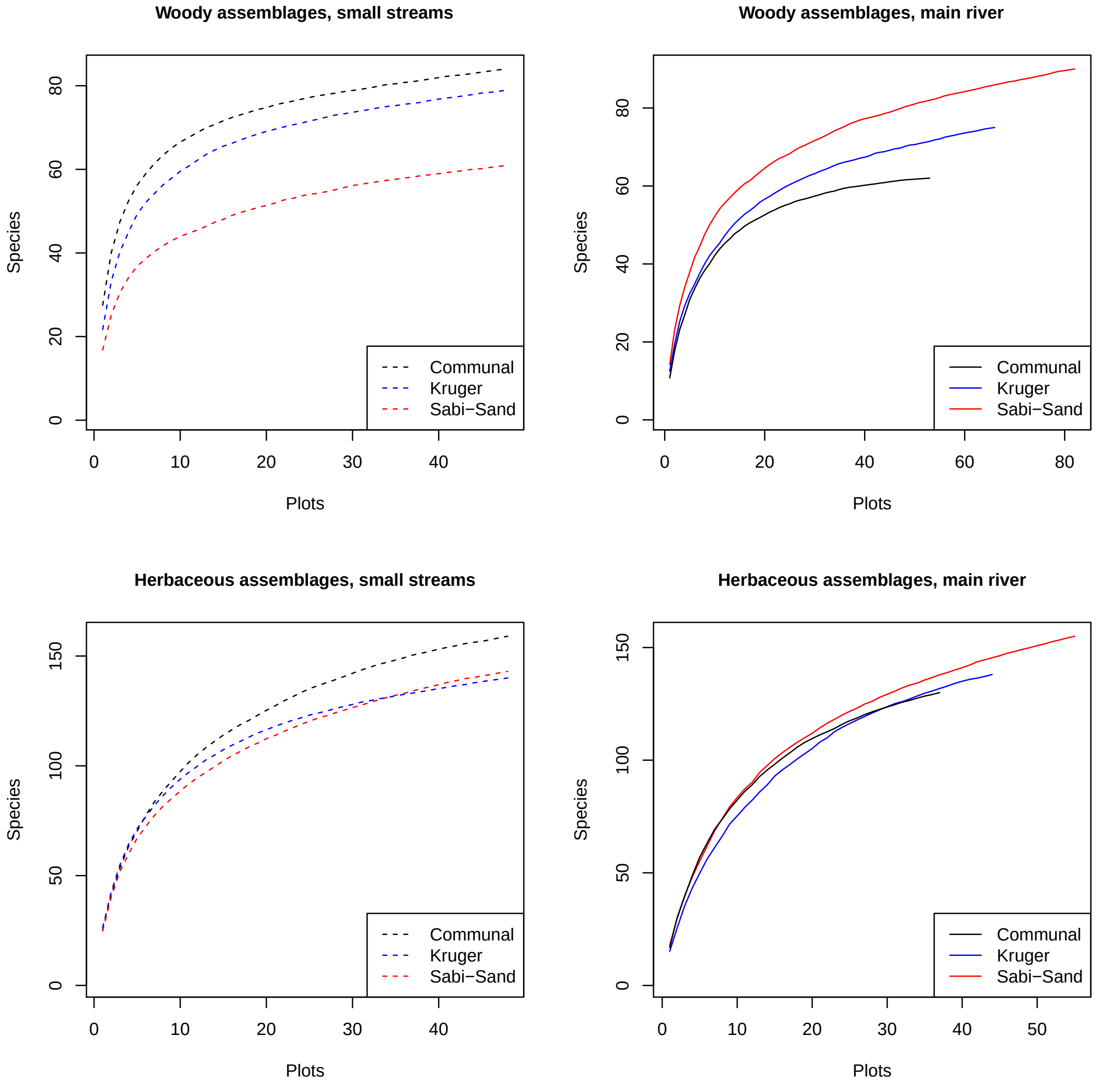


Figure 4.3: Sample–based rarefaction curves for woody and herbaceous assemblages in the three different management areas. These curves show the statistical expectation for the increase in species richness with the number of plots sampled, and are produced by repeatedly re–sampling the pool of samples at random and plotting the average number of species represented by increasing numbers of samples. Rarefaction methods allow for meaningful standardization and comparison of species richness across datasets (Colwell and Coddington, 1994).

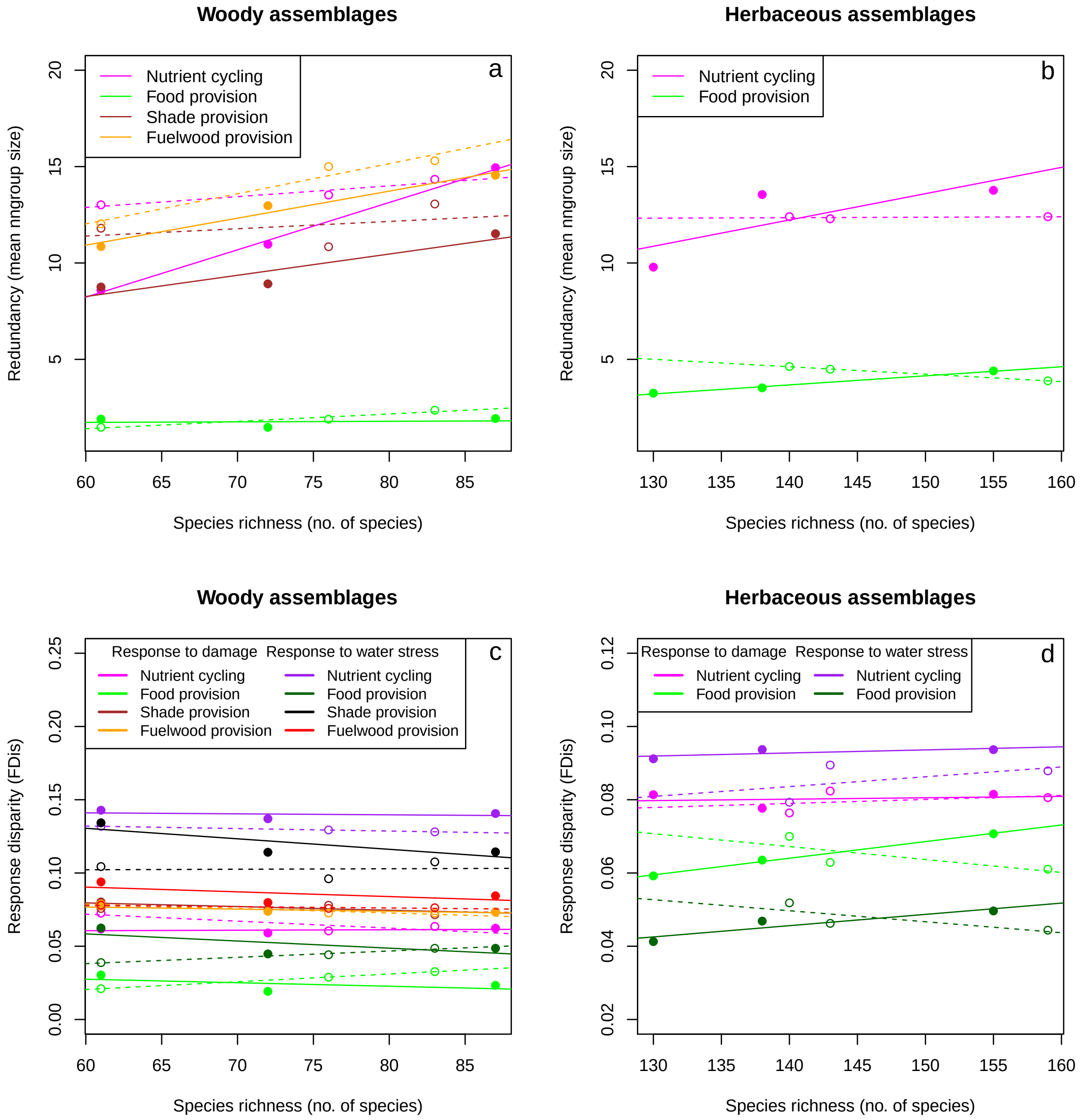


Figure 4.4: Relationships between species richness and resilience measures (redundancy - top, and response disparity - bottom), for different effect functions in woody (a, c) and herbaceous (b, d) riparian assemblages. Dashed lines: small streams, solid lines: main river. Different colours represent different functions.

Table 4.3: Results of weighted least squares regressions of the mean response disparity per assemblage on species richness, for woody and herbaceous assemblages from the small streams and the main river separately. Regression equations are of the form $y = a + bx$. Degrees of freedom = (1,1) in all cases.

	Intercept	**Slope**	**R^2**	**F**	**p-value**
Woody, small streams					
Nutrient cycling + response to damage	0.1	0	0.4	2.33	0.369
Food provision + response to damage	-0.01	0	1	18730.9	0.00465
Shade provision + response to damage	0.08	0	-0.55	0.29	0.687
Fuel provision + response to damage	0.1	0	0.83	10.56	0.19
Nutrient cycling + response to water stress	0.14	0	1	1147.34	0.0188
Food provision + response to water stress	0.01	0	0.96	49.65	0.0897
Shade provision + response to water stress	0.1	0	-1	0	0.986
Fuel provision + response to water stress	0.08	0	0.63	4.44	0.282
Woody, main river					
Nutrient cycling + response to damage	0.06	0	-0.56	0.28	0.689
Food provision + response to damage	0.04	0	-0.65	0.21	0.725
Shade provision + response to damage	0.09	0	0.71	5.93	0.248
Fuel provision + response to damage	0.08	0	0.42	2.42	0.364
Nutrient cycling + response to water stress	0.14	0	-0.95	0.03	0.897
Food provision + response to water stress	0.08	0	-0.2	0.66	0.566
Shade provision + response to water stress	0.17	0	0.29	1.82	0.406
Fuel provision + response to water stress	0.1	0	-0.54	0.3	0.682
Herbaceous, small streams					
Nutrient cycling + response to damage	0.07	0	-0.82	0.1	0.806
Food provision + response to damage	0.12	0	0.11	1.26	0.464
Nutrient cycling + response to water stress	0.04	0	-0.49	0.35	0.661
Food provision + response to water stress	0.09	0	0.22	1.57	0.429
Herbaceous, main river					
Nutrient cycling + response to damage	0.07	0	-0.83	0.09	0.81
Food provision + response to damage	0	0	0.99	258.36	0.0396
Nutrient cycling + response to water stress	0.08	0	0.08	1.17	0.475
Food provision + response to water stress	0	0	0.71	6.01	0.247

exception of the woody assemblage in small streams in Sabi–Sand). Between 11 and 30% of the species in each assemblage were recorded only in that assemblage.

A number of alien (non–indigenous) species were present. Although only 4.5% of all woody species surveyed were aliens, some of these were invasive species with relatively high abundances (Table 4.1). Woody invasive aliens were particularly abundant in the main river assemblage in the communal area, where three species were recorded (*Sesbania punicea*, *Lantana camara* and *Melia azedarach*, together making up 5.8% of abundance and 9.8% of cover). In Sabi–Sand only one species was recorded (*Lantana camara*, making up 6.3% of abundance and 2.3% of cover), while no woody alien species were recorded in the Kruger National Park. Herbaceous alien species made up 9% of the total number of herbaceous species in the species pool. These species made up around 10% of abundance and 5% of cover in the main river assemblages in all three management areas, but were insignificant in the assemblages from the small streams (Table 4.1).

All assemblages had highly skewed distributions of abundance and cover, with a few dominant species and a long tail of species with very low abundance or cover (Figures 4.6–4.9). Tail species that together contributed only 25% of the total cover, made up 75–95% of the total species richness (Table 4.1). The proportion of species in the tail was particularly high for the herbaceous component of the vegetation (87–95%). Many of these tail species were forbs (non–graminoid herbaceous plants), a component of the vegetation which is generally unknown and under–sampled.

Assemblages in the different management areas shared both core and tail species, and they also differed in both core and tail species (Figures 4.10 and 4.11). The differences in tail species composition contributed to the differences in redundancy and response disparity between the assemblages described in Chapter 3. The differences in core species composition opened up the possibility that assemblages from the three management areas differed in their functioning, depending on how similar the core species were to each other in their functional traits.

Assemblages from the small streams in the different management areas were each distinct in terms of species present, relative abundance and relative cover distributions of the species, particularly for the woody component (Figure 4.10). There were large differences in the composition of both the cores and the tails of the various assemblages. The herbaceous assemblages were more similar but still distinct, with those in the two reserves being more similar to each other than either was to the assemblage in the communal area (Figure 4.11).

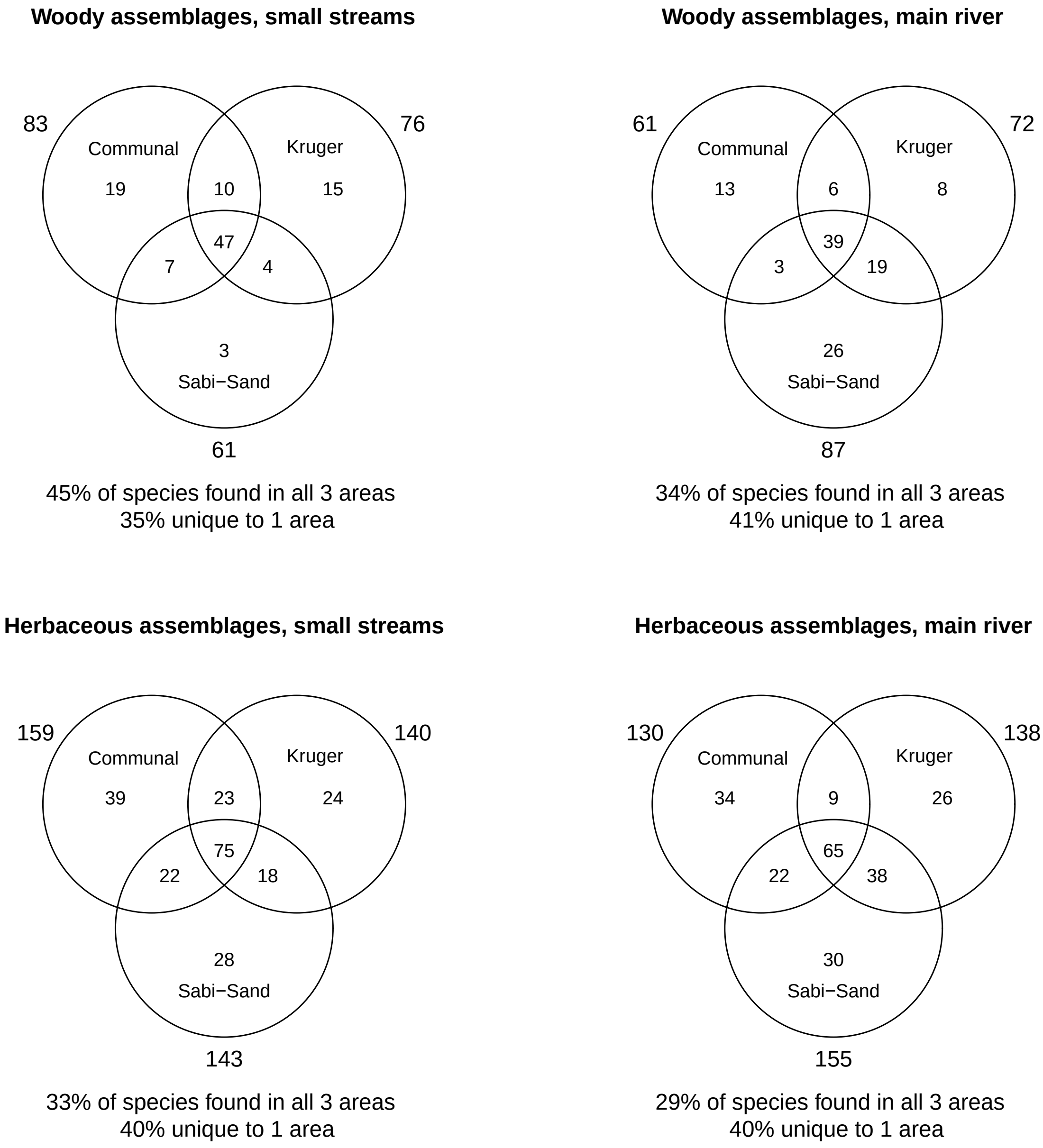
In the main river, the assemblage in the communal area was very different from the assemblages in the reserves, while the Kruger and Sabi–Sand assemblages were very similar, for both woody and herbaceous species (Figures 4.10 and 4.11).

The question now arises: what are the consequences of these differences in species composition for the functioning of the different assemblages? Did the differences in species composition translate into differences in functional composition?

4.3.3 A functional perspective on riparian assemblages from different management areas

Woody and herbaceous assemblages from the different management areas did indeed differ in functional composition, as shown by Principal Component Analysis of the functional composition data (Figures 4.12 and 4.14). The largest differences were between assemblages from the different sized streams, which were clearly separated along PCA axis 1. Axis 2 described differences between the three management areas. Interestingly, the differences in functional composition reflected the differences in species composition quite closely (Figures 4.10 and 4.11).

Woody assemblages along the small streams were dominated by nitrogen–fixing, spiny deciduous trees with hard wood and low riparian affinity (e.g. *Acacia* species). Assemblages on the main river had more evergreen, spineless and soft–wooded riparian species, and more shrubs and climbers (Figures 4.12 and 4.13). Shrubs made up 65–75% of the individuals present along the main river, but only 35–45% of the individuals along the small streams (Fig. 4.13). The mean potential height was therefore lower in assemblages along the main river (around 5.5 m). However, really large individual trees only occured along the main river. Many more riparian specialist or near–specialist species occurred along the main river, with individuals in these two categories making up 50–75% of the total, compared with less than 20% along the first order streams. These differences were largely expected, and are related to the greater availability of water in the main river than in the small streams, where surface water is not present for most of the year.



Woody assemblages, small streams

45% of species found in all 3 areas
35% unique to 1 area

Woody assemblages, main river

34% of species found in all 3 areas
41% unique to 1 area

Herbaceous assemblages, small streams

33% of species found in all 3 areas
40% unique to 1 area

Herbaceous assemblages, main river

29% of species found in all 3 areas
40% unique to 1 area

Figure 4.5: Venn diagrams showing numbers of unique and shared species in woody and herbaceous assemblages in the three different management areas. The numbers outside the circles indicate the total number of species in each assemblage.

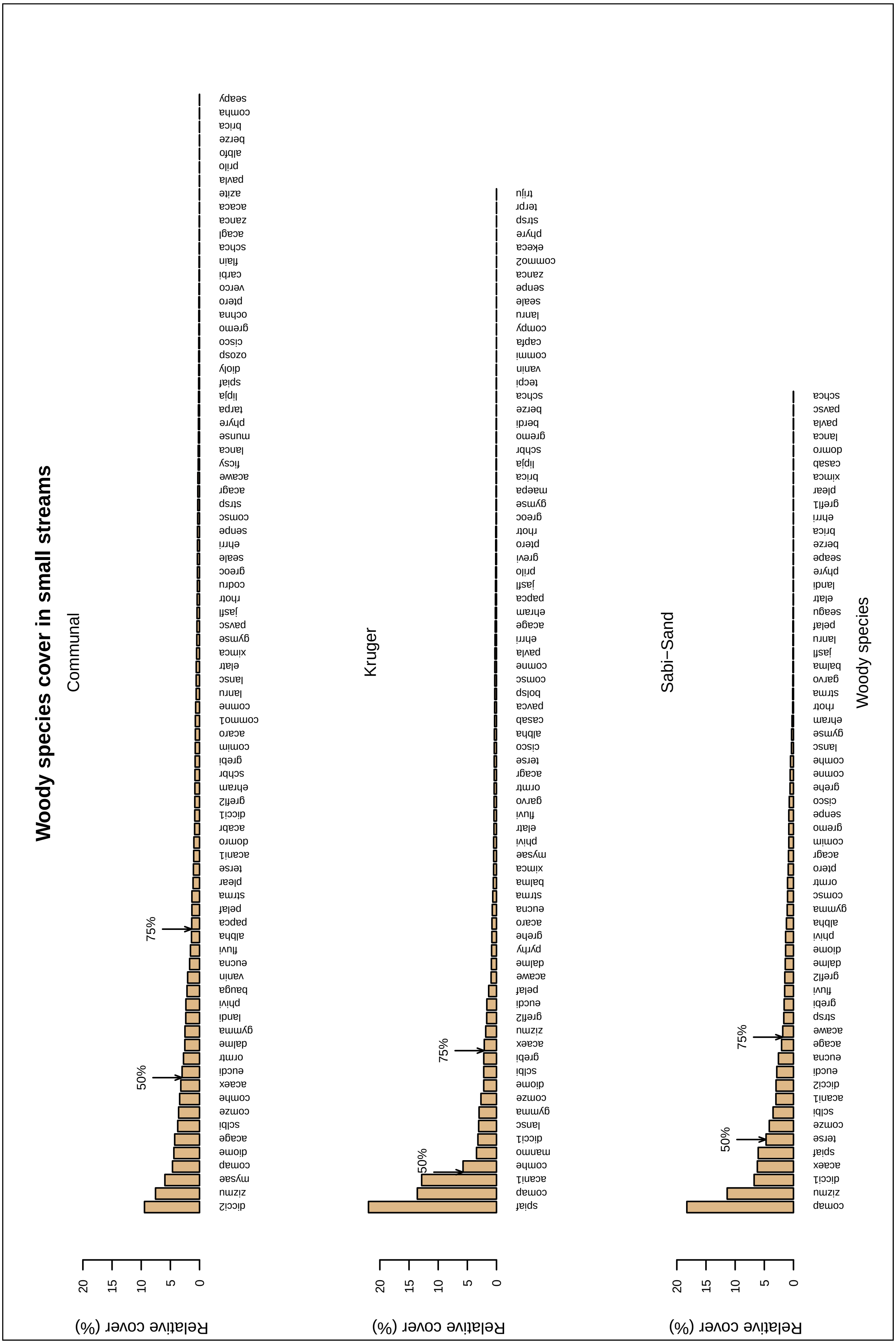


Figure 4.6: Species cover distributions in **woody riparian assemblages along small streams**, showing the highly skewed distribution of relative cover and the large number of species in the tail. Species to the left of the arrows make up 50% and 75% of the total cover respectively. The tail was defined as those species making up the remaining 25% of cover. Full species names (x axis) given in Appendix A.

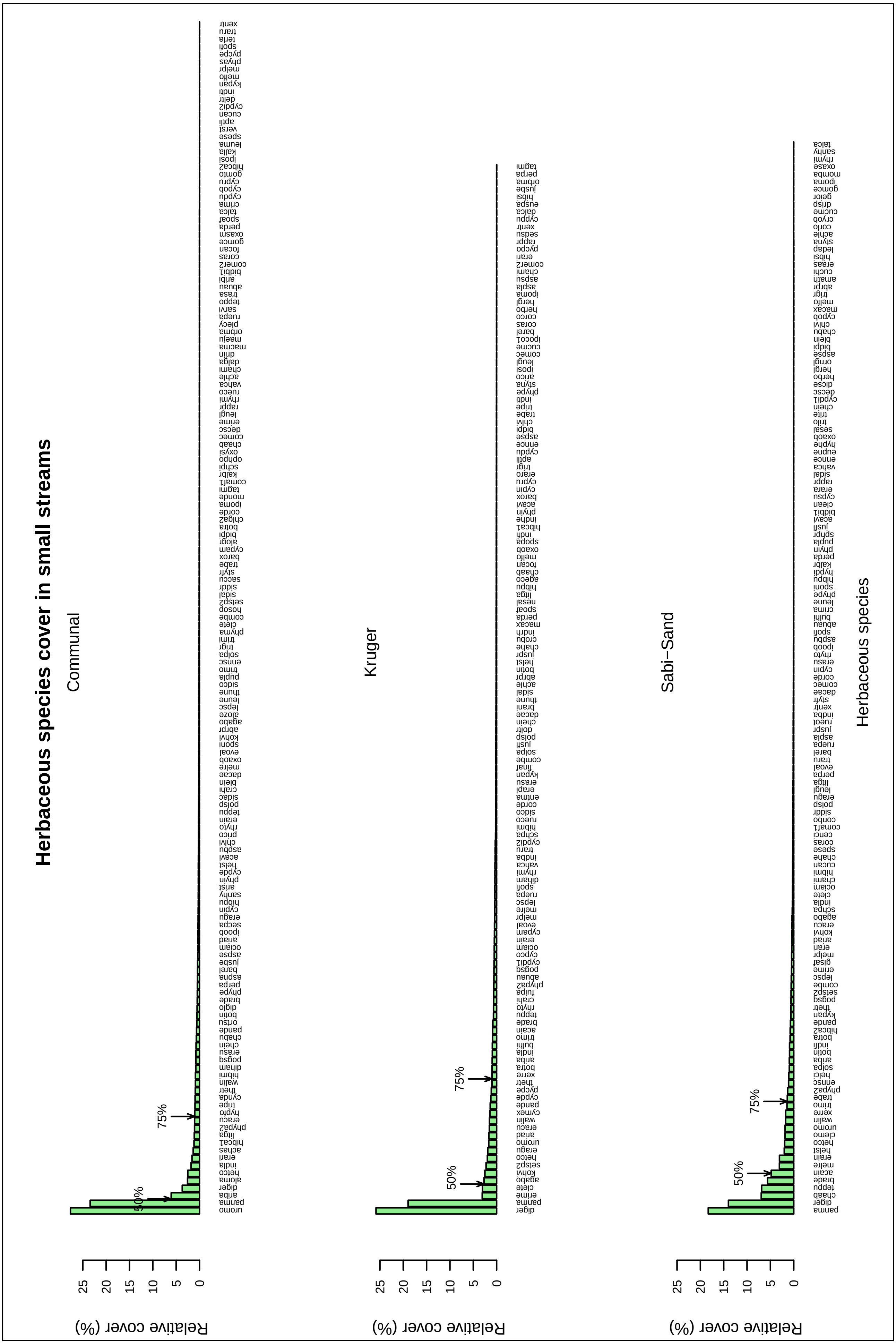


Figure 4.7: Species cover distributions in **herbaceous riparian assemblages along small streams**, showing the highly skewed distribution of relative cover and the large number of species in the tail. Details as in Fig. 4.6.

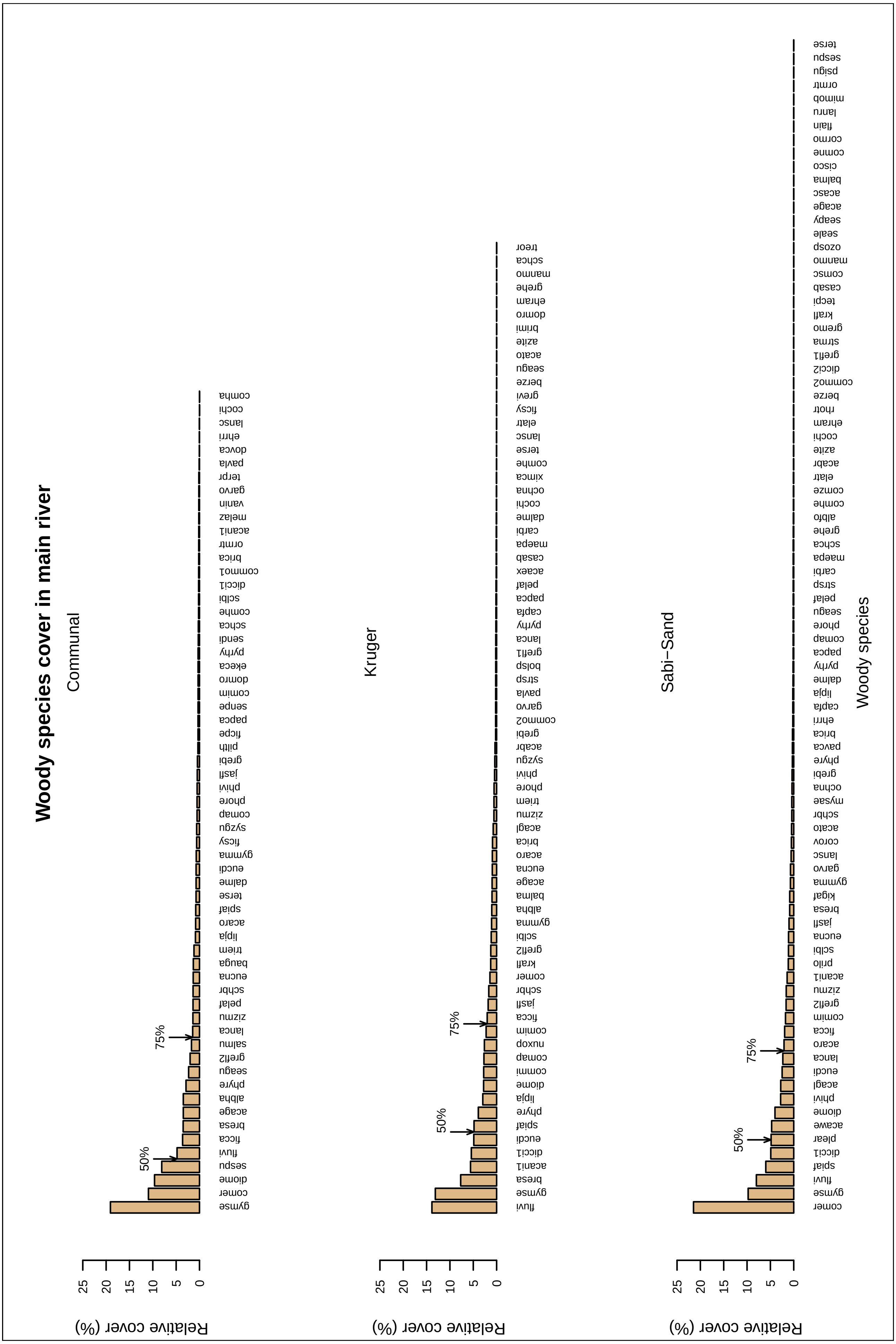


Figure 4.8: Species cover distributions in **woody riparian assemblages along the main river**, showing the highly skewed distribution of relative cover and the large number of species in the tail. Details as in Fig. 4.6.

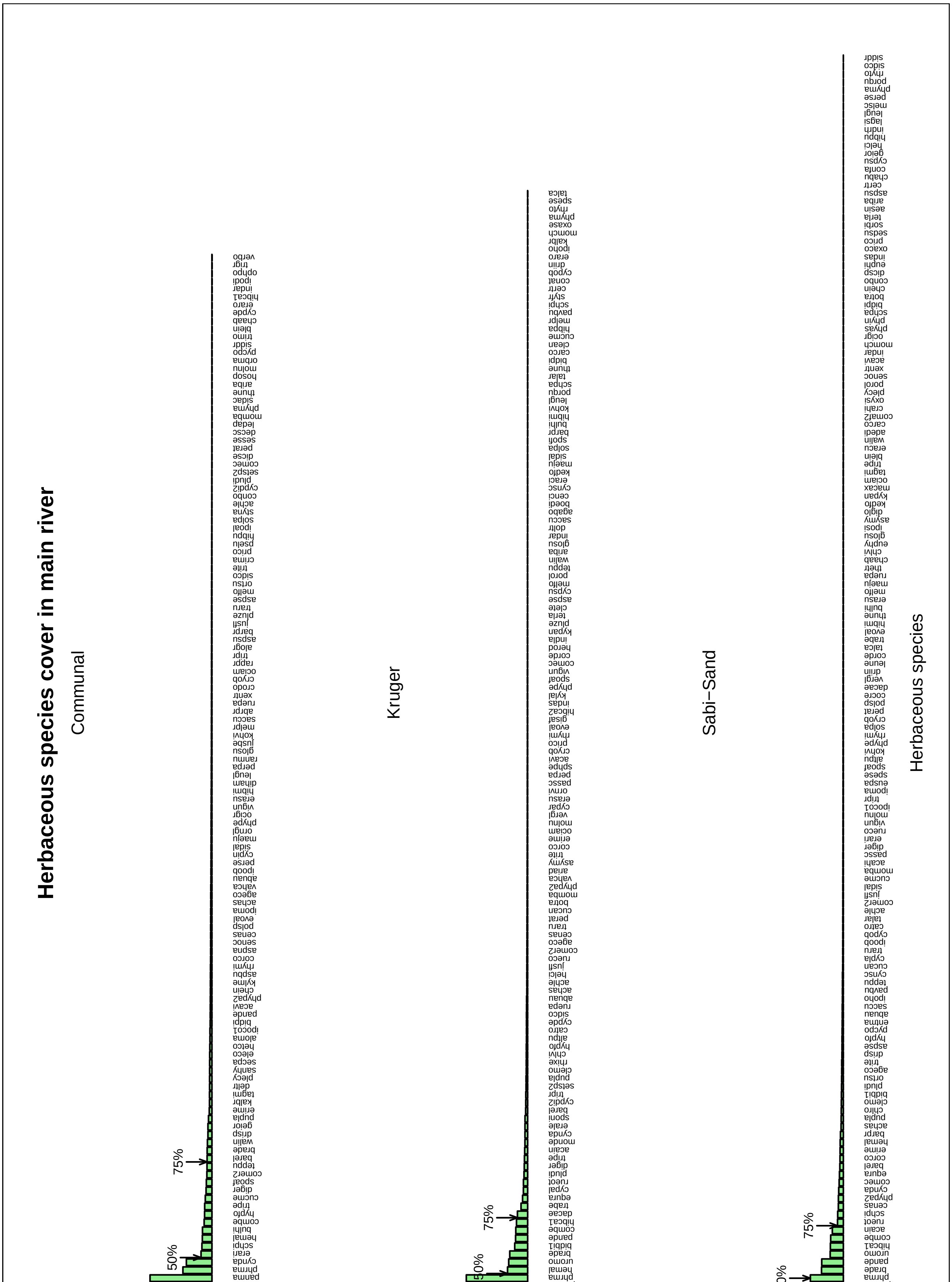
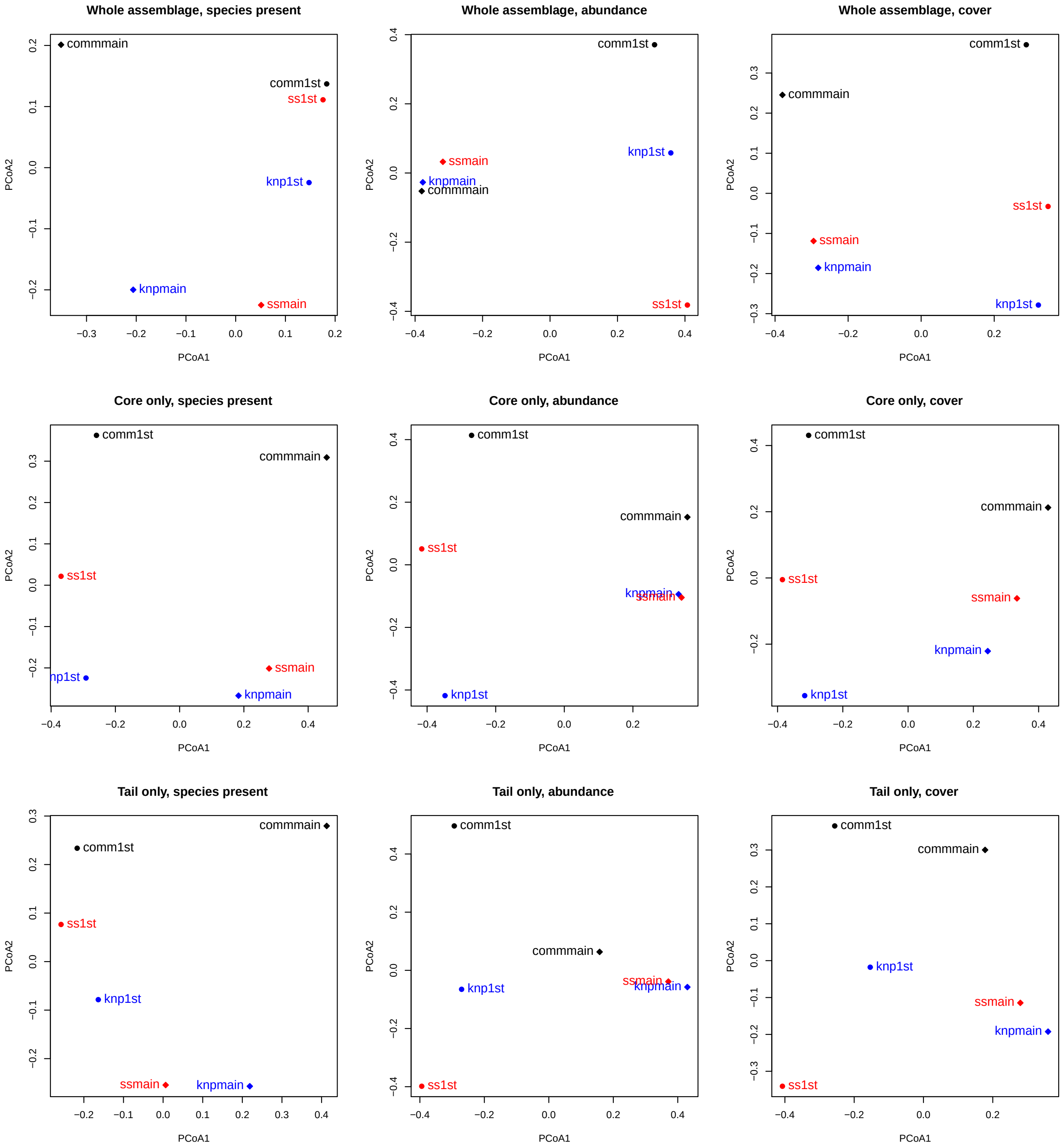


Figure 4.9: Species cover distributions in **herbaceous riparian assemblages along the main river**, showing the highly skewed distribution of relative cover and the large number of species in the tail. Details as in Fig. 4.6.



Whole assemblage, species present

Whole assemblage, abundance

Whole assemblage, cover

Core only, species present

Core only, abundance

Core only, cover

Tail only, species present

Tail only, abundance

Tail only, cover

Figure 4.10: Jaccard dissimilarity in woody species composition of assemblages in the different management areas. The dissimilarities between areas in three aspects of composition — species present (1st column), species relative abundances (2nd column) and relative cover (3rd column) — are represented using the first 2 axes of a multivariate Principal Coordinates space. Top row: whole assemblage, middle row: core species only (top 75% of cover), bottom row: tail species only. Acronyms: ‘comm’ = communal area, ‘knp’ = Kruger National Park, ‘ss’ = Sabi–Sand reserves, ‘1st’ = small (first order) streams, ‘main’ = main river.

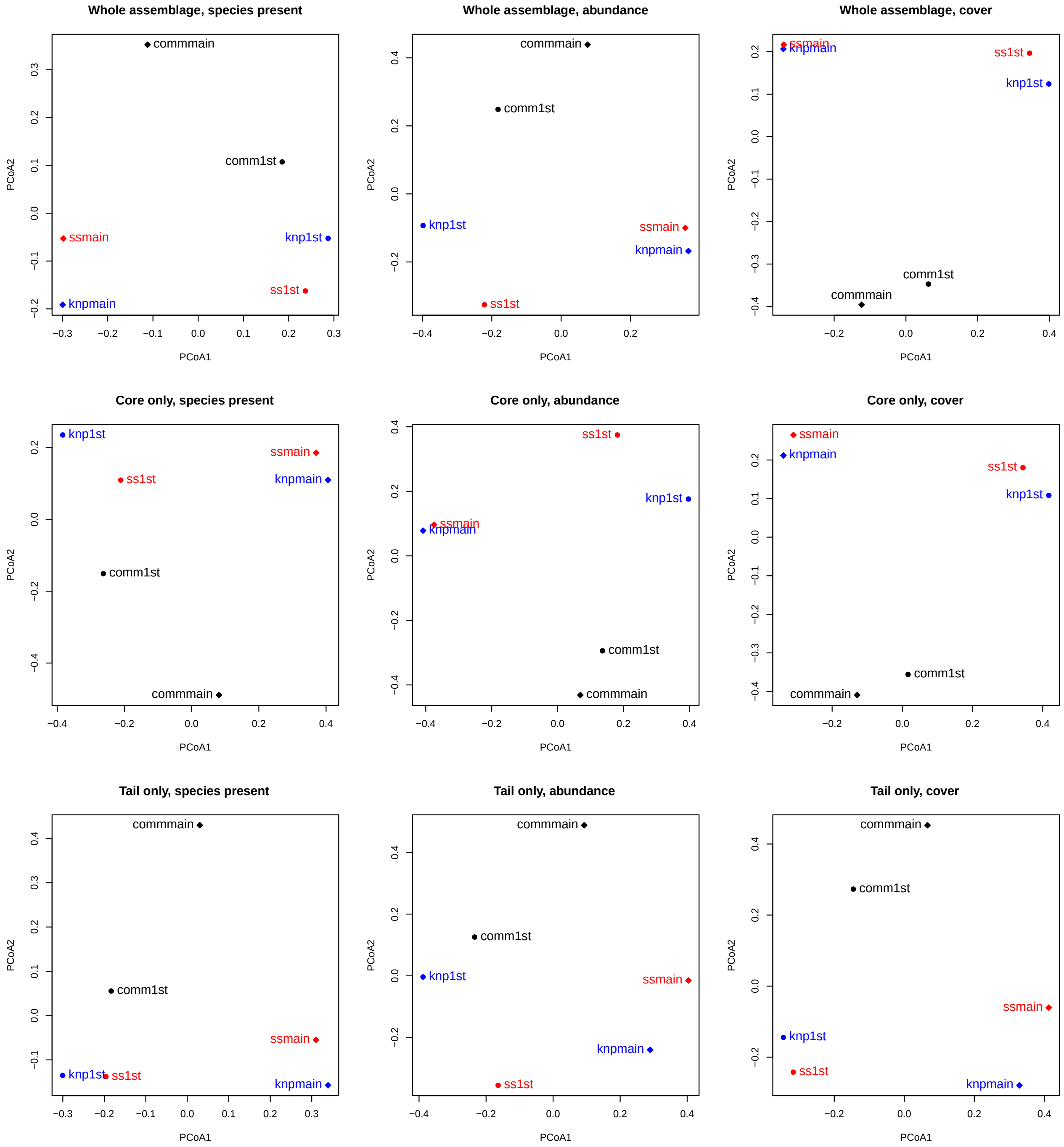


Figure 4.11: Jaccard dissimilarity in herbaceous species composition of assemblages in the different management areas. The dissimilarities between areas in three aspects of composition — species present (1st column), species relative abundances (2nd column) and relative cover (3rd column) — are represented using the first 2 axes of a multivariate Principal Coordinates space. Top row: whole assemblage, middle row: core species only (top 75% of cover), bottom row: tail species only. Acronyms: ‘comm’ = communal area, ‘knp’ = Kruger National Park, ‘ss’ = Sabi–Sand reserves, ‘1st’ = small (first order) streams, ‘main’ = main river.

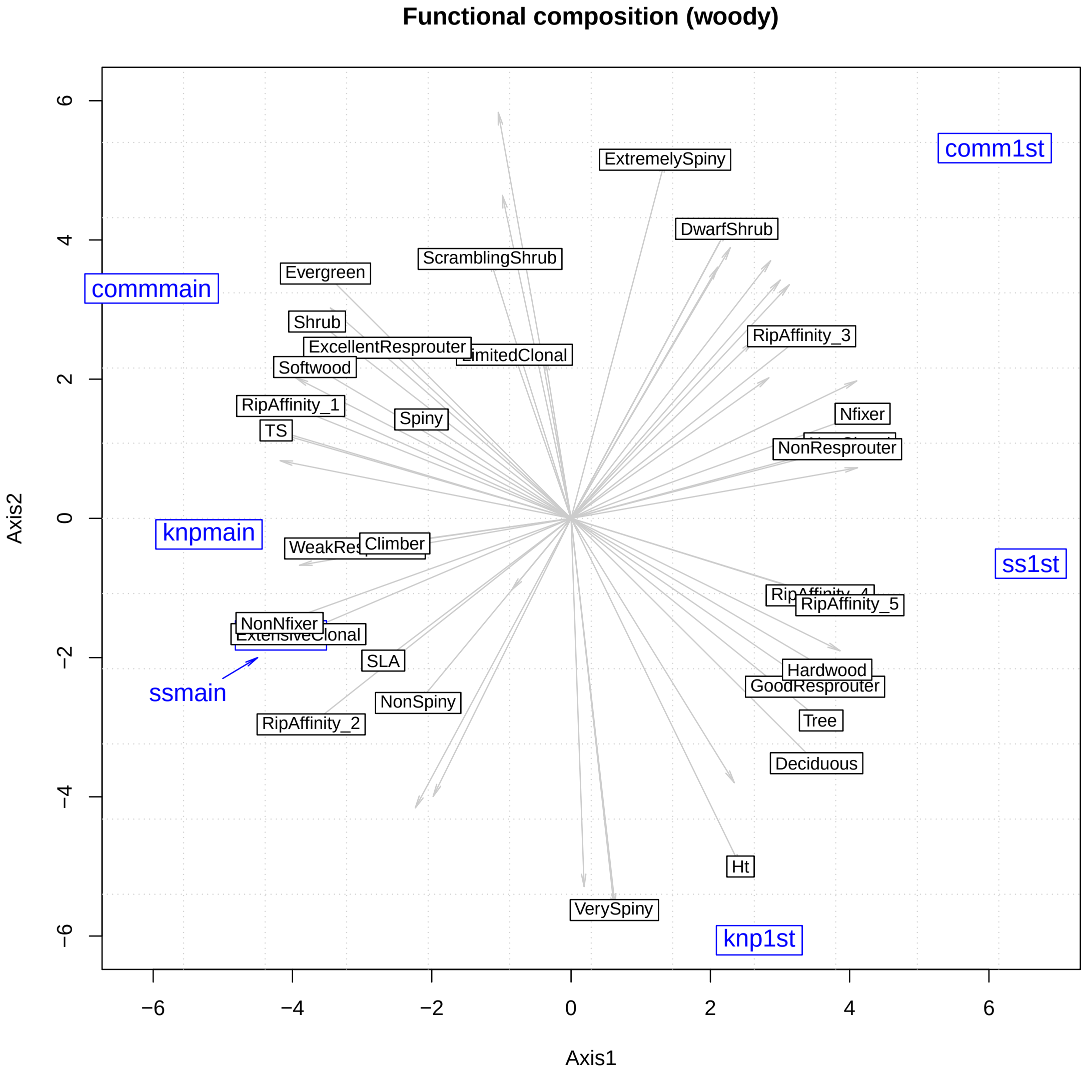


Figure 4.12: Principal Component Analysis showing the contribution of functional trait variables to the differences in functional composition among woody riparian assemblages. Axis 1 reflects the separation between assemblages from small streams and the main river, axis 2 the separation between management areas. For categorical, ordinal and binary traits, each category was treated as a separate variable with values reflecting the extent to which that trait category was represented in the assemblage. For continuous traits, the mean values of the trait were compared across assemblages. Some labels have been omitted to improve clarity.

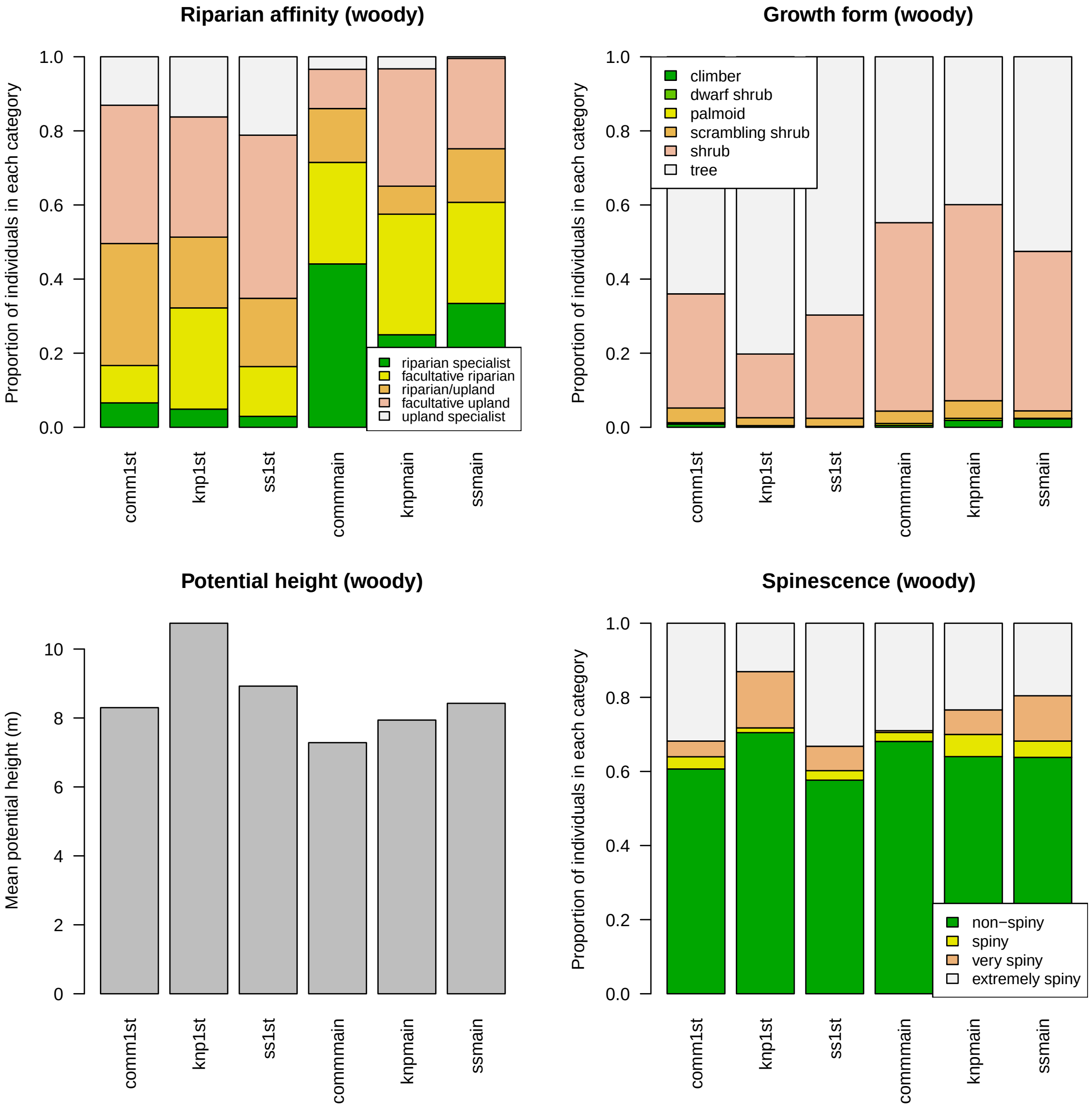


Figure 4.13: Comparison of selected aspects of functional composition in woody assemblages from the three management areas. Values for potential height are weighted means (weighted by species cover), so reflect mainly the dominant species. The x axis reflects the different assemblages: ‘comm’ = communal, ‘knp’ = Kruger National Park, ‘ss’ = Sabi–Sand reserves, ‘1st’ = small (1st order) streams, ‘main’ = main river.

Woody vegetation from small streams in the three management areas differed in riparian affinity, growth form, potential height and spinescence (Figure 4.12). Kruger had the most riparian specialists (mostly category 2), while Sabi–Sand was the most 'terrestrial' with the largest proportion of upland specialists (categories 4 and 5, Figure 4.13). The communal area had the largest proportion of 'generalist' individuals (category 3, which were neither riparian nor upland specialists). This suggests that assemblages from the three areas can be arranged on a continuum of riparian affinity, from most riparian (Kruger) to most terrestrial (Sabi–Sand), with the communal assemblage intermediate.

There were more trees and fewer shrubs in the assemblage in Kruger compared with the assemblages in the other areas, and consequently the mean potential height was greatest in Kruger (10.7 m, Figure 4.13). The communal assemblage had the most shrubby individuals, including *Dichrostachys* which is often implicated in 'bush encroachment' or 'woody thickening', and the dwarf shrub *Coddia rudis* which was not recorded in the reserves. The communal assemblage therefore had the lowest mean potential height (8.3 m, Figure 4.13). Note that this is *potential* height and not actual height, so it does not reflect the effects of wood harvesting directly but rather reflects a change in species composition, which changed the proportion of shrubs to trees. In keeping with its more riparian character, the assemblage in Kruger had more non–spiny individuals and fewer 'extremely spiny' individuals than assemblages in the other two areas (Figure 4.13).

Along the main river, the assemblage in the communal area had the most riparian character, with the highest proportion of riparian specialists and soft–wooded evergreen individuals, as well as the lowest mean potential height (Figure 4.12). This may be due to the loss of the more terrestrial species from the top of the macro–channel banks due to the clearing of fields for agriculture adjacent to the riparian zone. It is also partly due to the high cover of *Sesbania punicea*, an invasive woody species abundant on the macro–channel floor, which was not present in the reserves. Woody assemblages in Kruger and Sabi–Sand were similar to each other in functional composition and were characterised by taller trees, more woody climbers and more shrubs with the capacity for clonal spread (Figures 4.12 and 4.13).

In the herbaceous assemblages the distinction between small streams and the main river was less clear. This was mainly because of a convergence in functional composition between assemblages from small streams and the main river in the communal area (Fig. 4.14). The main traits distinguishing between the vegetation of small streams and the main river were the capacity for clonal spread, growth form, riparian affinity, potential height, specific leaf area (SLA) and leaf tensile strength (Fig. 4.14). Assemblages from the main river had more creeping graminoids and more strongly clonal species (*Cynodon*, reeds, sedges). As in the woody assemblages, riparian specialists were more common in assemblages from the main river. Mean potential height, SLA and leaf tensile strength were all higher in the main river assemblages, i.e. there were more tall, fast–growing individuals and also more individuals with tougher leaves than in the small streams (Fig. 4.15). Annuals were also more common in the main river assemblages. Nitrogen fixers were generally more common in the small stream assemblages, but there were also some important differences between management areas in the proportion of nitrogen fixing individuals (see below; Fig. 4.15).

Herbaceous assemblages from the small streams and the main river in the communal area stood out as different from their counterparts in Kruger and Sabi–Sand. Small streams in the communal area had a higher riparian affinity (dominated by category 3 individuals) than those in Kruger (category 4) or Sabi–Sand (category 5), while the assemblage from the main river had a lower riparian affinity (mainly category 3) than Kruger and Sabi–Sand (categories 1 and 2) (Figures 4.14 and 4.15). This represents a shift towards generalists among the dominant species in the communal area, and a reduction in the functional differences between small and large streams. On the other hand, assemblages in the communal area were also characterised by more perennials and more 'unusual' growth forms e.g. tubers, bulbs, rosettes, succulents, palmoids and herbaceous climbers (Figures 4.14 and 4.15). Possibly the lower herbaceous cover in the communal assemblages (Table 4.1) allowed these forb species to increase in abundance because of reduced shading in the herbaceous layer.

There was a subtle but interesting pattern of increased spinescence (more 'extremely spiny' individuals) in the communal assemblages, for woody and herbaceous assemblages, in small streams and in the main river (Figure 4.15). The pervasiveness of this effect suggests that it may be related to the management regime.

Herbaceous nitrogen–fixers were more common in the small streams than in the main river, and were particularly common in Sabi–Sand (Figure 4.15). This was due to the high cover of two leguminous forb species in particular, *Chamaecrista absus* and *Tephrosia purpurea.* The main river in the communal area also had a relatively large proportion of herbaceous nitrogen fixers.

In summary, small streams in the communal area were characterised by short, dense, shrubby woody vegetation, the presence of species with 'unusual' growth forms (geophytes, herbaceous climbers, rosettes,

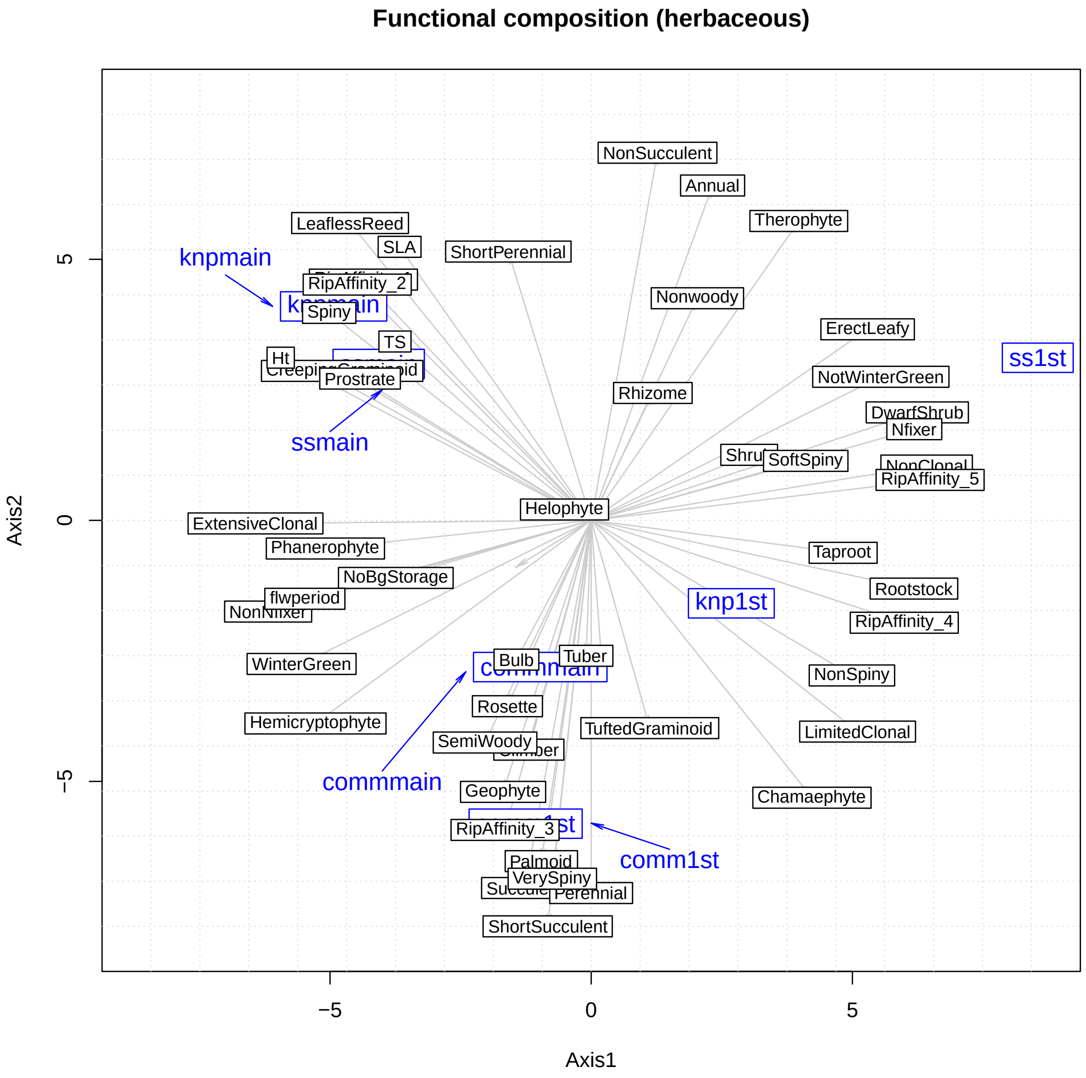


Figure 4.14: Principal Component Analysis showing the contribution of functional trait variables to the differences in functional composition among herbaceous riparian assemblages. Axis 1 reflects the separation between catchments of different sizes, axis 2 the separation between management areas. For categorical, ordinal and binary traits, each category was treated as a separate variable with values reflecting the extent to which that trait category was represented in the assemblage. For continuous traits, the mean values of the trait were compared across assemblages. Some labels have been omitted to improve clarity.

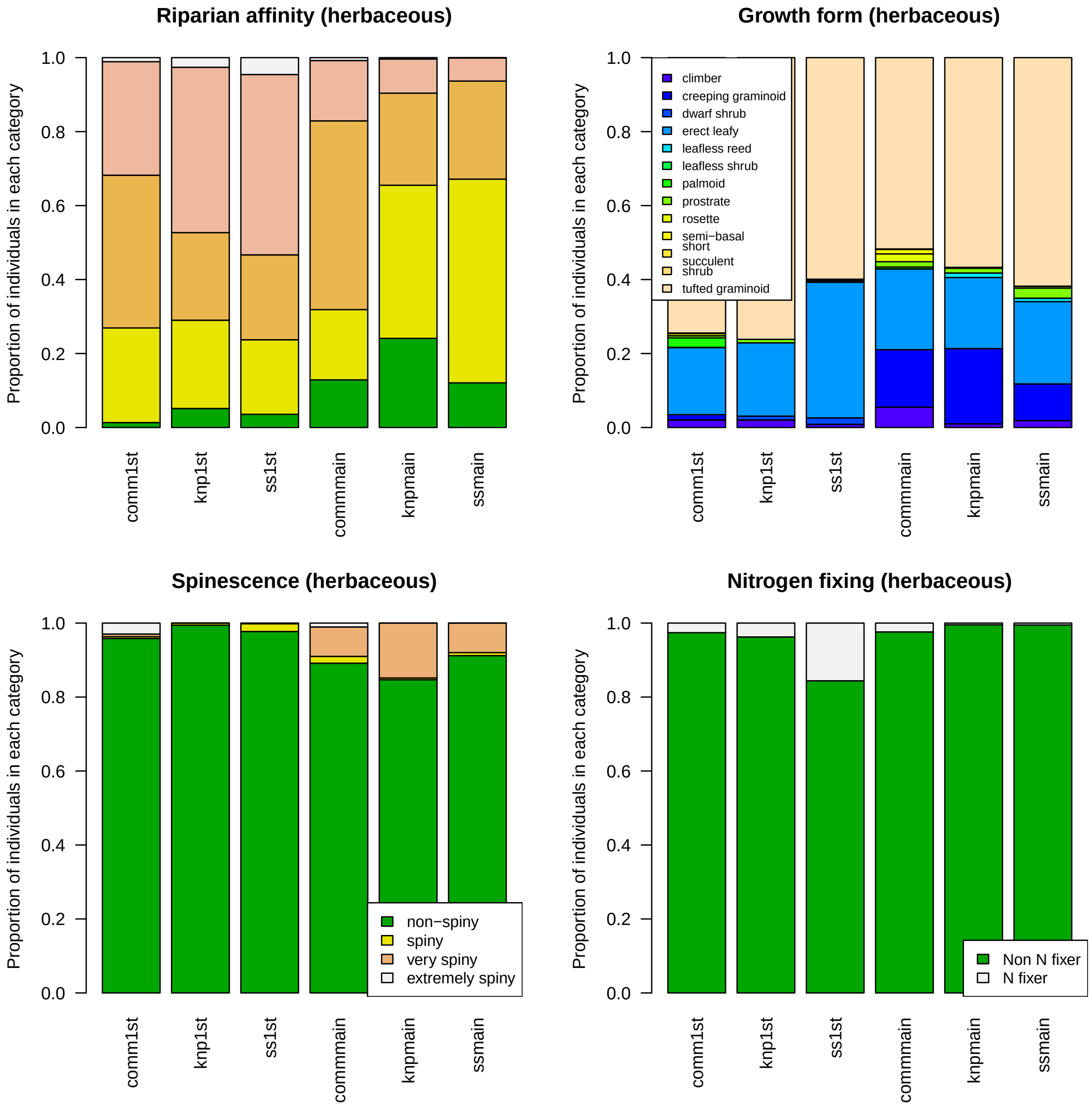


Figure 4.15: Comparison of selected aspects of functional composition in herbaceous assemblages from the three management areas. The x axis reflects the different assemblages: ‘comm’ = communal, ‘knp’ = Kruger National Park, ‘ss’ = Sabi–Sand reserves, ‘1st’ = small (1st order) streams, ‘main’ = main river.

succulents), higher spinescence, a higher proportion of perennials and a tendency towards intermediate riparian affinity among the core species. Small streams in Kruger had taller trees, fewer shrubs, lower spinescence, greater riparian affinity and a larger proportion of forbs with rootstocks or taproots (chamaephytes). Small streams in Sabi–Sand had the most open, herbaceous character, with the lowest woody cover and riparian affinity, and the highest proportions of nitrogen fixers and annual grasses and forbs. This did not reflect the effects of clearing directly, because clearing was only done in the upslope areas in the Sabi–Sand reserves and not in the riparian areas (§3.1.1).

The main river in the communal area had the largest proportion of climbers and geophytes and the lowest cover of tufted graminoids and reeds. In Kruger and Sabi–Sand, the main river assemblages were very similar in functional composition, with high riparian affinity, many clonal shrubs, high reed cover, and many short–lived perennial forbs, creeping graminoids and prostrate growth forms.

The differences in functional composition between the management areas have implications for the functioning of the assemblages and their responses to disturbance. In the main river the core species in the communal area would cycle nutrients slower than the core species in Kruger and Sabi–Sand (lower SLA, higher leaf tensile strength), and more nitrogen fixers were present. The communal assemblage from the main river also differed from the assemblages in the two reserves in food provision (more evergreen individuals to provide food in winter, but also more spiny and unpalatable individuals), shade provision (more woody evergreens but with lower potential height), fuelwood provision (more soft–wooded individuals less suitable for firewood), response to damage (more geophytes and more resprouting but fewer clonal shrubs) and response to water stress (more soft–wooded riparian specialists, which are less resistant to water stress, but fewer herbaceous riparian specialists).

In the small streams, the assemblage from Sabi–Sand differed from those in the other two areas in nutrient cycling (more nitrogen fixing forbs), food provision (more unpalatable grasses, more annual grasses and forbs that are not green in winter), shade provision (low woody cover), response to damage (fewer perennials that persist through disturbances) and response to water stress (low riparian affinity). The assemblage from the small streams in Kruger provided the most shade (taller trees and fewer shrubs, more evergreens). In the communal area, despite the high woody cover, less shade was available to animals because of the prevalence of thorny shrubs.

Functional composition therefore provides valuable insight into the functional differences between assemblages, which can help managers to evaluate observed changes by linking species composition with desired states or functions, via functional traits (Figure 4.1). To be most useful, however, compositional and functional perspectives such as those presented above need to be combined with a resilience perspective, to provide an understanding of how sustainable current functioning is. In the following section I will present some examples showing how information on species composition and functional composition can be combined with a resilience perspective to deal with specific management questions.

4.3.4 Linking the compositional, functional and resilience perspectives

Ecosystem managers are frequently required to interpret changes observed ‘on the ground’, to determine the implications of these changes for ecosystem integrity, functioning and resilience, and to make decisions as to whether the changes are desirable or undesirable. These changes may include species losses, establishment of invasive alien species, changes in species composition or balance, and changes in functional composition (such as the balance between trees and grasses, annuals and perennials, or grazers and browsers).

The approach and methods used in this study made it possible to investigate the impact of losses, gains or changes in abundance of a particular species on a particular function and on the resilience associated with particular functions. The way species were linked to functions via functional traits allowed the functioning of each species to be quantified (as its location in the functional space for a particular function). The amount of redundancy and response disparity associated with each species for each function were also quantified (redundancy as the size of the ‘nearest neighbour group’, response disparity as the dispersion of dissimilarities in response functions within each nearest neighbour group). Being able to quantify the contribution of each species to functioning and resilience, in the context of a particular assemblage, is extremely powerful because it becomes possible to address all sorts of questions about the impact of species losses or gains, or changes in composition or abundance. The power and flexibility of this approach will be demonstrated through the examples below.

Example 1: Effects of species losses on ecological functioning and resilience

Conservation managers are often concerned about species losses and the potential of species losses to affect ecological functioning and resilience. The positive relationship between species richness and the mean redundancy present in the riparian assemblages (§4.3.1) suggests that the effects of species losses on resilience will generally be negative. However, the large amount of variability in the redundancy associated with the functioning of individual species also suggests that the effects of species losses on the functioning or resilience of particular species may be quite variable.

The methods developed in this study make it possible to explore general patterns of species losses in different assemblages as well as how particular functions may be affected by the losses of particular species.

General patterns of species losses in assemblages from different management areas I used comparisons between the most species–rich and the most species–poor riparian assemblages to investigate how the redundancy of particular species (as opposed to the mean redundancy) was affected by the number of species present. Assemblages from the main river in the communal area had the lowest woody and herbaceous species richness. Assuming that the main river assemblages in the three management areas share the same species pool and would have similar species richness and functional composition if there were no differences in management practices (§3.1.1), I used the differences between the assemblages to investigate the effects of species losses on the functioning and resilience of the assemblage in the communal area.

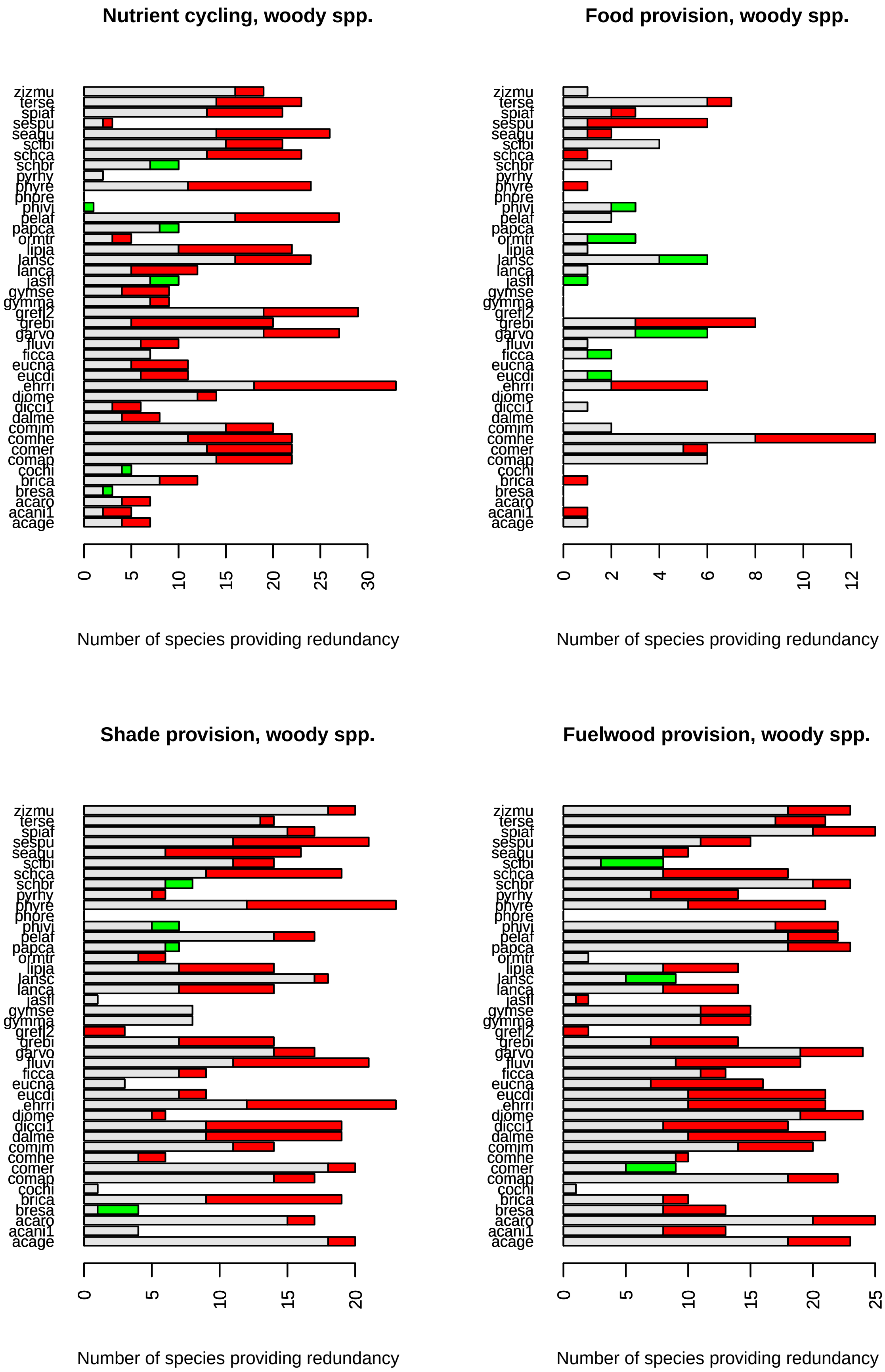
The negative effect of reduced species richness on the redundancy of the remaining species can be clearly seen in Figures 4.16 and 4.17, where the Sabi–Sand assemblages (highest richness) are compared with the communal assemblages (lowest richness). Species that were present in both assemblages had lower redundancy in the communal assemblages; there were simply fewer species available to provide redundancy. There were a few cases in which particular species had more redundancy in the communal assemblages (green bars), but these were far overshadowed by the loss of redundancy (red bars). The loss of species in the communal area therefore led to a general erosion of redundancy across all species and for all functions. The entire assemblage was negatively affected by the species losses, and not just particular species or groups of species.

There were 53 woody and 94 herbaceous species present in the main river assemblages in either Kruger, Sabi–Sand or both, that were missing from the assemblage in the communal area. Where were these species located in the various functional spaces? Did their absence reflect a systematic loss of particular functional traits in the communal area? I plotted the location of the species present in the communal assemblage in functional spaces calculated from the entire main river species pool. I then superimposed the species missing from the communal assemblage, to reveal which parts of each functional space were affected by the species losses.

The missing species occurred in similar parts of each functional space to the species that were present, and were scattered throughout the occupied portion of each space (Figures 4.18 and 4.19). There was no systematic loss of particular traits (e.g. large species, long–lived species, species with hard wood, species susceptible to water stress), which would have been indicated by clustering of missing species in particular parts of the occupied functional space. Species that were lost had a wide range of different traits. A similar pattern was found for all effect and response functions and for woody and herbaceous species (Figures 4.18 and 4.19). This strongly suggests that the species losses along the main river in the communal area did not occur because of direct targeting of species with particular traits by humans, but rather that these losses were an indirect result of land management practices.

It can therefore be concluded that the reduced species richness along the main river in the communal area was associated with a general erosion of redundancy across most species and most aspects of the functioning of the assemblage.

The picture was somewhat different in the small stream assemblages, however. Woody assemblages showed the same pattern as above, with across–the–board reductions of redundancy in the least species–rich assemblage (Sabi–Sand) (Figure 4.20). In the herbaceous assemblages, on the other hand, mean redundancy for the two effect functions, nutrient cycling and food provision, did not decrease with species richness (Figure 4.4). Comparing herbaceous assemblages with the highest (communal) and lowest (Kruger) species richness revealed the reason for this: while some species in the ‘species–poor’ assemblage had lost redundancy, others had actually gained redundancy, and the gains approximately balanced (or even slightly exceeded) the losses (Figure 4.21).



Nutrient cycling, woody spp.

Food provision, woody spp.

Shade provision, woody spp.

Fuelwood provision, woody spp.

Figure 4.16: Differences in redundancy between ‘species–rich’ (Sabi–Sand) and ‘species–poor’ (communal) woody assemblages from the main river. The species listed were present in both assemblages. The total length of each bar indicates the amount of redundancy present for each species in Sabi–Sand. Red bars indicate how much of this redundancy was lost in the communal assemblage. Green bars indicate that a species had more redundancy in the communal assemblage than in Sabi–Sand.

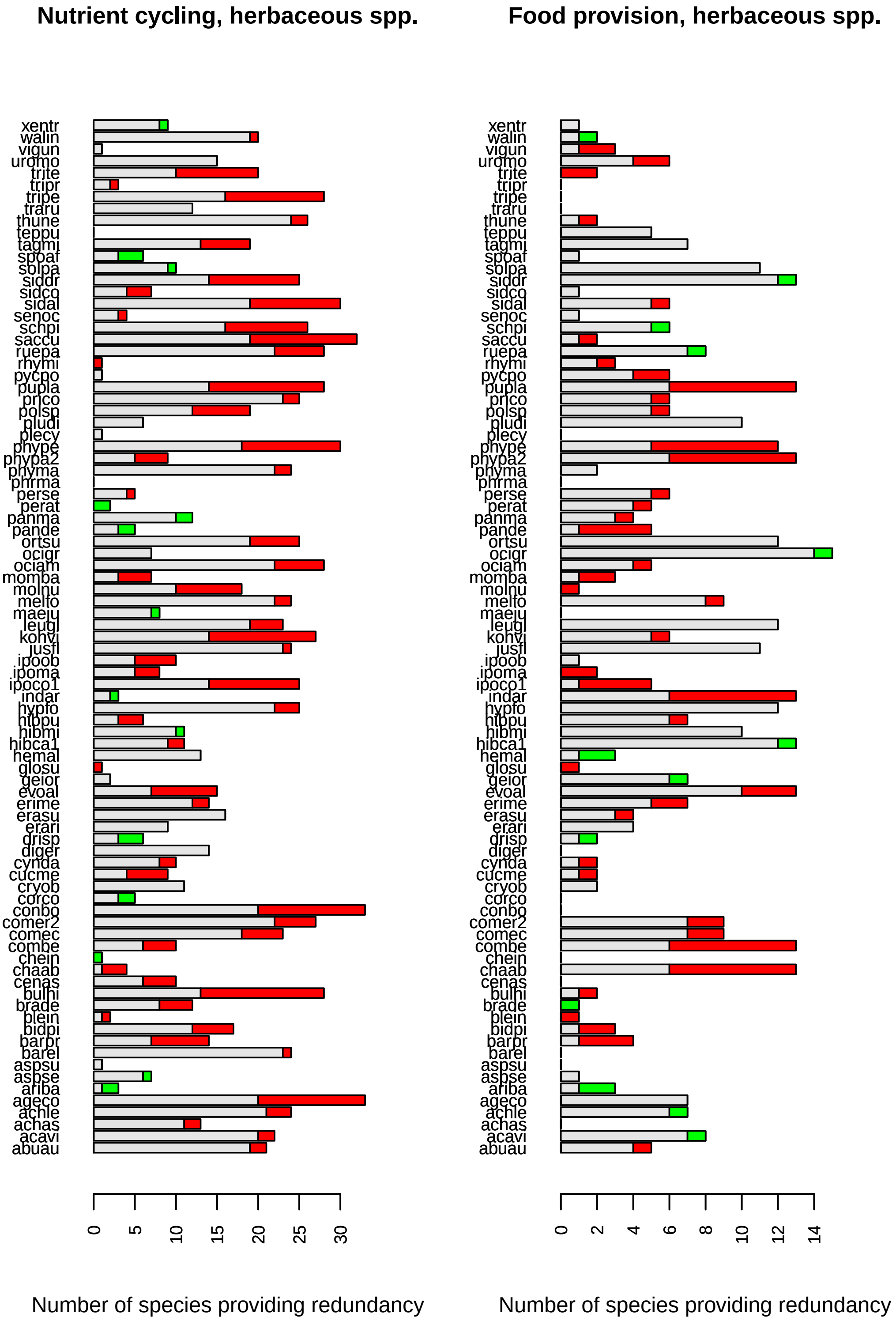


Figure 4.17: Differences in redundancy between ‘species–rich’ (Sabi–Sand) and ‘species–poor’ (communal) herbaceous assemblages from the main river. The species listed were present in both assemblages. Red bars indicate loss of redundancy in the ‘species–poor’ assemblage, green bars indicate gain, as in Figure 4.16.

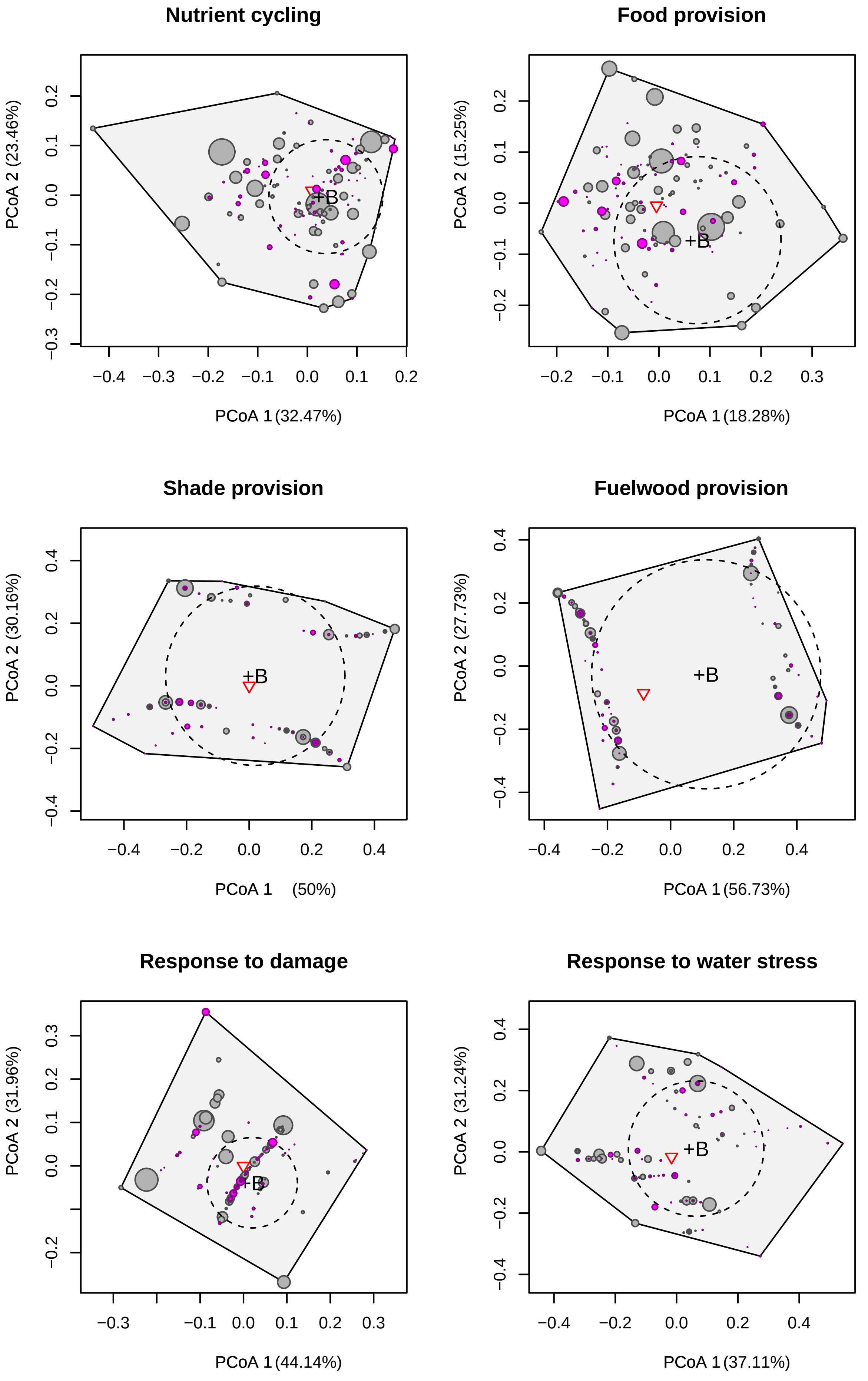


Figure 4.18: Distribution in functional space of woody species missing from the main river assemblage in the communal area (pink circles), in relation to the species present (grey circles). Size of circles indicates proportional cover of species in the communal assemblage (or in the assemblage in which they occur in the case of the missing species).

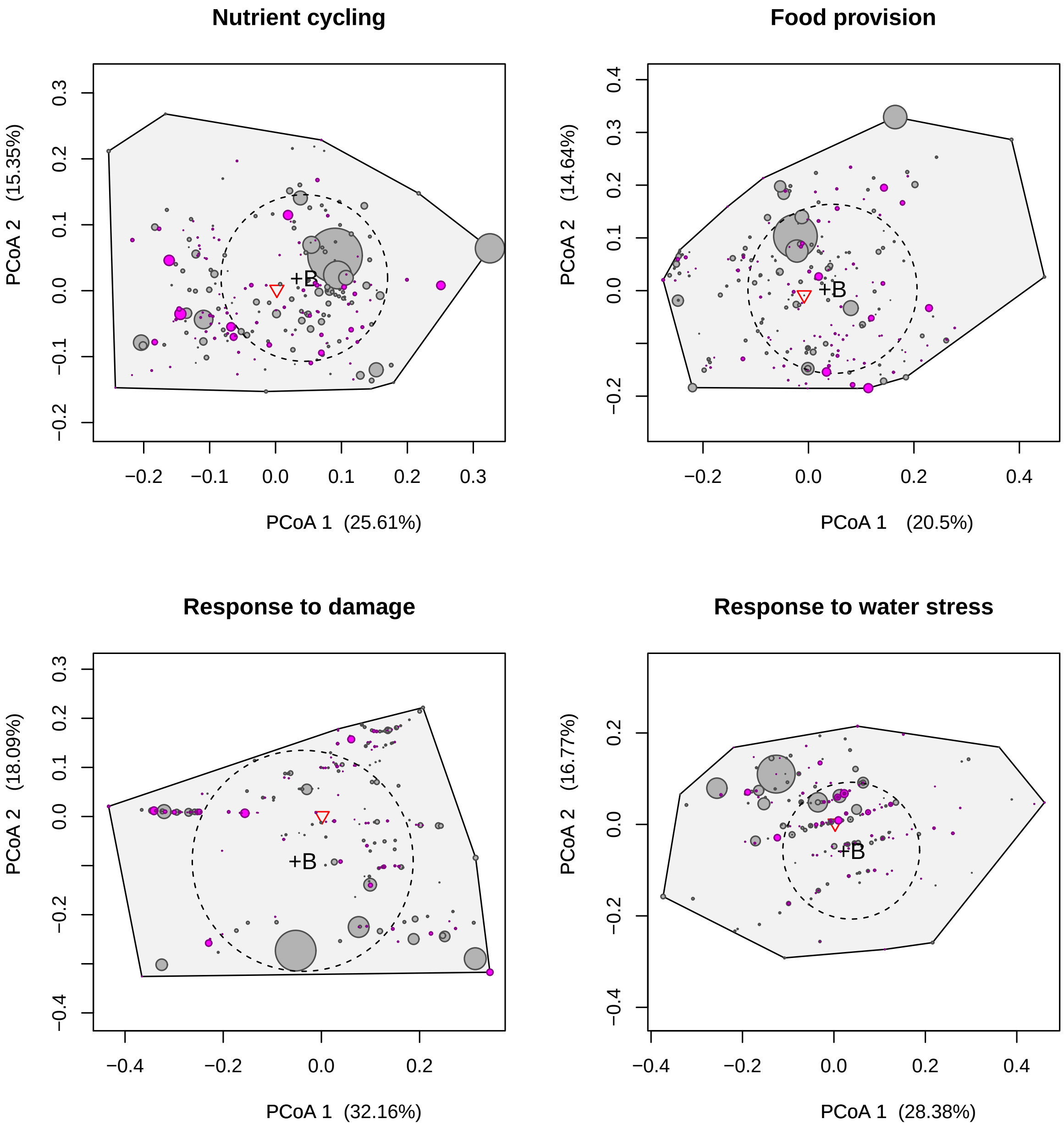


Figure 4.19: Distribution in functional space of herbaceous species missing from the main river assemblage in the communal area (pink circles), in relation to the species present (grey circles). Size of circles indicates proportional cover of species in the communal assemblage (or in the assemblage in which they occur in the case of the missing species).

How is it possible for species to gain redundancy in an assemblage with fewer species? The extra redundancy could only have been provided by the species present in the Kruger assemblage that were not shared with the communal assemblage. The results suggest that many of these non–shared species were functionally similar to the shared species and were therefore able to provide redundancy for them. In the communal assemblage, despite the fact that there were more species present, many of these species were functionally different from the shared species and therefore did not add redundancy.

Losses of particular species The example presented here concerns the loss of particular tall tree species from riparian assemblages along the main river. Tall trees are functionally important in riparian assemblages because they provide shade, which lowers soil and water temperatures and reduces evaporative losses. The presence of tall riparian trees may be considered an important part of the 'desired state' for a river system by managers, in which case an important question might be 'to what extent will the provision of shade be affected by the loss of tall tree species?'. I used data from the Sand River riparian assemblages to answer this question, as an illustration of the usefulness of my approach.

Sixteen potentially tall tree species were lost (missing) from the communal assemblage. However, 26 tall tree species were still present. The proportion of the total cover made up by tall tree species in the communal assemblage was much lower than the cover of tall tree species in Sabi–Sand (42% vs 54%), suggesting that less shade is available in the communal assemblage. However, the lower tall tree cover in the communal area was *not* caused by the absence of the 16 missing species, as none of these were particularly abundant in Kruger or Sabi–Sand. The lower cover was largely due to dramatic reductions in the cover of two species which were abundant in the reserves (*Acacia nigrescens* and *Spirostachys africana*; Figure 4.8). In other words, the differences in shade provision in the different management areas were due to differences in the abundances of tall tree species rather than to species losses.

Five tall tree species (*Combretum erythrophyllum*, *Diospyros mespiliformis*, *Breonadia salicina*, *Acacia gerrardii* and *Albizia harveyi*) made up 31% of the total cover and were therefore the most important shade providers in the communal assemblage. Four of these five species had lost redundancy for shade provision as a result of the species losses (Figure 4.16). *Breonadia salicina* gained a small amount of redundancy in the communal assemblage compared to Sabi–Sand, but its redundancy remained low. The lower redundancy means that fewer species would be available to compensate should the current dominant shade species decline. This implies a loss of resilience that may negatively affect the provision of shade in future.

The species losses did not, however, have a consistently negative effect on response disparity for the five important shade species in the communal assemblage. The range of responses to water stress were in fact bigger in the communal assemblage than in the reserves for *Diospyros mespiliformis* and *Breonadia salicina*, as seen by the fact that dissimilarity values for response to water stress within the shade nngroups for these species had a bigger range in the communal area than in the reserves (range of 0.43 in the communal area vs 0.22 and 0.19 in Kruger and Sabi–Sand respectively for *D. mespiliformis*, and 0.48 vs 0.16 and 0 for *B. salicina*). This means that species with similar shade provision characteristics to *D. mespiliformis* and *B. salicina* were more dissimilar in their responses to water stress in the communal area than in the reserves. This occurred because some riparian specialist species that provided redundancy for these five species in the reserves were missing from the communal assemblage (*Bridelia micrantha*, *Trema orientalis*, *Albizia forbesii*, *Balanites maughamii*, *Kigelia africana*, *Mimusops obovata*), leaving more 'terrestrial' species with very different water requirements to provide the redundancy. This means that shade could be provided under a wider range of hydrological conditions in the communal assemblage, because shade trees with a wide range of water requirements were present. Therefore, even if riparian specialist shade species were lost, shade could still be provided by more terrestrial species, although other functions may of course be affected differently.

Therefore, although losses of tall tree species in the communal area did not have a direct impact on the provision of shade in the riparian zone, they were detrimental to the resilience of this function. The species losses in the communal area therefore could be considered undesirable from this point of view.

Example 2: Effects of invasive alien species on functioning and resilience

Being able to examine the contribution of an invasive species to different functions separately, in relation to the contributions of the rest of the assemblage, can help managers to assess whether the new species is adding new functionality or simply adding redundancy to already existing functionality. If new functionality is added, the desirability of this functionality must then be assessed in relation to management aims or targets.

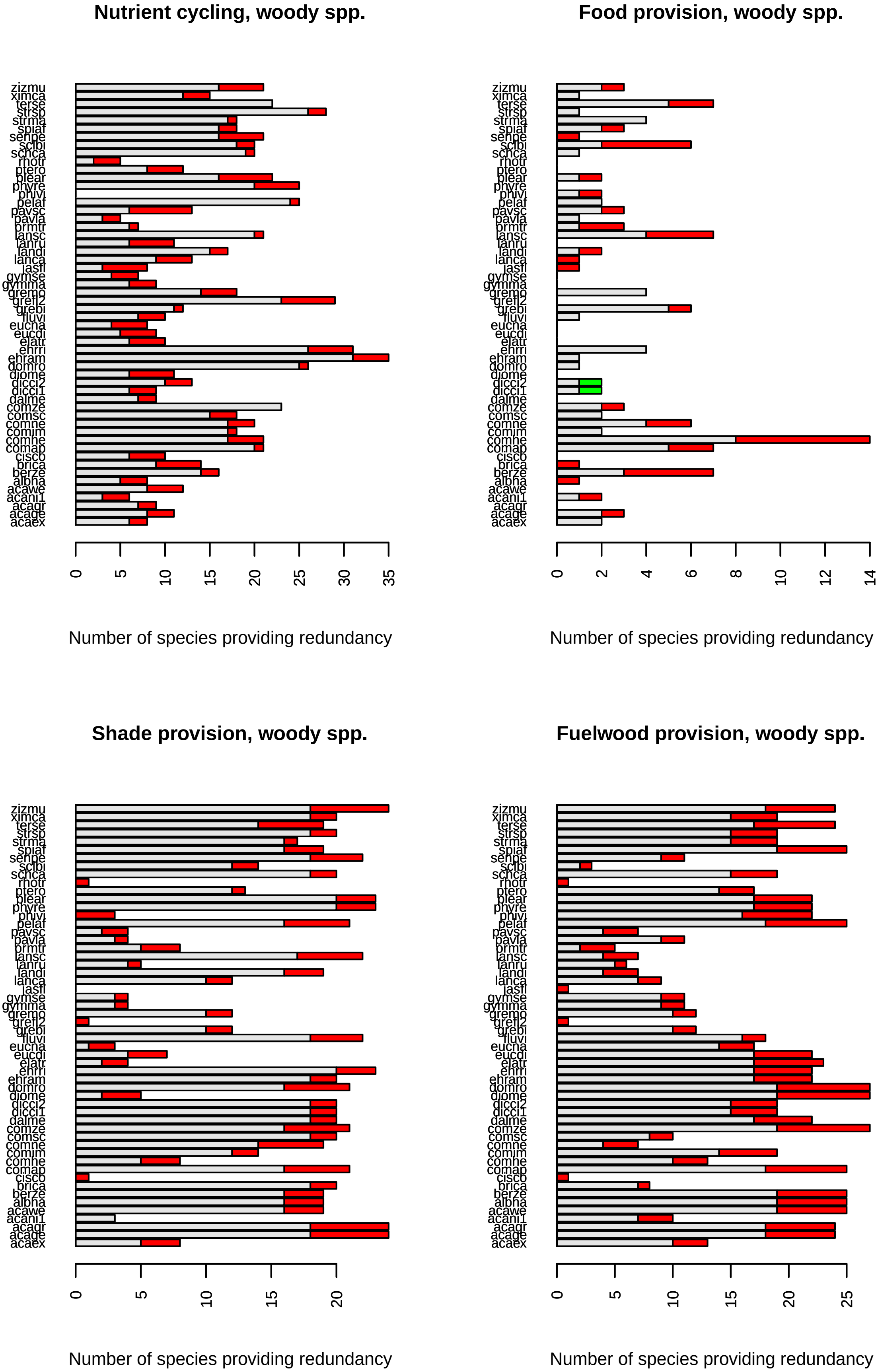


Figure 4.20: Differences in redundancy between 'species–rich' (communal) and 'species–poor' (Sabi–Sand) woody assemblages from the small streams. The species listed were present in both assemblages. Red bars indicate loss of redundancy in the 'species–poor' assemblage, green bars indicate gain, as in Figure 4.16.

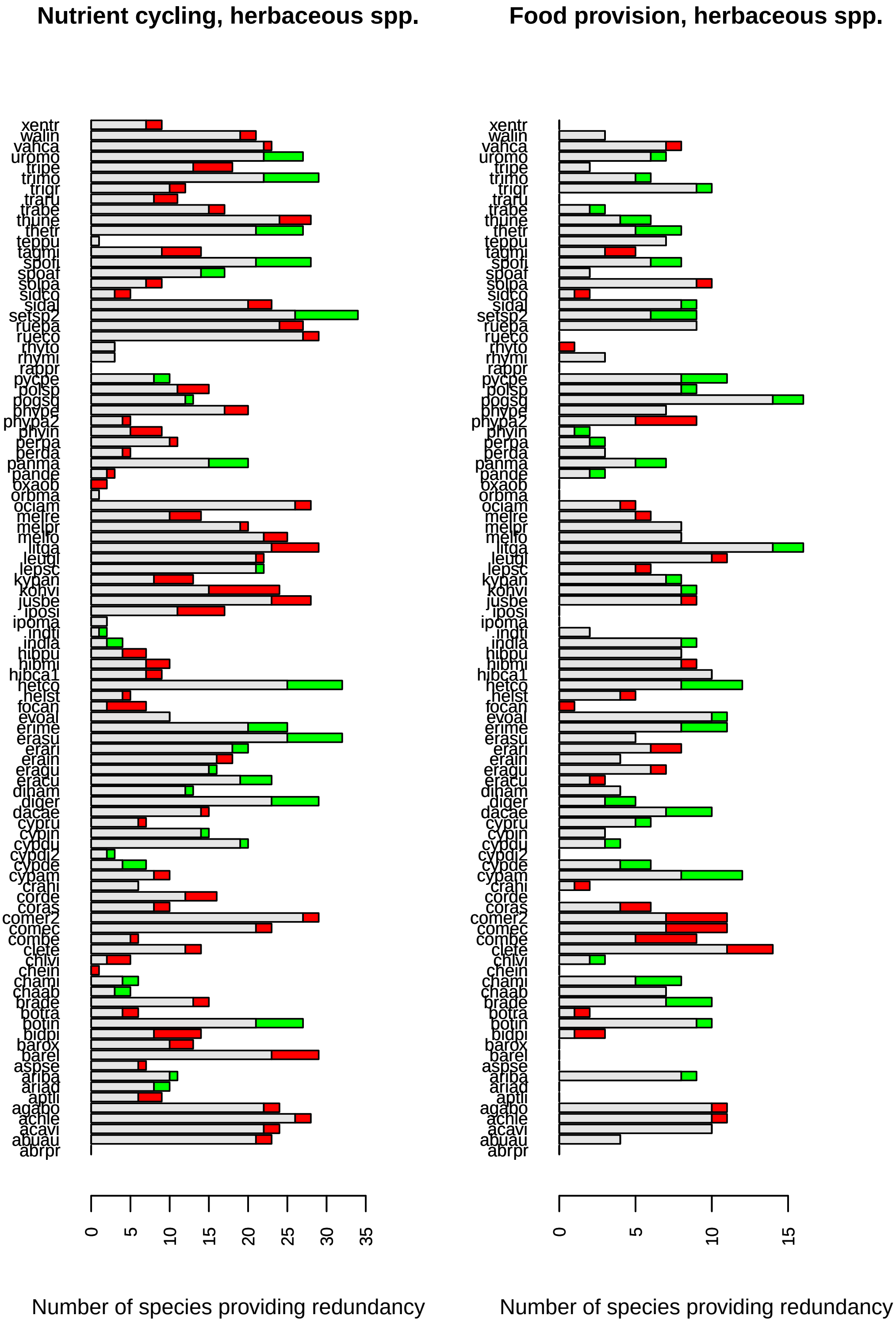


Figure 4.21: Differences in redundancy between 'species–rich' (communal) and 'species–poor' (Kruger) herbaceous assemblages from the small streams. The species listed were present in both assemblages. Red bars indicate loss of redundancy in the 'species–poor' assemblage, green bars indicate gain, as in Figure 4.16.

Figure 4.22: Woody invasive alien species present in riparian assemblages from the main–stem Sand River. (A) *Sesbania punicea*; (B) *Lantana camara*; and (C) *Melia azedarach*.

There were substantial differences in the abundance of woody alien species in the three management areas. No woody aliens were recorded in Kruger, possibly reflecting the success of alien clearing programmes. One species was recorded in Sabi–Sand, *Lantana camara*, which made up 6.3% of total abundance and 2.3% of cover. In the communal area, three species were recorded, *Sesbania punicea*, *Lantana camara* and *Melia azedarach*, together making up 5.8% of abundance and 9.8% of cover. The most abundant of these was *Sesbania punicea*, a large woody shrub originally from South America, with an abundance of 4.5% and cover of 8.1%.

The presence of *Sesbania punicea* in the communal assemblage has important functional implications because this species is a nitrogen fixer which grows on low elevation sand bars on the macro–channel floor. No indigenous woody nitrogen fixers occur in this habitat, so the alien species added functionality that was not previously present. This new functionality was mostly related to nutrient cycling and food provision, for which *Sesbania punicea* was most dissimilar from the indigenous species present. Only two indigenous species were similar to *Sesbania punicea* in nutrient cycling (*Ormocarpum trichocarpum* and *Dalbergia melanoxylon*), and one was similar in food provision (*Grewia bicolor*), but none of these species occurred in the same habitat as *Sesbania punicea* due to their very different water requirements — they were all more terrestrial species that occurred higher up on the bank. The contribution of the alien species to the provision of shade, and its responses to damage and water stress were not, however, unique and were shared by several other species.

The situation with *Lantana camara* was somewhat different, providing an interesting contrast. *Lantana camara* is a scrambling soft–wooded, spiny shrub which is widespread in the lowveld. There was a large amount of redundancy associated with most aspects of the functioning of this species, and the species was very similar to several indigenous species with which it co–occurred in the communal and Sabi–Sand assemblages, including *Flueggea virosa*, *Lippia javanica* and *Plectroniella armata*. *Lantana* did not, therefore, add new functionality to these assemblages. It appeared to have partially replaced *Flueggea virosa* (White Berry Bush). In Kruger, where *Lantana camara* was absent, *Flueggea virosa* had much higher cover (14% vs 8%). *Lantana* differs from *Flueggea* in its response to water stress, being much less tolerant of dry conditions than *Flueggea*. Changes in flow regime leading to drier conditions on the macro–channel floor may therefore cause compensatory changes in the cover or abundance of these two species without necessarily causing any change in function.

Including the functional and resilience perspectives provides a novel basis for assessing the impact of invasive alien species. We might conclude on the basis of the above that invasion by *Sesbania punicea* provides more cause for concern than invasion by *Lantana camara*, because the former alters the functional composition of the assemblage while the latter is simply one of a set of species providing redundancy for already–existing functionality. *Lantana camara* may even be considered to be adding to the resilience of the assemblage, by increasing the redundancy and response disparity associated with the indigenous species *Flueggea virosa*.

Example 3: Effects of changes in species abundance on functioning and resilience

Most often, changes in species composition involve changes in abundance rather than species gains or losses. The example presented here concerns the differences in grass species composition in assemblages from the small streams.

The assemblage in the communal area showed some notable differences in grass species abundance, compared with the assemblages in the reserves. The species with the highest proportional cover in the communal assemblage was *Urochloa mossambicensis* (27.6%). This species hardly featured in the other two assemblages (0.02% in both Kruger and Sabi–Sand). One of the dominant species in the two reserves, *Digitaria eriantha*, on the other hand, had much lower cover in the communal area (3.7%, compared to 25.8% in Kruger and 14% in Sabi–Sand). So essentially, *Urochloa mossambicensis* replaced *Digitaria eriantha* as a dominant species in the communal assemblage. There was also an increase in the cover of *Aristida congesta*, a wiry, unpalatable species, in the communal area (6.1% vs 1%). *Panicum maximum* was dominant in all three assemblages (Figure 4.7). What are the implications of these changes for ecological functioning and resilience?

Urochloa mossambicensis was in fact very similar to the other dominant grass species, *Panicum maximum*, in nutrient cycling and food provision, but less similar in its responses to damage and water stress. Replacing *D. eriantha* with *U. mossambicensis* therefore resulted in a situation where the top two species were very similar in functional effect (almost 'functional analogues'), but had different responses to disturbance. It could be argued that this reinforces the resilience of the functions performed by these species, by allowing each to compensate relatively rapidly for the other in response to changes in disturbance and available moisture. For example, if *P. maximum* declines due to heavy grazing and/or trampling, existing *U. mossambicensis* plants can increase their cover rapidly in response, allowing functioning to be maintained. The fact that both these species were so abundant and spatially widespread (found in 100% and 94% of 10 x 30 m plots respectively) further increases the likelihood of rapid compensation.

Panicum maximum and *Digitaria eriantha*, the dominant species in the Kruger and Sabi–Sand assemblages, were more different from each other than *Panicum maximum* and *Urochloa mossambicensis*. *Digitaria eriantha* was quite 'unusual' in these assemblages in its nutrient cycling and food provision traits (Figures 4.23). This can be seen by the fact that it was close to the convex hull (solid line), and its distance to the centre of the convex hull (+B) was greater than the mean (dashed circle). This means that *Digitaria eriantha* had a relatively unusual combination of traits, compared to the rest of the species in the assemblage. In this sense, *D. eriantha* can be considered relatively functionally specialised.

The shift from *D. eriantha* to *U. mossambicensis* in the communal area therefore represents a loss of functional specialisation among the dominant grasses, because *U. mossambicensis* is closer to the centre of the convex hull (Figure 4.23) and therefore less functionally specialised than *D. eriantha*. While both *Panicum maximum* and *Urochloa mossambicensis* can be considered specialists in the sense that they are found particularly in riparian areas and have a requirement for shade, they are relatively unspecialised in traits relating to nutrient cycling and food provision.

The herbaceous assemblages in the three management areas all contained similar numbers of grass species and similar proportions of unpalatable species (Table 4.4). However, overall grass cover and palatable vs unpalatable species cover varied substantially between areas (Table 4.4). The assemblage in the communal area actually had the highest cover of very palatable grasses (58%). The assemblage in Sabi–Sand had the lowest cover of very palatable grasses (38%), the highest cover of unpalatable grasses (12%), and a high forb cover due to the presence of a couple of very abundant forb species (Table 4.4, Figure 4.7). These differences suggest that plant assemblages from the different management areas function differently in terms of food provision to animals. For example, assemblages in the communal area may favour bulk grazers (such as cattle) more than assemblages in Sabi–Sand, and assemblages in Sabi–Sand may favour mixed feeders such as Kudu more than assemblages in the communal area.

More of the palatable and very palatable grass species had high redundancy for food provision in the communal area than in Sabi–Sand. Although many species had higher redundancy in Sabi–Sand (despite the lower species richness), many of these species were forbs and unpalatable grasses (Figure 4.24). For nutrient cycling, on the other hand, the palatable species generally had higher redundancy in Sabi–Sand than in the communal area, while the unpalatable species had less (Figure 4.24). The extra redundancy in Sabi–Sand was provided by a small number of palatable species that were not present in the communal area (*Schmidtia pappophoroides*, *Hyperthelia dissoluta*, *Cenchrus ciliarus* and *Eragrostis racemosa*) as well as a few sedges and forbs. Palatable grasses, considered important by pastoralists and wildlife managers, therefore had more redundancy for nutrient cycling in Sabi–Sand, but more redundancy for food provision in the communal area.

The results from the small streams, unlike those from the main river, do not support the commonly held view that communal rangelands are 'degraded', or that they are less able to support herbivores/livestock than assemblages in the reserves. Riparian assemblages from the communal rangelands had the highest palatable grass cover and the most redundancy for the food provision function. Although the top two species were functionally similar, it can be argued that this enhanced the resilience of the functions performed by these species by making rapid compensation possible. The communal assemblage had the highest herbaceous (and woody) species richness of the three areas, and had very similar numbers of palatable grass species to the reserves. It also had the highest functional richness or total range of traits present, and several unusual species were only found in the communal area. The assemblage in Sabi–

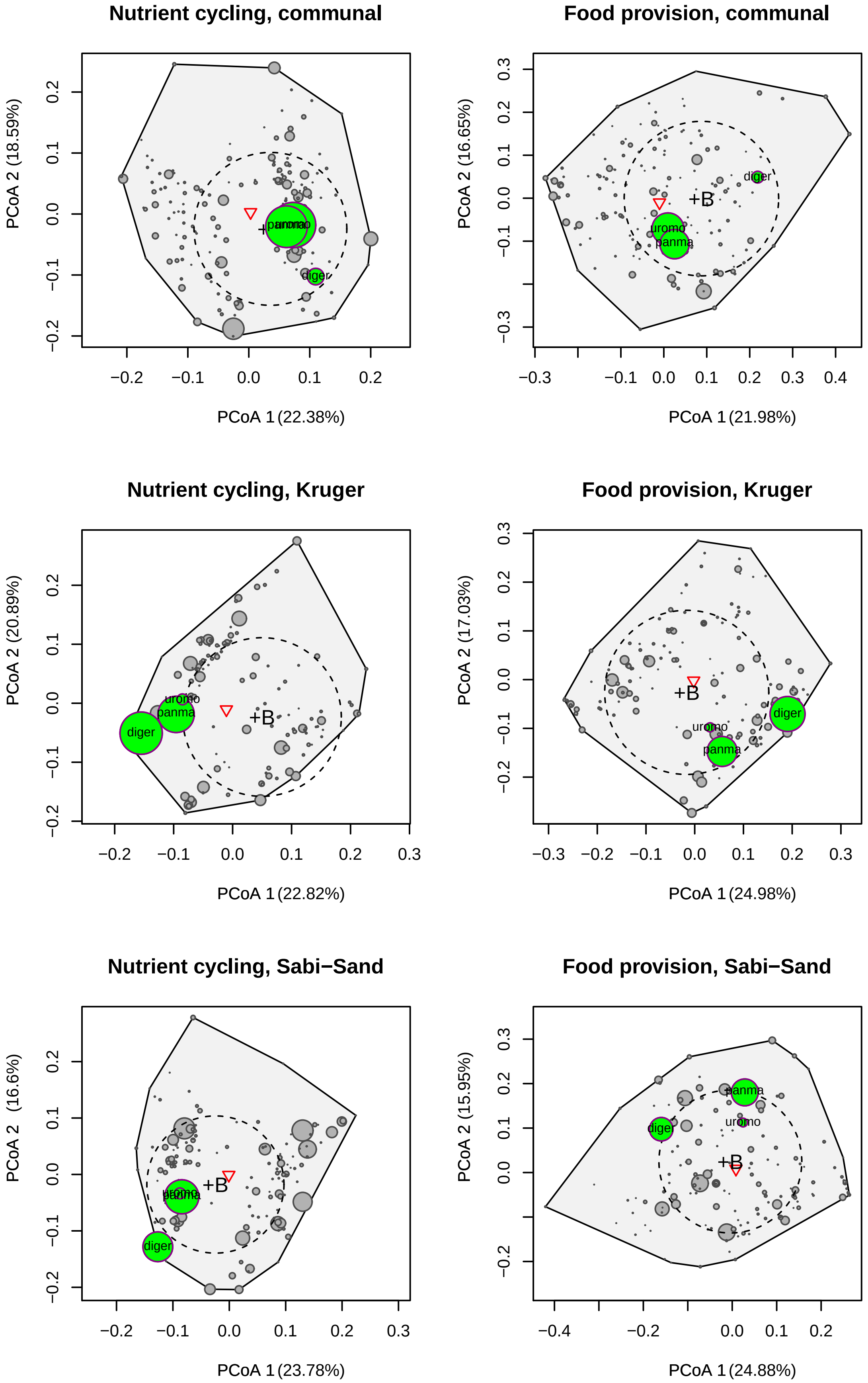


Figure 4.23: Distribution of herbaceous species from small streams in the nutrient cycling and food provision functional spaces, showing the differences in abundance and functional specialisation of three important grass species, *Panicum maximum* (panma), *Urochloa mossambicensis* (uromo) and *Digitaria eriantha* (diger) (green circles). Distance from the centre of gravity (+B) is a measure of functional specialisation because it indicates the relative 'unusualness' of a species with respect to the function being considered (Villéger *et al.*, 2010).

Table 4.4: Numbers of species and contribution to total herbaceous cover of palatable and unpalatable grasses in the three management areas. Palatability categories according to Van Oudtshoorn (2006).

		Very palatable	**Palatable**	**Unpalatable**	**Total**
Communal	No. of species	10	12	15	37
	% of cover	58.4	7.9	9	75.3
Kruger	No. of species	13	12	15	40
	% of cover	56.7	4.7	8.8	70.3
Sabi–Sand	No. of species	11	11	13	35
	% of cover	37.5	10.6	11.6	59.7

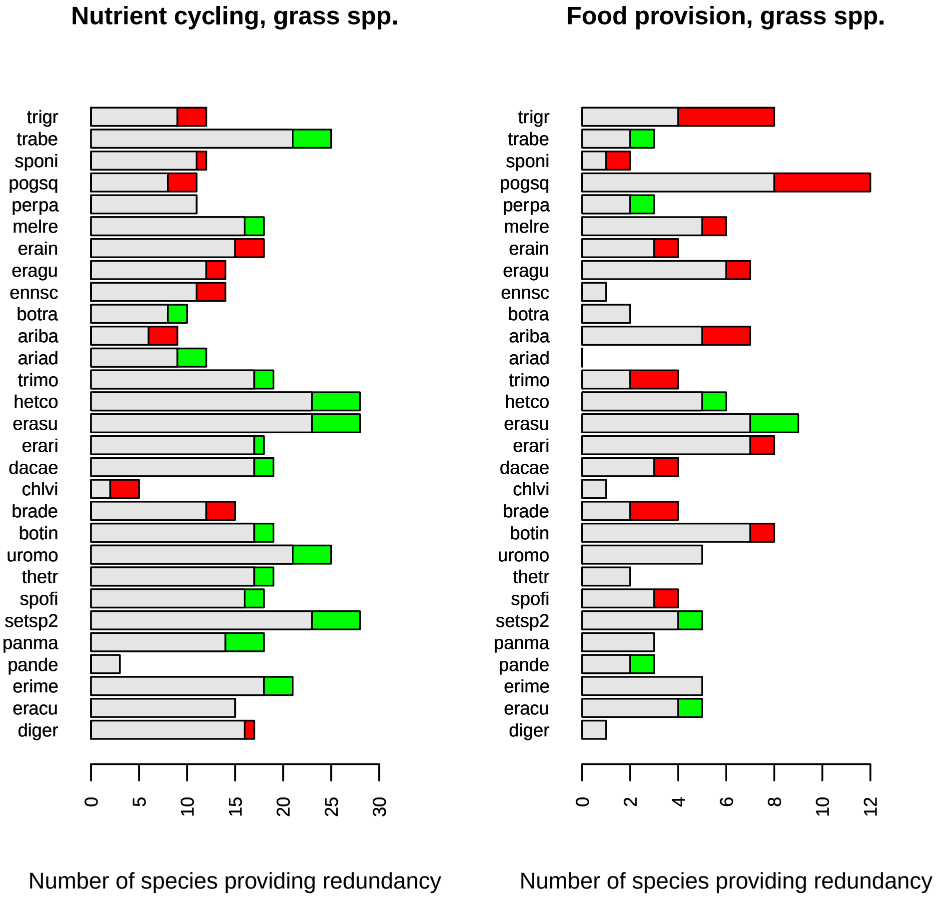


Figure 4.24: Differences in redundancy amongst grass species from small streams in the communal and Sabi–Sand assemblages. Species are listed according in the palatability categories of van Oudtshoorn, 2002 (unpalatable species at the top, palatable species in the middle and very palatable species at the bottom). The species listed were present in both assemblages. The total length of each bar indicates the amount of redundancy present for each species in the communal area. Coloured bars indicate the magnitude of the difference in redundancy, for each species, between the two assemblages. Red bars indicate lower redundancy in Sabi–Sand. Green bars indicate higher redundancy in Sabi–Sand.

Sand, despite being considerably less woody, was not more suitable for grazing than the assemblage in the communal area. These results have important implications for our understanding of ecosystem integrity and 'desired states' for riparian assemblages under different management regimes, as will be discussed below.

4.4 Discussion

The premise that biodiversity generally enhances resilience in ecosystems was the starting point for this thesis. Given the multidimensional, scale–dependent nature of both biodiversity and resilience, this statement is so general that it is of little use to managers trying to devise monitoring programmes or interpret changes observed in a particular system. This study has contributed to improving our understanding of the relationship between biodiversity and resilience, both conceptually (Chapter 1) and empirically (Chapter 3). Instead of simply assuming that a particular biodiversity measure can be used as an indicator of resilience, I have done the 'difficult work' of collecting empirical data which can help to unpack this relationship and advance our understanding of how, when and where it works.

The positive relationship between species richness (the variety component of diversity) and redundancy in the riparian assemblages studied here is an important first confirmation of the often–stated assumption that biodiversity enhances resilience. It provides empirical support to the theory upon which EBM is based, and suggests that maintaining species richness will tend to maintain redundancy in plant assemblages, and species losses will tend to reduce it. If two assemblages differ widely in species richness, the assemblage with lower species richness will generally have less redundancy and will therefore be less resilient. The more different the two assemblages are in species richness, the more sure we can be of this conclusion. This is a useful generalisation to be able to make, because species richness is relatively easy to monitor and species richness data are commonly available to managers. Despite the multifaceted nature of biodiversity, a single relatively easily measured aspect, species richness, does in fact have some value in predicting resilience. This generalisation goes some way towards providing the 'requisite simplicity' needed by managers (Figure 4.25).

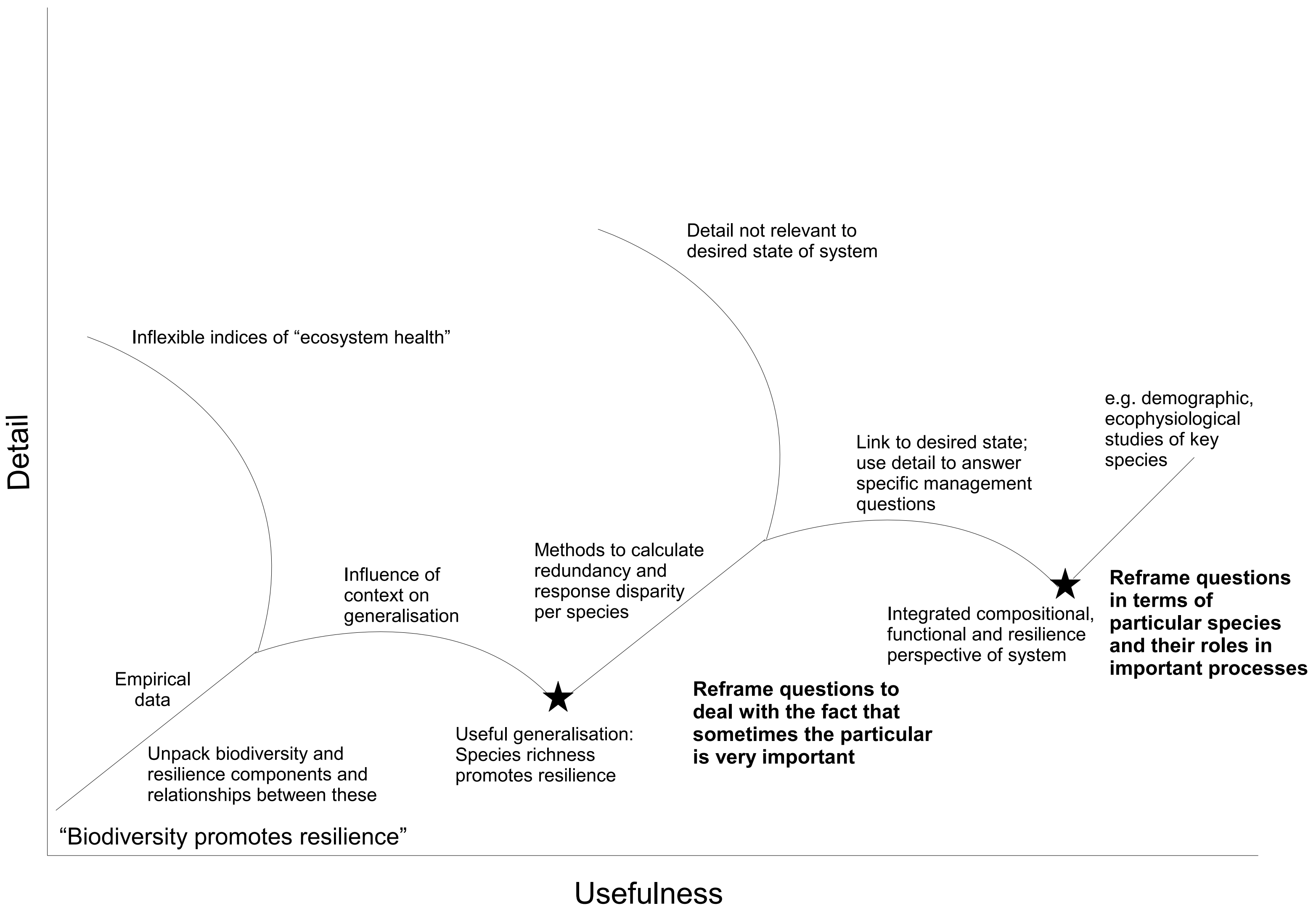


Figure 4.25: Contribution of this study to the production of information and methods useful for the implementation of ecosystem–based management.

Examining the relationship between species richness and resilience for different functions and different contexts separately (woody vs herbaceous species, small streams vs main river) increased the usefulness of the generalisation, because it provided insight into when and where in the landscape variations may occur. For example, the relationship between species richness and redundancy was stronger for assemblages from the main river than for assemblages from the small streams (Figure 4.4), and stronger for woody assemblages than it was for herbaceous ones (Figure 4.4, Figure 4.17 and Figure 4.21). Species losses are therefore more likely to cause a loss of redundancy in the main river, and losses of woody species are more likely to be detrimental to redundancy than losses of herbaceous species. Redundancy will also be lost at different rates for different functions, highlighting the need to consider different functions separately if we wish to understand the impacts of particular species gains or losses in a particular system. A possible ecological explanation for the stronger relationship between species richness and redundancy in assemblages from the main river is that species in these assemblages are more similar to each other than species in assemblages from the small streams, because of the operation of strong environmental filters such as flood disturbance (Poff, 1997). Environmental filters constrain the range of traits that species can possess in a particular environment; for example, species from the main river must be able to withstand flooding. If species from the main river are more similar to each other than species from the small streams, losing a species from an assemblage along the main river will cause more similarity (redundancy) to be lost than losing a species from an assemblage along a small stream.

However, species richness did not have a clear relationship with response disparity in this study (Figure 4.4), suggesting that species losses would have a variable, and not necessarily negative, effect on the range of responses to disturbance present in the assemblage. This is in agreement with the findings of Laliberté *et al.* (2010), who also described a variable effect of increasing intensity of land use on response disparity. It is important, therefore, not to assume that species losses *always* lead to a loss of resilience, as is often done in the conservation literature (Mayfield *et al.*, 2010).

An important aspect of the understanding gained during this study was that the effects of species losses (or gains) are sometimes irreducibly dependent on which species are involved. Species with little or no redundancy for particular functions were relatively common in all assemblages, even in assemblages with high species richness and high overall resilience (Chapter 3). If any of these species are important for the maintenance of a particular function ('keystone species'), their loss may have large or unexpected impacts on system functioning. The effects of species losses cannot therefore always be predicted from curves such as those in Figure 4.4. In other words, sometimes it is impossible to escape the need to consider the particular (such as *which* species and traits are present) to understand the impacts of species losses or changes in composition on functioning and resilience, or to address specific management questions. It is therefore necessary to retain the information on species identities and not to rely solely on generalisations based on assemblage–level properties such as species richness.

The methods developed in this thesis to consider the idiosyncratic effects of species composition on resilience rapidly produced a large amount of detail (redundancy and response disparity associated with each species, in each assemblage, for each of several different functions). Rather than attempting to find the requisite simplicity by summarising these data in the form of an index, I suggested an approach which retains the detail but concentrates on making it easier to interpret. This was done by developing compositional, functional and resilience perspectives on a particular assemblage and facilitating translation between these different perspectives. This provides a flexible way of using the detail to answer specific management questions, thus increasing its usefulness to managers (Figure 4.25). The desired states or functions identified for the system can be used as a guide to reduce the amount of detail that needs to be considered and increase the usefulness of the work to managers (Figure 4.25).

I have argued in this chapter that successful implementation of EBM requires integration between compositional, functional and resilience perspectives on ecosystems. This integration is difficult to achieve using index–based approaches to measuring diversity and ecosystem integrity because indices are inflexible and prescriptive about which data are important, and generally only provide an averaged, assemblage–level measure of diversity, function or resilience (§4.1.1). To successfully implement EBM, ecosystem managers need to be able to relate composition, function and resilience (Figure 4.1). For example, they need to be able to answer questions such as 'what are the functional implications of a particular observed change in species composition?', 'which species are responsible for an observed change in functional composition?', and 'how do observed compositional and functional changes affect resilience?'.

The approach used here, of placing species into various functional spaces on the basis of their disparities in different traits, has the benefit of allowing insight into the functional and resilience characteristics of each species, within the context of the assemblage (unlike index–based approaches). The fact that functioning, redundancy and response disparity were quantified for each species individually is much more flexible and useful than quantifying these aspects only for the assemblage as a whole, because it makes it possible to deal with a range of particular questions which cannot be answered using assemblage–level summaries.

For example, my approach allows identification of possible keystone species (those with low redundancy for one or more functions), unusual species that greatly increase the volume of functional space occupied (those on the convex hull) and species that are important providers of redundancy to many other species (those present in many nngroups). It is then possible to analyse the functioning, redundancy and response disparity associated with these important species, such as which other species provide redundancy for the various aspects of their functioning, and how this may change if particular species are lost from the assemblage. Species–level measures of resilience can always be aggregated to the level of the whole assemblage if required, but assemblage–level measures cannot be disaggregated to the level of species. My approach allows explicit consideration of the diversity within assemblages and guides exploration of the possible consequences of this diversity for functioning and resilience.

The graphical displays of species within each functional space (e.g. Figure 3.11) provide an informative summary of the species present in an assemblage, their relative abundances as well as their functional similarities/dissimilarities. The ability to highlight particular species or groups of species on these plots allows for much useful exploratory analysis. For example, one can highlight species with a particular trait (e.g. nitrogen fixers, palatable grasses), species with high/low redundancy, or species missing from a particular assemblage (as shown in Figures 4.23, 3.8 and 4.18, for example). These plots therefore facilitate integration of the different perspectives by making it easier to explore the relationships between composition, function and resilience, especially in cases where it is necessary to consider the particular details of the species involved.

The value of combining compositional and functional perspectives has previously been demonstrated by Villéger *et al.* (2010). These authors showed that in most areas of the Terminos Lagoon (Gulf of Mexico), changes in the species composition of fish assemblages did not lead to changes in functional composition and were therefore not considered cause for concern. In one area, however, the compositional changes were associated with a decrease in the disparity of fish feeding preferences, with specialist species being replaced by more similar generalist species. This allowed the authors to focus on identifying the causes and consequences of this functional change in that particular part of the lagoon (Villéger *et al.*, 2010). Similarly, I have shown that changes in riparian vegetation composition sometimes resulted in changes in functional composition, and sometimes did not. For example, woody assemblages in the communal area and Sabi–Sand were very different in species composition (Figure 4.10), but very similar in the relative proportions of shrubs vs trees (Figure 4.13). In herbaceous assemblages from the same two areas, on the other hand, differences in composition led to differences in nutrient cycling, because more nitrogen–fixing species were present in Sabi–Sand (Figure 4.11, Figure 4.15). The functional perspective provides a means of assessing whether particular compositional changes are cause for concern, as long as the functional changes can be related to what is considered desirable for the system.

The value of adding a resilience perspective is that it can provide an early warning signal for losses of ecosystem functioning. A trend of decreasing redundancy for particular functions may indicate an impending change in functioning which will only become apparent later, once a sufficient number of species have been lost, or once a particular disturbance occurs which reveals the weakness. The resilience perspective also provides information on how easy a particular change is to reverse (a large amount of redundancy and response disparity associated with a particular function will make it more resilient and difficult to change). The concept of ‘reversibility’ is useful in assessing the level of risk associated with a particular change. SANParks is currently experimenting with risk assessment processes as a way of prioritising park objectives (Gaylard and Ferreira, 2011). Comparative risk assessment (CRA) is applied towards the end of the adaptive planning process, once the park objectives have been decided upon. Objectives are prioritised according to the impact on the park’s vision and mission if the objective is not achieved, and the likelihood that this risk will be realised in the next 15 years. Processes that are irreversible or would take a long time to recover are not allowed to fluctuate as widely as processes that can easily be reversed (Gaylard and Ferreira, 2011). Such risk assessment processes would benefit greatly from the availability of information about the resilience associated with particular functions.

The approach to assessing the integrity of ecosystems suggested in this chapter, and discussed above, has several practical implications for conservation and resource managers. These implications will be explored in the following section.

4.4.1 Challenges to existing practice in EBM

The new ways of thinking about diversity and redundancy developed in this thesis generate four important challenges for conservationists, land managers or other stakeholders trying to implement EBM.

The need to include all the species when sampling assemblages

I have demonstrated in this study that species in the tail of the abundance distribution are important in providing redundancy and response disparity for the functions performed by the more abundant species in species assemblages (Chapter 3). Although some species will remain more functionally important than others because of their greater abundance, connectedness or contribution to key functions (Grime, 1998; Maclaurin and Sterelny, 2008), taking a longer–term perspective on functioning, by considering resilience, requires us to value even species that appear to be functionally unimportant at present (Walker *et al.*, 1999; Gamfeldt *et al.*, 2008; Perry, 2010). The tail species therefore need to be included in vegetation sampling if species composition data are to be informative about resilience.

While species composition data are one of the most common types of data collected by conservation and resource management agencies worldwide (Maclaurin and Sterelny, 2008; Lindenmayer and Likens, 2010; O'Connor, 2010; Ferreira *et al.*, 2011), many of these datasets are not suitable for studying resilience because the tail species are either excluded or not thoroughly sampled in the first place. Established procedures used to collect and analyse data on the species composition of plant communities (e.g. Clements, 1905; Braun-Blanquet, 1932; Bray and Curtis, 1957; Kent and Coker, 1992) often under–record or discard information on tail species, either because they are not considered functionally important, or because they are not considered 'permanent' members of the assemblage (Grime, 1998). Tail species are often not thoroughly sampled because a large amount of effort is required to do so, due to the asymptotic shape of species accumulation curves (Colwell and Coddington, 1994).

The need to include all the species, rather than just the dominant species, makes the collection of suitable data considerably more costly. Sampling designs will need to optimise detection of rare species, for example by deliberately including spatial and temporal heterogeneity in the sampling design, sampling across environmental gradients, and using nested sampling designs (see §3.2.2). It will also be important to maximise the accessibility of high–quality species composition datasets to conservation and land management agencies, by putting data standards and data sharing agreements in place and by ensuring that monitoring programmes are sustainable in the long term (Lindenmayer and Likens, 2010). The existence of organisations tasked with archiving and coordinating long–term datasets in a region is extremely valuable in this regard (e.g. the South African Environmental Observation Network, SAEON).

The need to collect functional data

Functional trait data or other data on the functioning of species are rarely included in monitoring schemes implemented by resource management or conservation agencies (Feld *et al.*, 2009). However, functional data are *absolutely critical* for any attempt to implement EBM, because of the strong emphasis in EBM on maintaining desirable functioning. I would argue that the collection of as much functional trait data, for as many species as possible, should be a priority for any organisation seeking to implement EBM, because of the usefulness of these data in addressing many different questions about functioning and resilience, as demonstrated in this thesis. Although time–consuming initially, collection of functional trait data is definitely a worthwhile investment. The initial outlay of resources needed to obtain the data is offset by the fact that these data only need to be collected once. Once a database of functional trait information has been built up, it can be used multiple times and in multiple different ways to add functional and resilience perspectives to compositional data. Functional data therefore greatly increases the value of all compositional data collected, whether in the past, present or future, for informing EBM.

The availability of functional trait information will allow methods for assessing ecosystem integrity to move away from their current strong focus on species richness and composition, which are not necessarily good indicators of functioning (Figure 4.2). For example, methods of 'veld condition assessment' (Tainton *et al.*, 1980; Tainton, 1999) are based largely on the composition of the dominant grass species, while in riparian areas the presence of invasive alien plant species in riparian areas is often taken as an indicator of functional impairment or degradation (Holmes *et al.*, 2005; Richardson *et al.*, 2007). The results of this study suggest that this may not always be a reasonable assumption. While in many cases alien species have been shown to have negative effects on the functioning and resilience of riparian vegetation (Richardson *et al.*, 2007), there may be cases where invasive alien species actually have a beneficial effect on the resilience of certain functions (see the example in §4.3.4). We should therefore avoid making assumptions about the integrity of an assemblage based on the presence of alien species.

The cost of collecting functional trait data can be reduced by collaboration and data–sharing among agencies and researchers in an area, to prevent duplication of effort. Several organisations around the world have implemented such collaborative efforts; examples include the TRY Global Plant Trait Database (`www.try-db.org`), the DiverSus network (`www.ecosystem-services.org`), and TraitNet (`www.columbia.`

`edu/cu/traitnet`). Where organisations do not have sufficient resources to collect functional data themselves, it is still possible to obtain useful information from published sources and online functional trait databases (see Appendix A). The choice of which traits to include should be guided by careful consideration of the functions/processes of interest, as was done in this study (§2.2.1).

The need to consider multiple functions

I have argued throughout this thesis that a more nuanced understanding of functioning is needed in our concepts of functional diversity, redundancy and ecosystem integrity. Measures of functional disparity and redundancy simply do not make sense unless the function for which they are being measured is clearly specified (Chapter 2). Our concepts of ecological functioning also need to recognise the fact that species and assemblages perform multiple functions, and therefore that functioning can be described in multiple different ways. While this multifunctionality may be intuitively obvious, it presents serious challenges to the scientist or manager wishing to measure functional diversity or integrity, because it vastly increases the amount of data that must be collected and analysed. Multifunctionality is therefore often ignored in order to make a particular problem more tractable. This can lead to a very narrow view of functioning which is ultimately not helpful for understanding ecosystem integrity or implementing EBM.

A good example of the problems caused by a failure to condider multiple functions when assessing ecosystem integrity is provided by the history of 'veld condition assessment' in savanna rangelands. The fact that large areas of the savanna biome around the world are used as rangelands for livestock or game (Tainton, 1999) has caused concepts of vegetation condition in savannas to revolve strongly around the ability of the vegetation to provide fodder to large herbivores. Commonly used indicators of rangeland integrity therefore also reflect this focus. These indicators include the amount of woody cover (because increases in woody cover, known in southern Africa as 'bush encroachment', are often associated with decreases in herbaceous cover and therefore in the biomass available to grazers; (Ben-Shahar, 1992; Teague and Smit, 1992; Smit *et al.*, 1996; Everson and Hatch, 1999)), the proportion of bare ground (increases in bare ground are associated with decreased grass cover, as well as with increased runoff and erosion; (Tongway and Hindley, 2004; Ludwig *et al.*, 2004)), the proportion of perennial to annual grass species (perennial species provide a more reliable food source to grazers; (Barnes *et al.*, 1984; Tainton, 1999; Van Oudtshoorn, 2006)), and the presence of grazing–tolerant or invasive species (taken to indicate 'overgrazing'; (Tainton, 1999; Van Oudtshoorn, 2006)). Areas which score poorly according to these indicators are labelled 'degraded' (e.g. Hudak, 1999; Hoffman and Todd, 2000). However, the application of such labels is problematic, because the label is often assumed to apply to other aspects of functioning besides the provision of food to herbivores, or to biodiversity in general. For example, bush encroachment is often assumed, on the basis of very little evidence, to have a negative impact on 'biodiversity' (e.g. O'Connor, 2001; Ward, 2005; Victor *et al.*, 2005; Tefera *et al.*, 2007). This is not always justifiable, as I will show below.

Communal rangelands in Africa and elsewhere have for most of this century been portrayed as overstocked, overgrazed, degraded and unproductive (reviewed by Smet and Ward, 2005; Vetter, 2005). This applies equally to the communal rangelands in the lowveld savannas of South Africa (Hoffman and Todd, 2000). These areas have been shown to display many of the characteristics of 'degradation' listed above, including bush encroachment, particularly by the fast–growing invasive shrub *Dichrostachys cinerea* (Roques and O'Connor, 2001), a higher proportion of bare ground compared to surrounding conservation areas (Parsons *et al.*, 1997; Shackleton, 2000), and a higher proportion of unpalatable grass species (Parsons *et al.*, 1997).

Perceptions of riparian vegetation integrity or condition in the communally–managed parts of the Sand River catchment have inevitably been influenced by the general perception that communal rangelands are degraded. The condition of the riparian vegetation in the communal area is considered less desirable by conservation managers than the condition of the riparian vegetation within the conservation areas (Ballance *et al.*, 2001). However, these perceptions are based on very little evidence. Few studies have specifically assessed the condition of the riparian vegetation. The River Health Programme assessments of vegetation condition along the main Sand River (Ballance *et al.*, 2001) were very superficial and qualitative, being based on the extent of vegetation cover, its structural intactness, the relative cover of indigenous vs alien species, and whether regeneration of indigenous species was occurring (Kemper, 2001). A problem with the Riparian Vegetation Index (RVI) used for these assessments is that the condition of the vegetation needs to be judged relative to a reference ('pristine') condition, and in most cases it is unknown what this reference condition should be (Jackie Jay, Department of Water Affairs and Forestry, pers. comm.). Perceptions of the integrity of riparian vegetation along the small streams are largely based on assumptions informed by the general perception of degradation. For example, riparian vegetation in the communal area is assumed to be undesirable because of the abundance of known 'bush–encroacher' species such as *Dichrostachys cinerea* along watercourses.

While this study has not sought to provide an assessment of riparian vegetation integrity in the Sand River catchment as a whole, it nevertheless provides valuable insight into the integrity (functioning and resilience) of riparian assemblages in the three different management areas. The results suggest that, in some respects, the label of 'degraded' applied to assemblages in the communal area is justified, while in others it clearly is not.

Assemblages from the main river in the communal area can be considered to be in a worse condition than assemblages in the reserves in one important respect: they had fewer woody and herbaceous species than assemblages from the reserves, which decreased the redundancy associated with most aspects of functioning considered in this study. This loss of redundancy from the communal assemblages should be considered undesirable, because it increases the risk that aspects of functioning may be lost in future. For the small streams, however, the results did not support the perception that riparian vegetation in the communal area is 'degraded'. There was no indication that the dense, shrubby thickets along the small streams in the communal area were detrimental to herbaceous species richness or resilience. The differences in grass species composition between the communal area and the reserves were consistent with known effects of heavy and sustained grazing, and included an increase in the proportion of annual grass species (mainly *Aristida congesta*), a decrease in certain palatable perennial grass species (*Digitaria eriantha*), and an increase in species tolerant of grazing and/or trampling (*Urochloa mossambicensis*) (O'Connor and Pickett, 1992). Despite these changes, however, the proportion and cover of palatable grass species was actually highest in the communal area (Table 4.4). In addition, the assemblages from the communal area had the highest woody and herbaceous species richness, the highest redundancy for most of the functions studied (Figure 4.4), the greatest variety of herbaceous growth forms (Figures 4.14 and 4.15), and several functionally unusual species. This all suggests that the dense riparian thickets along small streams in the communal area are not in fact detrimental to woody or herbaceous plant diversity, nor possibly even to the provision of food to large herbivores (cattle). The importance of small streams in the communal area from a conservation point of view should be noted. Far from being 'degraded', these areas are in fact valuable as biodiversity hotspots in the region as a whole, and this should be reflected in conservation planning for the area. The bush clearing carried out in the Sabi–Sand reserve, aimed specifically at preventing the type of situation seen in the communal areas (Ben-Shahar, 1992), should perhaps be re–evaluated.

It is therefore essential that concepts of riparian vegetation integrity (and rangeland integrity in general) move beyond their historical focus on single dimensions of functioning. An important step for starting to address other functions besides provision of food to herbivores in our concepts of savanna ecosystem functioning, is to begin to include the non–graminoid herbaceous (forb) species. Studies of rangeland integrity have focused largely on grass species composition and functional attributes (and possibly on woody species). However, most of the species richness in savanna plant assemblages is in fact provided by forbs. Forbs have been neglected in veld condition assessments (Zambatis, 2007; O'Connor *et al.*, 2011), and are also overlooked in landscape–scale assessments of vegetation functioning, in which herbaceous cover is usually called 'grass cover' and assumed to function in a uniform way (e.g. Simioni *et al.*, 2000; Sankaran *et al.*, 2004; Scanlon *et al.*, 2005; Archibald and Scholes, 2007). The multiple functional roles of forb species, and the redundancy and response diversity they provide, deserve much more attention.

The approach presented here, of using functional traits to describe the different functional roles of species, suggests a practical way in which a more nuanced understanding of functioning may be achieved. Instead of an index of ecosystem integrity or health, I have suggested that a combination of vegetation composition and functional trait data can be used to describe both functioning at a given point in time and the resilience associated with that functioning, for different functions separately. The desirability of a particular vegetation assemblage can then be discussed in relation to its actual functioning and resilience, rather than in relation to a (usually unknown) reference condition.

Rather than applying labels such as 'degraded/not degraded' or 'more degraded/less degraded' when assessing and comparing the functioning of systems, we should highlight the similarities and the differences between assemblages for different functions separately. For example, differences in functioning between herbaceous assemblages from the small streams in this study could be summarised as follows:

> The assemblages from the Kruger National Park and Sabi–Sand private reserve were more similar to each other than either was to the assemblage in the communal area with respect to response to water stress. The assemblage in the communal area had fewer species with strong terrestrial affinities, suggesting a greater susceptibility to water stress. However, the assemblages from Kruger and the communal area were more similar to each other in response to damage, nutrient cycling and provision of food to herbivores, even though they differed in

> the composition of the dominant grasses. The assemblage in Sabi–Sand was the most different in nutrient cycling, food provision and response to damage because of the larger proportion of annuals, nitrogen–fixing forbs and unpalatable grass species (see §4.3.3 for further details). In addition, the core herbaceous species from Sabi–Sand had less redundancy than the core species from the other assemblages for both nutrient cycling and food provision, suggesting lower resilience with respect to these functions.

Relating these differences in function to the desired states/functions defined for the system (Figure 4.2 will lead to a similarly nuanced description of the relative integrity of the assemblages being compared; along the lines of 'assemblage A is more desirable than assemblage B for function a, but less desirable than assemblage B for functions b and c'. Both scientists and managers need to become more comfortable with this more qualified kind of answer to the question of 'which assemblage has the greatest integrity or most closely achieves the goals of EBM?'.

The need for complexity thinking in the practice of EBM

In the riparian plant assemblages studied here, species able to provide functional compensation for each other were generally not 'drop–in replacements' that functioned similarly in all respects. Instead, species similar in one function were usually only partially similar when multiple functions were considered, differing in their responses to disturbance as well as in other effect functions (Chapter 3). This is important because it suggests that the different aspects of functioning are highly interdependent in real species assemblages. Compensatory changes in species abundances relevant to one function will necessarily affect other functions, because the compensating species (similar in that one function) also bring with them a number of functional differences. In a similar way, changes in the resilience associated with one function may lead to changes in the resilience of other functions, although it is not always easy to track or predict these changes. For example, species losses in the riparian assemblages were associated with losses of redundancy for most functions, but had variable effects on response disparity, sometimes even increasing it (§4.3.1). This interdependence, or interconnectedness, of functioning and resilience makes it ultimately necessary to consider the different functions simultaneously, including interactions and tradeoffs between them.

The interconnectedness of complex systems poses a major challenge to scientists and managers seeking to implement EBM, because the reductionism deeply ingrained in the minds of most scientists and ecosystem managers is not conducive to such integrated, holistic thinking (Rogers *et al.*, 2013). The reductionist mindset, which has dominated Western thought patterns for at least three centuries, seeks to understand the world as a collection of separable, independent units and rejects integration, ambiguity and paradox (Rogers *et al.*, 2013). The scientific method fathered by Newton is strongly reductionist in that it focuses on understanding the world by breaking it down into simpler components which can be understood using experiments (Carnap, 1995). It is assumed that understanding of these simpler components can and will lead to understanding of the whole system (Simon, 1962; Carnap, 1995; Ulanowicz, 2009).

However, it has become increasingly clear in recent years that reductionist scientific methods are not always useful for understanding complex systems or for solving complex environmental problems (Cilliers, 1998; Kay *et al.*, 1999; Levin, 1999; Wimsatt, 2007; Norberg and Cumming, 2008; Ulanowicz *et al.*, 2009). The highly interconnected, complex nature of ecosystems requires different ways of thinking, and different ways of solving problems. The new kind of thinking required has come to be called 'complexity thinking' (Zorach and Ulanowicz, 2003; Stirzaker *et al.*, 2010). Complexity thinking differs from reductionist thinking in that emphasis is placed on the organisation of, and interactions between, system elements, as well as on integration and the role of context and history in shaping observed phenomena (Levin, 1998; Ulanowicz, 2009; Rogers *et al.*, 2013). Multiple outcomes are accepted, and the emphasis is less on finding the 'right' way of framing a problem or its solution, but rather on exploring the range of possibilities (Kay *et al.*, 1999; Conklin, 2006). Rogers *et al.* (2013) use the following helpful analogy to describe problem–solving using complexity thinking. Addressing a problem is not a step–by–step process as reductionist thinking would suggest, but rather like trying to unravel the knots in a bundle of string. One cannot understand the bundle (issue) without trying to unravel it (solve it) and *vice versa.* Tugging at one point can loosen some parts of the knot but tighten others, so the process needs a holistic and empathetic approach (Rogers *et al.*, 2013).

However, complexity thinking is often not practised by those seeking to implement EBM (Rogers *et al.*, 2013), despite the fact that ecosystem–based management arose out of a recognition of the shortcomings of reductionist thinking for tackling complex problems (§4.1). In many cases people may simply be unaware of their own habitual thinking patterns, or there may be an intellectual acceptance of complexity, but a failure to fully appreciate or 'live out' its practical implications (Rogers *et al.*, 2013).

Reductionistic thinking habits are evident in the way scientists tend to divide problems into discrete elements which can each be tackled separately by disciplinary experts. For example, hydrologists, terrestrial plant and animal ecologists, limnologists and ecophysiologists each study different aspects of riparian ecosystem functioning. This separation of knowledge into 'disciplinary silos' does not foster the sort of integrated thinking required in complex systems (Kay *et al.*, 1999). Furthermore, when tackling particular problems, scientists have been trained to ignore or exclude any extraneous variables or phenomena that do not appear directly relevant to the problem at hand (Kay *et al.*, 1999). These habits do not make it easy to develop the integrated thinking which is necessary to understand functioning and resilience in ecosystems.

In an EBM context, both scientists and managers tend to see the role of science as providing 'the answers' (Kay *et al.*, 1999; Rogers *et al.*, 2013); for example providing objectively correct measures of ecosystem integrity. Scientists therefore hide the details of their analyses in simple indices to make transfer of their results to non–experts easier, assuming that these details have no further use in the framing of the problem or the solution. Managers, in turn, expect definitive, objective answers from scientists about the integrity of the ecosystem in question. And both scientists and managers expect that solutions found, and understanding gained, will be transferable to other situations. As discussed in §4.1.1, these attitudes are inappropriate in complex systems because they do not promote the flexibility of thinking required to 'untangle the knots' in an iterative, holistic way.

Changing to complexity thinking requires changing the mindset and behavior of people (Sterman, 1994). This is perhaps the biggest challenge of the four mentioned in this section, because changing the mindsets and behaviours of people and organisations is notoriously difficult (Senge *et al.*, 1999). Rogers *et al.* (2013) have suggested that fostering the following habits of mind can help to develop a more complexity–friendly mindset: openness, situational awareness and a healthy respect for the paradox of restraint *vs* action. Openness is a willingness to accept, engage with and internalize different perspectives, a willingness to affirm the legitimacy of multiple outcomes and to accept ambiguity, unpredictability and paradox (Rogers *et al.*, 2013). Situational awareness is an awareness of the importance of context when framing problems in complex systems. Context may include the historical and spatial context, but also the values and mindsets of the people involved (Rogers *et al.*, 2013). The ability to know when to practise restraint and when to take action is also important. Leaders in particular need the courage to take action in the midst of uncertainty, knowing that the consequences of their actions are never entirely predictable and there is never an objective 'right' decision (Rogers *et al.*, 2013). Models of learning and change (e.g. Argyris and Schön, 1974; Howell, 1982; Polanyi, 1983; Miller and Morris, 1999; Senge *et al.*, 1999) from the social and management sciences are useful in guiding attempts to bring about the required changes in thinking. Conservation and resource management agencies that have successfully transformed their management philosophy to a more complexity–friendly approach, such as the Kruger National Park (Rogers, 2003; Biggs and Rogers, 2003; Roux and Foxcroft, 2011) have noted the importance of attitudes such as a continual willingness to incorporate new knowledge into management and an acceptance of uncertainty (Venter *et al.*, 2008), the importance of developing integrative thinking (Biggs, 2003), as well as the importance of developing relationships between scientists, managers and other stakeholders to facilitate learning (Venter *et al.*, 2008; Stafford Smith *et al.*, 2009; Gaylard and Ferreira, 2011).

The first three needs identified above, namely the need to include all the species, the need to collect functional data and the need to consider multiple functions, all suggest that addressing the manager's dilemma in complex systems requires more data (and different data) than are usually collected during research and monitoring activities associated with EBM. Finding appropriate ways of acquiring and analysing these data is certainly challenging, but could, in theory at least, be achieved given sufficient manpower and computing power. However, simply acquiring more data would not on its own be sufficient to solve the manager's dilemma. I have argued in this chapter that to make progress in addressing the manager's dilemma we need to not only collect appropriate data, but also to use and think about these data in an appropriate way. In particular we need to use the data in a manner which takes into account the complexity inherent in ecosystems, while at the same time maximising their usefulness to ecosystem managers (see Figure 4.25). To do this it is necessary to develop a complexity mindset.

Unfortunately there are no easy solutions to the challenges of complexity for EBM practices, which include both a need for more information and a need to use that information differently. Old methods of ecosystem assessment, such as 'veld condition assessment' or the use of ecosystem health indices, cannot simply be replaced with new, better ones, because these approaches are based on a reductionistic mindset that has limited usefulness in complex systems. The need to include multiple species and multiple functions when assessing ecosystem integrity makes it difficult to recommend simple, practical methods that can be used by farmers or conservation managers.

In this chapter I have suggested a way forward for addressing the manager's dilemma of how to assess whether a system is functioning 'healthily' and sustainably. My approach involves using species composition and functional trait data to generate a multidimensional understanding of functioning and resilience in species assemblages. Statistical generalisations are used judiciously to help identify variables to measure or monitor. However, there is also an explicit attempt to retain as much flexibility as possible, so as to allow exploration of different scenarios, consideration of particular situations, and dealing with new and unexpected questions. This flexibility is achieved by avoiding summarising the data wherever possible, particularly by retaining the species–level information, and by viewing assemblages from different perspectives or points of view. These perspectives include a functional perspective, a compositional perspective, and a resilience perspective. The use of species–level measures of functioning and resilience provides a way of shifting flexibly between these different perspectives.

The composition–functioning–resilience approach described above can be distilled into the following principles:

- Don't look for a single all–encompassing measure of ecosystem integrity. Integrity or 'health' is multifaceted, like the biodiversity that underpins it.
- Include resilience when assessing integrity, because it provides a longer term perspective on functioning.
- Maximise the use of available information (avoid summarising data too much).
- View the system from multiple perspectives (e.g. composition, multiple functions, resilience).
- Build flexibility into the way ecosystems are assessed and monitored.

In the final chapter I provide a broader synthesis of the contributions of this thesis to our understanding of biodiversity, redundancy and resilience in complex systems. I present a vision for how biodiversity, redundancy and resilience should be understood, measured and applied in the context of EBM, and suggest future directions for research which will take this vision forward.

Chapter 5

Synthesis and conclusions

This chapter begins by providing a short synthesis of current thinking about biodiversity, redundancy and resilience. This is followed by a discussion of how this thesis has advanced thinking about these concepts, both in terms of theoretical understanding and in the way these concepts are used in conservation and land management. Finally, I point the way forward by identifying approaches and tools which will take this research agenda forward in the future.

5.1 Current thinking about biodiversity, redundancy and resilience in ecology

The study of biodiversity has a long history in ecology and a huge literature. Despite this, a universally agreed–upon definition is still lacking (DeLong, 1996; Oksanen and Pietarinen, 2004). The term 'biodiversity' is used in a number of different ways, reflecting different understandings of what is encompassed by the prefix 'bio'. It is now generally agreed that diversity can be described at many different levels of organisation including genomes, populations, assemblages and ecosystems (Maclaurin and Sterelny, 2008) and many different spatial scales (Crawley and Harral, 2001; Willis and Whittaker, 2002). The concept of 'diversity' itself is most commonly understood in terms of two components: the number of different types present (e.g. the number of species), and the number of individuals of each type (e.g. species relative abundances) (Magurran, 2004). Most ecological diversity indices therefore measure either the number of types (richness indices) or the distribution of abundance among types (evenness or dominance indices), or they combine these two quantities into various 'dual–concept' (Junge, 1994) diversity indices, such as the widely used Gini–Simpson, Shannon–Wiener and Hill (effective number of types) diversity indices (Magurran, 2004; Tuomisto, 2010).

However, if ecological concepts of diversity are compared to diversity concepts from the many other fields of study in which they are used (Stirling, 2007), it is clear that ecologists have generally neglected to include the differences (disparity) between types in their concepts of diversity. The recent interest in understanding the relationship between biodiversity and ecosystem functioning (Loreau *et al.*, 2002; Hooper *et al.*, 2005) has led to a growing recognition of the importance of disparity, particularly disparity in species' functional characteristics, for understanding functioning in ecosystems. However, there is still much confusion about how 'functional diversity' fits in with the concepts of diversity mentioned above, and there have been many different proposals for how it should be measured (e.g. Petchey and Gaston, 2002b; Mason *et al.*, 2003, 2005; Mouillot *et al.*, 2005; Mouchet *et al.*, 2008; Villéger *et al.*, 2008; Schmera *et al.*, 2009a; Schleuter *et al.*, 2010).

None of the existing approaches used by ecologists to measure disparity adequately addresses the multidimensional nature of disparity — species can be similar or different in many different ways, and the patterns of disparity pertaining to different functions are not necessarily correlated (Chapter 2). In particular, the intuitively obvious fact that species (or any other complex system components) generally have more than one functional role, is often ignored when measuring disparity. Functional disparity is commonly measured by collecting functional trait information for a set of species, assuming that this provides a sufficient measure of how these species 'function', and then calculating a single value for disparity (usually called 'functional diversity') in the assemblage as a whole (e.g. Walker *et al.*, 1999; Walker and Langridge, 2002; Flynn *et al.*, 2009; Petchey and Gaston, 2006; Villéger *et al.*, 2010; Cadotte *et al.*, 2011). There are two problems with this approach. Firstly, the link between the measured functional traits and particular functional roles are often insufficiently specified, so that it is unclear which function or functions are actually being considered, and 'functioning' is implicitly assumed to be a singular thing. Secondly, this approach provides a very one–dimensional view of disparity because it suggests that there is only one way of representing the differences among those particular species.

Early experimental work on the relationship between biodiversity and ecosystem functioning (so–called 'BEF' research) took a similarly one–dimensional view of disparity, attempting to use small numbers of species in artificially created assemblages to understand the effects of one aspect of diversity (species richness) on one or a few selected functions (Naeem *et al.*, 1994; Tilman *et al.*, 1996). Vigorous debate about the validity of these studies (Huston, 1997; Grime, 1997; Hooper and Vitousek, 1997; Tilman *et al.*, 1997; Hodgson *et al.*, 1998; Lawton *et al.*, 1998; Wardle, 1999) led to the establishment of larger experimental programs which included more species, more aspects of diversity, and more functions Hector *et al.* (1999); Spehn *et al.* (2005). However, for logistical reasons, the number of species in these experimental assemblages is always much smaller than in real species assemblages, usually below 20 (Hector *et al.*, 1999; Spehn *et al.*, 2005). Much BEF research has revolved around elucidating 'the relationship' between 'biodiversity' and 'ecosystem functioning' (e.g. Cadotte *et al.*, 2011). This assumes there is only one such relationship, and that both biodiversity and ecosystem functioning are singular things. More recently, a few authors have recognised that overall ecosystem functioning is in fact the combined effect of multiple functions which need to be considered jointly (Gamfeldt *et al.*, 2008; Isbell *et al.*, 2011; Mouillot *et al.*, 2011).

Functional diversity studies to date have predominantly focused on functional *differences* between species (e.g. Tilman *et al.*, 1997; Díaz *et al.*, 2004, 2007; de Bello *et al.*, 2010; Villéger *et al.*, 2010; Vogt *et al.*, 2010; Díaz *et al.*, 2011). Very little attention has been paid to the *similarities* between species. Similarities between species have been proposed by Walker (1992, 1995) to be particularly important in determining resilience, the ability of a system to maintain its functioning into the future, by ensuring that functional 'backup' or redundancy is present in the system. The concept of redundancy has, however, been contentious in ecology (Naeem, 1998; Fonseca and Ganade, 2001; Rosenfeld, 2002; Loreau, 2004; Gitay *et al.*, 1996; Jaksic *et al.*, 1996), largely because ecologists once again failed to fully appreciate the multidimensional nature of disparity (see Chapter 1). When only considering a single function, it is easy to make the implicit assumption that species similar in one function are also similar in other functions, like (functionally) interchangeable identical copies or 'analogues'. While the fact that species have multiple functional roles may be intuitively obvious, it has still not been sufficiently integrated into the way ecologists think about and measure functional disparity and redundancy.

The concept of resilience is used in a variety of interdisciplinary studies concerned with the interactions between people and nature (e.g. Holling and Gunderson, 2002; Walker *et al.*, 2002; Berkes *et al.*, 2003; Folke *et al.*, 2004; Suding *et al.*, 2004; Nyström *et al.*, 2008; Chapin *et al.*, 2009b). Resilience is generally recognised as a system–level property, and growing evidence suggests that resilience is an emergent property of complex systems in general (Carlson and Doyle, 2002), from social and economic systems (Holling, 2001; Folke, 2006; Goerner *et al.*, 2009), to complex technological systems (Csete and Doyle, 2002), to molecular and genetic systems (de Visser *et al.*, 2003; Stelling *et al.*, 2004; Whitacre and Bender, 2010). While there is still much disagreement about exactly how resilience arises in complex systems, it is generally accepted that diversity plays a central role (Levin, 1998; Carlson and Doyle, 2002; Norberg, 2004), hence the motivation for this thesis (Chapter 1).

Diversity is considered important for resilience because it provides a source of options for responding to change and disturbance (Walker and Salt, 2006; Worm *et al.*, 2006; Chapin *et al.*, 2009a). For example, the more different species, institutions or viewpoints are available, the greater will be the number of ways they can be combined, and the greater the likelihood that their interaction will produce useful novelty or innovation (Cumming *et al.*, 2005). More specifically, diversity has been proposed to lead to resilience by providing redundancy and response disparity, working together to allow functional compensation (Walker *et al.*, 1999; Elmqvist *et al.*, 2003; Nyström, 2006, see §1.2.6). However, besides the work of Walker *et al.* (1999) and Nyström (2006), these propositions have not been tested empirically. Most work on resilience is of a more theoretical or conceptual nature, and our ability to measure and evaluate resilience in real ecosystems is still in its infancy (Carpenter *et al.*, 2005; Groffman *et al.*, 2006).

So we therefore have a situation in which ecological studies of biodiversity, functional disparity and redundancy have tended to take a reductionistic approach and have focused strongly on measuring these properties and elucidating general relationships with ecological functioning, but have in most cases failed to take into account the multidimensional and interconnected nature of functioning. Much of this work is therefore not very useful for understanding resilience. Studies of resilience, on the other hand, have generally taken a more holistic, system–level approach, taking the multiple dimensions of functioning into account but producing little empirical evidence to support the contention that diversity is important for resilience, or why and how it is important.

In this thesis I have contributed to both the methods and the mindset needed to make biodiversity research more useful for understanding the relationships between diversity and resilience in complex systems. The analysis of resilience in real, riparian plant assemblages has also contributed to providing a stronger empirical foundation for resilience, by testing previously proposed hypotheses about the way in which functional redundancy and disparity influence resilience. In the following section I present a complex systems view of biodiversity, redundancy and resilience, as a synthesis of the results of my work and its contribution to the field.

5.2 A complex systems view of biodiversity, redundancy and resilience

The study of complex systems, bridging many natural and social scientific disciplines, has grown rapidly in recent years as the shortcomings of conventional science approaches to solving complex environmental and social problems have become apparent (Bar-Yam, 1997; Levin, 1998; Kay *et al.*, 1999; Cilliers, 1998; Holling, 2001; Wimsatt, 2007; Norberg and Cumming, 2008). A complex system is composed of a large number of heterogeneous components that interact in a non–simple way (Simon, 1962). Non–linear interactions and feedbacks between the components give complex systems a degree of unpredictability (Levin, 1999; Cilliers, 2005), which is exacerbated by the fact that present and future states are also determined by the history and spatial context of the system (Cilliers, 1998; Walker and Salt, 2006; Ulanowicz, 2009). Complex systems display emergent properties, properties which are not obvious from the properties of the components in isolation, but which arise because of the functional organisation and the interactions between the components (Cilliers, 1998; Wimsatt, 2007; Whitacre and Bender, 2010). The 'whole is more than the sum of the parts' in the sense that, given the properties of the components and the laws of their interaction, it is not a trivial matter to infer the properties of the whole (Simon, 1962).

Diversity is central to complexity, because complexity arises when there are large numbers of interacting components, as described above. However, it is not merely the number of components (the variety aspect of diversity) that generates complexity. The nature of the differences between the components (the disparity aspect of diversity) is also vitally important (Carlson and Doyle, 2002, see §1.2.1). Many macroscopic materials have a huge number of molecules, yet do not exhibit complex behaviour. But when the components are heterogeneous or differ from each other, especially when they do so in multiple ways, the number of possible interactions amongst them increases exponentially, thus giving rise to complex behaviour (Ulanowicz, 2009, p10). To understand the origins of resilience in complex systems, it is therefore essential that disparity be included in our concept of diversity. Disparity should be seen as an essential part of diversity itself, rather than as a mechanism which generates 'diversity' by allowing species to coexist (as assumed in theories of species coexistence and niche–based community assembly MacArthur and Levins, 1967; Abrams, 1983; Tokeshi, 1999; Weiher and Keddy, 1999; Keddy, 2001; Tilman and Lehman, 2001). Disparity describes the differences and heterogeneity which are an essential part of diversity, and which make complex behaviour possible in systems.

Ecological concepts of diversity that do not include disparity are therefore fundamentally incomplete and will hamper our ability to explore the relationship between biodiversity and resilience, or any other emergent property of complex systems, in a meaningful way. I propose that the framework provided by Stirling (2007), which presents variety, balance and disparity as three essential but individually insufficient aspects of diversity (Figure 1.1), be used to guide the further development of biodiversity concepts and terminology. Concepts of diversity which include only variety, or variety and balance, should not be called 'true diversity' (Tuomisto, 2010) or 'species diversity' (Magurran, 2004).

According to the variety–balance–disparity framework, *functional diversity* includes the variety (richness), balance (evenness) and disparity of the species or other entities of interest, where the disparity component describes *differences in function*, or functional disparity. Other types of diversity can be described in a similar way. For example, if the disparity component described differences in evolutionary history between species, we would have 'phylogenetic diversity', genetic differences between individuals in a population would be 'genetic diversity', and differences in land–use between different patches in a landscape 'land–use diversity'. These different types of diversity are all equally legitimate, and each provides a different perspective on 'biodiversity'.

Recognising the multidimensional nature of disparity is an essential first step towards developing an understanding of how functional diversity enhances resilience in complex systems. If we recognise that species perform many different functions, and that disparity and redundancy can be described for each different function separately, then we can move beyond a simplistic use of the term 'ecosystem functioning' and start to understand functioning in a manner more relevant to complex systems.

In the riparian plant assemblages studied here, patterns of disparity and redundancy were different for each different function considered (Chapter 3). Species similar in one function tended to differ in other functions, and species similar in all functions (functional 'analogues') were rare. This arrangement made it possible for both redundancy and disparity to be present in an assemblage simultaneously, for each different function considered, because each species contributed both to redundancy (for some functions) and disparity (for others). This kind of partial functional overlap between components has also been described in many other complex systems, including the immune system, the nervous system, human societies and commercial organisations (Gresov and Drazin, 1997; Edelman and Gally, 2001; Vavouri *et al.*, 2003; Whitacre and Bender, 2010, §3.4), suggesting that it may be an important general feature of complex systems. It is possible that this partial functional overlap arises because of some basic principles of statistics and combinatorics. As the number of different components increases, the probability increases that at least some of them will be similar in a particular aspect of functioning (Aarssen, 1997; Hector and Bagchi, 2007). This probabalistic argument may underlie the positive relationship between species richness (variety) and redundancy observed in this study (Chapter 4). At the same time, the more aspects of functioning are considered, the less likely it becomes that components will be identical in all their functional roles (Rosenfeld, 2002; Petchey and Gaston, 2002b; Ulanowicz, 2009), thus giving rise to complex patterns of similarity and difference among the species for the different functions.

Recognising the multiple functional roles of species helps to avoid the pitfall of assuming that species that perform one function similarly are also similar in the way they perform other functions, and successfully lays to rest the concerns that promoting redundancy will somehow be detrimental to diversity (§5.1). The commonly held view of redundancy as provided by identical copies or 'drop–in replacements' of system components is far too one–dimensional. Redundancy in real plant assemblages is provided by multiple 'non–identical copies' (species which function similarly with respect to a particular function, but differ in the way they perform other functions). No species in the assemblage are functionally 'redundant' in the sense that they are dispensible; rather all species are 'in–use' components (Low *et al.*, 2003) contributing to the functioning of the assemblage, while at the same time providing redundancy for various different aspects of each others' functioning.

The empirical evidence for redundancy and response disparity in the riparian assemblages supported two existing hypotheses (Walker *et al.*, 1999) about patterns of functional organisation in species assemblages: (1) minor species in the tail of the abundance distribution provide redundancy for functions performed by the dominant species, and (2) groups of species that provide redundancy for each others' functioning differ in their response traits, thus providing response disparity. This is the first time such patterns have been described in real, species–rich assemblages. The pervasiveness of both redundancy and response disparity in these assemblages suggests that the type of functional compensation proposed by (Walker *et al.*, 1999) and (Elmqvist *et al.*, 2003) is certainly possible (compensation for loss of functioning caused by a decline in one of the dominant species through increases in the abundance of one or more minor species from the tail of the abundance distribution). However, the highly interconnected nature of functioning in these assemblages, described above, also suggests that this concept of functional compensation is far too simplistic.

In a functionally interconnected system with multiple partial functional overlaps between species, functional compensation cannot be studied for one function in isolation, because changes in the abundance of one species will affect multiple functions simultaneously, and probably in different ways. Functional compensation will seldom be a simple matter of species replacing each other as 'drop–in replacements'. Rather, compensatory changes in species composition or balance will have knock–on effects that affect many other species and lead to many 'readjustments' in species' functioning, responses to disturbance, interactions and abundances. This may lead to complicated patterns of change which are much more difficult to interpret as functional compensation than suggested by Walker *et al.* (1999). While I did not measure functional compensation directly, the fact that species co–occurrence patterns in the different assemblages were only consistent with functional compensation in about half the cases studied, and that in about one quarter of the cases the patterns were unclear (Chapter 3), supports this contention.

Functional compensation therefore needs to be studied more holistically, considering the effects of changes in species abundances on functioning and resilience for multiple functions simultaneously. The interactions and tradeoffs between compensation processes for different functions require further study, as does the possibility of different types of functional compensation such as the 'networked buffering' proposed by Whitacre and Bender (2010), which involves more subtle changes distributed across a large number of entities (see Chapter 3). The overall resilience of an assemblage is determined by the full set of redundancy and response disparity patterns among the species for all the different functions, and the multiple possibilities for functional compensation arising from these patterns.

The interconnectedness of functioning and resilience in complex systems makes it essential for scientists to develop a complex systems mindset when studying the relationship between biodiversity and resilience. The fact that many of the measures of diversity and resilience currently used by ecologists do not adequately recognise the multidimensional and interconnected nature of functioning in ecosystems (§5.1), and therefore are not always appropriate for gaining an understanding of resilience, is not so much a fault of the methods themselves. Rather, it reflects the mindset of the scientists devising the methods.

At the end of the previous chapter I argued that the reductionist mindset dominant in the Western world is in some ways a hindrance to successful implementation of ecosystem–based natural resource management policies, and showed that recognising the complexity in ecosystems has implications for the way we collect data, the type of data collected, and the way the data are used in an applied context (§4.4.1). In fact, the need to develop a more complexity–friendly mindset also extends to the study of biodiversity and resilience, and, it could be argued, to all fields of study involving complex systems.

I have shown in this study that taking a more nuanced view of 'ecosystem functioning' that recognises the multiple functional roles of species is a good starting point for building a complexity–friendly view of ecosystems. The use of different sets of traits to describe individual species' contributions to different functions, the distinction between effect and response functions (essential for measuring response disparity), and the development of measures of redundancy and response disparity which took into account the multidimensional nature of differences between species, all allowed me to advance our understanding of the way in which diversity enhances resilience in species assemblages.

The complex systems perspective on diversity and resilience presented above should caution us against focusing only on the characteristics of the system components (e.g. species) when seeking to understand how resilience arises in ecosystems. While the characteristics of the components are important, because they determine the amount of diversity and redundancy present, and hence the functional organisation of the system, other features of complex systems have also been proposed to affect resilience. These include the interactions between the components, the hierarchical organisation of the system and the arrangement of the components in space and time (Carpenter *et al.*, 2001; Cumming *et al.*, 2005; Cumming, 2011). The measures of resilience developed and used in this thesis were based on the diversity of the system components (functional disparity and redundancy among species), as a reasonable (and tractable) starting point for understanding resilience. Diversity is an important, but not the only, aspect of complexity that produces resilience in complex systems. Future work therefore needs to explore the role of other aspects of complexity in generating resilience.

In the following section I suggest what sort of research is necessary to take our understanding of the relationship between biodiversity and resilience forward, and highlight research directions and approaches which are both compatible with complexity thinking and which will help to embed a complexity–friendly mindset more firmly in the minds of ecologists.

5.3 Future research directions

5.3.1 Put redundancy back on the research agenda

It is time to put redundancy back on the research agenda, as an important aspect of functional organisation which leads to resilience in complex systems. This thesis has provided a platform and a starting point from which to do this. Walker's concept of redundancy is a valid and useful way of examining resilience in ecosystems, if it is applied in a way which recognises the multifunctionality of species and the multiple ways in which species may differ from each other.

However, the term 'redundancy' is not the ideal term to describe this important aspect of resilience. 'Redundancy' is often used to describe the existence of identical copies of system components (in genetics and electrical engineering, for example). The negative connotations of the term have in fact been central to the debate about redundancy in the ecological literature (see Chapter 1). The term 'degeneracy', used in genetics, is equally negative, and its reference to the degeneration of similarity between duplicate gene copies over time would be obscure to ecologists. 'Partial redundancy' suggests that the redundancy provided is somehow incomplete, and still retains the negative connotation. I have retained the term redundancy in this thesis in order to relate my work clearly to the concept originally proposed by Walker (1992). However, a better term would be 'excess functional capacity' after Whitacre and Bender (2010), or even better, 'reserve functional capacity', after Ulanowicz *et al.* (2009). The co–occurrence of a number of species similar in the way they perform a particular function represents excess capacity with respect to that function. While this capacity may not always be required, it provides the buffering or insurance

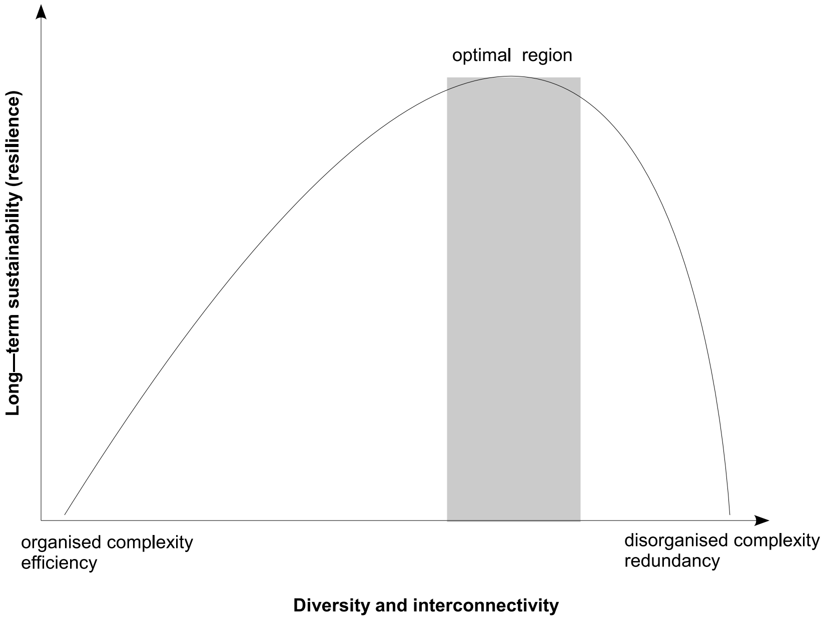


Figure 5.1: Balance between organised and disorganised complexity in ecosystems (modified from Lietaer *et al.* (2010)). The optimal region represents a statistical tendency towards balance rather than a fixed optimum.

that is so important for resilience. 'Reserve functional capacity' has the benefit of sounding more like a positive attribute than a negative one, and I propose that it be used instead of 'redundancy' in future.

5.3.2 Develop a network perspective on resilience

Biodiversity concepts currently used in ecology are focused only on the system components (e.g. species) themselves and not on the interactions between components. However, interactions between components play a key role in generating complexity in systems and are therefore thought to be important in determining emergent properties such as resilience (Simon, 1962; Levin, 1999; Cilliers, 1998; Wimsatt, 2007). Network analysis is a promising approach to measuring functional organisation in ecosystems, allowing analysis of interactions between species or other system components, connections with the abiotic environment, and overall network topology. Network approaches have the potential to greatly improve our understanding of the interconnectedness of functioning and resilience in ecosystems, by focusing specifically on the interactions.

A fascinating network perspective on resilience has been developed by Ulanowicz and colleagues (Ulanowicz, 2009; Ulanowicz *et al.*, 2009; Lietaer *et al.*, 2010). They portray ecosystems as complex flow networks which maintain a balance between order (efficiency, structure, directionality, non–randomness, organisation), and disorder (entropy, randomness, disorganisation) (Figure 5.1). A system is seen to have maximum sustainability when it has an optimal balance between these two opposing pulls. Too much efficiency in the flows of energy or matter through the system make it too tightly constrained or 'honed' to a particular environment, making it vulnerable to even minor novel disturbances, or 'brittle' in the sense of Holling and Gunderson (2002). Too little efficiency, and the system does not have the extent of activity or internal organisation needed to survive because flows are dissipated in many different directions (Ulanowicz, 2009).

Figure 5.1 encapsulates the idea that maintaining diversity is costly (to efficiency of flows; x axis), but necessary for long–term sustainability of the system. The 'diversity and connectivity' on the x axis of Figure 5.1 are, however, measures derived from network theory, and represent the effective number of roles and the connectance in a flow network (Zorach and Ulanowicz, 2003). These measures cannot be simply equated to species diversity or species richness, which only deal with the nodes (species) and not the flows between them. Much work is still needed to better understand the interplay between the species diversity perspective and the flow diversity perspective.

Network approaches are becoming increasingly common in ecology (Solé and Montoya, 2001; Pimm, 2002; Memmott *et al.*, 2004; Ings *et al.*, 2009; Ulanowicz *et al.*, 2009, e.g.), as well as in a wide range of other fields including molecular biology/genetics (Calvano *et al.*, 2005; Zhu *et al.*, 2007; Macía *et al.*, 2009) and various social sciences from psychology to economics (Borgatti *et al.*, 2009). While the data needed to construct ecological interaction networks are difficult to obtain, where they are available ecologists can make use of the great strides made by molecular biologists in analysing and visualising such data (Pavlopoulos *et al.*, 2008).

Various properties of networks can be related to both diversity and resilience. For example, food webs dominanted by generalists (which have a greater diversity of connections within the network) have been predicted to exhibit less variable dynamics than those dominated by specialists (McCann *et al.*, 1998). Evidence from plant–pollinator networks suggests that a core of generalist species is important for maintaining network structure over time (Bascompte *et al.*, 2003; Martín González *et al.*, 2010; Díaz-Castelazo *et al.*, 2010). These generalist species provide resilience by ensuring that most plants can be pollinated even in the absence of specialist pollinators, and are important in maintaining connectance among specialist species, which interact with the generalists but seldom with each other (Díaz-Castelazo *et al.*, 2010). Species that are highly connected are important because their loss would have a bigger impact on the rest of the assemblage than loss of specialist species (Memmott *et al.*, 2004).

Recent studies of network topology have shown that both flexible (generalist) and specialised network motifs or 'wiring patterns' occur in complex biological systems (Macía *et al.*, 2009). A specialised motif has a high probability of performing a particular function, while a generalist one has similar probabilities of performing several different functions. Similarly, the human immune system produces both generalist antibodies, which partially match many different antigens, and specialist antibodies, which match only a few antigens with high specificity (Forrest *et al.*, 1993). The role of diversity in generating these different types of 'wiring patterns' is a fruitful avenue for further research.

A network perspective on resilience is essential for understanding the 'alternative pathways' type of functional compensation, also known as 'networked buffering', which requires explicit consideration of context–dependent changes in interaction patterns among network components (Whitacre and Bender, 2010).

With network analysis, as with functional diversity, we need to be careful to take the multifunctionality of species into account in order to avoid reductionist thinking about functioning and resilience. Figure 5.1 represents only a single perspective, or a single way of representing a particular system (as a network of energy flows between species, for example). The meaning of 'efficiency' or 'organisation' is therefore dependent on this perspective. For example, viewing the system in terms of energy transfers leads us to define efficiency as the ability of the system to channel energy flows preferentially through a small number of routes for particular purposes, such as growth and development (Ulanowicz, 2009). However, the same system components are also related in numerous other ways, and many different interaction networks can be drawn, representing flows of various types of matter or information. We might equally validly study flows of carbon, nitrogen (or any other element), pollen or parasites in an assemblage of species. Each of these would represent a different perspective, effectively making Figure 5.1 multi–dimensional. Each of these perspectives could have different regions of optimality in the overall possibility space (Stirling, 2006).

Studies of 'biodiversity–ecosystem functioning' relationships in the last two decades have shown that if only one function is considered there is a saturating relationship between diversity and functioning, so that diversity is only beneficial to functioning up to a point (Kinzig *et al.*, 2001). However, if multiple functions are considered, the relationship between diversity and functionality becomes linear and positive (Hector and Bagchi, 2007; Gamfeldt *et al.*, 2008; Isbell *et al.*, 2011). In a similar way, I suspect that flow diversity and connectivity would have a consistently positive effect on resilience if multiple perspectives were taken into account.

5.3.3 Study different types of functional compensation

As discussed in Chapter 3, functional compensation by changes in species balance is only one way in which compensation may be achieved. It can also be achieved by developmental or functional plasticity (DeWitt and Scheiner, 2004), genetic variability within populations of species (Welham *et al.*, 2002), or 'networked buffering' involving compensation via alternative pathways in a network (Whitacre and Bender, 2010). An intriguing possibility is that different types of compensation may allow different speeds of response to change (Figure 5.2).

Certain types of physiological, developmental or behavioural plasticity allow individuals to respond rapidly to disturbance, through rapid and often reversible changes to their appearance, behaviour or functioning (Hart and Strathmann, 1994; Piersma and Drent, 2003; Gabriel, 2005; Kishida *et al.*, 2010). If such plasticity occurs among the core species in an assemblage, it will facilitate rapid functional compensation (Figure 5.2). Since the core species are mainly responsible for determining the functional profile

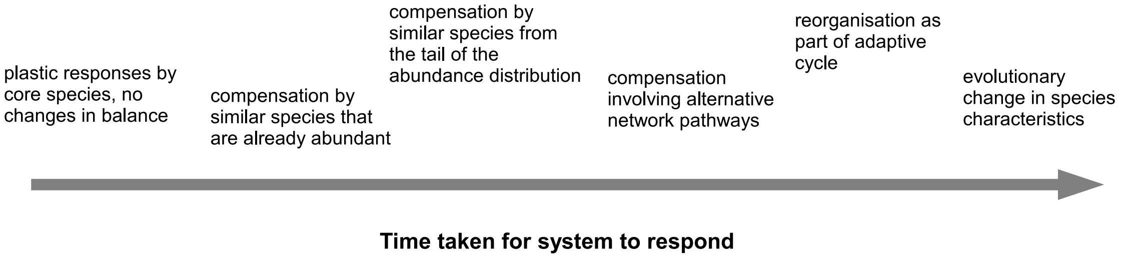


Figure 5.2: Proposed relative time taken for different types of compensatory responses to disturbance in ecosystems.

of the assemblage (Grime, 1998), plasticity which allows these species to adjust to change while maintaining their abundance and functioning will involve minimal disruption to the structure of interaction networks. Likewise, core species with generalist habitat requirements may facilitate rapid responses to change because they are able to persist in a wider range of conditions than habitat specialists (McPeek, 1996).

The type of compensation that was the focus of this thesis, involving changes in the abundances of functionally similar species, would be slower than compensation by plastic/generalist species, because changes in abundance take time. If the compensating species are already reasonably abundant or widespread in the assemblage, they may be able to increase their abundance more rapidly than rare or spatially restricted tail species.

There are several reasons why species may be in the tail of the abundance distribution at a given spatial and temporal scale (Nee *et al.*, 1991; Wisheu and Keddy, 1992; Murray *et al.*, 2002; Shipley *et al.*, 2006; Green and Plotkin, 2007). These need to be taken into account when determining which species are actually able to compensate for a given loss of functioning, and the time scale of the response. Species may be low in abundance because the conditions at the time favor the dominants, e.g. they may be competitively inferior to similar but more abundant species, and thus competitive interactions suppress their abundance in the community (Tokeshi, 1999). For example, weedy annuals are characteristic of early successional stages but decline in abundance over time as they are out–competed by later successional species (van der Maarel, 2005). Alternatively, species may form part of the tail of the abundance distribution because their populations are held in check by dynamic interactions with other species, e.g. by consumers at higher trophic levels (Ives and Carpenter, 2007). Some tail species may be habitat specialists that are locally abundant but confined to small or rare patches of habitat e.g. rock outcrops, termite mounds, permanent pools (Joseph *et al.*, 2011). Habitat specialists may not be able to replace dominant species that do not occur in the same specialised habitat, no matter how similar they are in other respects (McPeek, 1996).

Compensation involving switching between alternative network pathways could occur rapidly or slowly, depending on the number of species involved and the extent to which changes in abundance are required. Reorganisation of assemblages due to extensive disruption of their structure or species composition may provide a yet slower type of functional compensation, while evolutionary changes are proposed to be the slowest (Breuker *et al.*, 2006) (Figure 5.2). Future work needs to focus on these different types of functional compensation to understand the different ways in which functioning may be maintained in ecosystems.

5.3.4 Explore the effects of spatial and temporal organisation on resilience

The field of landscape ecology has produced a wealth of knowledge about how the spatial and temporal configuration of system components affect particular aspects of functioning (e.g. Turner, 1989; Hutchings *et al.*, 2000; Turner, 2005), but less attention has been paid to how spatial and temporal organisation affect resilience (but see Peterson *et al.*, 1998; Nyström and Folke, 2001; van Nes and Scheffer, 2005; Cumming, 2011). The spatial and temporal organisation of system components are important aspects of complex systems expected to affect emergent properties such as resilience (Cumming *et al.*, 2005; Ulanowicz, 2009). Exploring these effects will require simultaneous consideration of the connectivity, interaction and mobility of system components (see §5.3.2). The role of seed banks, patches of remnant vegetation and other forms of 'ecological memory' in resilience must also be addressed (e.g. Seymour *et al.*, 2010; White and Stromberg, 2011; Joseph *et al.*, 2011).

A large body of work in ecology and evolutionary biology attempts to explain how patterns of trait dissimilarity (disparity) arise in species assemblages (MacArthur and Levins, 1967; Abrams, 1983; Harvey *et al.*, 1983; Poff, 1997; Tokeshi, 1999; Weiher and Keddy, 1999; Cornwell and Ackerly, 2009). Although the aim of this work is usually to explain species coexistence and community assembly, it is also relevant to the study of resilience because patterns of trait dissimilarity underlie patterns of functional redundancy and response disparity in species assemblages. The amount of trait dissimilarity present in an assemblage is typically compared to the amount expected if the assemblage was randomly assembled, according to a specified null model. Trait convergence (traits underdispersed compared to random expectation) is generally taken to indicate the operation of a strong environmental filter — a set of conditions that only allows species with a certain combination and range of traits to persist (Poff, 1997; Cornwell *et al.*, 2006; Cornwell and Ackerly, 2009). Species in the assemblage tend to be more similar than expected, because they share traits that allow them to persist in that habitat. Trait divergence (traits overdispersed compared to random expectation) is usually interpreted as evidence that niche–based processes related to species interactions and/or resource utilisation are important, mainly interspecific competition (Tokeshi, 1999). A large amount of work on resource utilisation curves and 'limiting similarity' addresses niche–based processes, mostly in animal assemblages (MacArthur and Levins, 1967; Abrams, 1983, and many recent studies).

Studying patterns of trait convergence and divergence at different scales and in different contexts may be a fruitful avenue for research into the effects of spatial and temporal organisation on resilience. However, evidence for trait convergence or divergence should be interpreted with caution. Environmental filters and biological interactions such as competition may occur at very different scales. For example, competition usually only occurs between species actually occurring in close proximity (ie. small scales), whereas environmental filters related to climate, geology or disturbance may operate at much broader scales (de Bello *et al.*, 2009; Ackerly and Cornwell, 2007; Thompson *et al.*, 2010). Competitive interactions may, however, not be limited to local scales if multiple trophic levels are considered (Kraft *et al.*, 2008). In addition, environmental filters may be complex and involve several different factors with different patterns in time or space (Vamosi *et al.*, 2009). Different traits may also vary differently across environmental gradients, and simultaneous over– and under–dispersion may obscure each other (Anderson *et al.*, 2011). Phylogenetic structure, or the degree of evolutionary relatedness between species, also affects patterns of trait disparity (Webb *et al.*, 2002; Kraft *et al.*, 2007; Vamosi *et al.*, 2009). It is therefore necessary to examine patterns of trait disparity for different functions separately, across various environmental gradients, ecosystem types and disturbance regimes, and to carefully specify the temporal and spatial scale involved. Further work using the data collected in this study could explore changes in patterns of resilience across the elevation gradient in rivers (equivalent to a gradient of water availability and disturbance frequency).

When analysing resilience in ecosystems, it is important to keep in mind the broader social–ecological systems to which they belong. A system may appear resilient according to the kind of (ecologically based) resilience measures developed in this study, but it may in fact be highly vulnerable in the broader context, for example if the area is due to be cleared for an alternative land use. Alternatively, human activities and traditions may actually enhance the resilience of a system, and policy decisions which restrict these activities can be detrimental to resilience (e.g. Li and Huntsinger, 2011). The integration of social, economic and ecological understanding of systems is ultimately essential when addressing resilience (Walker *et al.*, 2002; Berkes *et al.*, 2003). This leads us to the final research thrust important for understanding the relationship between diversity and resilience in complex systems, the need to investigate the tradeoffs and interactions between different aspects of functioning.

5.3.5 Investigate the effect of interactions and tradeoffs between functions on resilience

Considering patterns of redundancy and response disparity for multiple different functions separately is an important first step towards developing a complex systems understanding of the relationship between biodiversity and resilience. However, the interconnectedness of complex systems demands that we go further, and find ways of considering these different functions *jointly*. It is not sufficient simply to average across functions, because 'overall resilience' (resilience of the whole system, all functions considered) depends on the interactions and tradeoffs among the full set of functions.

Analysing functioning or resilience jointly is difficult, but some suggestions have been provided by Gamfeldt *et al.* (2008), Stirling (2007) and de Bello *et al.* (2010). A complexity mindset is needed to 'untangle the knots', as in the bundle of string analogy in the previous chapter (Rogers *et al.*, 2013). Rather than attempting to find 'the correct way' of integrating different functions and perspectives, we need to focus on developing tools which enable systematic exploration of these different perspectives. For example, different assumptions about the functioning of the system components, the type of disparity that is relevant, and the scale(s) at which tradeoffs occur (Stirling, 2007); in other words the many different ways in which diversity, functioning and resilience may be related. Exploring these different perspectives will provide a better platform for decision–making and management, as discussed in Chapter 4.

Taking an integrated view of functioning and resilience may fundamentally alter our perception of the value associated with a system. For example, communal rangelands in Africa are generally perceived to be 'degraded' (§4.4.1). However, while commercial ranches are able to maximise meat production over the short term, and hence to be more efficient with respect to this single goal, communal production systems are more resilient in the long term (Behnke and Kerven, 1994; Scoones, 1994). This greater resilience is achieved by mechanisms that allow pastoralists to track environmental variability in time and space (Sullivan and Homewood, 2003; Niamir-Fuller, 2003), and also by the fact that cattle have a greater diversity of uses in communal systems (meat, milk, traction power, hides, social status) (Behnke and Kerven, 1994). These multiple benefits, in the long term, are equal to or greater than the benefits derived from meat alone in commercial production systems (Behnke and Kerven, 1994). Communal production systems therefore maximise multiple functions as opposed to one function, at the cost of lower efficiency in any one of these functions, but with the benefit of greater overall resilience and no loss in overall value. These sorts of interactions and tradeoffs among functions need to be considered when developing a complex systems understanding of diversity and resilience.

Scenario–building is becoming a favoured approach for exploring different possible futures in complex social–ecological systems (Kay *et al.*, 1999; Bennett *et al.*, 2003; Peterson *et al.*, 2003; Carpenter *et al.*, 2006). Scenarios are narrative accounts of plausible alternative futures for a particular system (Bennett *et al.*, 2003). Scenario planning involves constructing and using a small number of different scenarios to explore the uncertainty around the consequences of particular management choices (Peterson *et al.*, 2003); in other words, to play out the consequences of choosing different options. Each scenario may represent a different set of tradeoffs among functions or values (Kay *et al.*, 1999) and can include a variety of quantitative and qualitative information (Peterson *et al.*, 2003; Carpenter *et al.*, 2006). Quantitative analyses of diversity and resilience such as those in this thesis can be included in scenarios, and used together with scenario planning to explore the consequences of varying levels or types of diversity on ecosystem service provision and resilience (Carpenter *et al.*, 2006; Stirling, 2007). Scenarios can also help scientists to organize their views of how ecosystems work (Bennett *et al.*, 2003) and develop research questions appropriate for studying the relationship between diversity and resilience in complex systems.

The emphasis throughout this thesis has been on developing a thoughtful and critical evaluation of current thinking and practice in the study of the relationship between biodiversity and resilience. One of the major shortcomings identified has been the tendency to approach the study of resilience in an overly reductionistic manner, for example by selecting only a few species or functions to study in an attempt to elucidate general principles or management guidelines. I have argued that this is inappropriate in compex systems, and hampers our ability to understand emergent properties such as resilience. The approach I have used to study resilience, while reductive at times, has also sought to take complexity into account. This was achieved by recognising that species have multiple functional roles and by developing species–level measures of redundancy and response disparity that allowed me to describe the patterns of functional overlap between species, for multiple functions, in a highly detailed way. This highlighted the interconnectedness of functioning in species assemblages and suggested that future research should aim to further develop our ability to study resilience in a holistic manner. The composition–function–resilience approach presented here for assessing the integrity of ecosystems for EBM, was also designed to take the complexity of ecosystems into account. This was done by avoiding prescriptive indices and excessive data summarisation, thereby retaining the ability to consider the 'particularities' of a given situation, which are often so important in determining outcomes in complex systems.

In conclusion, this thesis has made contributions to the conceptual understanding (Chapter 1), the methods required to measure (Chapter 2), and the empirical evidence for (Chapter 3), two important manifestations of diversity which have been proposed to affect resilience in species assemblages, namely functional redundancy and response disparity. In so doing it has contributed to developing a stronger empirical foundation for ecosystem–based management (Chapter 4), and has advanced our understanding of the relationship between the multifaceted concepts of biodiversity and resilience.

Appendix A

Details of methods

A.1 Functional trait data

A.1.1 Details of leaf trait measurements

A description of how leaves were collected and selected for measurement of leaf traits was given in Chapter 2. This section contains further details of the apparatus and methods used, as well as a record of how special cases were handled, as recommended by Cornelissen *et al.* (2003).

Specific leaf area

Specific leaf area is the one–sided area of a fresh leaf divided by its oven–dry mass (the inverse of leaf mass per area or LMA). It was calculated by measuring the projected area of fresh leaves, then drying the leaves and weighing them (Cornelissen *et al.*, 2003).

Leaf area was measured using an EPSON Perfection 3200 Photo scanner together with Leaf Area Measurement software (version 1.3, A. P. Askew, University of Sheffield, June 2003; `www.shef.ac.uk/~nuocpe/`). Images were scanned at 600 dpi (800 dpi for very small leaves), using the 'black and white' output mode, no scaling options, and the default brightness, contrast and threshold settings, as recommended by the authors of the software. A calibration constant of 0.00561 was used.

The area measured included the petiole (or the rachis for compound leaves). Large leaves and leaves that could not easily be placed flat in the scanner, including curved and rolled leaves and compound leaves with overlapping leaflets, were cut into pieces and the areas of the pieces summed. The very large leaves of the palm *Phoenix reclinata* had to be cut into a large number of pieces. The spines present on the rachis of this species were included in the area measurement. For geophytes with no above–ground stem, including *Stylochiton natalensis*, *Gonatopus angustus* and *Ophioglossum polyphyllum*, leaf area was measured from the point of attachment to the bulb or rhizome.

For grasses and sedges the leaf sheath was removed together with the leaf, by cutting the stem at the point of attachment of the sheath. The sheath was then separated from the blade and the two parts scanned separately. In most species, the leaf sheaths were difficult to unroll and lay flat on the scanner without breaking them, so they were rather folded in half and flattened before scanning. Leaf area A was then calculated as:

$$A = blade\ area + (2 \times sheath\ area)$$

Translucent parts of the sheaths were darkened using a black permanent marker to ensure proper scanning and area calculation. A few other non–graminoid species with leaf sheaths were treated in the same way (e.g. *Commelina* species).

For species with no leaves, the photosynthetically active stems were used. For the succulent cactus *Opuntia ficus-indica* I used whole cladodes, sectioned longitudinally to allow them to be placed flat in the scanner. For *Sarcostemma viminale* and *Orbea maculata*, which have cylindrical succulent stems, I used the smallest branches, from the point at which they branched off from another stem. The relatively short stems of *Orbea maculata* were sectioned longitudinally and one of the resulting two half–cylinder sections

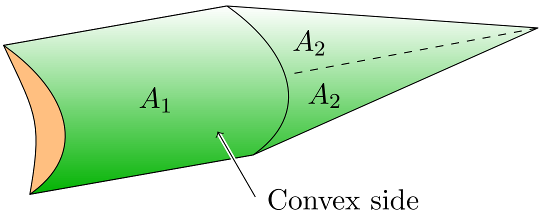


Figure A.1: Idealisation of a leaf of *Aloe marlothii* for calculating its leaf area. The area of the convex side of the leaf is approximated as $A_1 + 2A_2$. The area of the concave side is approximated as $A'_1 + 2A'_2$ (not shown).

was then cut in half again lengthways to increase the accuracy of the projected area measurement. The long succulent stems of *Sarcostemma viminale* were not scanned because this was difficult to do accurately, and the sticky white latex was problematic while scanning. Area of these stems was calculated as:

$$A = \frac{1}{2}(circumference)/diameter$$

For the horsetail *Equisetum ramosissimum*, I also used the smallest branches as leaf equivalents, and flattened the hollow stems before scanning.

The large (75–150 cm long, 15 cm wide, 5 cm thick) succulent, spiny leaves of *Aloe marlothii* were not scanned because this would have required extensive cutting to obtain pieces that could be laid flat in the scanner, and the gelatinous orange sap on the glass of the scanner interfered with the scanning process. The area A of these leaves was therefore calculated using the following formula and using the leaf shape idealisation shown in Figure A.1:

$$A = \frac{1}{2}(A_1 + 2A_2 + A'_1 + 2A'_2)$$

Scanned leaves were labelled (taking care to keep all cut pieces of a particular leaf together) and dried in an oven at 80^oC for 48 h (or longer for large succulent species). Leaves were then weighed using an analytical balance (Denver Instrument, model PI-114), to an accuracy of 0.1 mg. The SLA values for the two leaves from each plant were averaged to give a mean value per plant, then the mean values for each plant were used to calculate the mean and standard deviation for the species (i.e. each plant used as one statistical observation).

Leaf tensile strength

Leaf tensile strength was measured using a simple custom–built ‘leaf tearing apparatus’, similar to the one described in Hendry and Grime (1993). The apparatus was built by the University of Cape Town Life Sciences Workshop as a copy of the device used in functional trait screening programmes around the world (Díaz *et al.*, 2004), according to specifications and a sample provided by Sandra Diaz. The device essentially records the force required to tear a leaf fragment which is held in place with clamps at each end (Figure A.2).

Fragments of leaf blade were cut from the central section of the leaf, avoiding the midrib if present, as described by Cornelissen *et al.* (2003). These fragments were 20–30 mm long and 10 mm wide in most cases, but where leaves were too small or too tough, narrower strips were used and the calculation adjusted accordingly (minimum width was 1 mm). For compound leaves strips were taken from one leaflet only. For grasses and sedges I used the full width of the leaf blade if this was less than 10 mm, or slightly less than half the width if a clear midrib was present. If strips of 1 mm wide could still not be broken, I first tried securing the ends more firmly by placing double–sized tape at the ends of the strip and tightening the clamps, failing which I recorded tensile strength as the maximum value obtainable with the apparatus (60 N.mm^{-1}).

Species with very finely divided bipinnately compound leaves, such as many *Acacia* species, presented a particular problem, as even whole pinnules were too tiny to clamp into the device. For these species whole pinnae were used (pinnules plus axis), as the axis was judged to be equivalent to the main veins of simple leaves. For species with very small simple leaves, such as *Asparagus* species, the largest possible leaves were used. If no leaves were large enough to use (e.g. *Asparagus minutiflorus*), tensile strength was estimated from the values obtained for other species in the genus. For plants with succulent leaves or succulent stems, I used fragments of epidermis, while for leafless species with hollow stems, such as *Equisetum ramosissimum*, I used fragments of unrolled stem.

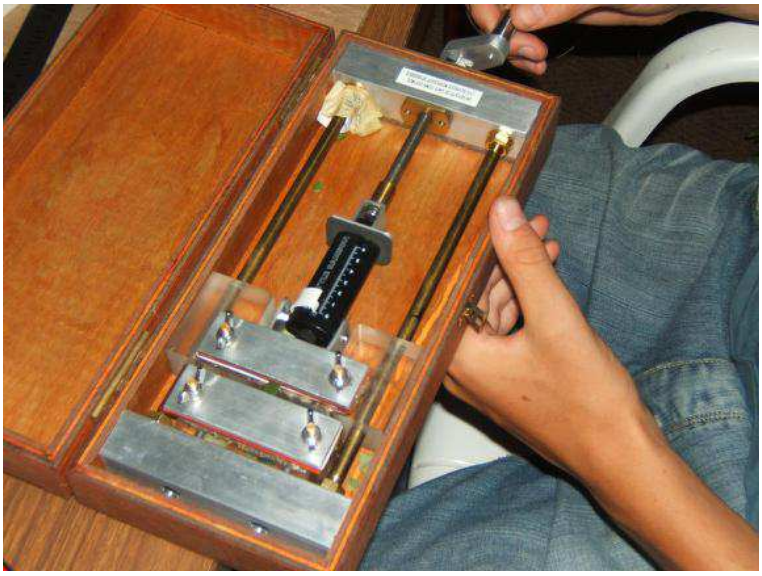


Figure A.2: Custom–built device for measuring leaf tensile strength.

As for SLA, I calculated mean tensile strength values per plant, and means and standard deviations per species.

A.1.2 Details of how literature–based trait information was collected and recorded

Growth form

Each species was assigned to one of 23 possible growth form categories (Table 2.5). The categories were those proposed by Cornelissen *et al.* (2003), with a few modifications. Within the category 'shrub' I created a subcategory 'scrambling shrub', because of the abundance of this growth form in the riparian assemblages. I also split the category 'short basal' into the subcategories 'rosette', 'prostrate' and 'creeping graminoid', and called the 'tussock' category of Cornelissen *et al.* (2003) 'tufted graminoid'. I created an additional category, 'leafless reed' to accommodate *Equisetum ramosissimum.* Woody species occupied six categories (tree, shrub, scrambling shrub, dwarf shrub, palmoid and climber), while herbaceous species occupied 15 categories (shrub, dwarf shrub, leafless shrub, leafless reed, climber, palmoid, erect leafy, prostrate, rosette, long basal, semi–basal, short succulent, creeping graminoid, tufted graminoid and aquatic floating).

Information was obtained primarily from Schmidt *et al.* (2002), Germishuizen and Meyer (2003), Retief and Herman (1997) and Van Oudtshoorn (2006). Plants described as 'prostrate' or 'procumbent' were assigned to the 'prostrate' category, those described as 'decumbent' to 'erect leafy', and those described as 'scandent' were placed in the category 'climber'. Where species were described as having more than one possible growth form (e.g. 'large shrub/small tree'), the most usual growth form was chosen, based on comparisons among different reference books and my experience of the plants in the field within the study area. Soft herbaceous shrubs such as species in the genera *Abutilon, Tephrosia* and *Indigofera* were placed in the 'erect leafy' category rather than the 'shrub' category, which was reserved for woody or semi–woody species. *Aloe* species without significant stems were assigned to the 'rosette' category, while tall Aloes such as *Aloe marlothii* were assigned to the 'palmoid' category. Other petaloid Monocotyledons such as *Crinum, Chlorophytum, Drimia, Hypoxis, Ornithogalum* and *Trachyandra* species were all assigned to the 'rosette' category.

Life form

The categories for this alternative description of plant form originally designed by Raunkiaer (1934) are described in Cornelissen *et al.* (2003). Each species was assigned to one of the seven categories (phanerophyte, chamaephyte, hemicryptophyte, geophyte, therophyte, helophyte and hydrophyte).

Almost all woody species were assigned to the category 'phanerophyte', as their perennating buds remain $\geq$ 0.5 m above the ground. All prostrate and rosette growth forms, as well as all perennial grasses and terrestrial sedges were considered ‘hemicryptophytes’. Species with below–ground bulbs or tubers were considered ‘geophytes’ only if their stems or leaves are annual (die back in winter). Species with tubers and perennial stems (such as *Asparagus* species) were placed in the categories ‘chamaephyte’ or ’phanerophyte’, depending on the height of the perennating buds. Species with a maximum potential height a little above 0.5 m, but which are usually shorter than 0.5 m, were considered chamaephytes. Aquatic sedges and grasses such as *Phragmites mauritianus* were assigned to the category ’helophyte’, and all annuals to the category ‘therophyte’.

Life span

Species were assigned to one of three categories ordered by increasing life span (annual, biennial/short–lived perennial and perennial). Species described as ‘annual/occasionally perennial’ or ‘perennial/occasionally annual’ were assigned to category 2 (biennial/short–lived perennial).

Leaf phenology

Woody species were classified as either deciduous or evergreen based on information provided in the literature sources cited above. Leaf phenology was treated as an ordinal trait (Table 2.5), with the evergreen category representing a longer period of greenness than the deciduous category. For herbaceous species, information on leaf phenology was more difficult to find. Consequently, I only recorded whether species are green during the dry season or not, which was considered important for the food provision function (Table 2.5, §2.2.1). Information from the literature was supplemented with field observations and information from herbarium specimens (C. E. Moss Herbarium, J) where necessary. Annuals were generally considered not to be green in winter unless there was evidence to the contrary. Species closely associated with aquatic habitats on the other hand, were generally considered to remain green in winter even if this was not explicitly stated.

Flowering and fruiting phenology

The months in which flowering and fruiting started and ended for each species were recorded as circular variables (months 1–12), and the length of the flowering and fruiting periods as continuous variables (Table 2.5). Fruiting information was only recorded for the woody species because this information was not available for many of the herbaceous species. Information on flowering phenology obtained from the literature was supplemented with information from herbarium specimens (at J) and field notes made during the course of this study.

Succulence

This binary trait was recorded for herbaceous species only (succulent/not succulent). A species was considered succulent if the stems, leaves or both were fleshy and served to store water.

Woodiness

Woodiness was recorded as an ordinal trait with four categories of increasing woodiness (non–woody, semi–woody, soft wood, hard wood), as described in Table 2.5. Herbaceous species described as ‘a suffrutex’, ‘becoming woody’, ‘woody at the base’ or ‘with a woody rootstock’ were placed in the ‘semi–woody’ category. Woody species were assigned to the ‘soft wood’ or ‘hard wood’ categories on the basis of quantitative wood density or air–dry mass data, which were available for many species in Van Wyk (1972, 1984), the Inside Wood Database and SEPASAL. For cases in which no quantitative data were available, wood hardness was inferred from published descriptions and uses of the species. For example, species with wood described as ‘hard’, ‘heavy’, ‘fine–grained’ or ‘termite resistant’ were assigned to the ‘hard wood’ category, as were species used to make implement handles or fence posts and species favoured for firewood. Species with wood described as ‘easy to break’, ‘soft’, ‘worthless’ or ‘light’ were assigned to the ‘soft wood’ category. In cases where no information was available for a particular species, information about similar species or species in the same genus was used to infer woodiness. Published information was not available for 20% of the woody species. These were assigned to a woodiness category on the basis on my field knowledge of the species or its close relatives, with substantial uncertainty associated with only four of the 130 species.

Riparian affinity

Species were assigned to one of five categories representing decreasing riparian affinity, from obligate riparian species (category 1), where most individuals occur only in riparian zones and are dependent on water at or near the soil surface, to obligate upland species (category 5) which are not water–dependent and where most individuals occur on hillslopes or crests rather than in riparian areas (Table 2.5).

Species were assigned to categories on the basis of published descriptions of their habitat requirements. Information from several different sources was compared, and where these sources were not in agreement a ‘weight of evidence’ approach was used. Local sources were given priority over more general sources or sources from outside South Africa. Where published information could only be obtained from a source outside the region, the habitat description was interpreted in terms of the habitats available in the study area. For example, a species described as occurring in ‘rainforest’ was assumed to have a requirement for water and/or shade, and therefore to occur mainly in riparian zones in this area. Locality information from herbarium specimens was used in a few cases to supplement the published information (for some of the rarer herbaceous species only).

Only species explicitly described as having a strong affinity for water were placed in category 1 (e.g. ‘riparian’ ‘riverbanks’ or ‘growing in or next to water’). Reference to ‘swamps’ ‘vleis’ (pans) or ‘damp soil’ was taken to indicate a need for permanent or seasonal flooding (category 1 or 2). If a species was described as occurring in riparian areas or vleis, but also in non–riparian habitats, it was placed in category 2 or 3. Weedy species associated with ‘disturbed areas’ (including riparian zones but also roadsides, fields and human settlements) were placed in category 3 if an association with water was specifically mentioned, or category 4 otherwise. Mention of ‘saline or brackish soil’ or ‘brackish flats’, without any other reference to riparian areas or any sort of water, caused species to be placed in categories 3 or 4 rather than category 5, because of the association between sodic areas and riparian zones in this landscape. Few species were assigned to category 5; this was only done when ‘dry’, ‘arid’ or similar words were used in the habitat description. Where descriptions were not very specific (e.g. ‘bushveld’), I put the species in category 4 rather than in category 5. Species described as occurring in ‘thickets’, with no mention of riparian areas or water, were also placed in category 4 rather than 5, because of the possibility that these could include riparian thickets.

Spinescence

The categories for this ordinal trait were obtained from Cornelissen *et al.* (2003). The five categories indicate increasing spinescence and are based on the density of spines or spine equivalents as well as the length and hardness of the spines, all of which influence the extent of the damage that can be inflicted on large herbivores. Information for this trait was obtained primarily from my experience of the plants in the field, as well as from herbarium specimens. Published information was used only to resolve uncertainties.

Several woody species had sharp, rigid branchlets that can be considered spine equivalents (e.g. several *Searsia* and *Combretum* species, and *Pyrostria hystrix*). Certain species with high densities of hard, sharp hook thorns were put into category 3 even though the thorns were less than 5 mm long, because the amount of damage that can be inflicted by these species was considered equivalent to or greater than that inflicted by species with longer straight thorns (*Acacia nigrescens*, *Acacia brevispica*, *Acacia schweinfurthii*, *Acacia caffra*, *Ziziphus mucronata* and *Capparis fascicularis*). No species in the survey were placed in category 5 (intermediate or high density of hard, sharp spines longer than 100 mm).

Resprouting ability

Resprouting ability was recorded for all woody and herbaceous species, but the data for the herbaceous species was excluded from the analysis because of strong correlations with other traits (Chapter 2). I defined four categories, representing increasing ability to resprout after severe physical damage such as being pushed over, uprooted, or having the main stem broken (Table 2.5).

Quantitative data on the resprouting behaviour of some (36%) of the woody species in response to severe (flood) damage were available from a previous study (Kotschy et al., in prep.). Information on resprouting for 31% of the species was obtained from published sources including Van Wyk (1972), Angassa and Oba (2009), Neke *et al.* (2006), Nzunda *et al.* (2008), Pandey and Shukla (2001), Pote *et al.* (2006), and the Agroforestree and SEPASAL electronic databases. Species for which sources stated ‘coppicing possible’ or ‘coppicing practised’ were assigned to category 3, while species ‘coppicing well’ or ‘regenerating by coppice and root suckers’ were assigned to category 4. However, information on resprouting was generally difficult to find, and the remaining one third of the species were assigned to a category using educated guesses based on my field knowledge of the species or its close relatives. There was substantial uncertainty about the resprouting abilities of around 10% of the 130 woody species.

Data for the herbaceous species was even more difficult to obtain, so for these species resprouting was recorded as a binary trait (able/unable to resprout). All perennial grasses and sedges were assumed to be able to resprout, as were all perennial species with woody rootstocks, tubers or bulbs. Annuals and short–lived perennials were assumed not to be able to resprout, as well as perennial forb species with no special below–ground storage organs.

Clonal spread

Cornelissen *et al.* (2003) suggested three categories (with subcategories): non–clonal, clonal aboveground, and clonal belowground. I did not use this classification because I considered the extent (distance) of clonal spread to be more important for describing a species' response to disturbance in riparian zones than the type of clonal organs present. I therefore used three categories ordered by increasing extent of clonal spread (non–clonal, limited and extensive; Table 2.5). 'Limited' clonal spread was defined as clonal spread that does not result in ramets being established much beyond the perimeter of the parent plant, such as production of daughter bulbs or expansion by means of short rhizomes. 'Extensive' clonal spread was defined as clonal spread that establishes ramets well beyond the perimeter of the parent plant, for example via stolons, long rhizomes, or dispersal of clonal fragments. Information on the type of storage organs present was captured with the trait 'below–ground storage' (see below).

Information on clonal spread was obtained from a wide range of literature sources, together with the information on below–ground storage. Lateral spread by climbing, scrambling or prostrate growth forms was not considered clonal, unless there was specific mention of rooting at the nodes, allowing ramets to potentially become independent. Rhizomes were generally considered to provide limited clonal spread unless they were specifically described as 'long' or 'spreading'. Bulbs and corms were also considered to provide limited clonal spread. Tubers were generally not considered organs of clonal spread, unless they occurred on a spreading root system (e.g. *Asparagus, Commelina*). Species for which no information was available were assumed to be non–clonal.

Below–ground storage

This was recorded as a categorical trait with six categories describing different types of below–ground storage organs (none, taproot, rootstock, rhizome, bulb, tuber). It was only recorded for herbaceous species, because very little information was available on the root systems of the woody species in this study.

All annuals and short–lived perennials were assumed to have no specialised below–ground storage organs unless stated otherwise. Likewise, stoloniferous or tufted graminoids were placed in the category 'none'. 'Tuberous roots' or 'swollen roots' were assumed to refer to tubers. 'Rootstock' refers to a swollen woody root and/or stem base that facilitates resprouting after damage but not clonal spread (not equivalent to rhizomes).

Information was obtained from many different sources including books, Floras, electronic databases and journal articles (§A.1.3), supplemented with my field knowledge and observation of herbarium specimens. After extensive searching, I was able to find information on below–ground storage for 98% of the herbaceous species. The remaining 2% of species were assumed to have no special below–ground storage organs.

Nitrogen–fixing ability

Nitrogen–fixing ability was recorded as a binary trait (ability to fix nitrogen present or absent), where the presence of root nodules was taken to indicate an ability to fix nitrogen. Root nodulation information was obtained from the GRIN Taxonomy for Plants website (`www.ars-grin.gov/~sbmljw/cgi-bin/taxnodul.pl`).

Potential height

The potential maximum height attained by each species was obtained from literature sources. Local sources (pertaining to the study area only) were given preference over more general sources (pertaining to the whole country) wherever possible, e.g. values given by Schmidt *et al.* (2002), Retief and Herman (1997) and van der Walt (2009) were given preference over values given by Germishuizen and Meyer (2003). I used the 'usual' maximum height value given. For example, if a species' height was given as '3–5 m, occasionally to 10 m', I used the value of 5 m rather than the 'unusual' value of 10 m.

A.1.3 Literature sources for functional trait data

Publications

The following publications were used to obtain functional trait data for one or more species. Further details on the sources used for each species are available in the electronic data files (Open Office spreadsheets).

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Electronic databases

The following online databases were accessed between Februaray 2009 and March 2010 to obtain functional trait information:

1. South African National Biodiversity Institute. PlantzAfrica.com database (`www.plantzafrica.com`).
2. South African National Biodiversity Institute. SANBI Integrated Biodiversity Information System (SIBIS) (`sibis.sanbi.org`).

3. Royal Botanic Gardens, Kew. Survey of Economic Plants for Arid and Semi–Arid Lands (SEPASAL) database (`www.kew.org/ceb/sepasal`).
4. World Agroforestry Centre. Agroforestree database (`www.worldagroforestry.org/resources/databases/agroforestree`).
5. Plant Resources of Tropical Africa Programme. PROTA4U database (`www.prota4u.org`).
6. Plants for a Future. A Resource and Information Centre for Edible and Otherwise Useful Plants (`www.pfaf.org`).
7. FAO. Indigenous multipurpose trees of Tanzania: uses and economic benefits for people (`www.fao.org/docrep/x5327e/x5327e0b.htm`).
8. North Carolina State University. Inside Wood database (`insidewood.lib.ncsu.edu`).
9. USDA, ARS, National Genetic Resources Program. Germplasm Resources Information Network (GRIN). Taxonomy for Plants: rhizobial nodulation data (`www.ars-grin.gov/~sbmljw/cgi-bin/taxnodul.pl`).

I also used the following Floras: *Flora Capensis, Flora Zambesiaca, Flora of Southern Africa, Flora of Tropical East Africa, Flora of West Tropical Africa, Flora of Tropical Africa, Flora Somalia and Useful Plants of West Tropical Africa.* These were accessed via Aluka (`www.aluka.org`), now available in the JSTOR Plant Science online environment (`plants.jstor.org`).

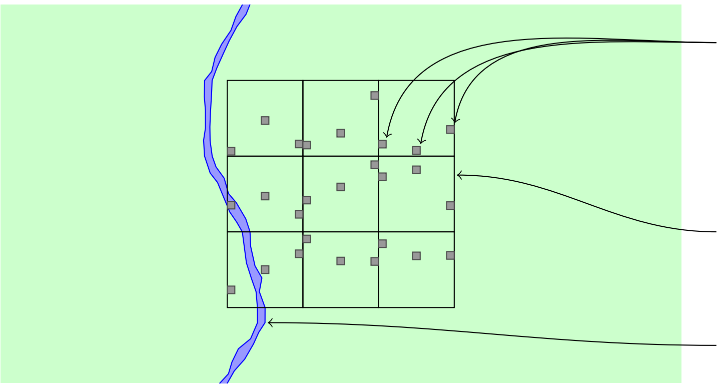
A.2 Vegetation survey data

The layout of the plots and quadrats used for sampling the woody and herbaceous riparian vegetation is illustrated in Figure A.3. The reasons for the differences in layout between the small streams and the main river were given in §3.2.2.

The cover and abundance of each woody species present in each 10 × 10 m plot was recorded. A stratified random sampling design was used for the herbaceous vegetation. Three 1m×1m quadrats were placed within each 10 × 10 m plot. One of these was constrained to be located along an imaginary line against the top side (shown here as the right edge) of each plot, one along an imaginary line across the middle of the plot, and one along an imaginary line against the bottom side (shown here as the left edge) of the plot (Figure A.3). This was done to ensure adequate capturing of the lateral (and vertical) heterogeneity (§3.2.2). However, the exact position of these quadrats along each imaginary line was random, and was determined in each case by drawing a card from a set of well–shuffled playing cards numbered 1–9. If, for example, the number 5 was drawn, the centre of the quadrat was located 5 m from the upstream side of the plot, along the appropriate imaginary line. This random component to the quadrat layout increased the amount of micro–scale heterogeneity captured. Linear sampling generally fails to capture diversity adequately when micro–scale heterogeneity is high, because it captures a lot of redundant information (due to spatial autocorrelation) while missing non–linear variation in the surrounding area, such as that due to animal disturbance, micro–scale soil differences and topographic features (Stohlgren *et al.*, 1998). Herbaceous vegetation cover and abundance was recorded within the 1 × 1 m quadrats, with an additional record of the presence of any extra species not found within the quadrats, within each 10 × 10 m plot.

Global Positioning System (GPS) readings were taken at the corners of each 10 × 10 m plot, and also in the centre of each 1 × 1 m quadrat, using a Trimble GPS PFPower-RSA receiver connected to a Trimble Recon 400C running TerraSync software. Post–processing was done using Trimble Pathfinder Office software, version 3.1. Base station files from the Nelspruit base station (L1-5 second files) for the appropriate Julian days were downloaded from the Trignet website (`www.trignet.co.za`). GPS readings were accurate to within 2 m after post–processing, and in $\geq 70\%$ of cases, to within 1 m.

(a) First order stream



Three 1m×1m quadrats placed randomly against the top side (shown here as the right edge of each plot), the bottom side (shown here as the left edge) and along the middle of each plot.

10×10m plot area

Channel

(b) Main-stem river

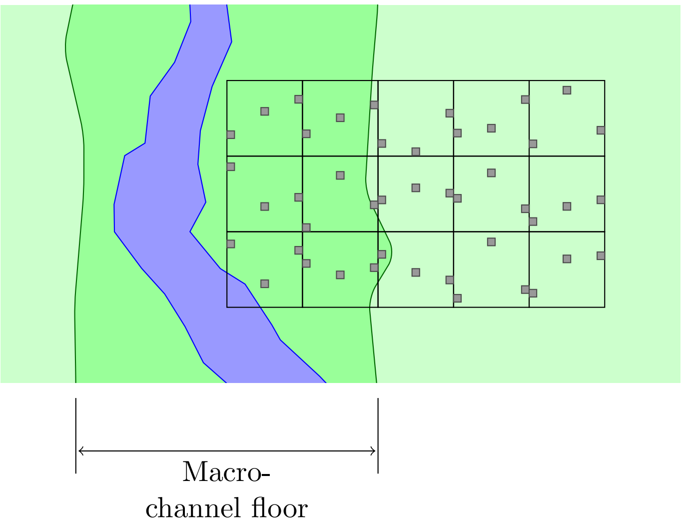


Figure A.3: Layout of plots and quadrats for the riparian vegetation surveys.

Table A.1: Acronyms and full species names for all woody species recorded in this study. Alien species are indicated with a '⋆' (Germishuizen and Meyer, 2003).

Acronym	Full name	Common name	Family	Growth form
acabr	*Acacia brevispica* Harms subsp. *dregeana* (Benth.) Brenan	Prickly Thorn	Fabaceae	Scrambling shrub
acaca	*Acacia caffra* (Thunb.) Willd.	Common Hook Thorn	Fabaceae	Tree
acaex	*Acacia exuvialis* I.Verd.	Flaky-bark Thorn	Fabaceae	Tree
acage	*Acacia gerrardii* subsp. *gerrardii* var. *gerrardii* Benth.	Red Thorn	Fabaceae	Tree
acagl	*Acalypha glabrata* Thunb.	Forest no-nettle	Euphorbiaceae	Shrub
acagr	*Acacia grandicornuta* Gerstner	Horned Thorn	Fabaceae	Tree
acani1	*Acacia nigrescens* Oliv.	Knob Thorn	Fabaceae	Tree
acaro	*Acacia robusta* Burch. subsp. *clavigera* (E.Mey.) Brenan	Robust Thorn	Fabaceae	Tree
acasc	*Acacia schweinfurthii* var. *schweinfurthii* Brenan & Exell	River Climbing Thorn	Fabaceae	Scrambling shrub
acato	*Acacia tortilis* (Forssk.) Hayne subsp. *heteracantha* (Burch.) Brenan	Umbrella Thorn	Fabaceae	Tree
acawe	*Acacia welwitschii* Oliv. subsp. *delagoensis* (Harms) J.H.Ross & Brenan	Delagoa Thorn	Fabaceae	Tree
ademu	*Adenium multiflorum* Klotzsch	Impala Lily	Apocynaceae	Shrub
albfo	*Albizia forbesii* Benth.	Broad-pod Albizia	Fabaceae	Tree
albha	*Albizia harveyi* Fourn.	Bushveld Albizia	Fabaceae	Tree
azite	*Azima tetracantha* Lam.	Needle-bush	Salvadoraceae	Scrambling shrub
balma	*Balanites maughamii* Sprague	Green-thorn	Balanitaceae	Tree
bauga	*Bauhinia galpinii* N.E.Br.	Pride-of-de-kaap	Fabaceae	Scrambling shrub
berdi	*Berchemia discolor* (Klotzsch) Hemsl.	Brown Ivory	Rhamnaceae	Tree
berze	*Berchemia zeyheri* (Sond.) Grubov	Red Ivory	Rhamnaceae	Tree
bolsp	*Bolusanthus speciosus* (L.Bolus) Harms	Tree Wistaria	Fabaceae	Tree
bresa	*Breonadia salicina* (Vahl) Hepper & J.M.Wood	Matumi	Rubiaceae	Tree
brica	*Bridelia cathartica* G.Bertol. subsp. *melanthesoides* (Baill.) J.Léonard	Blue Sweetberry	Phyllanthaceae	Shrub
brimi	*Bridelia micrantha* (Hochst.) Baill.	Mitzeerie	Phyllanthaceae	Tree
capfa	*Capparis fascicularis* var. *fascicularis* DC.	Zigzag Caper-bush	Capparaceae	Scrambling shrub
carbi	*Carissa bispinosa* (L.) Desf. ex Brenan subsp. *bispinosa*	Num-num	Apocynaceae	Shrub
casab	*Cassia abbreviata* Oliv. subsp. *beareana* (Holmes) Brenan	Long-tail Cassia	Fabaceae	Tree
cisca	*Cissus cactiformis* Gilg.	Cactus Vine	Vitaceae	Climber
cisco	*Cissus cornifolia* (Baker) Planch.	Ivy-grape	Vitaceae	Scrambling shrub
cismu	*Cissampelos mucronata* A.Rich.	Heart-leaved Vine	Menispermaceae	Climber
cochi	*Cocculus hirsutus* (L.) Diels	Boom Creeper/Ink Berry	Menispermaceae	Climber
codru	*Coddia rudis* (E.Mey. ex Harv.) Verdc.	Small Bone-apple	Rubiaceae	Dwarf shrub
comap	*Combretum apiculatum* Sond. subsp. *apiculatum*	Red Bushwillow	Combretaceae	Tree
comer	*Combretum erythrophyllum* (Burch.) Sond.	River Bushwillow	Combretaceae	Tree
comha	*Commiphora harveyi* (Engl.) Engl.	Copperstem Corkwood	Burseraceae	Tree
comhe	*Combretum hereroense* Schinz	Russet Bushwillow	Combretaceae	Tree
comim	*Combretum imberbe* Wawra	Leadwood	Combretaceae	Tree
commi	*Combretum microphyllum* Klotzsch	Flame Climbing Bushwillow	Combretaceae	Scrambling shrub

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Acronym	Full name	Common name	Family	Growth form
commo1	*Combretum molle* R.Br. ex G.Don	Velvet Bushwillow	Combretaceae	Tree
commo2	*Combretum mossambicense* (Klotzsch) Engl.	Knobbly Climbing Bushwillow	Combretaceae	Scrambling shrub
comne	*Commiphora neglecta* (I. Verd.)	Sweet-root Corkwood	Burseraceae	Tree
compy	*Commiphora pyracanthoides* Engl.	Firethorn Corkwood	Burseraceae	Shrub
comsc	*Commiphora schimperi* (O.Berg) Engl.	Glossy-leaved Corkwood	Burseraceae	Shrub
comze	*Combretum zeyheri* Sond.	Large-fruit Bushwillow	Combretaceae	Tree
cormo	*Cordia monoica* R.Br. ex A.DC.	Sandpaper Saucer-berry	Boraginaceae	Shrub
corov	*Cordia ovalis* R.Br. ex A.DC.	Satin-bark Saucer-berry	Boraginaceae	Shrub
dalme	*Dalbergia melanoxylon* Guill. & Perr.	Zebrawood	Fabaceae	Shrub
dicci1	*Dichrostachys cinerea* (L.) Wight & Arn. subsp. *africana* Brenan & Brummitt	Sickle Bush	Fabaceae	Shrub
dicci2	*Dichrostachys cinerea* (L.) Wight & Arn. subsp. *nyassana* (Taub.) Brenan	Large-leaved Sickle Bush	Fabaceae	Shrub
dioly	*Diospyros lycioides* Desf. subsp. *sericea* (Bernh.) De Winter	Eastern Bluebush	Ebenaceae	Shrub
diome	*Diospyros mespiliformis* Hochst. ex A.DC.	Jackal-berry	Ebenaceae	Tree
domro	*Dombeya rotundifolia* (Hochst.) Planch.	Wild Pear	Malvaceae	Tree
dovca	*Dovyalis caffra* (Hook.f & Harv.) Hook.f.	Kei-apple	Flacourtiaceae	Shrub
ehram	*Ehretia amoena* Klotzsch	Sandpaper-bush	Boraginaceae	Shrub
ehrri	*Ehretia rigida* (Thunb.) Druce	Puzzle-bush	Boraginaceae	Shrub
ekeca	*Ekebergia capensis* Sparrm.	Cape Ash	Meliaceae	Tree
elatr	*Elaeodendron transvaalense* (Burtt Davy) R.H.Archer	Bushveld Saffron	Celastraceae	Tree
eucdi	*Euclea divinorum* Hiern	Magic Guarri	Ebenaceae	Shrub
eucna	*Euclea natalensis* A.DC. subsp. *natalensis* F.White	Bushveld Hairy Guarri	Ebenaceae	Shrub
ficca	*Ficus capreifolia* Delile	Sandpaper Fig	Moraceae	Shrub
ficpe	*Ficus petersii* Warb.	Peters Fig	Moraceae	Tree
ficsy	*Ficus sycomorus* L. subsp. *sycomorus*	Sycamore Fig	Moraceae	Tree
flain	*Flacourtia indica* (Burm.f) Merr.	Governor's Plum	Flacourtiaceae	Tree
fluvi	*Flueggea virosa* (Roxb. ex Willd.) Pax & K.Hoffm. subsp. *virosa*	Feverberry	Phyllanthaceae	Shrub
garvo	*Gardenia volkensii* K.Schum. subsp. *volkensii*	Bushveld Gardenia	Rubiaceae	Tree
grebi	*Grewia bicolor* Juss.	White-leaved Raisin	Malvaceae	Shrub
grefl1	*Grewia flava* DC.	Velvet Raisin	Malvaceae	Shrub
grefl2	*Grewia flavescens* var. *flavescens* Juss.	Soft-leaved Sandpaper Raisin	Malvaceae	Scrambling shrub
grehe	*Grewia hexamita* Burret	Giant Raisin	Malvaceae	Shrub
gremo	*Grewia monticola* Sond.	Grey Raisin	Malvaceae	Shrub
greoc	*Grewia occidentalis* L.	Cross-berry	Malvaceae	Shrub
grevi	*Grewia villosa* Willd.	Mallow Raisin	Malvaceae	Shrub
gymma	*Gymnosporia maranguensis* (Loes.) Loes.	Tropical Spikethorn	Celastraceae	Shrub
gymse	*Gymnosporia senegalensis* (Lam.) Loes.	Red Spikethorn	Celastraceae	Shrub
jasfl	*Jasminum fluminense* Vell.	Jasmine	Oleaceae	Climber
kigaf	*Kigelia africana* (Lam.) Benth.	Sausage Tree	Bignoniaceae	Tree
krafl	*Kraussia floribunda* Harv.	Rhino-coffee	Rubiaceae	Shrub

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Acronym	Full name	Common name	Family	Growth form
lanca ⋆	*Lantana camara* L.	Christmas Berry	Verbenaceae	Shrub
landi	*Lannea discolor* (Sond.) Engl.	Live-long	Anacardiaceae	Tree
lanru	*Lantana rugosa* Thunb.	Bird‘s Brandy	Verbenaceae	Shrub
lansc	*Lannea schweinfurthii* (Engl.) Engl. var. *stuhlmannii* (Engl.) Kokwaro	False Marula	Anacardiaceae	Tree
lipja	*Lippia javanica* (Burm.f) Spreng.	Fever-tea	Verbenaceae	Shrub
maepa	*Maerua parvifolia* Pax	Dwarf Bush-cherry	Capparaceae	Shrub
manmo	*Manilkara mochisia* (Baker) Dubard	Lowveld Milkberry	Sapotaceae	Tree
melaz ⋆	*Melia azedarach* L.	Syringa	Meliaceae	Tree
mimob	*Mimusops obovata* Sond.	Bush Red-Milkwood	Sapotaceae	Tree
munse	*Mundulea sericea* (Willd.) A.Chev.	Cork-bush	Fabaceae	Tree
mysae	*Mystroxylon aethiopicum* (Thunb.) Loes. subsp. *schlechteri* (Loes.) R.H.Archer	Bushveld Kubu-berry	Celastraceae	Tree
nuxop	*Nuxia oppositifolia* (Hochst.) Benth.	Water Elder	Buddlejaceae	Tree
ochna	*Ochna natalitia* (Meisn.) Walp.	Natal Plane	Ochnaceae	Shrub
opufi ⋆	*Opuntia ficus-indica* (L.) Mill.	Sweet Prickly Pear	Cactaceae	Shrub
ormtr	*Ormocarpum trichocarpum* (Taub.) Engl.	Hairy Catterpillar-pod	Fabaceae	Tree
ozosp	*Ozoroa sphaerocarpa* R. & A.Fern.	Currant Resin-tree	Anacardiaceae	Tree
papca	*Pappea capensis* Eckl. & Zeyh.	Jacket-plum	Sapindaceae	Tree
pavca	*Pavetta catophylla* K.Schum.	Sand Brides-bush	Rubiaceae	Shrub
pavla	*Pavetta lanceolata* Eckl.	Weeping Brides-bush	Rubiaceae	Shrub
pavsc	*Pavetta schumanniana* F.Hoffm. ex K.Schum.	Poison Brides-bush	Rubiaceae	Tree
pelaf	*Peltophorum africanum* Sond.	African-wattle	Fabaceae	Tree
phivi	*Philenoptera violacea* (Klotzsch) Schrire	Apple-leaf	Fabaceae	Tree
phore	*Phoenix reclinata* Jacq.	Wild Date Palm	Arecaceae	Palmoid
phyre	*Phyllanthus reticulatus* var. *reticulatus* Poir.	Potato-bush	Phyllanthaceae	Shrub
pilth	*Piliostigma thonningii* (Schumach.) Milne-Redh.	Camel-foot	Fabaceae	Tree
plear	*Plectroniella armata* (K.Schum.) Robyns	no Turkey-berry	Rubiaceae	Shrub
prilo	*Pristimera longipetiolata* (Oliv.) N.Hall	Bushveld Paddle-pod	Celastraceae	Climber
psigu ⋆	*Psidium guajava* L.	Guava	Myrtaceae	Shrub
ptero	*Pterocarpus rotundifolius* (Sond.) Druce subsp. *rotundifolius*	Round-leaved Bloodwood	Fabaceae	Shrub
pyrhy	*Pyrostria hystrix* (Bremek.) Bridson	Porcupine-bush	Rubiaceae	Shrub
rhotr	*Rhoicissus tridentata* (L.f) Wild & R.B.Drumm. subsp. *cuneifolia* (Eckl. & Zeyh.) Urton	Northern Bushman‘s Grape	Vitaceae	Climber
salmu	*Salix mucronata* Thunb. subsp. *woodii* (Seemen) Immelman	Flute Willow	Salicaceae	Shrub
schbr	*Schotia brachypetala* Sond.	Weeping Boer-bean	Fabaceae	Tree
schca	*Schotia capitata* Bolle	Dwarf Boer-bean	Fabaceae	Shrub
sclbi	*Sclerocarya birrea* (A.Rich.) Hochst. subsp. *caffra* (Sond.) Kokwaro	Marula	Anacardiaceae	Tree
seagu	*Searsia gueinzii* (Sond.) F.A.Barkley	Thorny Karree	Anacardiaceae	Shrub
seale	*Searsia leptodictya* (Diels) T.S.Yi, A.J.Mill. & J.Wen	Mountain Karree	Anacardiaceae	Shrub
seape	*Searsia pentheri* (Zahlbr.) Moffett	Crow-berry	Anacardiaceae	Shrub
seapy	*Searsia pyroides* var. *pyroides* (Burch.) Moffett	Common Wild Currant	Anacardiaceae	Shrub

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Acronym	Full name	Common name	Family	Growth form
sendi ⋆	*Senna didymobotrya* (Fresen.) Irwin & Barneby	Peanut Senna	Fabaceae	Shrub
senpe	*Senna petersiana* (Bolle) Lock	Eared Senna	Fabaceae	Shrub
sespu ⋆	*Sesbania punicea* (Cav.) Benth.	Red Sesbania	Fabaceae	Shrub
spiaf	*Spirostachys africana* Sond.	Tamboti	Euphorbiaceae	Tree
strma	*Strychnos madagascariensis* Poir.	Black Monkey-orange	Strychnaceae	Shrub
strsp	*Strychnos spinosa* Lam.	Spiny Monkey-orange	Strychnaceae	Shrub
syzgu	*Syzygium guineense* (Willd.) DC. subsp. *guineense*	Bushveld Waterberry	Myrtaceae	Tree
tarpa	*Tarchonanthus parvicapitulatus* P.P.J.Herman	Small-head Camphor-bush	Asteraceae	Shrub
tecpi	*Teclea pilosa* (Engl.) I.Verdc.	Winged Cherry-orange	Rutaceae	Shrub
terpr	*Terminalia prunioides* C.Lawson	Purple-pod Cluster-leaf	Combretaceae	Tree
terse	*Terminalia sericea* Burch. ex DC.	Silver Cluster-leaf	Combretaceae	Tree
treor	*Trema orientalis* (L.) Blume	Pigeonwood	Celtidaceae	Tree
triem	*Trichilia emetica* Vahl. subsp. *emetica*	Natal Mahogany	Meliaceae	Tree
triju	*Tricalysia junodii* var. *junodii* (Schinz) Brenan	Fluffy-flowered Jackal-coffee	Rubiaceae	Scrambling shrub
vanin	*Vangueria infausta* Burch. subsp. *infausta*	Velvet Wild-medlar	Rubiaceae	Tree
verco	*Vernonia colorata* (Willd.) Drake subsp. *colorata*	Lowveld Vernonia	Asteraceae	Shrub
ximca	*Ximenia caffra* var. *natalensis* Sond.	Sourplum	Olacaceae	Shrub
zanca	*Zanthoxylum capense* (Thunb.) Harv.	Small Knobwood	Rutaceae	Tree
zizmu	*Ziziphus mucronata* Willd. subsp. *mucronata*	Buffalo-thorn	Rhamnaceae	Tree

Ends

Table A.2: Acronyms and full species names for all herbaceous species recorded in this study. Alien species are indicated with a '⋆' (Germishuizen and Meyer, 2003).

Acronym	Full name	Family	Growth form
abrpr	*Abrus precatorius* L. subsp. *africanus* Verdc.	Leguminosae	Climber
abuau	*Abutilon austro-africanum* Hochr.	Malvaceae	Erect leafy
abugr	*Abutilon grandiflorum* G. Don	Malvaceae	Erect leafy
acahi ⋆	*Acanthospermum hispidum* DC.	Asteraceae, Heliantheae sens. lat.	Erect leafy
acain	*Acalypha indica* var indica	Euphorbiaceae	Erect leafy
acavi	*Acalypha villicaulis* Hochst.	Euphorbiaceae	Erect leafy
achas ⋆	*Achyranthes aspera* L.	Amaranthaceae	Erect leafy
achle	*Achyropsis leptostachya* (E.Mey. ex Meisn.) Baker & C.B.Clarke	Amaranthaceae	Erect leafy
adedi	*Adenia digitata* (Harv.) Engl.	Passifloraceae	Climber
adeha	*Adenia hastata* (Harv.) Schinz var. *glandulifera* W.J.de Wilde	Passifloraceae	Climber
aesin	*Aeschynomene indica* L.	Leguminosae	Erect leafy
agabo	*Agathisanthemum bojeri* Klotzsch subsp. *bojeri*	Rubiaceae	Erect leafy
ageco ⋆	*Ageratum conyzoides* L.	Asteraceae	Erect leafy
alcla	*Alchornea laxiflora* (Benth.) Pax & K.Hoffm.	Euphorbiaceae	Shrub
alogr	*Aloe greatheadii* Schönland var. *davyana* (Schönland) Glen & D.S.Hardy	Liliaceae	Rosette
aloma	*Aloe marlothii* A.Berger subsp. *marlothii*	Liliaceae	Palmoid
aloze	*Aloe zebrina* Baker	Liliaceae	Rosette
altpu ⋆	*Alternanthera pungens* Humb., Bonpl. & Kunth	Amaranthaceae	Prostrate
amapr	*Amaranthus praetermissus* Brenan	Amaranthaceae	Erect leafy
amast ⋆	*Amaranthus standleyanus* Parodi ex Covas	Amaranthaceae	Erect leafy
amath	*Amaranthus thunbergii* Moq.	Amaranthaceae	Semi-basal
ampob	*Ampelocissus obtusata* (Welw. ex Baker) Planch. subsp. *kirkiana* (Planch.) Wild & R.B.Drumm.	Vitaceae	Climber
aptli	*Aptosimum lineare* Marloth & Engl.	Scrophulariaceae	Dwarf shrub
argoc ⋆	*Argemone ochroleuca* Sweet subsp. *ochroleuca*	Papaveraceae	Erect leafy
ariad	*Aristida adscensionis* L.	Poaceae	Tufted graminoid
ariba	*Aristida congesta* Roem. & Schult. subsp. *barbicollis* (Trin. & Rupr.) De Winter	Poaceae	Tufted graminoid
aribi	*Aristida bipartita* (Nees) Trin. & Rupr.	Poaceae	Tufted graminoid
arico	*Aristida congesta* Roem. & Schult. subsp. *congesta*	Poaceae	Tufted graminoid
arist	*Aristida stipitata* Hack. subsp. *graciliflora* (Pilg.) Melderis	Poaceae	Tufted graminoid
aspbu	*Asparagus buchananii* Baker	Liliaceae	Climber
aspex	*Asparagus exuvialis* Burch.	Liliaceae	Climber
aspla	*Asparagus laricinus* Burch.	Liliaceae	Shrub
aspmi	*Asparagus minutiflorus* (Kunth) Baker	Liliaceae	Shrub
aspna	*Asparagus natalensis* (Baker) Fellingham & N.L.Mey.	Liliaceae	Climber
aspse	*Asparagus setaceus* (Kunth) Jessop	Liliaceae	Erect leafy
aspsu	*Asparagus suaveolens* Burch.	Liliaceae	Erect leafy

Continued on next page.

Acronym	Full name	Family	Growth form
aspvi	*Asparagus virgatus* Baker	Liliaceae	Erect leafy
asymy	*Asystasia mysorensis* (Roth) T. Anderson	Acanthaceae	Erect leafy
barel	*Barleria elegans* S.Moore ex C.B.Clarke	Acanthaceae	Erect leafy
barox	*Barleria oxyphylla* Lindau	Acanthaceae	Erect leafy
barpr	*Barleria prionitis* L.	Acanthaceae	Erect leafy
bidbi1 ⋆	*Bidens bipinnata* L.	Asteraceae	Erect leafy
bidpi ⋆	*Bidens pilosa* L.	Asteraceae	Erect leafy
blein	*Blepharis integrifolia* (L.f.) E. Mey. ex Schinz	Acanthaceae	Prostrate
boedi ⋆	*Boerhavia diffusa* L.	Nyctaginaceae	Prostrate
botin	*Bothriochloa insculpta* (A.Rich.) A.Camus	Poaceae	Tufted graminoid
botra	*Bothriochloa radicans* (Lehm.) A.Camus	Poaceae	Tufted graminoid
brade	*Brachiaria deflexa* (Schumach.) C.E.Hubb. ex Robyns	Poaceae	Tufted graminoid
brani	*Brachiaria nigropedata* (Ficalho & Hiern) Stapf	Poaceae	Tufted graminoid
bulhi	*Bulbostylis hispidula* (Vahl) R.Haines	Cyperaceae	Tufted graminoid
carco	*Cardiospermum corindum* L.	Sapindaceae	Climber
catro ⋆	*Catharanthus roseus* (L.) G.Don	Apocynaceae	Erect leafy
cenas ⋆	*Centella asiatica* (L.) Urb.	Apiaceae	Prostrate
cenci	*Cenchrus ciliarus* L.	Poaceae	Tufted graminoid
certr	*Ceratotheca triloba* (Bernh.) Hook.f.	Pedaliaceae	Erect leafy
chaab	*Chamaecrista absus* (L.) Irwin & Barneby	Fabaceae	Erect leafy
chabu	*Chaetacanthus burchellii* Nees	Acanthaceae	Erect leafy
chahe	*Chascanum hederaceum* (Sond.) Moldenke	Verbenaceae	Erect leafy
chami	*Chamaecrista mimosoides* (L.) Greene	Fabaceae	Erect leafy
checa ⋆	*Chenopodium carinatum* R. Br.	Chenopodiaceae	Erect leafy
chein	*Cheilanthus involuta* (Sw.) Schelpe & N.C.Anthony var. *obscura* (N.C.Anthony) N.C.Anthony	Adiantaceae	Erect leafy
chlga2	*Chlorophytum galpinii* var. *galpinii* Baker	Liliaceae	Rosette
chlro	*Chloris roxburghiana* Schult.	Poaceae	Tufted graminoid
chlvi	*Chloris virgata* Sw.	Poaceae	Tufted graminoid
citla	*Citrullus lanatus* (Thunb.) Matsum. & Nakai	Cucurbitaceae	Climber
clean	*Cleome angustifolia* Forssk. subsp. *petersiana* (Klotzsch ex Sond.) Kers	Capparaceae	Erect leafy
clemo	*Cleome monophylla* L.	Capparaceae	Erect leafy
clete	*Clerodendrum ternatum* Schinz	Verbenaceae	Erect leafy
cocad	*Coccinia adoensis* (A.Rich.) Cogn.	Cucurbitaceae	Climber
cocre	*Coccinia rehmannii* Cogn.	Cucurbitaceae	Climber
comaf1	*Commelina africana* L. var. *krebsiana* (Kunth) C.B.Clarke	Commelinaceae	Erect leafy
comaf2	*Commelina africana* var. *africana* L.	Commelinaceae	Erect leafy
comaf3	*Commelina africana* L. var. *lancispatha* C.B.Clarke	Commelinaceae	Erect leafy
combe	*Commelina benghalensis* L.	Commelinaceae	Erect leafy
comec	*Commelina eckloniana* Kunth	Commelinaceae	Erect leafy

Continued on next page.

Acronym	Full name	Family	Growth form
comer2	*Commelina erecta* L.	Commelinaceae	Erect leafy
compl	*Commicarpus plumbagineus* (Cav.) Standl.	Nyctaginaceae	Erect leafy
conal ⋆	*Conyza albida* Spreng.	Asteraceae	Erect leafy
conat	*Conyza attenuata* DC.	Asteraceae	Erect leafy
conbo ⋆	*Conyza bonariensis* (L.) Cronquist	Asteraceae	Semi-basal
confa	*Convolvulus farinosus* L.	Convolvulaceae	Climber
coras	*Corchorus asplenifolius* Burch.	Malvaceae	Prostrate
corco	*Corchorus confusus* Wild	Malvaceae	Prostrate
corde	*Corbichonia decumbens* (Forssk.) Exell	Aizoaceae	Prostrate
corlo	*Corchorus longipedunculatus* Mast.	Malvaceae	Erect leafy
cortr2 ⋆	*Corchorus tridens* L.	Malvaceae	Erect leafy
crahi	*Crabbea hirsuta* Harv.	Acanthaceae	Prostrate
crave	*Crabbea velutina* S.Moore	Acanthaceae	Semi-basal
crima	*Crinum macowanii* Baker	Amaryllidaceae	Rosette
crobu	*Crotalaria burkeana* Benth.	Fabaceae	Erect leafy
crodo	*Crotalaria doidgeae* I.Verd.	Fabaceae	Erect leafy
crola2	*Crotalaria laburnifolia* L. subsp. *australis* (Baker f.) Polhill	Fabaceae	Erect leafy
cryob	*Cryptolepis obtusa* N.E.Br.	Periplocaceae	Climber
cucan	*Cucumis anguria* L.	Cucurbitaceae	Climber
cuchi	*Cucumis hirsutus* Sond.	Cucurbitaceae	Climber
cucme	*Cucumis metuliferus* Naudin	Cucurbitaceae	Climber
cucmy	*Cucumis myriocarpus* Naudin subsp. *myriocarpus*	Cucurbitaceae	Climber
cymex	*Cymbopogon excavatus* (Hoschst.) Stapf ex Burtt Davy	Poaceae	Tufted graminoid
cynda	*Cynodon dactylon* (L.) Pers.	Poaceae	Creeping graminoid
cynsc	*Cynanchum schistoglossum* Schltr.	Asclepiadaceae	Climber
cypal	*Cyperus albostriatus* Schrad.	Cyperaceae	Tufted graminoid
cypam	*Cyperus amabilis* Vahl	Cyperaceae	Tufted graminoid
cypar	*Cyperus articulatus* L.	Cyperaceae	Tufted graminoid
cypco	*Cyperus compressus* L.	Cyperaceae	Tufted graminoid
cypde	*Cyperus denudatus* L.f.	Cyperaceae	Tufted graminoid
cypdi1	*Cyperus distans* L.f.	Cyperaceae	Tufted graminoid
cypdi2	*Cyperus dives* Delile	Cyperaceae	Tufted graminoid
cypdi3	*Cyperus difformis* L.	Cyperaceae	Tufted graminoid
cypdu	*Cyperus dubius* Rottb.	Cyperaceae	Tufted graminoid
cypin	*Cyperus indecorus* var. *indecorus* Kunth	Cyperaceae	Tufted graminoid
cypla	*Cyperus latifolius* Poir.	Cyperaceae	Tufted graminoid
cypob	*Cyperus obtusiflorus* Vahl	Cyperaceae	Tufted graminoid
cyppu	*Cyphostemma puberulum* (C.A.Sm.) Wild & R.B.Drumm.	Vitaceae	Climber
cypru	*Cyperus rupestris* var. *rupestris* Kunth	Cyperaceae	Tufted graminoid

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Acronym	Full name	Family	Growth form
cypse	*Cyperus sexangularis* Nees	Cyperaceae	Tufted graminoid
cypsu	*Cyphostemma subciliatum* (Baker) Desc. ex Wild & R.B.Drumm.	Vitaceae	Climber
cypwo	*Cyphostemma woodii* (Gilg & M.Brandt) Desc.	Vitaceae	Climber
dacae	*Dactyloctenium aegyptium* (L.) Willd.	Poaceae	Tufted graminoid
dalca	*Dalechampia capensis* A.Spreng.	Euphorbiaceae	Climber
dalga	*Dalechampia galpinii* Pax	Euphorbiaceae	Climber
decsc	*Decorsea schlechteri* (Harms) Verdc.	Fabaceae	Climber
deltr	*Delosperma tradescantioides* (A.Berger) L.Bolus	Mesembryanthemaceae	Prostrate
dicga	*Dicoma galpinii* F.C.Wilson	Asteraceae	Erect leafy
dicse	*Dicerocaryum senecioides* (Klotzsch) Abels subsp. *transvaalense* Abels	Pedaliaceae	Prostrate
dicsp	*Dicliptera spinulosa* Hochst. ex K.Balkwill	Acanthaceae	Erect leafy
diger	*Digiteria eriantha* Steud.	Poaceae	Tufted graminoid
diglo	*Digiteria longiflora* (Retz.) Pers.	Poaceae	Creeping graminoid
diham	*Diheteropogon amplectens* (Nees) Clayton	Poaceae	Tufted graminoid
doltr	*Dolichos trilobus* L. subsp. *transvaalicus* Verdc.	Fabaceae	Climber
dribu	*Drimiopsis burkei* Baker subsp. *burkei*	Hyacinthaceae	Rosette
driin	*Drimia indica* (Roxb.) Jessop	Hyacinthaceae	Rosette
drisp	*Drimia sp.* -	Hyacinthaceae	Rosette
dysro	*Dyschoriste rogersii* S.Moore	Acanthaceae	Erect leafy
eclpr ⋆	*Eclipta prostrata* (L.) L.	Asteraceae	Erect leafy
eleco	*Eleusine coracana* (L.) Gaertn. subsp. *africana* (Kenn.-O'Byrne) Hilu & De Wet	Poaceae	Tufted graminoid
ennce	*Enneapogon cenchroides* (Roem. & Schult.) C.E.Hubb	Poaceae	Tufted graminoid
ennsc	*Enneapogon scoparius* Stapf	Poaceae	Tufted graminoid
entma	*Enteropogon macrostachyus* (A.Rich.) Benth.	Poaceae	Tufted graminoid
equra	*Equisetum ramosissimum* Desf.	Equisetaceae	Leafless reed
eraas	*Eragrostis aspera* (Jacq.) Nees	Poaceae	Tufted graminoid
eraci	*Eragrostis cilianensis* (All.) F.T.Hubb.	Poaceae	Tufted graminoid
eracu	*Eragrostis curvula* (Schrad.) Nees	Poaceae	Tufted graminoid
eragu	*Eragrostis gummiflua* Nees	Poaceae	Tufted graminoid
erain	*Eragrostis inamoena* K.Schum.	Poaceae	Tufted graminoid
erale	*Eragrostis lehmanniana* var. *lehmanniana* Nees	Poaceae	Tufted graminoid
erapl	*Eragrostis plana* Nees	Poaceae	Tufted graminoid
erara	*Eragrostis racemosa* (Thunb.) Steud.	Poaceae	Tufted graminoid
erari	*Eragrostis rigidior* Pilg.	Poaceae	Tufted graminoid
eraro	*Eragrostis rotifer* Rendle	Poaceae	Tufted graminoid
erasu	*Eragrostis superba* Peyr.	Poaceae	Tufted graminoid
erime	*Eriochloa meyeriana* (Nees) Pilg. subsp. *meyeriana*	Poaceae	Tufted graminoid
euphi	*Euphorbia hirta* (L.) Millsp.	Euphorbiaceae	Prostrate
euphy ⋆	*Euphorbia hypericifolia* (L.) Millsp.	Euphorbiaceae	Erect leafy

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Acronym	Full name	Family	Growth form
eupne	*Euphorbia neopolycnemoides* (Pax & K.Hoffm.) Koutnik	Euphorbiaceae	Erect leafy
euspa	*Eustachys paspaloides* (Vahl) Lanza & Mattei	Poaceae	Tufted graminoid
evoal	*Evolvulus alsinoides* (L.) L. var. *linifolius* (L.) Baker	Convolvulaceae	Erect leafy
finaf	*Fingerhuthia africana* Lehm.	Poaceae	Tufted graminoid
focan	*Fockea angustifolia* K.Schum.	Asclepiadaceae	Erect leafy
fuipa	*Fuirena pachyrrhiza* var. *pachyrrhiza* Ridl.	Cyperaceae	Tufted graminoid
geior	*Geigeria ornativa* O.Hoffm.	Asteraceae	Erect leafy
gisaf	*Gisekia africana* var. *africana* (Lour.) Kuntze	Aizoaceae	Erect leafy
glosu	*Gloriosa superba* L. subsp. *superba*	Liliaceae	Climber
gomce ⋆	*Gomphrena celosioides* Mart.	Amaranthaceae	Prostrate
gomto	*Gomphocarpus tomentosus* Burch. subsp. *tomentosus*	Asclepiadaceae	Erect leafy
gonan	*Gonatopus angustus* N.E.Br.	Araceae	Erect leafy
helci	*Heliotropium ciliatum* L.Kaplan	Boraginaceae	Erect leafy
helst	*Heliotropium strigosum* Willd.	Boraginaceae	Erect leafy
hemal	*Hemarthria altissima* (Poir.) Stapf & C.E.Hubb	Poaceae	Creeping graminoid
herbo	*Hermannia boraginiflora* Hook.	Sterculiaceae	Erect leafy
hergl	*Hermannia glanduligera* K.Schum.	Sterculiaceae	Erect leafy
herod	*Hermbstaedtia odorata* var. *odorata* (Burch.) T. Cooke	Amaranthaceae	Erect leafy
hetco	*Heteropogon contortus* (L.) Roem. & Schult.	Poaceae	Tufted graminoid
hibca1	*Hibiscus calyphyllus* Cav.	Malvaceae	Erect leafy
hibca2 ⋆	*Hibiscus cannabinus* L.	Malvaceae	Erect leafy
hibmi	*Hibiscus micranthus* var. *micranthus* L.f.	Malvaceae	Erect leafy
hibpa	*Hibiscus palmatus* Forssk.	Malvaceae	Erect leafy
hibpu	*Hibiscus pusillus* Thunb.	Malvaceae	Erect leafy
hibsi	*Hibiscus sidiformis* Baill.	Malvaceae	Erect leafy
hibvi	*Hibiscus vitifolius* L. subsp. *vulgaris* Brenan & Exell	Malvaceae	Erect leafy
hosop	*Hoslundia opposita* Vahl	Lamiaceae	Erect leafy
hyben	*Hybanthus enneaspermus* (L.) F.Muell.	Violaceae	Erect leafy
hypdi	*Hyperthelia dissoluta* (Nees ex Steud.) Clayton	Poaceae	Tufted graminoid
hypfo	*Hypoestes forskaolii* form B	Acanthaceae	Erect leafy
hyphe	*Hypoxis hemerocallidea* Fisch., C.A.Mey. & Avé-Lall.	Hypoxidaceae	Rosette
indar	*Indigofera arrecta* Hochst. ex A.Rich.	Fabaceae	Erect leafy
indas	*Indigofera astragalina* DC.	Fabaceae	Erect leafy
indba	*Indigofera bainesii* Baker	Fabaceae	Erect leafy
indfi	*Indigofera filipes* Benth. ex Harv.	Fabaceae	Erect leafy
indhe	*Indigofera heterotricha* DC.	Fabaceae	Erect leafy
indla	*Indigofera laxeracemosa* Baker f.	Fabaceae	Erect leafy
indrh	*Indigofera rhytidocarpa* Benth. ex Harv. subsp. *rhytidocarpa*	Fabaceae	Erect leafy
indti	*Indigofera tinctoria* L. var. *arcuata* J.B.Gillett	Fabaceae	Erect leafy

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Acronym	Full name	Family	Growth form
ipoal	*Ipomoea albivenia* (Lindl.) Sweet	Convolvulaceae	Climber
ipoco1	*Ipomoea coptica* var. *coptica* (L.) Roth ex Roem. & Schult.	Convolvulaceae	Climber
ipoco2	*Ipomoea coscinosperma* Hochst. ex Choisy	Convolvulaceae	Prostrate
ipocr	*Ipomoea crassipes* var. *crassipes* Hook.	Convolvulaceae	Prostrate
ipodi	*Ipomoea dichroa* Choisy	Convolvulaceae	Climber
ipoho	*Ipomoea hochstetteri* House	Convolvulaceae	Climber
ipoma	*Ipomoea magnusiana* Schinz	Convolvulaceae	Climber
ipoob	*Ipomoea obscura* var. *obscura* (L.) Ker Gawl	Convolvulaceae	Climber
iposi	*Ipomoea sinensis* (Desr.) Choisy subsp. *blepharosepala* (Hochst. ex A.Rich.) Verdc.	Convolvulaceae	Climber
jasmu	*Jasminum multipartitum* Hochst.	Oleaceae	Shrub
jusbe	*Justicia betonica* L.	Acanthaceae	Erect leafy
jusfl	*Justicia flava* (Vahl) Vahl	Acanthaceae	Erect leafy
juspr	*Justicia protracta* (Nees) T.Anderson	Acanthaceae	Erect leafy
kalbr	*Kalanchoe brachyloba* Welw. ex Britten	Crassulaceae	Semi-basal
kalla	*Kalanchoe lanceolata* (Forssk.) Pers.	Crassulaceae	Semi-basal
kalro	*Kalanchoe rotundifolia* (Haw.) Haw.	Crassulaceae	Erect leafy
kedfo	*Kedrostis foetidissima* (Jacq.) Cogn.	Cucurbitaceae	Climber
kohvi	*Kohautia virgata* (Willd.) Bremek.	Rubiaceae	Erect leafy
kylal	*Kyllinga alba* Nees	Cyperaceae	Tufted graminoid
kylme	*Kyllinga melanosperma* Nees	Cyperaceae	Tufted graminoid
kypan	*Kyphocarpa angustifolia* (Moq.) Lopr.	Amaranthaceae	Erect leafy
lagsi	*Lagenaria siceraria* (Molina) Standl.	Cucurbitaceae	Climber
ledap	*Ledebouria apertiflora* (Baker) Jessop	Liliaceae	Rosette
lepsc	*Lepidagathis scabra* C.B.Clarke	Acanthaceae	Erect leafy
leugl	*Leucas glabrata* var. *glabrata* (Vahl) Sm.	Lamiaceae	Erect leafy
leuma	*Leucas martinicensis* (Jacq.) R.Br.	Lamiaceae	Erect leafy
leune	*Leucas neuflizeana* Courbai	Lamiaceae	Erect leafy
litga	*Litogyne gariepina* (DC.) Anderb.	Asteraceae	Erect leafy
ludad	*Ludwigia adscendens* (L.) Hara subsp. *diffusa* (Forssk.) P.H. Raven	Onagraceae	Aquatic floating
macax	*Macrotyloma axillare* var. *axillare* (E.Mey.) Verdc.	Fabaceae	Climber
macma	*Macrotyloma maranguense* (Taub.) Verdc.	Fabaceae	Climber
maeju	*Maerua juncea* Pax subsp. *crustata* (Wild) Wild	Capparaceae	Climber
malco ⋆	*Malvastrum coromandelianum* (L.) Garcke	Malvaceae	Erect leafy
melfo	*Melhania forbesii* Planch. ex Mast.	Malvaceae	Erect leafy
melpr	*Melhania prostrata* DC.	Malvaceae	Erect leafy
melre	*Melinis repens* (Willd.) Zizka subsp. *repens*	Poaceae	Tufted graminoid
melsc	*Melanthera scandens* (Schumach. & Thonn.) Roberty subsp. *dregei* (DC.) Wild	Asteraceae	Erect leafy
molnu ⋆	*Mollugo nudicaulis* Lam.	Aizoaceae	Rosette
momba	*Momordica balsamina* L.	Cucurbitaceae	Climber

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Acronym	Full name	Family	Growth form
momch ⋆	*Momordica charantia* L.	Cucurbitaceae	Climber
monde	*Monechma debile* (Forssk.) Nees	Acanthaceae	Erect leafy
mongl	*Monsonia glauca* R.Knuth	Geraniaceae	Erect leafy
nesal	*Nesaea alata* Immelman	Lythraceae	Erect leafy
ociam	*Ocimum americanum* var. *americanum* L.	Lamiaceae	Erect leafy
ocigr	*Ocimum gratissimum* subsp. *gratissimum* var. *gratissimum* L.	Lamiaceae	Erect leafy
ophpo	*Ophioglossum polyphyllum* A.Braun	Opioglossaceae	Rosette
orbma	*Orbea maculata* (N.E.Br.) L.C.Leach subsp. *maculata*	Asclepiadaceae	Short succulent
orngl	*Ornithogalum glaucescens* J.C.Manning & Goldblatt	Hyacinthaceae	Rosette
ornte	*Ornithogalum tenuifolium* F.Delaroche subsp. *tenuifolium*	Hyacinthaceae	Rosette
ornvi	*Ornithogalum viride* (L.) J.C.Manning & Goldblatt	Hyacinthaceae	Rosette
ortsu	*Orthosiphon suffrutescens* (Thonn.) J.K.Morton	Lamiaceae	Erect leafy
oxaco ⋆	*Oxalis corniculata* L.	Oxalidaceae	Prostrate
oxaob	*Oxalis obliquifolia* Steud. ex A.Rich.	Oxalidaceae	Prostrate
oxase	*Oxalis semiloba* Sond. subsp. *semiloba*	Oxalidaceae	Prostrate
oxasm	*Oxalis smithiana* Eckl. & Zeyh.	Oxalidaceae	Prostrate
oxysi	*Oxygonum sinuatum* (Hochst. & Steud. ex Meisn.) Dammer	Polygonaceae	Semi-basal
pande	*Panicum deustum* Thunb.	Poaceae	Tufted graminoid
panma	*Panicum maximum* Jacq.	Poaceae	Tufted graminoid
passc	*Paspalum scrobiculatum* L.	Poaceae	Tufted graminoid
pavbu	*Pavonia burchellii* (DC.) R.A.Dyer	Malvaceae	Erect leafy
pegse	*Pegolettia senegalensis* Cass.	Asteraceae	Erect leafy
penpe	*Pentodon pentandrus* (Schumach. & Thonn.) Vatke var. *minor* Bremek.	Rubiaceae	Erect leafy
perat	*Persicaria attenuata* (R.Br.) Soják subsp. *africana* K.L.Wilson	Polygonaceae	Erect leafy
perda	*Pergularia daemia* (Forssk.) Chiov. subsp. *daemia*	Asclepiadaceae	Climber
perpa	*Perotis patens* Gand.	Poaceae	Tufted graminoid
perse	*Persicaria serrulata* (Lag.) Webb & Moq.	Polygonaceae	Erect leafy
phrma	*Phragmites mauritianus* Kunth	Poaceae	Creeping graminoid
phyas	*Phyllanthus asperulatus* Hutch.	Euphorbiaceae	Erect leafy
phyde	*Phyllanthus delagoensis* Hutch.	Euphorbiaceae	Erect leafy
phyin	*Phyllanthus incurvus* Thunb.	Euphorbiaceae	Erect leafy
phyma	*Phyllanthus maderaspatensis* L.	Euphorbiaceae	Erect leafy
phyoc ⋆	*Phytolacca octandra* L.	Phytolaccaceae	Erect leafy
phypa2	*Phyllanthus parvulus* var. *gariepensis* Sond.	Euphorbiaceae	Erect leafy
phype	*Phyllanthus pentandrus* Schumach. & Thonn.	Euphorbiaceae	Erect leafy
plalo	*Plantago longissima* Decne.	Plantaginaceae	Rosette
plecy	*Plectranthus cylindraceus* Hochst. ex Benth.	Lamiaceae	Semi-basal
pludi	*Pluchea dioscoridis* (L.) DC.	Asteraceae	Erect leafy
pluze	*Plumbago zeylanica* L.	Plumbaginaceae	Shrub

Continued on next page.

Acronym	Full name	Family	Growth form
pogsq	*Pogonarthria squarrosa* (Roem. & Schult.) Pilg.	Poaceae	Tufted graminoid
polsp	*Polygala sphenoptera* Fresen.	Polygalaceae	Erect leafy
porol ⋆	*Portulaca oleracea* L.	Portulacaceae	Prostrate
porqu	*Portulaca quadrifida* L.	Portulacaceae	Prostrate
prico	*Priva cordifolia* (L.f.) Druce	Verbenaceae	Erect leafy
pselu	*Pseudognaphalium luteo-album* (L.) Hilliard & B.L.Burtt	Asteraceae	Erect leafy
psevi	*Pseudoconyza viscosa* (Mill.) D'Arcy	Asteraceae	Erect leafy
pupla	*Pupalia lappacea* var. *lappacea* (L.) Juss.	Amaranthaceae	Erect leafy
pycpe	*Pycreus pelophilus* (Ridl.) C.B.Clarke	Cyperaceae	Tufted graminoid
pycpo	*Pycreus polystachyos* var. *polystachyos* (Rottb.) P.Beauv.	Cyperaceae	Tufted graminoid
ranmu	*Ranunculus multifidus* Forssk.	Ranunculaceae	Rosette
rappr	*Raphionacme procumbens* Schltr.	Asclepiadaceae	Climber
rhixe	*Rhinacanthus xerophilus* A.Meeuse	Acanthaceae	Erect leafy
rhymi	*Rhynchosia minima* var. *minima* (L.) DC.	Fabaceae	Climber
rhyto	*Rhynchosia totta* var. *totta* (Thunb.) DC.	Fabaceae	Climber
ricbr ⋆	*Richardia brasiliensis* Gomes	Rubiaceae	Prostrate
rueco	*Ruellia cordata* Thunb.	Acanthaceae	Erect leafy
rueot	*Ruellia otaviensis* P.G.Mey.	Acanthaceae	Erect leafy
ruepa	*Ruellia sp.* nov. 2 aff. R. patula	Acanthaceae	Erect leafy
saccu	*Sacciolepis curvata* (L.) Chase	Poaceae	Tufted graminoid
sanhy	*Sansevieria hyacinthoides* (L.) Druce	Liliaceae	Rosette
sarvi	*Sarcostemma viminale* (L.) R.Br.	Asclepiadaceae	Leafless shrub
schpa	*Schmidtia pappophoroides* Steud.	Poaceae	Tufted graminoid
schpi ⋆	*Schkuhria pinnata* (Lam.) Cabrera	Asteraceae	Erect leafy
secpa	*Secamone parvifolia* (Oliv.) Bullock	Asclepiadaceae	Climber
sedsu	*Seddera suffruticosa* (Schinz) Hallier f. var. *hirsutissima* Hallier f.	Convolvulaceae	Erect leafy
senba	*Senecio barbertonicus* Klatt	Asteraceae	Erect leafy
senoc ⋆	*Senna occidentalis* (L.) Link	Fabaceae	Erect leafy
sesal	*Sesamum alatum* Thonn.	Pedaliaceae	Erect leafy
sesbi ⋆	*Sesbania bispinosa* var. *bispinosa* (Jacq.) W.Wight	Fabaceae	Erect leafy
sesse	*Sesbania sesban* subsp. *sesban* var. *nubica* (L.) Merr.	Fabaceae	Erect leafy
setsa	*Setaria sagittifolia* (A.Rich.) Walp.	Poaceae	Tufted graminoid
setsp2	*Setaria sphacelata* (Schumach.) Moss subsp. *sphacelata*	Poaceae	Tufted graminoid
sidac	*Sida acuta* Burm. f.	Malvaceae	Erect leafy
sidal	*Sida alba* L.	Malvaceae	Erect leafy
sidco	*Sida cordifolia* L.	Malvaceae	Erect leafy
siddr	*Sida dregei* Burtt Davy	Malvaceae	Erect leafy
solac	*Solanum aculeastrum* Dunal	Solanaceae	Shrub
solpa	*Solanum panduriforme* E.Mey.	Solanaceae	Erect leafy

Continued on next page.

Acronym	Full name	Family	Growth form
sorbi	*Sorghum bicolor* (L.) Moench	Poaceae	Tufted graminoid
spese	*Spermacoce senensis* (Klotzsch) Hiern	Rubiaceae	Erect leafy
sphpe	*Sphaeranthus peduncularis* DC. subsp. *peduncularis*	Asteraceae	Erect leafy
sphpr	*Sphedamnocarpus pruriens* (Juss.) Szyszyl. subsp. *pruriens*	Malpighiaceae	Climber
spoaf	*Sporobolus africanus* (Poir.) Robyns & Tournay	Poaceae	Tufted graminoid
spofi	*Sporobolus fimbriatus* (Trin.) Nees	Poaceae	Tufted graminoid
sponi	*Sporobolus nitens* Stent	Poaceae	Tufted graminoid
spopa	*Sporobolus panicoides* A.Rich.	Poaceae	Tufted graminoid
styfr	*Stylosanthes fruticosa* (Retz.) Alston	Fabaceae	Erect leafy
styna	*Stylochiton natalensis* Schott	Araceae	Erect leafy
synca	*Syncolostemon canescens* (Gürke) D.F.Otieno	Lamiaceae	Erect leafy
tagmi ⋆	*Tagetes minuta* L.	Asteraceae	Erect leafy
talar	*Talinum arnotii* Hook.f.	Portulacaceae	Erect leafy
talca	*Talinum caffrum* (Thunb.) Eckl. & Zeyh.	Portulacaceae	Erect leafy
tarof ⋆	*Taraxacum officinale* Weber	Asteraceae	Rosette
teppo	*Tephrosia polystachya* E.Mey var. *hirta* Harv.	Fabaceae	Shrub
teppu	*Tephrosia purpurea* subsp. *leptostachya* (DC.) Brummitt var. *leptostachya* (L.) Pers.	Fabaceae	Erect leafy
terla	*Teramnus labialis* (L.f.) Spreng. subsp. *labialis*	Fabaceae	Climber
thede	*Thelypteris dentata* var. *dentata* (Forssk.) E.St.John	Thelypteridaceae	Long basal
thetr	*Themeda triandra* Forssk.	Poaceae	Tufted graminoid
thune	*Thunbergia neglecta* Sond.	Acanthaceae	Climber
trabe	*Tragus berteronianus* Schult.	Poaceae	Tufted graminoid
traru	*Tragia rupestris* Sond.	Euphorbiaceae	Climber
trasa	*Trachyandra saltii* var. *saltii* (Baker) Oberm.	Liliaceae	Rosette
trigr	*Trichoneura grandiglumis* (Nees) Ekman	Poaceae	Tufted graminoid
trilo	*Tricliceras longepedunculatum* var. *longipedunculatum* (Mast.) R.Fern.	Turneraceae	Erect leafy
trimi	*Tripogon minimus* (A.Rich.) Steud.	Poaceae	Tufted graminoid
trimo	*Tricholaena monachne* (Trin.) Stapf & C.E.Hubb.	Poaceae	Tufted graminoid
tripe	*Triumfetta pentandra* A.Rich.	Malvaceae	Erect leafy
tripr ⋆	*Tridax procumbens* L.	Asteraceae	Prostrate
trite	*Tribulus terrestris* L.	Zygophyllaceae	Prostrate
uromo	*Urochloa mossambicensis* (Hack.) Dandy	Poaceae	Tufted graminoid
vahca	*Vahlia capensis* subsp. *vulgaris* Bridson var. *vulgaris* (L.f.) Thunb.	Vahliaceae	Erect leafy
verbo ⋆	*Verbena bonariensis* L.	Verbenaceae	Erect leafy
verfa	*Vernonia fastigiata* Oliv. & Hiern	Asteraceae	Erect leafy
vergl	*Vernonia glabra* (Steetz) Vatke	Asteraceae	Erect leafy
verol	*Vernonia oligocephala* (DC.) Sch. Bip. ex Walp.	Asteraceae	Erect leafy
verst	*Vernonia steetziana* Oliv. & Hiern	Asteraceae	Erect leafy
vigun	*Vigna unguiculata* subsp. *dekindtiana* (Harms) Verdc. var. *dekindtiana* (L.) Walp.	Fabaceae	Climber

Continued on next page.

Acronym	Full name	Family	Growth form
walin	*Waltheria indica* L.	Malvaceae	Erect leafy
xentr	*Xenostegia tridentata* (L.) D.F.Austin & Staples subsp. *angustifolia* (Jacq.) Lejoly & Lisowski	Convolvulaceae	Climber
xerre	*Xerophyta retinervis* Baker	Velloziaceae	Dwarf shrub

Ends

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Appendix B

R Code

B.1 Circular variables

A circular variable is a special type of variable associated with cyclical time series (Table 2.1). This type of variable is frequently encountered in functional trait studies, particularly when dealing with phenological traits (e.g. month in which flowering or fruiting starts or ends, where December is equally close to January and November). Circular variables cannot be handled in the same way as other variables when calculating dissimilarities, because range needs to be calculated differently to account for the circular structure of the data.

A formal analysis of circular variables follows. Sensible distance measures are derived for when a circular variable is continous and for when it is discrete.

B.1.1 Continuous circular variables

The analysis begins by considering the simple real line. Each point on the real line is uniquely assigned a single real number, so that two different numbers denote two different points, as shown in Figure B.1.

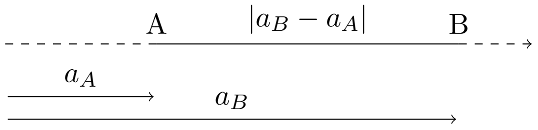

Figure B.1: Two points A and B are located at the positions a_A and a_B on the real line. Their separation is, trivially, $|a_B - a_A|$.

The calculation of the distance between any two such points is, trivially, the difference between their two assigned real numbers.

But if the real line is wrapped around a circular cylinder, say, then the unique assignment fails because there are infinitely many numbers each referring to the same point. That is, one number is assigned for each wrapping instance. And the calculation of a distance measure between two such points is therefore no longer as trivial.

Consider two points A and B located at the angular positions α_A and α_B on the circumference of a circle of radius r, as shown in Figure B.2. The two points' smallest circumferential separation, $S(\alpha_A, \alpha_B, r)$, is

$$S(\alpha_A, \alpha_B, r) = \min(|\alpha_B - \alpha_A|, 2\pi - |\alpha_B - \alpha_A|)r$$

The use of functional notation for "$S(\alpha_A, \alpha_B, r)$" indicates explicitly the dependence of the circumferential separation S on three variables, namely, A's angular position α_A, B's angular position α_B, and the radius r of the circle. The 'min' function accepts two arguments, returning the numerically lesser of the two. And conventionally, the angular positions α_A and α_B are measured in radians, so that a single angular revolution equals 2π radians.

The point circumferentially furthest from A is located at an angle $\alpha_A + \pi$. Its circumferential separation from A is therefore

$$S(\alpha_A, \alpha_A + \pi, r) = \min(\pi, 2\pi - \pi)r = \pi r$$

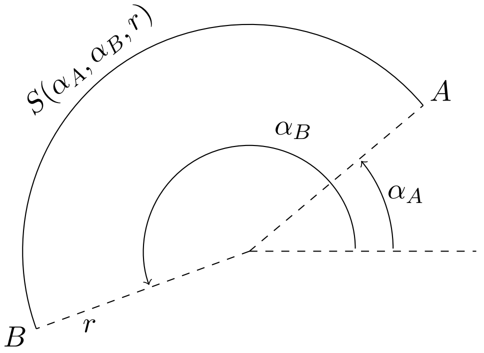

Figure B.2: Two points A and B are located at the angular positions α_A and α_B on the circumference of a circle of radius r. Their circumferential separation is denoted $S(\alpha_A, \alpha_B, r)$.

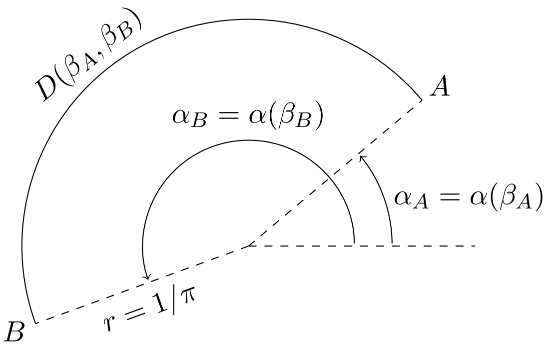

Figure B.3: Two points A and B are located at the angular positions $\alpha(\beta_A)$ and $\alpha(\beta_B)$ on the circumference of a circle of radius $r = 1/\pi$, with $\alpha(\beta)$ given by (B.2). Their normalised circumferential separation $D(\beta_A, \beta_B)$ is given by (B.3).

as expected.

However, while geometrically, a furthest distance equal to πr is sensible, it may seem arbitrary for a variable for which no obvious geometric scale is apparent. Specifically, the choice of value for the radius r is arbitrary. We therefore define a "normalized" separation D by setting $r = 1/\pi$ so that the furthest point from A is at a distance 1 from A. That is

$$\begin{aligned} D(\alpha_A, \alpha_B) &= \frac{1}{\pi r}\, S(\alpha_A, \alpha_B, r) \\ &= \frac{1}{\pi} \min(|\alpha_B - \alpha_A|\,, 2\pi - |\alpha_B - \alpha_A|) \end{aligned} \tag{B.1}$$

Thus $D(\alpha_A, \alpha_A + \pi) = 1$ for all α_A.

The definition of separation $D(\alpha_A, \alpha_B)$ suffices as a normalised distance measure between points whose angular position assignments are constrained to lie in the interval $[0, 2\pi)$. But this is restrictive. For example, for a variable used to store the day of the week, an appropriate interval is $[1, 8)$. And for a variable used to store the day of the year, an appropriate interval is $[1, 366)$ (or $[1, 367)$ to account for leap years). It is therefore necessary to relax the constraints that $0 \leq \alpha_A < 2\pi$ and $0 \leq \alpha_B < 2\pi$.

Consider the linear transformation:

$$\alpha(\beta) = \left(\frac{\beta - \beta_{\text{lo}}}{\beta_{\text{hi}} - \beta_{\text{lo}}}\right) 2\pi \tag{B.2}$$

for some arbitrary β_{lo} and β_{hi}. It is clear that when $\beta = \beta_{\text{lo}}$, $\alpha = 0$. And when $\beta = \beta_{\text{hi}}$, $\alpha = 2\pi$. Thus, by considering the α_A and α_B in (B.1) as functions of β, namely, $\alpha_A = \alpha(\beta_A)$ and $\alpha_B = \alpha(\beta_B)$, and provided that we ensure that the circular variable value lies in the interval $[\beta_{\text{lo}}, \beta_{\text{hi}})$, we may happily shift our attention from α as being the circular variable to β, as shown in Figure B.3.

Substituting (B.2) in (B.1) gives

$$D(\beta_A, \beta_B) = \frac{2}{\beta_{\text{hi}} - \beta_{\text{lo}}} \min(|\beta_A - \beta_B|\,, \beta_{\text{hi}} - \beta_{\text{lo}} - |\beta_A - \beta_B|) \tag{B.3}$$

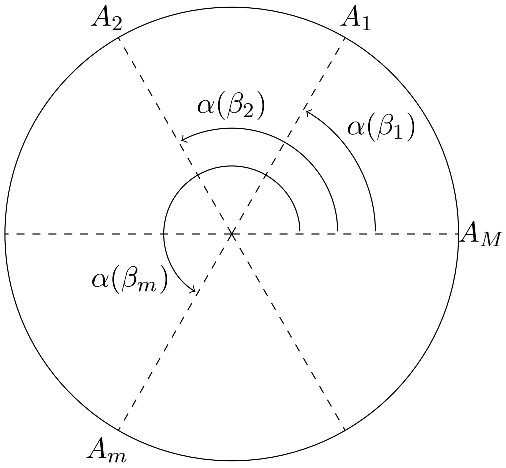

Figure B.4: Points $A_1, \ldots, A_M$ are located at the angular positions $\alpha(\beta_1), \ldots, \alpha(\beta_M)$ on the circumference of a circle of radius $r = 1/\pi$, with $\alpha(\beta_m)$ given by (B.2).

with the functional notation "$D(\beta_A, \beta_B)$" now indicating explicit dependence of D on β_A and β_B instead of on α_A and α_B.

$D(\beta_A, \beta_B)$ is defined using the 'min' and absolute value functions. It may alternatively be defined with the absolute value function only. To achieve this we rely on the easily verifiable result that for any real a and b,

$$\min(a, b-a) \;=\; \frac{b}{2} - \left|a - \frac{b}{2}\right|$$

Recognising that (B.3) contains the form $\min(a, b-a)$, we obtain after some algebraic manipulation

$$D(\beta_A, \beta_B) = 1 - \left|1 - \frac{2}{\beta_{\text{hi}} - \beta_{\text{lo}}}\,|\beta_B - \beta_A|\right| \tag{B.4}$$

How may we assess the validity of this result? Firstly, consider any given value β_A for the circular variable β. We expect that the value "furthest" from β_A is $\beta_A + \frac{1}{2}(\beta_{\text{hi}} - \beta_{\text{lo}})$. Secondly, we expect the separation between the values β_{lo} and β_{hi} to vanish. Using (B.4)

$$D(\beta_A, \beta_A + \tfrac{1}{2}(\beta_{\text{hi}} - \beta_{\text{lo}})) \;=\; 1 - \left|1 - \frac{2}{\beta_{\text{hi}} - \beta_{\text{lo}}}\left|\frac{\beta_{\text{hi}} - \beta_{\text{lo}}}{2}\right|\right| \;=\; 1 \;\text{ for any } \beta_A$$

And

$$D(\beta_{\text{lo}}, \beta_{\text{hi}}) \;=\; 1 - \left|1 - \frac{2}{\beta_{\text{hi}} - \beta_{\text{lo}}}\,|\beta_{\text{hi}} - \beta_{\text{lo}}|\right| \;=\; 0$$

B.1.2 Discrete circular variables

Suppose that instead of our circular variable β being continuous over the interval $[\beta_{\text{lo}}, \beta_{\text{hi}})$, its range of values is restricted to a finite set of M evenly spaced discrete values. That is, suppose $\beta = \beta_m$, $m = 1, 2, \ldots, M$. The circularity of β is represented in Figure (B.4).

With β now discrete, what is the meaning of β_{hi}? To be sure, $\beta_{\text{hi}} \neq \beta_M$, because if it was, then the distance separation of the final "sector" between A_M and A_1 (Figure (B.4)) would be lost when moving from a continuous distance measure (B.4) to a discrete one. Instead, β_{hi} must be thought of as "lying alongside" β_1, so that:

$$\beta_{\text{hi}} = \beta_{\text{lo}} + M(\beta_2 - \beta_1)$$

Substituting into (B.4) gives

$$D(\beta_A, \beta_B) = 1 - \left|1 - \frac{2}{M(\beta_2 - \beta_1)}\,|\beta_B - \beta_A|\right| \tag{B.5}$$

For example, consider a discrete circular variable having 5 allowable values ($M = 5$), as represented in Figure B.5. We expect the point "furthest" from the discrete point A_1 (with circular variable $\beta = \beta_1$) to be located midway between points A_3 and A_4. The value of the circular variable corresponding to that

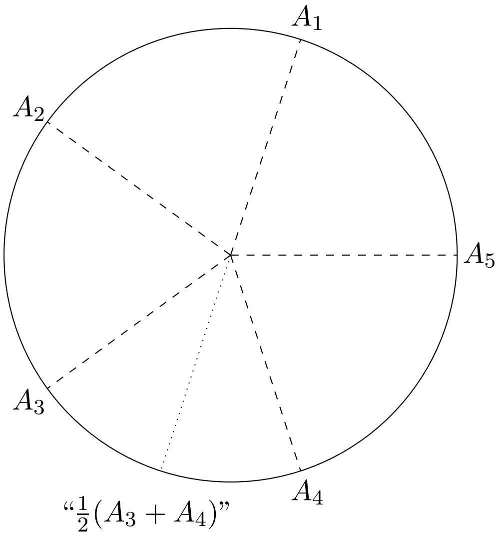

Figure B.5: Points $A_1, \ldots, A_5$ are located at the angular positions $\alpha(\beta_1), \ldots, \alpha(\beta_5)$ on the circumference of a circle of radius $r = 1/\pi$, with $\alpha(\beta_m)$ given by (B.2).

midway point is $\beta_3 + \frac{1}{2}(\beta_2 - \beta_1)$, notwithstanding that in this example, such a point is inadmissable. Then using (B.5) to calculate their separation,

$$\begin{aligned} D(\beta_1, \beta_3 + \tfrac{1}{2}(\beta_2 - \beta_1)) &= 1 - \left|1 - \frac{2}{5(\beta_2 - \beta_1)} \left|\beta_3 + \tfrac{1}{2}(\beta_2 - \beta_1) - \beta_1\right|\right| \\ &= 1 - \left|1 - \frac{2}{5(\beta_2 - \beta_1)} \left|\beta_1 + 2(\beta_2 - \beta_1) + \tfrac{1}{2}(\beta_2 - \beta_1) - \beta_1\right|\right| \\ &= 1 \end{aligned} \tag{B.6}$$

as expected. For any set $\{\beta_1, \beta_2, \beta_3, \beta_4, \beta_5\}$ of 5 evenly spaced values, the matrix of separation values may easily be calculated using (B.5) as:

	β_1	β_2	β_3	β_4	β_5
β_1	0	$\frac{2}{5}$	$\frac{4}{5}$	$\frac{4}{5}$	$\frac{2}{5}$
β_2	$\frac{2}{5}$	0	$\frac{2}{5}$	$\frac{4}{5}$	$\frac{4}{5}$
β_3	$\frac{4}{5}$	$\frac{2}{5}$	0	$\frac{2}{5}$	$\frac{4}{5}$
β_4	$\frac{4}{5}$	$\frac{4}{5}$	$\frac{2}{5}$	0	$\frac{2}{5}$
β_5	$\frac{2}{5}$	$\frac{4}{5}$	$\frac{4}{5}$	$\frac{2}{5}$	0

In summary, combining the continuous (B.4) and the discrete distance measure (B.5) gives

$$\boxed{D(\beta_A, \beta_B) = \begin{cases} 1 - \left|1 - \dfrac{2}{\beta_{\text{hi}} - \beta_{\text{lo}}} \left|\beta_B - \beta_A\right|\right|, & \beta_A \text{ and } \beta_B \text{ continuous.} \\ 1 - \left|1 - \dfrac{2}{M(\beta_2 - \beta_1)} \left|\beta_B - \beta_A\right|\right|, & \beta_A \text{ and } \beta_B \text{ discrete. } \beta_A, \beta_B = 1 \ldots M. \end{cases}} \tag{B.7}$$

B.1.3 Comparison with Pavoine's result

Pavoine *et al.* (2009) proposed an alternative distance measure for discrete circular variables, as:

$$D(\beta_A, \beta_B) = \begin{cases} \sqrt{1 - \left|1 - \dfrac{2}{M} \left|\beta_B - \beta_A\right|\right|}, & M \text{ even.} \\ \sqrt{1 - \left|1 - \dfrac{2}{M - 1} \left|\beta_B - \beta_A\right|\right|}, & M \text{ odd.} \end{cases} \tag{B.8}$$

When comparing (B.8) with (B.7), it is clear that Pavoine's inclusion of the square root, as well as the treatment of the case M odd, are dubious. Furthermore, Pavoine's result must assume that the increment between adjacent possible discrete values is always equal to 1. For, as above in (B.6), consider a discrete circular variable having 5 allowable values ($M = 5$), as represented in Figure B.5. Then Pavoine's result gives

$$\begin{aligned}
D(\beta_1, \beta_3 + \tfrac{1}{2}(\beta_2 - \beta_1)) &= \sqrt{1 - \left|1 - \frac{2}{5-1}\left|\beta_3 + \tfrac{1}{2}(\beta_2 - \beta_1) - \beta_1\right|\right|} \\
&= \sqrt{1 - \left|1 - \frac{2}{4}\left|\beta_1 + 2(\beta_2 - \beta_1) + \tfrac{1}{2}(\beta_2 - \beta_1) - \beta_1\right|\right|} \\
&= \sqrt{1 - \left|1 - \frac{5}{4}(\beta_2 - \beta_1)\right|} \\
&= \frac{\sqrt{3}}{2} \quad \text{provided } \beta_2 - \beta_1 = 1
\end{aligned}$$

I cannot find any compelling justification for this result.

B.1.4 Implementation

To implement (B.7) in R, I wrote a function called `prepcircvars`, and also extended the code for the function `gowdis` in the `FD` package to include handling of circular variables.

The helper function `prepcircvars` was necessary because of the need to calculate range differently for circular variables. This function was loosely based on R code by Pavoine *et al.* (2009) in their implementation of the Gower dissimilarity measure (function `dist.ktab` in the package `ade4`). To use `prepcircvars`, circular variables must first be placed in a separate data matrix or data frame, if they are mixed with other data types. The function is then run on the circular variable data matrix/frame. The function checks the variables, calculates the circular range appropriately and adds it to each variable as an attribute (`"crange"`). It also changes the class of each variable to `"circular"`. It does not, however, change the actual data values. The prepared circular data can then be joined back onto the data matrix/frame containing the rest of the variables (if necessary).

The `prepcircvars` function requires the following input for each circular variable:

1. `type`, i.e. whether the variable is continuous or discrete (see (B.7))
2. `tmax`, the theoretical maximum value of m
3. `tmin`, the theoretical minimum value of m, and
4. `tstep`, the size of the increment between successive levels for discrete variables (NA for continuous variables). This cannot be 0.

The modified version of `gowdis` described below will give an error if circular variables are not prepared using `prepcircvars`.

Function to prepare circular variables for dissimilarity calculation

```
#
# Function to prepare circular variables for use in gowdis().
# Refer to the sibling file 'gowdis.R'.
#
# For each circular variable, the existing attribute "class"
# is set to equal "circular", and the new attribute "crange"
# introduced here is set to an appropriately calculated
# circular range.  This allows the gowdis() function to
# recognise and handle these variables appropriately when
# calculating Gower dissimilarity.
#
# Notes:
#
```

```
#  - ’x’ must be a data frame or numeric matrix.
#  - ’type’, ’tmax’, ’tmin’ and ’tstep’ must be vectors of length
#     ncol(x).
#  - NA’s are allowed in ’x’.
#  - Negative values are allowed in all arguments.
#  - ’tstep’ is only needed for discrete variables. If you
#    have mixed discrete and continuous data, you must supply
#    ’tstep’ (but can use NA for continuous variables).
#
#                                         KA Kotschy
#                                         16Dec10.
#

prepcircvars <- function(x, type, tmax, tmin, tstep)
{
   #
   # Input validation.
   #
   if (length(dim(x)) != 2 || !(is.data.frame(x) || is.numeric(x)))
      stop ("x is not a dataframe or a numeric matrix.\n")
   #
   # NB: When the members of the columns of x are integer,
   #     the result of data.class(xcol) is "numeric", where xcol
   #     is a column of x.  See help(data.class).
   #
   if (any(sapply(x, data.class) != "numeric"))
      stop ("Circular variables should be of class ’numeric’ or ’integer’.\n")
   if (any(!(type %in% c("discrete", "continuous"))))
      stop ("’type’ may only contain ’discrete’ or ’continuous’.\n")
   if (length(type) != ncol(x))
      stop ("’type’ must have length = number of circular variables in ’x’.\n")
   buf <- list(tmax, tmin, tstep)
   if (any(sapply(buf, length) != ncol(x)))
      stop ("’tmax’, ’tmin’ and ’tstep’ must have length = number of circular variables in ’x’.\n")
   if (any(!sapply(buf, is.numeric)))
      stop ("’tmax’, ’tmin’ and ’tstep’ must be numeric vectors.\n")
   veriffun <- function(i){
      if (tmin[i] > min(x[,i], na.rm = TRUE))
         stop ("tmin is larger than min in data.\n")
      if (tmax[i] < max(x[,i], na.rm = TRUE))
         stop ("tmax is smaller than max in data.\n")
   }
   sapply(1:ncol(x), veriffun)

   #
   # Private utility function for discrete variables.
   #
   prepdiscretevars <- function(xcol,j){
      if (is.null(tstep[j]))
         stop ("’tstep’ must be supplied for discrete circular variables.\n")
      if (tstep[j] == 0)
         stop ("’tstep’ cannot be 0.\n")

      #
      # When calculating datastep using diff(), any
      # vanishing differences (i,e., equal to 0) between
      # two successive entries in xcol must not be
      # considered.
      #
      datastep <- abs(diff(xcol))
      datastep <- min(datastep[datastep>0], na.rm=T)
      if (abs(tstep[j]) > datastep)
         stop ("’abs(tstep)’ is larger than smallest step in data.\n")

      #
      # NB Note: The ’+1’ is very important.
      #
```

```
      levels <- (tmax[j]-tmin[j])/tstep[j] + 1
      crange <- levels * tstep[j]
      attr(xcol, "crange") <- crange
      return(xcol)
   }

   #
   # Private utility function for continuous variables.
   #
   prepcontinuousvars <- function(xcol,j){
      crange <- tmax[j] - tmin[j]
      attr(xcol, "crange") <- crange
      return(xcol)
   }

   #
   # This is the heart of prepcircvars().
   #
   res <- x
   for (k in 1:ncol(x)){
      class(x[,k]) <- "circular"
      #class(res[,k]) <- "circular"
      if (type[k] == "discrete")
         res[,k] <- prepdiscretevars(x[,k],k)
      else
         res[,k] <- prepcontinuousvars(x[,k],k)
   }

   return(res)
}
```

Modifications to the `gowdis` function to allow handling of circular variables

The R function `gowdis` in the package `FD`, written by Etienne Laliberté, calculates pairwise dissimilarities between entities using the Gower dissimilarity metric (§**??**). The main engine of the function, called `gowdis.c`, is written in C for improved speed, and is contained inside an R wrapper named `gowdis.R`.

Modifications to the R code include the addition of an extra type of variable (“circular”, case 6) and modifications to the internal function used to calculate range (`range2`). Calculation of dissimilarities using (B.7) is performed within `gowdis.c`.

Modifications to the R code (`gowdis.R`)

```
# This function has been modified to handle the existence of circular variables. It is
# important to note that circular variables must be prepared using the preparatory function
# ’prepcircvars()’. Please note that elements of the layout, such as indentation, have been
# changed to match that in the file ’prepcircvars.R’.  KA Kotschy 10Nov10.

‘gowdis‘ <- function(x, w, asym.bin = NULL, ord = c("podani", "metric"))
{
   #
   # Input validation starts.
   #
   if (length(dx <- dim(x)) != 2 || !(is.data.frame(x) || is.numeric(x)))
      stop("x is not a dataframe or a numeric matrix.\n")

   # n = number of rows, p = number of variables.
   n <- dx[1]
   p <- dx[2]

   ord <- match.arg(ord)

   varnames <- dimnames(x)[[2]]
```

```

   # Check for weight vector.  Add equal weights if missing.
   if (!missing(w)){
      # Check if correct class and length.
      if (length(w) != p | !is.numeric(w))
         stop("w needs to be a numeric vector of length equal to the number of variables in x.\n")
      if (all(w == 0) )
         stop("Cannot have only 0’s in ’w’.\n")
      w <- w / sum(w)
   } else {
      w <- rep(1, p) / sum(rep(1, p))
   }
   #
   # Input validation ends.
   #

   #
   # Setting the class of each variable starts.
   #
   if (is.data.frame(x)) {
      type <- sapply(x, data.class)
   } else {
      type <- rep("numeric", p)
      names(type) <- colnames(x)
   }

   # Replace character variables by factors.
   if (any(type == "character")) {
      for (i in 1:p) {
         if (type[i] == "character")
            x[,i] <- as.factor(x[,i])
      }
   }

   # Check for binary variables.
   is.bin <- function(k) all(k[!is.na(k)] %in% c(0,1))

   bin.var <- rep(NA,p); names(bin.var) <- varnames
   for (i in 1:p)
      bin.var[i] <- is.bin(x[,i])

   if (any(type[bin.var] != "numeric"))
      stop("Binary variables should be of class ’numeric’.\n")

   type[type %in% c("numeric", "integer")] <- 1
   type[type == "ordered"] <- 2
   type[type %in% c("factor", "character")] <- 3
   type[bin.var] <- 4

   # Convert asymmetric binary variables, if present.
   if (!is.null(asym.bin) ){
      if (!all(bin.var[asym.bin]))
         stop("Asymetric binary variables must only contain 0 or 1.\n")
      else
         type[asym.bin] <- 5
   }

   # Added to account for "circular variables". KA Kotschy. 27Oct10.
   type[type == "circular"] <- 6
   #
   # Setting the class of each variable ends.
   #

   type <- as.numeric(type)

   # Convert ordinal variables to ranks, following Podani (1999).
   if (any(type == 2)) {
```

```
      for (i in 1:p) {
         if (type[i] == 2)
            x[,i] <- rank(x[,i], na.last = "keep")
      }
   }

   #
   # Calculation of range starts. This has been modified from
   # the original to add clarity, and because the range attribute
   # "crange" for circular variables must be used *before* the
   # data frame is 'downgraded' to a matrix via data.matrix(),
   # otherwise the "crange" attributes are lost.
   #
   # Note that range is not actually used in calculating
   # dissimilarities (in gowdis.c) for factor,
   # binary or asymmetric binary variables, so for these types
   # of variables the entry in the range2 vector will be 0 (the
   # default). KA Kotschy. 18Dec10.
   #
   #range2 <- vector("numeric", length=p)
   range2 <- rep(0.0, p)
   for (i in 1:p) {

       if (type[i] == 1) {

          #
          # "Numeric" type.
          #
          maxmin <- range(x[,i], na.rm = T)
          range2[i] <- maxmin[2] - maxmin[1]

       } else if (type[i] == 2) {

          #
          # "Factor" type.
          #
          # Convert ordinal variables to ranks, following Podani (1999).
          #
          x[,i] <- rank(x[,i], na.last = "keep")

          #
          # Using unclass() converts
          # factor levels to their internal numeric codes.
          #
          #x[,i] <- unclass(x[,i])
          maxmin <- range(x[,i], na.rm = T)
          range2[i] <- maxmin[2] - maxmin[1]

       } else if ((type[i] == 3) || (type[i] == 4) || (type[i] == 5)) {

          #
          # Do nothing.
          #

       } else if (type[i] == 6) {

          #
          # "Circular" type.
          #
          # Circular range is calculated and added as an attribute of
          # the circular variable(s) in the function prepcircvars(),
          # which must be used to prepare circular data prior
          # to using gowdis().
          #
          range2[i] <- attr(x[,i],"crange")

       } else {
```

```

          #
          # Error.
          #
          stop("Variable type is invalid.\n")

       }

   }
   #
   # Calculation of range ends.
   #
   ## Original function to calculate range, replaced by section above.
   ##range.Data <- function(v){
   ##   r.Data <- range(v, na.rm = T)
   ##   res <- r.Data[2]-r.Data[1]
   ##   return(res)
   ##}
   ##range2 <- apply(x, 2, range.Data)

   ## Convert factors to their internal numeric codes.
   # Convert x to a matrix if it is not already. This is
   # necessary here because gowdis.c cannot accept a data
   # frame as input. Conversion of ordered factors to their
   # numeric codes has already been done in the calculation
   # of range (above). KA Kotschy. 18Dec10.
   x <- data.matrix(x)

   #
   # Compute Timax, and Timin for each variable (these will
   # only apply to ordinal variables, see Podani [1999], eq. 2b.)
   #
   comp.Timax <- function(v){
      Ti.max <- max(v, na.rm = T)
      no.na <- v[!is.na(v)]
      res <- length(no.na[no.na == Ti.max])
      return(res)
   }

   Timax <- apply(x, 2, comp.Timax)

   comp.Timin <- function(v){
      Ti.min <- min(v, na.rm = T)
      no.na <- v[!is.na(v)]
      res <- length(no.na[no.na == Ti.min])
      return(res)
   }

   Timin <- apply(x, 2, comp.Timin)

   if (ord == "podani")
      pod <- 1
   else
      pod <- 2

   res <- .C("gowdis", as.double(x), as.double(w), as.integer(type), as.integer(n), as.integer(p),
             as.double(range2), as.integer(pod), as.double(Timax), as.double(Timin),
             res = double(n*(n-1)/2), NAOK = T, PACKAGE = "FD")$res

   type[type == 1] <- "C"
   type[type == 2] <- "O"
   type[type == 3] <- "N"
   type[type == 4] <- "B"
   type[type == 5] <- "A"
   #
   # Added equivalent character code for circular
   # variables. KA Kotschy. 18Dec10.
```

```
   #
   type[type == 6] <- "Ci"

   if (any(is.na(res)))
      attr(res, "NA.message") <- "NA’s in the dissimilarity matrix!"

   attr(res, "Labels") <- dimnames(x)[[1]]
   attr(res, "Size") <- n
   attr(res, "Metric") <- "Gower"
   attr(res, "Types") <- type
   class(res) <- "dist"

   return(res)
}
```

Modifications to the C code (`gowdis.c`)

```
/*
 * Etienne Laliberte, October 26, 2009
 * etiennelaliberte[AT]gmail.com
 */

#include <R.h>
#include <math.h>

static int dequal(double d1, double d2)
{
  double diff = fabs(d1 - d2);
  return (diff < 0.00000001);
}

/*
 * This function has been modified as follows:
 *
 * 1. Cosmetics, such as:
 *
 *    - Changing the indenting layout to better conform to
 *      C coding conventions.
 *
 *    - Adding some blank lines to aid readability.
 *
 *    - Ensuring that at most 1 expression or expression
 *      clause resides on 1 line.
 *
 *    - Ensuring consistent use of whitespace, e.g., ’(1 + 2 )’
 *      was changed to ’(1 + 2)’.
 *
 *    - Migrating the declaration of the ’l’ integer counter
 *      to lie within the scope of its use.
 *
 *    - Changing all ’1’s and ’2’s to ’1.0’ and ’2.0’ where real
 *      values were expected.
 *
 * 2. Accounting for the presence of "circular variables".
 *    See type[k] case ’6’ below.
 *
 * Paul Kotschy. 27Oct10.
 */
void gowdis( double *x,         /* Data frame of species (Species are the rows; traits are */
                                /* the columns). */
             double *win,       /* Vector of weights.  Length equals no. of traits. */
             int *type,         /* Vector of integers indicating trait data type. Length */
                                /* equals no. of traits. */
             int *nin,          /* No. of rows of ’x’, i.e., no. of species, say. */
```

```
             int *pin,          /* No. of columns of ’x’, i.e., no of traits, say. */
             double *range2,    /* Vector of (max-min) of each column of ’x’. */
             int *podin,        /* Flag specifying how to treat ordinal variables [1|2]. */
             double *tmax,      /* Vector of some "maximum" for each column of ’x’. */
             double *tmin,      /* Vector of some "minimum" for each column of ’x’. */
             double *res )      /* ? */
{
   int i,
       n = *nin;
   double ti, tj;

   /*printf("Paul Kotschy: nin=%d. pin=%d. res=%f\n", *nin, *pin, *res); exit(0);*/

   for (i = 0; i < n-1; i++) {

      /*printf("Species %d: *nin=%d, *pin=%d.\n",i+1,*nin,*pin);*/
      int j;

      for (j = i+1; j < n; j++) {

         int k;
         double wsum = 0.0,
                tmp = 0.0;

         for (k = 0; k < *pin; k++) {

              double psim = 0.0;
              double w = 0.0;

              if (R_FINITE(x[i + n * k]) && R_FINITE(x[j + n * k])) {

                 w = win[k];

                 /*printf("type[%d]=%d\n",k,type[k]);*/
                 switch (type[k]) {
                    case 1:
                       psim = w * (1.0 - (fabs(x[i + n * k] - x[j + n * k])) / range2[k]);
                       break;
                    case 2:
                       switch (*podin) {
                          case 1: {
                             if (dequal(x[i + n * k], x[j + n * k])) {
                                psim = w * 1.0;
                             } else {
                                int l;
                                ti = 0.0;
                                tj = 0.0;
                                for (l = 0; l < n; l++) {
                                   if (R_FINITE(x[l + n * k]) && dequal(x[l + n * k], x[i + n * k]))
                                      ti = ti + 1.0;
                                   if (R_FINITE(x[l + n * k]) && dequal(x[l + n * k], x[j + n * k]))
                                      tj = tj + 1.0;
                                }
                                psim = w * ( 1.0 - ( ( fabs(x[i + n * k] - x[j + n * k])
                                                       - (ti-1.0)/2.0 - (tj-1.0)/2.0 )
                                                     / ( range2[k] - (tmax[k]-1.0)/2.0
                                                         - (tmin[k]-1.0)/2.0 ) ) );
                             }
                             break;
                          }
                          case 2: {
                            psim = w * ( 1.0 - (fabs(x[i + n * k] - x[j + n * k])) / range2[k] );
                            break;
                          }
                       }
                       break;
                    case 3:
```

```
case 4:
   if (dequal(x[i + n * k], x[j + n * k]))
      psim = w * 1.0;
   break;
case 5:
   if (dequal(x[i + n * k], 0) && dequal(x[j + n * k], 0)) {
      w = 0.0;
      psim = 0.0;
   } else {
     if (dequal(x[i + n * k], x[j + n * k]))
        psim = w * 1.0;
   }
   break;
case 6:
   /*
    * Case ’6’ added to account for circular
    * variables in the specified ’x’ dataframe.
    *
    * Consider the following important point.  When a
    * k-th trait is "circular", the question arises
    * whether the trait is "continuous" or "discrete".
    * A continuous trait can assume any real value
    * between two extrema, and the value of range[k]
    * must contain the absolute value of the difference
    * between these two extrema.
    *
    * In contrast, a discrete trait can only take on a
    * value from a finite set of evenly spaced real
    * values.  In this case, range[k] is not just the
    * difference between the extrema in this set.
    * Instead, range[k]’s value must equal m*dX, where
    * m is the number of such possible values, and dX
    * is the spacing between two adjacent values in the
    * abovementioned finite set.  E.g.:
    *
    * 1. If the k-th trait is continuous in the range
    *    [Xmin,Xmax], then range[k] must equal
    *    |Xmax-Xmin|.
    *
    * 2. If the k-th trait is discrete, and its
    *    possible values are, say:
    *
    *         { X1=Xmin, X2,     X3,      ..., Xm          }
    *       = { Xmin,    Xmin+D, Xmin+2D, ..., Xmin+(m-1)D }
    *
    *    Then range[k] must equal Xm+D-Xmin = m*D.
    *
    *    But since it is likely that the ecologist will have
    *    available the set {X1,...,Xm}, in which case
    *    m must be derived as
    *
    *       m = (Xm-X1)/D + 1
    *
    * PJ Kotschy. 27Oct10.
    */
   /*printf("   Species pair=(%d,%d). Trait=%d.\n",i+1,j+1,k+1);*/
   if (dequal(x[i + n * k], x[j + n * k])) {
      psim = w * 1.0;
   } else {
      psim = w * fabs(1.0 - 2.0*fabs(x[i + n * k] - x[j + n * k])/range2[k]);
      /*if ( i+1 == 3  &&  j+1 == 4 ) {
       *   printf( "i=%d, j=%d, n=%d, k=%d: i+n*k=%d, j+n*k=%d, xi=%f, xj=%f, "
       *           "w=%f, range2[k]=%f: psim=%f\n",
       *           i,
       *           j,
       *           n,
       *           k,
```

```
                           *           i+n*k,
                           *           j+n*k,
                           *           x[i + n * k],
                           *           x[j + n * k],
                           *           w,
                           *           range2[k],
                           *           psim );
                           *}*/
                       }
                       break;
                    default:
                       psim = 0.0;
                       break;
                 }

             }

             tmp += psim;
             wsum += w;

         }

         if (wsum == 0)
            *res = NA_REAL;
         else
            *res = 1.0 - (tmp / wsum);

         /*if ( i+1 == 3  &&  j+1 == 4 ) {*/
         /*   printf("Species pair=(%d,%d). res=%f.\n",i+1,j+1,*res);*/
         /*}*/

         res++;

      }

   }

   return;
}
```

B.2 Developing a measure of the contribution of each trait to the overall dissimilarity

As argued in §**??**, it is useful to be able to differentially weight the trait variables used to calculate between–species dissimilarities, either to reflect the differences in importance of the traits for a particular function, or to remove any unintentional weighting effects caused by differences in trait data types (assuming that we are interested in more than one trait variable).

The first step in developing weightings for a set of traits is to evaluate the relative contribution of each *unweighted* trait to the overall dissimilarity, i.e. the dissimilarity obtained when all the variables are combined. The fact that traits are not differentially weighted does *not* mean that they will all contribute equally to the overall dissimilarity (§**??**).

The contribution of each trait can be calculated from the correlation between the dissimilarities obtained using each individual trait in turn and the dissimilarities obtained using all the traits together. This approach has been implemented in R by Pavoine *et al.* (2009), in the function `kdist.cor` (package `ade4`). This function was designed to work with the function `dist.ktab (ade4)`, which calculates Gower dissimilarities but does not allow for weighting of traits, and requires input in a particular format which is not compatible with the output from the `gowdis` function. I therefore wrote a new function `traitcontrib`, based on `kdist.cor`, which is compatible with `gowdis`.

```
#
# Function to calculate the contribution of each functional trait to
```

```
# the global distance (dissimilarity) between species. Weighting of
# traits can be specified using ‘w’. To apply no weighting, make
# w = c(rep(1, ncol(x))).This function is based on ade4::kdist.cor.
#
# x = trait data frame or matrix, with species as rows and traits as
# cols.  w = vector of numerical weights, of same length as no. of
# trait vars. Cannot contain zeroes.  asym.bin indicates if binary
# vars should be treated as asymmetric (double zeroes become NA);
# specify col nos containing these vars as asym.bin=7:10 or
# asym.bin=c(7:10,14).
#
#                                           KA Kotschy
#                                           27Aug10.
#
traitcontrib <- function(x, w, asym.bin = NULL, squared = FALSE)
{
   weight.global <- w
   weight.indiv <- diag(weight.global)
   gowdis.global <- gowdis(x, weight.global, asym.bin = asym.bin)
   ldis <- vector("list", length = length(weight.global))
   for(i in seq_along(weight.global))
   {
      ldis[[i]] <- gowdis(x, w = weight.indiv[i,], asym.bin = asym.bin)
      names(ldis) <- names(x)
   }
   tabvec <- cbind.data.frame(lapply(ldis, as.vector))
   vecglo <- as.vector(gowdis.global)
   if (squared){
      paircov <- cov(tabvec^2, use = "pairwise.complete.obs")
      paircor <- cor(tabvec^2, use = "pairwise.complete.obs")
      glocor <- cor(tabvec^2, vecglo^2, use = "pairwise.complete.obs")
      colnames(glocor) <- "contrib to global distance"
   }
   else{
      paircov <- cov(tabvec, use = "pairwise.complete.obs")
      paircor <- cor(tabvec, use = "pairwise.complete.obs")
      glocor <- cor(tabvec, vecglo, use = "pairwise.complete.obs")
      colnames(glocor) <- "contrib"
   }
   return(list(paircov = paircov, paircor = paircor, glocor = glocor))
}
```

Using the `traitcontrib` function with all trait variables assigned equal weights (or, using `kdist.cor`) provides a measure of the relative influence of each trait on the overall dissimilarity. This should be done before applying any weighting, as it reveals inherent differences in trait contributions due to data type or correlations among traits. Trait weightings can then be applied as desired using `gowdis`.

Once weightings have been applied, it is necessary to be able to evaluate the effects of these weightings and how they modify the relative contributions of the different traits. I originally intended to use `traitcontrib` to do this. However, calculating the contributions of weighted traits using this method is problematic. Although it is logistically possible to run such an analysis, the meaning of the results would be unclear. This is because the effect of weighting a particular trait cannot be seen in isolation; it depends on the weightings given to all the other traits. In `traitcontrib`, trait contributions are calculated by calculating the distance matrices for each trait separately and then correlating each of these with the overall distance matrix. However, a trait cannot be weighted when it is the only one in the analysis, so the distance matrices for each of the traits separately do not properly reflect their *weighted* contribution to the global distance within the context of the weights given to all the other traits.

I therefore developed a new method for calculating the contribution of trait variables to the overall dissimilarity. This method allows the contribution of unweighted and weighted traits to be calculated. Trait contributions to the overall dissimilarity are calculated by the effect on the overall dissimilarity of removing each trait in turn. This is similar to the approach suggested by Petchey and Gaston (2002a) for calculating the contribution of individual species to the disparity of a whole assemblage. First, an overall (weighted or unweighted) distance matrix is calculated, then each trait is removed one at a time, without changing the weights of the remaining traits. The amount of change occurring with the removal of each trait is measured by simple matrix correlations.

The new method is implemented in R as the function `wtraitcontrib` below.

```
#
# Function to calculate WEIGHTED contribution of each functional
# trait to the global distance (dissimilarity) between species.
#
# x = a trait data frame or matrix, with species as rows and traits as
#     columns.
# w = a vector of numeric weights, of the same length as ncol(x).
#
#                                             KA Kotschy
#                                             2Sep10.
#
wtraitcontrib <- function(x, w)
{
   gowdis.global <- gowdis(x, w)
   gowdis.drop1 <- vector("list", length = ncol(x))
   contrib <- data.frame(row.names = names(x))
   for(i in 1:ncol(x))
   {
      gowdis.drop1[[i]] <- gowdis(x[-i], w[-i])
      names(gowdis.drop1) <- paste("drop.", names(x), sep = "")
      contrib[i,1] <- 1 - cor(gowdis.global, gowdis.drop1[[i]], use = "pairwise.complete.obs")
   }
   names(contrib) <- "contrib"
   return(contrib)
}
```

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