

Biodiversity and Ecosystem Functioning

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Synthesis and Perspectives

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Preface

The study of biodiversity and ecosystem functioning has followed a pattern that often characterizes history in science. This pattern is best described as periods of empirical and theoretical development bracketed by periods of synthesis (Kuhn 1962; Kingsolver and Paine 1991). This is not an even course; new developments are often accompanied by debate or controversy (Dunwoody 1999).

A conference, entitled *Biodiversity and ecosystem functioning: synthesis and perspectives*, was held in Paris, France, on 6–9 December 2000 under the auspices of the International Geosphere–Biosphere Programme—Global Change and Terrestrial Ecosystems (IGBP–GCTE) and DIVERSITAS, international programmes that foster communication among scientists involved in global change and biodiversity research. The conference was designed to facilitate synthesis of nearly a decade of observation, theory, and experiment in biodiversity and ecosystem functioning research. Its goals were to identify central principles, certainties, uncertainties, future directions, and policy implications in this area. A brief report of the conference was published in *Trends in Ecology and Evolution* (Hughes and Petchey 2001), and a summary of its main findings was published in *Science* (Loreau *et al.* 2001). This volume provides overviews, position papers, and reports from the synthesis workshops of the conference, which together give a synthetic and balanced account of the current knowledge and future challenges in the fast growing area of biodiversity and ecosystem functioning.

The conference was a delight. Virtually every invitation was accepted (indeed, many could not

be invited or were turned away to keep the workshops of manageable size) in the interest of resolving the issues. The distribution of participants was broad, most importantly being weighted towards junior and emerging researchers. The presentations, workshops, and panel discussions were extraordinarily cordial, friendly, and interactive. Not unexpectedly, some left with as strong an opinion as they arrived with, but all were encouraged to explore the issues in greater depth and all had a greater appreciation of the perspectives and the fascinating science behind the varied perspectives.

The conference was made possible by the financial support provided by the European Science Foundation LINKECOL programme, the Centre National de la Recherche Scientifique (France), and the US National Science Foundation (DEB NSF DEB 973343). Some who attended contributed to the workshops and panel discussions although they could not contribute to the chapters. In addition, we wish to acknowledge the help of many anonymous individuals who provided critical reviews of the chapters, and Paola Paradisi, Régine Mfoumou, Christelle Blée, Marie-Bernadette Tesson and Susie Dennison who helped with logistics. And to all those that space does not provide for a proper acknowledgment, we thank for help in making the conference the success that it was.

Michel Loreau, Shahid Naeem and Pablo Inchausti
14 January 2002

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PART V

Extending the scope to other dimensions

Species diversity, functional diversity, and ecosystem functioning

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17.1 Introduction

Experiments assessing the effects of biodiversity on ecosystem functioning initially aimed at establishing whether such relationships exist (e.g. Naeem *et al.* 1995; Tilman *et al.* 1996; Jonsson and Malmqvist 2000; Engelhardt and Ritchie 2001). These phenomenological studies were useful for helping to identify patterns and articulate further questions. However, using species richness as a simple measure of biotic diversity, as they did, had no explicit explanatory power: ecosystem level processes are affected by the functional characteristics of organisms involved, rather than by taxonomic identity (Odum 1969; Pugh 1980; Grime 1988). Therefore, functional attributes of species must be considered if a mechanistic understanding of biodiversity effects is sought. In attempting to understand mechanisms, several subsequent experiments have manipulated either the diversity of functional groups (i.e. functional diversity) alone (Hooper and Vitousek 1997, 1998; Symstad and Tilman 2001) or functional group diversity in concert with species diversity (McGrady-Steed *et al.* 1997; Naeem and Li 1997; Tilman *et al.* 1997a; Hector *et al.* 1999; Petchey *et al.* 1999; McGrady-Steed and Morin 2000; Emmerson *et al.* 2001) (see Díaz and Cabido 2001 for a recent review for plants). Here we discuss species and functional-group approaches and compare their suitability for understanding the effects of organismic diversity on ecosystem functioning.

There is a vast literature on functional classification in both terrestrial and aquatic ecosystems

(e.g. see reviews on soil organisms: Faber 1991; Brussaard *et al.* 1997; animals in general, guild concept: Simberloff and Dayan 1991; marine sediment organisms: Swift 1993; Snelgrove *et al.* 1997; stream invertebrates: Wallace and Webster 1996; plants: Smith *et al.* 1997; Díaz and Cabido 2001; general: Lavorel and Garnier 2001). Our goal is not to recapitulate the extant literature, but to address three questions of importance to biodiversity–ecosystem functioning research. First, of the various approaches used for functional classification, which are most useful for investigating diversity effects on ecosystem functioning? Second, how are functional and species diversity related in terms of their effects on ecosystem processes? Third, what is the relevance of using a functional versus species diversity approach for understanding the implications of recent experiments to ecosystem management?

17.2 Defining functional groups

Ecologists have used a variety of ways to define functional groups, and such delineation has a long history in ecology (e.g. Raunkiaer 1934). Functional groups have been defined as sets of species showing either similar *responses* to the environment or similar *effects* on major ecosystem processes (Gitay and Noble 1997). In addition, functional groups can be identified as clusters in trait space through multivariate statistics, without *a priori* classifications regarding particular responses to environment or

influences on ecosystem processes (i.e. emergent groups, Lavorel *et al.* 1997). The terms 'functional group' and 'functional type' are sometimes used synonymously. We will generally use the term 'functional group' for simplicity. Other related terms include 'guild' and 'ecological groups' (Root 1967; Simberloff and Dayan 1991; Wilson 1999), and there is a close relation of these to various forms of the niche concept (Leibold 1995). Functional diversity refers to the range and value of organismal traits that influence ecosystem properties (Tilman 2001). This can be expressed in a variety of ways, including the number and relative abundance of functional groups (e.g. Tilman *et al.* 1997a; Hooper 1998; Spehn *et al.* 2000b), 'the variety of interactions with ecological processes' (Martinez 1996), or the average difference among species in functionally related traits (Walker *et al.* 1999). In this section, we examine different approaches to delineating functional groups, whether these approaches might be merged and whether functional classifications are hierarchical.

17.2.1 Multiple approaches

A number of approaches for defining functional groups have been used in different ecosystems, at different scales, and for different types of organisms (plants, microorganisms, soil mesofauna, etc). This is not necessarily a problem; it usually reflects current knowledge of organisms and ecosystems and the particular questions being addressed. Indeed, it is unlikely that there will be a single functional classification that is appropriate universally. Instead, what might be called a 'trait toolkit' may be more appropriate, whereby the organisms, their traits, and the scales of diversity (genotype, species, higher taxa, community type) for functional classification (the tools) will be defined in accordance with the job at hand: the processes of interest, the ecosystem type, and the suitable spatial and temporal scale (Fig. 17.1). The number of traits in such a toolkit are not infinite, however, because there are often correlations among traits due to physiological or fitness tradeoffs. For example, drought-tolerant plants may share traits such as position of stomata, cuticle thickness, and photosynthetic pathways even though taxonomically quite different (e.g.

cacti and euphorbs). Exhibiting sets of traits that are collectively associated with adaptation to particular environmental challenges is known as an 'ecological syndrome' or 'primary strategy' (Lavorel *et al.* 1997; Grime 2001). Primary strategies among many different types of organisms yield predictable effects on ecosystem properties (Chapin 1980; Chapin *et al.* 1993; Elser *et al.* 1996; Grime *et al.* 1997b; Reich *et al.* 1997) and may help simplify functional classifications in the trait toolkit. We discuss this approach more in the following sections.

17.2.2 Effect and response groups

Functional classification often has two relatively distinct goals, one of which is to investigate the effects of species on ecosystem properties (functional effect groups) and another which is to investigate the response of species to changes in the environment, such as disturbance, resource availability, or climate (functional response groups) (Landsberg 1999; Walker *et al.* 1999). The distinction between functional effect groups and functional response groups is directly analogous to the distinction between the functional and habitat niche concepts (e.g. Leibold 1995), where the functional niche encompasses the effects that a species has on community and ecosystem dynamics, and the habitat niche encompasses the environmental parameters necessary for a species' survival. Most studies on biodiversity/ecosystem functioning have focused on functional effect groups, rather than using groupings based on species' responses. We suggest, however, that merging these two perspectives is useful for understanding biodiversity effects on ecosystem properties.

Functional effect groups

Two alternate approaches have been applied for categorizing species into functional effect groups. The first uses *ad hoc* groups based on physiognomic attributes of organisms in the ecosystem studied (Table 17.1), while the second approach looks for general tradeoffs in organism traits as a way of constraining the axes of differentiation for functional classification (e.g. Grime 1979, 2001). These approaches are described below.

Table 17.1 Examples of *ad hoc* functional groups for a variety of organisms and ecosystems. Many of these examples at least partially follow taxonomic lines. This list is meant to be illustrative, not comprehensive. See Díaz and Cabido (2001) and Smith *et al.* (1997) for a more complete listing for plants; See Simberloff and Dayan (1991) for more animal examples. ANPP = Above-ground net primary production

Organism type	Ecosystem	Functional effect groups	Ecosystem properties influenced	References
Plants	Perennial grasslands	C ₃ grasses, C ₄ grasses, forbs, N-fixers	ANPP	Tilman <i>et al.</i> 1997; Hector <i>et al.</i> 1999
Plants	Perennial grasslands	C ₃ grasses, C ₄ grasses, forbs	Soil food webs, microbial dynamics	Wardle <i>et al.</i> 1999
Plants	Annual grasslands	Early season annual forbs, late season annual forbs, perennial bunchgrasses, N-fixers	ANPP, soil nutrient pools, ecosystem nutrient retention	Hooper and Vitousek 1997, 1998
Plants	Alaskan tundra	Evergreen shrubs, deciduous shrubs, forbs, sedges, mosses	Decomposition, nutrient cycling, primary productivity	Hobbie <i>et al.</i> 1993; Chapin <i>et al.</i> 1996
Plants	Costa Rican rainforest	Short and long lifespan monocots and dicots	ANPP	Haggar and Ewel 1997
Herbivorous insects	Various	Leaf-chewers, leaf miners, seed-feeders, phloem-feeders, xylem-feeders, root-feeders, whole-cell-feeders	Plant consumption, secondary production, nutrient cycling	Bezemer and Jones 1998
Ungulates	Savanna	Grazers, browsers	Plant consumption, nutrient cycling	Du Toit and Cumming 1999
Soil organisms	Boreal forests	Fungi, bacteria, saprophytic animals, fungal feeders, protozoa, nematodes, intermediate predators (e.g. mites, nematodes), large, top predators (mites, spiders, coleoptera, ants)	Decomposition	Bengtsson <i>et al.</i> 1996
Aquatic consumers (zooplankton and fish)	Freshwater pelagic	Size of prey consumed	Energy flow Response to increased productivity	Hrbáček <i>et al.</i> 1961; Brooks and Dodson 1965; Dodson 1974; Hulot <i>et al.</i> 2000

Ad hoc groups. Many proposed functional classifications have been on an *ad hoc* basis, depending on the ecosystem in question and the major physiognomic forms of the organisms present (Table 17.1). Often the most general grouping in functional effect classifications, either implicitly or explicitly, is by trophic level. Trophic groupings are fundamental to carbon and energy fluxes through ecosystems, and linked to nutrient cycles as well (Naeem, in press). Microbial functional groups based on metabolic capacity and its biogeochemical consequences (heterotrophs, nitrifiers, denitrifiers, nitrogen (N) fixers, etc.) are in some ways similar to trophic groups in that they are based on who consumes what resources. Trophic groupings are not always clear-cut for either micro or macroorganisms. Omnivores are common (Persson *et al.* 1992; Power 1992; Strong 1992; Mittelbach and Osenberg 1993) and even some relatively clear-cut groups include multiple trophic types or levels. For example, nitrifying bacteria include autotrophic, heterotrophic and mixotrophic nitrifiers (Steinmüller and Bock 1976; Degrange *et al.* 1997). Even with these complexities, however, trophic groups are often the most obvious place to start.

Studies explicitly manipulating diversity within and across multiple trophic levels are most common in micro and mesocosms for aquatic (Naeem *et al.* 1994; Degrange *et al.* 1997; McGrady-Steed *et al.* 1997; Naeem and Li 1997; Petchey *et al.* 1999; Hulot *et al.* 2000) and soil ecosystems (e.g. de Ruiter *et al.* 1994; van der Heijden *et al.* 1998; Mikola *et al.*, Chapter 15; Wardle and van der Putten, Chapter 14), although there are some examples from natural and semi-natural systems as well (e.g. Ingham *et al.* 1985; Mulder *et al.* 1999; van der Heijden and Cornelissen, Chapter 16; Raffaelli *et al.*, Chapter 13). However, many biodiversity–ecosystem functioning studies have investigated effects of diversity in only one trophic level, so that a hierarchy of functional effect classification starting with trophic groups is implicit rather than explicit.

A major exception to functional characterizations that either implicitly or explicitly start with trophic categories is that of ecosystem engineers (Jones *et al.* 1994; Lavelle *et al.* 1997). For example, at the water–sediment interface of all aquatic systems, benthic invertebrates living in the sediment regulate a

variety of processes, including organic matter degradation, carbon burial, microbial grazing and gardening, bioturbation, and biogenic structure formation (Aller 1983; Krantzberg 1985; Van de Bund *et al.* 1994; Mermillod-Blondin *et al.* 2000). The large heterogeneity of activities necessitates classifying these invertebrates into groups with distinct attributes. For marine bioturbators, organism size, type of biogenic structure produced, and feeding location (sediment surface, within sediment, or both) are primary axes of differentiation and these traits cut across multiple trophic levels (bioturbation groups, François *et al.* 1997) (for feeding groups of invertebrates in rivers, see Cummins 1974; Cummins and Klug 1979).

For some applications, the trophic level of resolution is clearly quite coarse and the crux of functional classification comes with trying to delineate groups within trophic levels. Most approaches to defining functional groups within trophic levels have started with *a priori* designations based on combinations of anatomy, physiology, or behaviour. Plant functional classifications often rely on combinations of physiognomy, phenology, and photosynthetic pathway (e.g. associations with N-fixing bacteria, woodiness, phenology, rooting depth, C₃, C₄ or CAM photosynthetic mechanism and associated tissue quality), whereas functional groupings for animals often reflect guilds based on consumption (Simberloff and Dayan 1991) (Table 17.1). Many animal studies, however, have focused on guilds in relation to forces influencing community composition and trophic structure, rather than effects on ecosystem properties—with the notable exceptions of soil and stream fauna (e.g. de Ruiter *et al.* 1994; Wallace and Webster 1996), pelagic foodwebs (e.g. Carpenter and Kitchell 1993; Schindler *et al.* 1997; Hulot *et al.* 2000), and benthic invertebrates (e.g. Emmerson *et al.* 2001).

Functional effect groups based on complementary resource use (niche differentiation) among species of the same trophic group provide a method to test for effects of functional diversity on ecosystem-level resource use and productivity. If species use different portions of the total resource pool, then greater species diversity should lead to greater utilization of resources and a corresponding increase in productivity (Trenbath 1974; Harper 1977;

Ewel 1986; Vandermeer 1989; Haggard and Ewel 1997; Hooper 1998; Loreau and Hector 2001; Tilman *et al.* 2001). Although complementarity has been applied mostly to plants, it applies equally well to animals (e.g. Simberloff and Dayan 1991; Fox and Brown 1993; Kelt *et al.* 1995).

Competition among plants is presumed to be a common feature of communities given the frequency of shared resources, such as light, space, and nutrients (Tilman 1988). Questions about the degree of overlap (competition) and non-overlap (complementarity) in resource use in a number of studies have raised debate about the effects of plant diversity on ecosystem processes (e.g. Tilman *et al.* 1996; Aarssen 1997; Huston 1997; Wardle 1999; Tilman *et al.* 2001). Distinguishing among complementarity, facilitation, and sampling effects in observed responses to biodiversity requires careful attention to experimental design and analysis (Allison 1999; Loreau and Hector 2001; Hector *et al.*, Chapter 4). Clearly, identifying complementary functional groups should be a priority for a better understanding of how diversity affects ecosystem functioning, particularly primary production, secondary production, and ecosystem-level resource use.

Primary strategies: general tradeoffs in organisms' traits. The search for functional groups that are applicable across ecosystem types focuses on tradeoffs among traits based on evolutionary constraints on the trait space that organisms occupy. The search is based on the simultaneous consideration of multiple individual traits and observations of different species' responses to environmental gradients and effects on ecosystem processes. The traits usually involve key aspects of the organisms' life history, resource use, reproduction, and responses to external factors. Rather than attempting to identify discrete groups, species can then be placed across continuous axes or planes that define evolutionarily realized combinations of interrelated traits. This approach has been applied most often to terrestrial plants (e.g. Chapin *et al.* 1996b; Díaz and Cabido 1997; Grime *et al.* 1997b). For example, plant growth form, leaf turnover, and nutrient status covary with maximum photosynthesis, defence against herbivory, and effects on decomposition and mineralization (Chapin 1980; Coley 1983;

Grime and Campbell 1991; Chapin *et al.* 1993; Reich *et al.* 1997; Grime 2001). However, a similar approach has also been applied to stoichiometry of organismic element ratios and their ecosystem consequences, especially in pelagic systems (Elser *et al.* 1996, 2000). Zooplankton growth rates may define the C:N:P ratios of their cells, with consequences for ecosystem nutrient cycling.

Such correlated suites of traits may help simplify functional designations because one suite of traits may influence several related ecosystem processes in similar ways. In such cases, so-called 'soft traits', those that encapsulate a suite of 'hard traits' (those that actually affect the process), are often comparatively easy to measure and may be useful for designating functional groups (Hodgson *et al.* 1999). For example, increasing leaf toughness or sclerophylly (a soft trait) is often correlated with greater amounts of carbon-based defences, slower decomposition rates and slower rates of N mineralization (hard traits; Coley 1983; Herms and Mattson 1992; Cornelissen *et al.* 1999). Correlation among traits will limit the number of axes across which species are differentiated, and thus the number of functional groups. If these associations among traits can be proven consistent, it would not be necessary to measure all traits to classify taxa into functional groups.

Work on primary organism strategies suggests that the resource environment of a site may select for suites of covarying traits that control entry of species into a given community (Grime *et al.* 1997a). For example, low resource environments select for plants that have low growth rate, high nutrient use efficiency, low litter quality, and high allocation to defence (Chapin 1980). In other words, the resource environment acts as an environmental filter on community composition (Pearson and Rosenberg 1978; Weiher *et al.* 1995; Díaz *et al.* 1998). (These traits may then feed back to further alter resource availability as well; Chapin *et al.* 1986; Hobbie 1992.) One hypothesis in this case is that because traits relating to such a primary strategy will be similar among species, the traits of the dominant species, rather than species richness and complementarity, will exert the strongest control on ecosystem properties (e.g. Solan and Kennedy, in press). However, other forces, such as variability in environmental conditions,

selection for trait differentiation due to competition (Bazzaz 1987; Weiher *et al.* 1995), trophic dynamics, or disturbance may counteract such a trend. Empirical studies are needed to address these issues.

Functional response groups

Identification of functional response groups can help understand and predict how communities and ecosystem properties might be affected by environmental change, variability, or disturbance. The task is to define the potential disturbances or environmental fluctuations to which a given system may be subjected, and identify the functional traits relevant to either tolerating or recovering from those conditions (Landsberg 1999; Walker *et al.* 1999). Examples include differential response to extreme climatic events, directional climatic change, grazing, or pathogens; differential recruitment abilities, differential sensitivity to pollutants, or other traits that influence an individual's or population's sensitivity to or recovery from different stresses (Noble and Slatyer 1980; McIntyre *et al.* 1995; Box 1996; Chapin *et al.* 1996a; Buckland *et al.* 1997; Westoby 1998; Díaz *et al.* 1999; Walker *et al.* 1999).

Traits useful for delineating functional response groups may vary independently from those used for delineating functional effect groups. For example, in plants, regeneration traits (e.g. seed size, number of seeds per plant, dispersal mode, pollination mode), which often affect response to disturbance, tend to be only loosely correlated with vegetative characteristics, which often have more direct effects on process rates (Grime 1979; Díaz and Cabido 1997). However, because traits that affect response to disturbance also influence an individual's or population's sensitivity to or recovery from different stresses (e.g. seed size and shape are related to seed persistence in the soil bank: Thompson *et al.* 1994; Funes *et al.* 1999), they may indirectly influence an ecosystem process under consideration.

While functional response groups often have been delineated independently of functional effect classifications, a better integration of these approaches could help understanding of how diversity within functional effect groups influences stability of processes to non-equilibrium conditions or new disturbance regimes (Naeem 1998; Walker *et al.* 1999). For example, as species richness within functional

effect groups (trophic groups of producers, bacterivores, herbivores, and predators) was increased in an aquatic microcosm experiment, total respiration became more predictable and temporal variation in the abundance of trophic groups declined (McGrady-Steed *et al.* 1997; McGrady-Steed and Morin 2000; Petchey *et al.*, Chapter 11).

17.2.3 Testing the predictive value of functional traits

An additional, but necessary step for refining knowledge of functional classifications is iteration of the testing process. If initial classifications do not accurately reflect species' effects on ecosystem properties, re-classification and re-testing help to more closely delineate which particular functional traits are important for which processes. Two approaches that explicitly incorporate this step are the Integrated Screening Program (ISP) for plants (Grime *et al.* 1997b; Díaz and Cabido 1997), and screening for bioturbator functional groups on estuarine mudflats (Swift 1993; Solan 2000) (Fig. 17.2). Grime's ISP starts with individual species and measurements of many functional traits related to life history, physiology, and morphology (Fig. 17.2(a)). Following ordination of these traits, the ISP allocates species into emergent groups based on similar traits, which are then used to predict effects on ecosystem processes or responses to perturbation. Researchers then test those predictions by long-term monitoring in natural systems and experiments in the field or microcosms (e.g. Leps *et al.* 1982; Grime *et al.* 1987; MacGillivray *et al.* 1995). It is an explicitly iterative process: if initial predictions don't hold up, functional classification and testing start again. For example, laboratory screening of plant traits was used to predict the resistance and resilience of five grassland ecosystems subjected to drought, late frost and burning treatments (MacGillivray *et al.* 1995). Results indicated that the same traits were good predictors of both drought and frost resistance, but also that it was necessary to weight predicted ecosystem responses according to the abundance of species in the vegetation (i.e. the mass ratio hypothesis of Grime 1998).

Because of the large amount of effort involved in these studies, it is not practical to apply these

techniques whenever ecologists need functional information for research or management purposes. The hope is that intensive studies on multiple species in one system or a small number of systems will provide enough experience to recognize predictive traits in other species and other systems. For example, for bioturbators, the iterative testing process has identified four primary groups into which organisms can be placed without detailed taxonomic information (Fig. 17.2(b)). Classification is based on whether the species primarily acts above the sediment (epifaunal), within the uppermost sediment layer (surficial modifier), throughout the sediment (biодiffusers) or within select areas of the sediment (advective mixing) (Gardner *et al.* 1987; François *et al.* 1997). For both the ISP and the bioturbator example, the functional effects and responses of the organisms cut across taxonomic boundaries.

17.2.4 A simple functional hierarchy

Hierarchical classifications have a couple of advantages. First, they allow researchers to identify different traits of interest for particular groups (i.e. the same set of traits might have different response implications for different life forms). Second, additional levels of detail on traits may be necessary to understand mechanisms of species' effects on processes or responses to environmental changes (Lavorel *et al.* 1997). While there is likely no single correct functional hierarchy, even *ad hoc* hierarchies can be useful. For example, a hierarchical functional classification for plant responses to disturbance (grazing) effectively predicted species' responses to

altered grazing regime (Mcintyre and Lavorel 2001).

We propose a simple hierarchy of nesting response groups into effect groups as a good strategy for understanding effects of functional diversity on ecosystem processes (Fig. 17.1). Studies of biodiversity and ecosystem functioning often have two different, albeit related, goals: investigating diversity effects on process rates and investigating diversity effects on stability of processes. The first takes a short-term, equilibrium view—a necessary simplification for initial understanding of species effects on ecosystem properties. The second takes an explicitly non-equilibrium view, allowing a more complex and realistic perspective for understanding how environmental fluctuations, mediated through changes in species composition, might influence those processes (Chapin *et al.* 2000). Once functional effect groups have been delineated, species within each group can be characterized by their responses to various environmental perturbations, which will determine how species diversity within those functional effect groups influences stability of ecosystem processes (McNaughton 1977; Yachi and Loreau 1999). This approach forms the basis of many discussions of diversity effects on ecosystem process rates and stability (e.g. Naeem 1998; Walker *et al.* 1999; Griffiths *et al.* 2000 to name just a few).

We acknowledge that there is no *a priori* reason for nesting response groups within effect groups. In many cases, response strategies will cut across effect groups, and vice versa. If the primary goal is to understand how global environmental change will affect species' distributions (e.g. Cramer 1997),

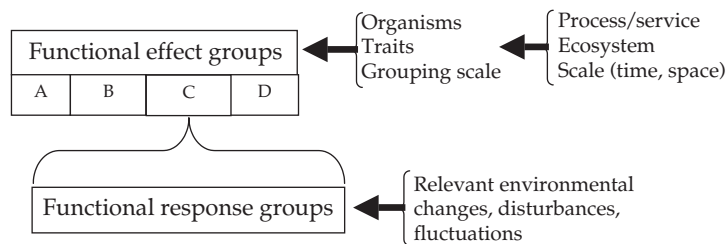


Figure 17.1 A simple hierarchy of functional groups for relating the effects of biodiversity on ecosystem functioning. In general, the process in question, the ecosystem type and the spatio-temporal scales will determine the appropriate organisms, traits, and levels of grouping into functional effect groups. Functional response groups within each effect group are determined by species' responses to relevant environmental stresses.

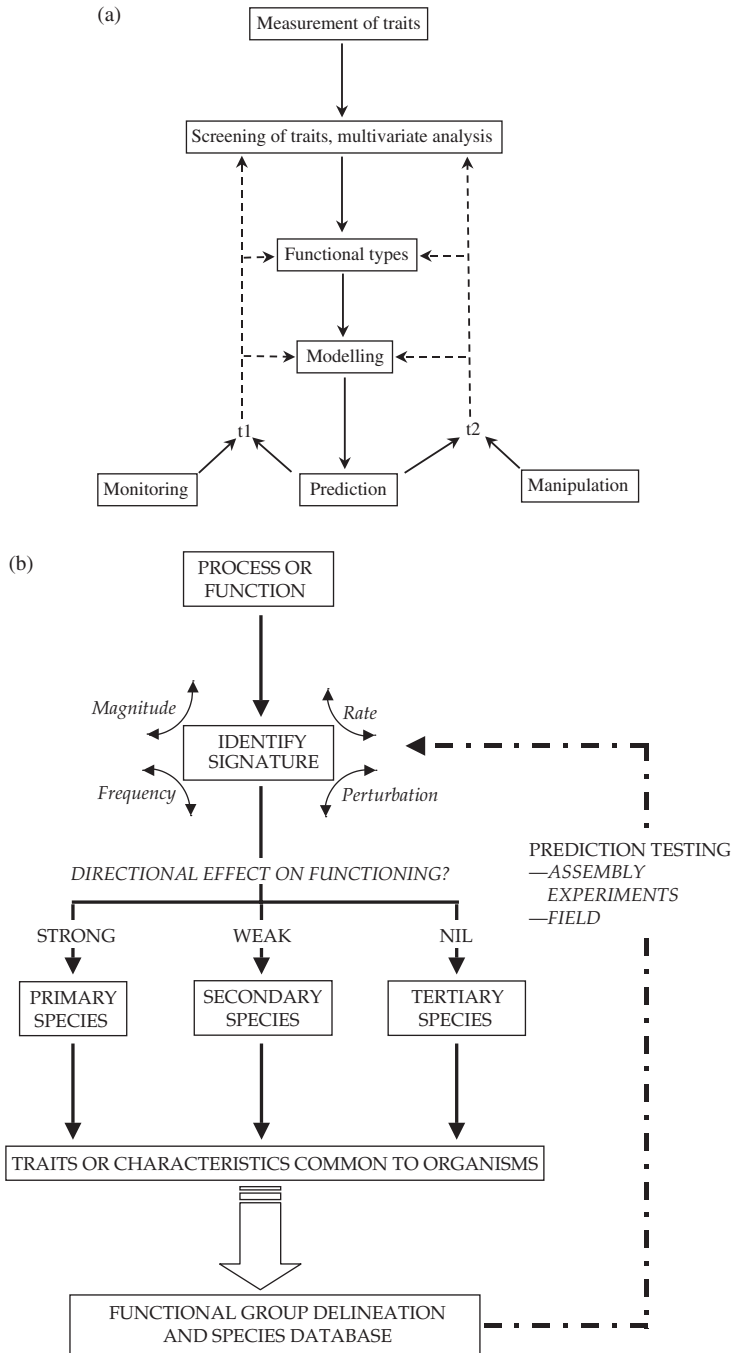


Figure 17.2 Iterative processes of functional group classification. (a) Integrative Screening Process (ISP) for plants. The ISP leads to predictions of functional groups and their effects on ecosystem processes. These predictions are then tested by monitoring and experiments (t1 and t2), whereupon the relevant traits, initial functional groupings, or models of predicted effects or responses may be modified. Redrawn from Grime *et al.* (1997a) (© Cambridge University Press). (b) Definition of functional groups for estuarine macrofaunal invertebrates based upon body size, mobility, and bioturbation reworking mode (Solan 2000). The process starts with a priori predictions as to what traits are likely to modify a given ecosystem process and in which ways they are likely to make these modifications (the 'signatures'). Species are then categorized according to their potential effects. The actual effects on ecosystem processes of species in isolation and in mixture are tested in mesocosm experiments, and predictions are refined.

response groups will most likely be at the top of the hierarchy. On the other hand, if understanding effects on ecosystem properties is the goal, then effect groupings will be foremost.

17.3 Relationships between functional and species diversity

Experiments investigating the effects of diversity on ecosystem properties have manipulated functional composition (presence of certain plant functional effect groups or functional traits), functional richness (number of different plant functional effect groups), and species richness. However, separating the effects of species diversity from those of functional group diversity in experiments manipulating both can prove difficult: in many experiments using randomly assembled communities, the two types of diversity are correlated across much of the experimental space (Tilman *et al.* 1997b; Allison 1999; Schmid *et al.* 2001) (Fig. 17.3). Here, we discuss the importance and difficulties of empirical evaluations of the relative contributions of functional and taxonomic diversity to ecosystem functioning.

17.3.1 Disentangling diversity components in biodiversity–ecosystem functioning relations

Correlation between species and functional diversity leads to a trade-off between two common experimental goals in biodiversity/ecosystem functioning studies: (1) that of examining the broadest range of species richness possible and (2) that of examining the relative effects of functional richness and species richness. One typically cannot have more functional effect groups than species (though see below for counter-examples), and most experiments have limited numbers of species to add within functional groups. For example, if researchers are working with a total pool of four species from each of four functional groups, and examine a range of species richness from 1 to 16 in a logarithmic series, species and functional richness will be strongly correlated (Fig. 17.3(a)). This problem can be reduced by using many species in each functional group and constraining the total range of species richness

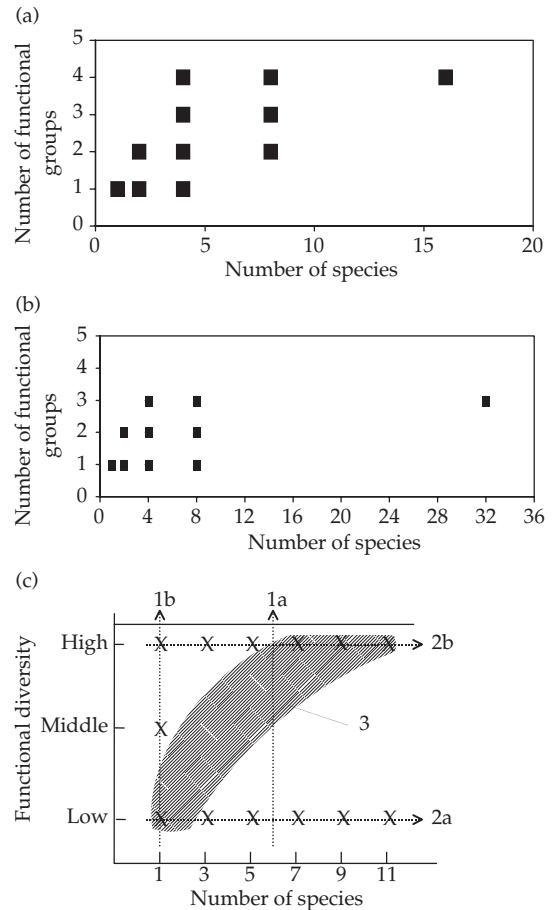


Figure 17.3 The correlation between species richness and functional richness in biodiversity experiments. Graphs show (a) the arrangement of treatments for a hypothetical experiment using four species in each of four functional groups across a logarithmic species richness gradient from one to sixteen species; (b) the arrangement of treatments in the Swiss BioDEPTH site where researchers attempted to minimize the correlation between species and functional group richness (Spehn *et al.* 2000); and (c) a general scheme for how species and functional richness might be related. In (c), along the vertical lines, the number of species is kept constant but the number of functional groups (1a) or the phenotypic or genetic variability of species (1b) is increased. Along the horizontal lines, the number of functional groups is kept constant but the number of species ((2a) narrow-niched species, (2b) broad-niched species) is increased. Most empirical studies lie in the shaded area, 3 (from Schmid *et al.* 2001) (© Princeton University Press).

examined. For example, in an experimental study of grasslands in Switzerland, researchers used a total pool of 48 species in three functional groups (grasses, legumes, and non-leguminous forbs)

across a range of species richness from 1 to 32 (Fig. 17.3(b)) (Diemer *et al.* 1997; Spehn *et al.* 2000b). The relatively large number of species compared to the low number of functional groups allowed testing various species compositions within richness levels and increasing species richness without adding more functional effect groups. With the hierarchical structure discussed above, however, adding more species within functional effect groups may add a diversity of functional response types. Alternatively, experiments may be replicated with entirely different sets of species (e.g. MacGrady-Steed *et al.* 1997). Constraining the species pool, however, does not solve all problems. For example, there can still be a high correlation between species and functional diversity at low diversity levels where much of the effect on ecosystem properties often occurs.

However, a direct correlation between species richness and functional diversity may not always hold at low diversity ends of a gradient. For example, morphological or behavioural plasticity could lead to a breadth of functional attributes with relatively few species (Fig. 17.3(c)). Such a relationship does not necessarily solve the experimental problems addressed above, however, because it just raises the important (and largely unanswered) question of how important genetic diversity within species is in affecting ecosystem processes. Differences in behaviour, size, diet, and habitat preferences between sexes and life-history stages (and social status in social arthropods such as termites) also contribute to functional diversity within species. Furthermore, animals may significantly change behaviour patterns in response to external stimuli, behavioural variation, or season/time, which could alter their functional roles. For example, a common polychaete, *Nereis diversicolor*, has several feeding modes that directly affect its bioturbatory capacity. When deposit feeding, it is actively foraging, but when suspension feeding, it is relatively sedentary and has little impact on the sediment profile. Therefore, presence of a single species may equate to the presence of several functional groups, although they may not all occur simultaneously (Solan 2000). If functional groups are to be meaningful in those cases, they must be conditioned on environmental factors that influence functioning.

17.3.2 Is species diversity a surrogate for functional diversity?

While correlation between species and functional group richness often occurs in experiments, the relevance of this correlation to natural communities is subject to debate. With little prior knowledge of a system, and for practical reasons, species diversity may serve as a surrogate for functional diversity. From a bottom-up approach, the concepts of niche differentiation and limiting similarity imply that functional characteristics of coexisting organisms must differ at some level, which means that increasing species diversity should lead to increasing functional diversity, especially if it also broadens the total range of functional traits present (Schmid *et al.* 2001).

Whether species richness is an adequate surrogate for functional diversity in natural systems depends in part on patterns of community assembly. Species richness and functional diversity will tend to correlate if there is a linear increase in niche space 'coverage' as species richness increases (Díaz and Cabido 2001). This situation could happen either if species are assembled at random, as in situations in which disturbance regimes lead to a predominance of stochastic colonization (e.g. Grime 1979; Hobbs and Mooney 1991; Fridley 2001), or if complementarity in species' functional traits is an important component of community assembly (Bazzaz 1987; Weiher and Keddy 1998; Kelt and Brown 1999). On the other hand, Díaz and Cabido (2001) argue, based on the concept of environmental filters, that plant communities are non-random assemblages from the regional species pool. They suggest that climate, disturbance, and biotic interactions impose increasingly fine-grained constraints on the composition of communities (Pearson and Rosenberg 1978; Díaz *et al.* 1998). In this scenario, the same amount of functional variation (or niche space) is just more finely divided as more species are added (Schmid *et al.* 2001), and therefore, functional diversity may not increase with increasing species richness. The crux of the question with regard to diversity effects on ecosystem processes is the degree to which abiotic conditions constrain the functional variation within communities that influences processes within that system. Merging our understanding of

ecosystem level controls with our understanding of community dynamics and assembly is an important focus of future study (Thompson *et al.* 2001).

The relationship between diversity of taxa and functional diversity in natural systems will also depend on the level of taxonomic resolution. Adding increasing numbers of genotypes of a given species will likely add some degree of functional diversity (Fig. 17.4). On an average, randomly adding new species within a genus or family would add more functional diversity than adding new genotypes of the same species, and adding new species from different families would likely add even more. Adding species from known different functional groups would give the greatest increase in functional diversity per species added. The relationship of number of genotypes, species, families or functional groups with functional diversity for these different taxa are not likely to be simple lines, but rather broad, potentially overlapping areas. For some processes and species, adding more genotypes of the same species might add relatively more functional diversity than others (Fig. 17.4).

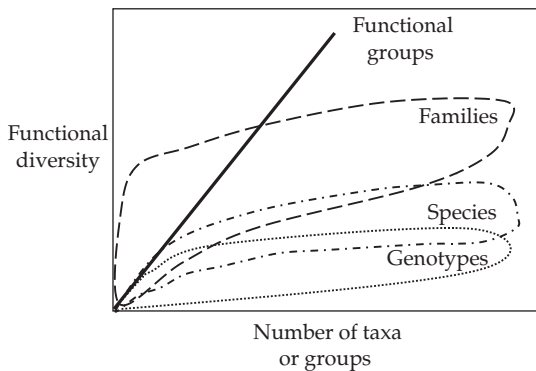


Figure 17.4 Hypothesized relationships between richness of various taxa in an ecosystem and the total amount of trait variation, i.e. functional diversity. On an average, adding more families within a trophic type would add more functional trait variation than adding more species within a genus or family, which in turn would add more variation than adding genotypes within a species. Variability in the general relationship results from genetic variation and plasticity within species, and the variation in traits within families or genera. By definition, the number of functional groups would have the strongest and most linear relationship with total trait variation.

17.3.3 Limitations of species and functional groupings

Species richness has been the most common measure of diversity in biodiversity–ecosystem functioning experiments. While often done for practical reasons, this approach starts from the premise that species’ delineations both embody functionally significant information and are distinct. While this approach works in some cases, it clearly will not in many others. Reflecting population and evolutionary processes, species are usually delineated based on genetic or morphological traits. Functional traits are more directly related to ecosystem processes, but organisms with vastly different phylogenies can be very much alike functionally—one of the original reasons for using guilds (Root 1967). Hybridization and variability in mutualistic associations can also confound species designations in diversity/ecosystem functioning experiments. The definition of what is a species also has limitations, both of a theoretical and practical nature, and these have given rise to a multitude of alternate species concepts (e.g. Bisby and Coddington 1995; Hey 2001). In addition, notorious identification problems exist within many groups. Greatest problems are probably encountered with microorganisms, notably bacteria and fungi, whose body forms are simple and whose sexuality and genetics fundamentally differ from those of plants and animals (e.g. Kück 1995; Pace 1997; Staley 2001). In many cases, basing functional classifications on taxonomy is difficult, especially because the number of microbial functions known to be affected by horizontal gene transfer is increasing (e.g. plant pathogenicity supported by the plasmid Ti in *Agrobacterium*; Teyssier-Cuvellé *et al.* 1999). On the other hand, some microbial functional groups in fact define taxonomic families. For example, N-fixers associated with legumes belong to the Rhizobiaceae family, and nitrifiers belong to the Nitrobacteriaceae family (Krieg and Holt 1984). All these reasons suggest that a mechanistic understanding of biodiversity–ecosystem functioning relationships ultimately requires a functional approach to classifying organisms even when species richness may serve as a convenient starting point.

A common criticism of studying the effects of functional group diversity on ecosystem processes

is that the underlying rationale is circular. If the functional effect groups in question have been defined by their influence on an ecosystem process, then by definition, adding and removing these groups will alter that process. In most experiments, however, the functional effect groups used are based on (1) traits that are known to influence a process but the generality of the functional grouping has not been tested, or (2) a mixture of taxonomic and physiognomic features ('soft traits') that are more general, and not specifically related to any particular process. As such, these groupings might be more appropriately termed 'candidate functional groups' (cf Vitousek and Hooper 1993). A goal of such experiments should be to verify if the functional effect groups are accurate by testing if they have, both alone and in combination, the hypothesized influences on ecosystem processes (see Section 17.2.3 above). This approach differs from the tautology described above, though the design of the experiment is critical for accurately discriminating functional group versus species richness effects (Allison 1999). In the past, however, many biodiversity–ecosystem functioning experiments have not actually carried out explicit tests of candidate functional effect groups (but see Hooper and Vitousek 1998; Symstad and Tilman 2001).

Reliance on functional classification (effect or response) can have several difficulties as well, however. Functional classifications are often not discrete—many traits vary continuously and cut-offs for inclusion/exclusion for a given group may be arbitrary. Recognizing axes of general functional tradeoffs (Chapin *et al.* 1993; Grime 2001), and using continuous, quantitative trait axes (Walker *et al.* 1999) could help remedy this problem. Even more difficult are situations in which it is not possible to discern the summary traits by which to classify species with respect to a given process or response (e.g. inability to predict which types of plants will have strong growth responses to elevated CO₂; Körner 2000). In addition, microcosm or greenhouse experiments may not be adequate to identify functional groups if interactions with other species are important in affecting certain processes (e.g. Chapin *et al.* 2000; Newton *et al.* 2001).

Despite these difficulties, functional characterizations offer the best hope of gaining a mechanistic

understanding of diversity effects on ecosystem properties. Should we be able to clearly delineate both the functional effect groups and functional response groups for a given system, future management could rely on the functional traits toolbox rather than the black box of random species diversity.

17.4 Implications for management and policy

Although the conservation of biodiversity has been linked with the sustainability of ecosystems (Naeem *et al.* 1994a, 1995; Tilman *et al.* 1996), the relevance of these experiments to ecosystem management remains controversial (Schwartz *et al.* 2000; Wardle *et al.* 2000b; but see Hector *et al.* 2001b). Changes in species composition have been shown to influence ecosystem processes and services, often with large economic impacts (Chapin *et al.* 2000). The primary cause is often gain or loss of single species with key functional traits. The following discussion focuses on management and policy objectives concerning functional groups and ecosystem processes and services.

The particular needs for understanding biodiversity effects on ecosystem processes and services depend on the type of management being used or investigated. Management is a broad term encompassing small-scale, local issues (e.g. how many and which species are necessary to produce food and reduce erosion for a farmer in the tropics), regional issues (e.g. how to manage forest lands for wood production, fish and wildlife habitat, and recreation), and global issues (e.g. how might shifts in species composition associated with climate change influence carbon sequestration in the biosphere?). Management can mean setting aside a parcel of land or water and doing nothing, or it can involve intensive manipulation of both biota and the physical environment. The common thread is that whatever action (or inaction) takes place is done by human choice to achieve some goal or maximize a particular ecosystem service (this includes setting aside wilderness areas or wildlife refuges). At the same time, lack of management can affect biotic diversity outside of the manipulated

system (e.g. agricultural runoff affecting water quality in nearby lakes and rivers) (Silver *et al.* 2001), whereupon policy decisions should be made about how to incorporate those effects into more comprehensive management. From the practical standpoint of maintaining ecosystem services in all of these situations, it may be necessary to maintain species and functional diversity for several reasons:

1. To ensure that for key services, important functional groups are present and active;
2. To ensure survival of rare or occasional species, which may resume critical processes following disturbance or gradual changes of environmental conditions (Grime 1998);
3. To maintain a diversity of services in natural or semi-natural systems (e.g. provision of food and fibre, recreation, wildlife habitat, catchment protection and maintenance of water quality, protection against natural hazards).

Managers need to be aware of species composition as well as of richness. Management- or disturbance-related species losses may not be at random, nor are they necessarily equally distributed among different functional groups (Díaz and Cabido 2001). Loss of species diversity to the point that entire functional effect groups disappear will clearly have the greatest influence on ecosystem processes. Such loss of entire functional effect groups is most probable when only one or a few species are responsible for a given process in a given ecosystem (Hooper *et al.* 1995). Loss of functioning in ecosystems can sometimes be restored by changes in environmental conditions if the organismal diversity has remained intact. When viewed from a functional perspective, management practices should aim to ensure that the species present are the ones with traits that will maintain the desired ecosystem properties within acceptable bounds. (Definition of what those desired properties are raises a variety of questions at the intersection of ecology and societal values, but we will not address those issues here: Rapport 1995; Wicklum and Davies 1995).

The key question for all of these issues is what level of functional diversity is needed to sustain the ecosystem services in question in response to loss of biodiversity resulting from a variety of global

changes (Sala *et al.* 2000). This issue has two components, both of which require functional group classifications: (1) identification of which species and traits have a large influence on processes under current conditions, and (2) the delineation of functional response groups to improve our ability to predict which organisms might be lost from ecosystems in response to given environmental perturbations.

The pattern of response of ecosystem services to altered diversity will likely depend on patterns of loss of diversity. For example, gradual losses of species as abiotic conditions begin to exceed tolerance limits (e.g. with climatic change) could result in random losses of functional effect groups if functional effect and response groups are independent from one another. In such a situation, average patterns of process response to changes in diversity could be similar to those observed in randomly assembled communities (Tilman *et al.* 1996, 1997a; Hector *et al.* 1999; but see also Wardle 1999). At the other extreme, as in situations involving land-use transformation, gross changes in abiotic conditions and loss of a majority of the functionally important biota may have a greater impact on ecosystem processes and services than the decline of species richness *per se*. Between the two extremes of complete dependence on abiotic conditions and complete dependence on species or functional richness, is probably where many real world situations will fall. For example, landscape fragmentation involves both gross transformation in some areas and subsequent more gradual species loss in remaining fragments (under island biogeographic models), so both abiotic and diversity drivers could apply depending on the area involved.

In other cases, species losses may not be random with respect to species effects on ecosystem processes because certain traits related to response to the environment also affect ecosystem processes (Díaz and Cabido 2001). For example, there has been debate about whether plant diversity or traits of certain species are responsible for decreased resistance of grassland production to drought in the experiment by Tilman and Downing (1994) because the gradient in species richness was caused by N fertilization (Givnish 1994; Huston 1997). The mechanistic debate may be moot from the practical

perspective of managing N within landscapes, however, if changes in both diversity and traits of the dominant species are consistently correlated across gradients of N deposition (Berendse *et al.* 1993; Tilman 1996). Thus, effective ecosystem management requires an integrated understanding of the relative effects of individual species traits, species or functional richness, and abiotic drivers of ecosystem processes.

17.5 Conclusion

A hierarchy of functional response groups nested within functional effect groups is one way to approach questions of how changes in biotic diversity might affect ecosystem properties, both on short time scales and in response to changing environmental conditions. Progress in three key areas will substantially further efforts to gain a rigorous understanding of how functional attributes of species, and their interactions, influence the response of ecosystem properties to changing biodiversity:

1. Synthesis of the *ad hoc* and primary strategies approaches for defining functional groups, in concert with development of methods for quantitatively measuring functional diversity (e.g. Walker *et al.* 1999);
2. Better understanding of which functional response and effect traits are correlated versus independent, particularly with respect to the predominant forces of global change; and
3. Better understanding of how patterns of community assembly influence relationships between species and functional diversity in natural communities, and how this might differ in different environments.

Knowledge of the effects of species and functional diversity on ecosystem services, particularly in the context of abiotic drivers, individual species effects, and global change, will be critical where management priorities seek to manipulate species

composition directly. Intensive management often relies on the functional characteristics of one or a few species and substitution of human inputs for biotic processes. Clearly this reliance decreases the planned diversity of these systems, but the unplanned (i.e. associated) diversity may also decline (Ewel 1991, 1999; Vandermeer *et al.*, Chapter 19). However, the insurance hypothesis (Naeem 1998; Yachi and Loreau 1999) and the precautionary principle emphasize that land managers and policy makers also must be prepared for unpredictable events and a changing world. Faced with the unpredictable, preserving species or taxonomic diversity (e.g. Clarke and Warwick 1998; Warwick and Clarke 1998; von Euler and Svensson 2001) within functional effect and response groups may better allow long-term, internal dynamics and evolution of managed systems as they face new environmental conditions.

A critical question for the future is how to balance patterns of human use and biotic diversity at the landscape scale to maintain (a) local diversity within sites, (b) regional diversity among sites, (c) ecosystem services that depend on small-scale functions (e.g. crop productivity in a field), and (d) ecosystem services that depend on interactions among different landscape components (e.g. nutrient transformations in riparian zones). Answering this question will require a rigorous synthesis across all scales of ecological organization, from physiological to landscape levels.

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