epidemiological study from the international clearing house for birth defects monitoring systems. *Am. J. Med. Genet.* 93, 110–116

42 Froster-Iskenius, U.G. and Baird, P.A. (1989). Limb reduction defects in over one million consecutive livebirths. *Teratology* 39, 127–135

43 MacDorman, M.F. and Atkinson, J.O. (1999) Infant mortality statistics from the 1997 period linked birth/infant death data set. *Natl. Vital Stat. Rep.* 47, 1–23

44 Digilio, M.C. *et al.* (1997) Atrioventricular canal defect and postaxial polydactyly indicating phenotypic overlap of Ellis–van Creveld and Kaufman–McKusick Syndromes. *Pediatr. Cardiol.* 18, 74–75

45 Dipple, K.M. and McCabe, E.R.B. (2000) Phenotypes of patients with 'simple' Mendelian disorders are complex traits: thresholds, modifiers, and systems dynamics. *Am. J. Hum. Genet.* 66, 1729–1735

46 Kaplan, B.S. and Bellah, R.D. (1999) Postaxial polydactyly, ulnar ray dysgenesis, and renal cystic dysplasia in sibs. *Am. J. Med. Genet.* 87, 426–239

47 Wright, S. (1935) A mutation of the guinea pig, tending to restore the pentadactyl foot when heterozygous, producing a monstrosity when homozygous. *Genetics* 20, 84–107

48 Detwiler, S.R. (1930) Observations upon the growth, function, and nerve supply of limbs when grafted to the head of salamander embryos. *J. Exp. Zool.* 55, 319–370

49 Trueb, L. (1973) Bones, frogs and evolution. In *Evolutionary Biology of the Anurans* (Vial, J.L., ed.), pp. 65–132, University Missouri Press

50 Gollmann, G. (1991) Osteological variation in *Geocrinia laevis*, *Geocrinia victoriana*, and their hybrid populations (Amphibia, Anura, Myobatrachinae) *Z. zool. Syst. Evolutionsforsch.* 29, 289–303

51 Rienesl, R. and Wagner, G.P. (1992) Constancy and change of basipodial variation patterns: a comparative study of crested and marbled newts – *Triturus cristatus*, *Triturus marmoratus* – and their natural hybrids. *J. Evol. Biol.* 5, 307–324

52 Shubin, N. *et al.* (1995) Morphological variation in the limbs of *Taricha granulosa* (Caudata: Salamandridae): evolutionary and phylogenetic implications. *Evolution* 49, 874–884

53 Hanken, J. (1982) Appendicular skeletal morphology in minute salamanders, genus *Thorius* (Amphibia: Plethodontidae): growth regulation, adult size determination and natural variation. *J. Morphol.* 174, 57–77

54 Hanken, J. (1983) High incidence of limb skeletal variants in a peripheral population of the red-backed salamander, *Plethodon cinereus* (Amphibia: Plethodontidae), from Nova Scotia. *Can. J. Zool.* 61, 1925–1931

55 Lynch, J.D. (1971) Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. *Univ. Kansas Mus. Nat. Hist. Misc. Publ.* 53, 1–238

56 Alberch, P. and Gale, E.A. (1983) Size dependence during the development of the amphibian foot. Cochicine-induced digital loss and reduction. *J. Embryol. Exp. Morphol.* 76, 177–197

57 Parker, H.W. (1940) The australasian frogs of the family *Leptodactylidae*. *Novitates Zoologicae* 42, 1–107

58 Galis, F. (1999) Why do almost all mammals have seven cervical vertebrae? Developmental constraints, *Hox* genes and cancer. *J Exp. Zool.* 285, 19–26

59 Langecker, T.G. *et al.* (1993) Transcription of the opsin gene in degenerate eyes of cave-dwelling *Astyanax fasciatus* (Teleostei, Characidae) and of its consepecific epigean ancestor during early ontogeny. *Cell Tissue Res.* 273, 183–192

60 Carroll, T. *et al.* (1999) Molecular regulation of pronephric development. *Curr. Top. Dev. Biol.* 44, 67–100

61 Seiferle, E. (1927) Atavismus und Polydaktylie der hyperdaktilen Hinterpfote des Haushundes. *Morph. Jb.* 57, 313–380

62 Flower, W.H. (1888) *Einleitung in die Osteologie der Säugethiere*, Wilhelm Engelmann

63 Owen, R. (1866) *On the Anatomy of Vertebrates*, Longmans Green

64 Emery, C. (1890) Zur Morphologie des Hand – und Fussskeletts. *Anat. Anz.* 5, 283–294

65 Steiner, H. (1921) Hand und Fuss der Amphibien, ein Beitrag zur Extremitätenfrage. *Anat. Anz.* 22, 513–542

Vive la différence: plant functional diversity matters to ecosystem processes

Sandra Díaz and Marcelo Cabido

The links between plant diversity and ecosystem functioning remain highly controversial. There is a growing consensus, however, that functional diversity, or the value and range of species traits, rather than species numbers *per se*, strongly determines ecosystem functioning. Despite its importance, and the fact that species diversity is often an inadequate surrogate, functional diversity has been studied in relatively few cases. Approaches based on species richness on the one hand, and on functional traits and types on the other, have been extremely productive in recent years, but attempts to connect their findings have been rare. Crossfertilization between these two approaches is a promising way of gaining mechanistic insight into the links between plant diversity and ecosystem processes and contributing to practical management for the conservation of diversity and ecosystem services.

Diversity is being lost at an unprecedented rate at the global level, as a consequence of land use, biotic exchanges and changes in atmospheric composition and climate, potentially threatening major ecosystem processes and the ECOSYSTEM SERVICES (see Glossary) that humans derive from them[1]. The issue of whether plant diversity influences ecosystem processes has received increasing attention in the past five years, as a consequence of the publication of several groundbreaking theoretical developments and experiments[2–13].

There is now general agreement that diversity (a synonym of biodiversity and biological diversity) includes both number and composition of the genotypes, species, functional types and landscape units in a given system. However, diversity is often equated to SPECIES RICHNESS, and other components of diversity have frequently been underestimated. In particular, FUNCTIONAL DIVERSITY[14], which has received much less attention in the literature, is now emerging as an aspect of crucial importance in determining ecosystem processes.

The role of plant diversity in ECOSYSTEM FUNCTIONING has been the focus of high-profile debates in the literature[15–18]. Much controversy still remains regarding issues of experimental design[19–21], statistical interpretation of results[5,21], and factors controlling and being influenced by diversity at different scales[11,21,22]. However, there is a growing consensus that the effects of diversity on ecosystem processes should be attributed to the functional traits (value and range) of individual species and their interactions (how they compete directly or indirectly, and how they modify each other's biotic and abiotic environment), rather than to species number *per se*[1,3,6,7,11,12,17,18,23–25]. Empirical and theoretical support is accumulating for the idea that functional diversity might affect short-term ECOSYSTEM RESOURCE DYNAMICS and long-term ECOSYSTEM STABILITY.

Species richness, functional richness and functional composition: the empirical evidence

Recent reviews[20,21,25] of experimental findings generally indicate a positive relationship between plant species richness and ecosystem processes, notably in aboveground primary production. However, this link is neither simple nor universal, and the range of ecosystem types studied to date is extremely limited (mostly synthetic herbaceous assemblages). Only a fraction of these studies have explicitly tested for the role of FUNCTIONAL COMPONENTS OF DIVERSITY, such as functional richness and functional composition (Table 1). Even fewer studies have addressed all three components of diversity, perhaps partly because the effects of species richness, functional richness and functional composition are difficult to tease apart[19,21,26], and their relative contributions can be affected by experimental design[19]. In general, studies that have jointly addressed species richness, functional richness and functional composition suggest that the components of variance for functional composition and functional richness tend to be larger than the component of variance for species richness in influencing ecosystem processes (Table 1).

Rates and magnitudes of ecosystem processes have been found to be more consistently associated with functional composition (presence of certain plant FUNCTIONAL TYPES or traits) and functional richness (number of different plant functional types) than with species richness. With few exceptions (e.g. Ref. 27), whenever a positive effect of species richness has been recorded, so too were effects of functional richness and/or functional composition (Table 1). Functional composition has been found to be associated with ecosystem processes more often than has functional richness. This could be an ecologically meaningful trend, but could also be attributed to the fact that functional richness has been addressed in so few studies, often *a posteriori*. The overall trend emerging from Table 1 is consistent with the idea that the range, and especially the values, of FUNCTIONAL TRAITS carried by plants (e.g. whether plants are nitrogen-fixing legumes, warm-season bunchgrasses, or rosette forbs) are strong drivers of ecosystem processes, even where the range of functional types is small and the distribution of relative abundance is kept unnaturally even, such as in synthetic assemblages[4,6,9,12,26–35].

Caution is necessary when comparing the results from microcosms and field studies shown in Table 1, for two reasons. First, few diversity/ecosystem functioning studies have been performed on natural communities. Second, the nature and strength of the links between diversity and ecosystem functioning vary strongly across spatial scales, from local plots to regional gradients. In experiments involving synthetic assemblages, diversity at the local level is manipulated with all environmental factors held constant. By contrast, in field situations, diversity variation among sites is almost always accompanied by variation in environmental factors (e.g. climate, soil resources and disturbance), which directly influences both diversity and ecosystem processes. Therefore, in natural communities, diversity is both a variable responding to the environment and a factor influencing ecosystem functioning. The local effects of diversity on ecosystem processes are thus often masked by effects caused by environmental conditions[11]. Given the extremely different scale and nature of the processes involved, field and synthetic assemblage studies often focus on rather different questions, and extrapolation between them is problematic[7,9,11,15–19]. That said, it is from the comparison and integration of results coming from these contrasting approaches that some of the most substantial advances in this field will probably arise.

Species richness and functional traits: two lines of enquiry

Strong links between the presence and abundance of certain plant functional traits and types and the rate and magnitude of ecosystem processes are well documented for a variety of systems[36–44]. For example, the presence of trees with complex aboveground woody structures and extensive root systems has important effects on soil, water and sediment retention, climate buffering, and animal diversity[1,37,41]; graminoids and mosses have different effects on carbon and nitrogen cycling in tundra ecosystem[38]; and the relative abundance of tall tussock grasses strongly determine fire regime in seminatural vegetation[1]. Ecosystem resilience and resistance are strongly influenced by the traits of the dominant plant species: communities dominated by fast-growing plants tend to have high resilience and low resistance, with the opposite being true for communities dominated by slow-growing plants[36,42,43].

Sandra Díaz*
Marcelo Cabido
Instituto Multidisciplinario de Biología Vegetal (CONICET–UNC) and FCEFyN, Universidad Nacional de Córdoba, Casilla de Correo 495, 5000 Córdoba, Argentina.
*e-mail: sdiaz@ com.uncor.edu

Table 1. Empirical evidence of relations between ecosystem processes and different components of plant diversity[a]

Ecosystem	Experimental set-up	Ecosystem processes[b]	Positive effects reported[c]			Functional types (*sensu lato*)	Refs
			Species richness	Functional richness	Functional composition		
Synthetic assemblages							
Serpentine grassland, USA	Plant mixtures planted in the field	N retention in ecosystem Aboveground biomass Inorganic N pools in soil	NA NA NA	No No Yes	Yes Yes Yes	Bunchgrasses, N-fixers, early and late-season annual forbs	4
Savannah-grassland, USA	Plant mixtures planted in the field	Aboveground biomass, light penetration, and plant % and total N	No	Yes	Yes	C3 grasses, C4 grasses, legumes, forbs and woody plants	6
Mesic grassland, UK	Plant mixtures planted in the field	No. of invading species and total biomass of invasives	No	NA	Yes	Perennial grasses and forbs	12
Grasslands, Germany, Portugal, Switzerland, Greece, Ireland, Sweden, UK	Plant mixtures planted in the field	Total aboveground biomass	Yes	Yes	Yes	Grasses, legumes, herbs	9
Annual grassland, France	Plant mixtures planted in the field	No. of invasives from soil seed bank and survival of seedlings of the exotic annual forbs *Coniza bonariensis* and *C. canadensis*	No	No	Yes	Annual grasses, annual legumes and annual Asteraceae	28
Acid grassland, UK	Plant mixtures planted in the field	Decomposition of standard material Decomposition of litter mixtures	Yes No	No No	No Yes	Grasses, legumes and herbs	27
Grasslands on old fields, Switzerland and Sweden	Plant mixtures planted in the field	No. of leafhoppers (Cicadellidae) No. of wingless aphids (Aphididae) No. of hymenopteran parasitoids No. of grasshoppers (Acrididae) and slugs (Gastropoda) No. of carabid beetles (Carabidae) and spiders (Araneae)	No No No No No	No Yes No No No	Yes Yes No No Yes	Grasses, legumes and forbs	29
Calcareous grassland on old field, Switzerland	Plant mixtures planted in the field	Preference by voles[d] Earthworm biomass[d] Plant aboveground biomass, soil microbial biomass, LAI, plant light absorbance per unit ground area Mesofauna feeding activity Decomposition of standard material Soil moisture	Yes Yes Yes No No No	No Yes Yes No No No	Yes No Yes No Yes Yes	Grasses, legumes and forbs	30, 31
Grassland, Greece	Plant mixtures planted in the field	Total aboveground biomass	Yes	NA	Yes[e]	Annuals and perennial grasses, geophytes and legumes	32
Serpentine grassland, USA	Plant mixtures planted in the field	Aboveground biomass of invasive forb *Centaurea solstitialis* Impact of invader on aboveground biomass of resident species and whole-system evapotranspiration	No Yes	Yes Yes	Yes Yes	Annual grasses, perennial grasses bunchgrasses, early-season and late-season annual forbs	33
Grasslands on old fields, Czech Republic, The Netherlands, UK Sweden and Spain	Plant mixtures planted in the field	Total aboveground biomass Suppression of natural colonizers	Yes Yes	NA NA	Yes Yes	Grasses, forbs and legumes	34
Grassland, USA	Plant mixtures planted in greenhouse microcosms	Aboveground biomass N retention	Yes No	NA NA	Yes Yes	C3 grasses, C4 grasses, legumes and forbs	53
Annual grassland, France	Plant mixtures in greenhouse microcosms	Invasibility (establishment of the forb *Echium plantagineum*)	No	No	Yes	Grasses, legumes and rosette dicots	28
Prairie grassland, USA	Plant mixtures in greenhouse microcosms	Above- and belowground biomass, light transmission, and water retention in soil Decomposition of standard material	Yes No	Yes No	Yes Yes	Grasses, legumes and forbs	26
Prairie grassland, USA	Plant mixtures planted in the field and in greenhouse microcosms	Resistance to invasion (total biomass of invasive)	Yes	NA	Yes	C3 grasses, C4 grasses, legumes and forbs	35

Table 1. continued[a]

Ecosystem	Experimental set-up	Ecosystem processes[b]	Positive effects reported[c]			Functional types (*sensu lato*)	Refs
			Species richness	Functional richness	Functional composition		
Grassland-crop site, New Zealand	Litter bags placed in the field	Decomposition rate of, rate of N release from, and active microbial biomass on litter	No	NA	Yes	Grasses, weedy forbs, forbs from grasslands and trees	8
Grasslands, UK	Litter bags placed in indoor soil microcosms	Soil microbial biomass	No[f]	NA	Yes	Dominant species in intensively managed fertile grasslands, or traditionally managed unfertilized grasslands	54

Manipulation of natural communities

Ecosystem	Experimental set-up	Ecosystem processes[b]	Species richness	Functional richness	Functional composition	Functional types (*sensu lato*)	Refs
Grassland, Argentina	Mostly perennial grassland in neighbouring paddocks under different grazing regimes	Aboveground net primary production	No	No	Yes	Cool-season graminoids, warm-season grasses, cool-season and warm-season forbs	55
Boreal forest, Sweden	Vegetation on islands of different area, subjected to different frequencies of wildfires	Aboveground biomass, litter decomposition, N mineralization and humus accumulation	No	NA	Yes	Early versus late successional species	56
Savannah-grasslands, India	Vegetation along a productivity, diversity and disturbance gradient, with different burning and grazing experimental treatments	Resistance to compositional change across communities	No[g]	NA[g]	Yes[g]	Not explicit, communities dominated by the grasses *Cymbopogon flexuosus* or *Aristida setacea*	22
		Resistance to species turnover across communities	Yes[g]	NA	No		
		Resistance to compositional change and to species turnover within communities	No[g]	NA	No		
Calcareous grasslands, UK	Contrasting grasslands subjected to temperature and precipitation manipulations in the field	Resistance of total aboveground biomass and species compositions	No	NA	Yes	Communities dominated by fast-growing early successional species or by slow-growing, stress-tolerant perennial grasses and sedges	10
Mediterranean shrublands, Greece	Sites naturally differing in species diversity and growth-form composition	Aboveground biomass	Yes	NA	Yes	*Cistus* sp., other shrubs and herbs	57
Sand prairie-grassland, USA	Experimental removal from natural communities on old fields	No. of individuals and cover of invaders	NA	Yes	Yes	C3 graminoids, C4 graminoids and forbs	58
		Light transmittance through canopy	NA	Yes	Yes		
		Soil moisture, soil extractable N, and aboveground biomass	NA	No	Yes		
Dairy grasslands, New Zealand	Grasslands differing in climate and seasonal vegetation, subjected to experimental extreme temperature and rainfall events	Stability of biomass production after extreme events	No	NA	Yes	C3 or C4 species	59
Sand prairie-grassland, USA	Old-field communities subjected to removal of different functional types	Total aboveground biomass	NA	No	Yes	C3 graminoids, C4 graminoids and forbs	60
		Community drought resistance	NA	No	Yes		

[a]Only studies assessing the impact of at least two components of plant diversity on ecosystem processes, and published in 1995 or later, were considered. Comparisons are qualitative and should be taken with caution, because unless a study explicitly has a test for species richness, functional richness and functional composition in its design, it might lead to underestimation or misrepresentation of different components of diversity[19]. Field studies[10,22,55–60] differ markedly among themselves and with synthetic assemblage studies in approach, design and intervening factors and thus strict comparison is not possible.

[b]Abbreviations: LAI, leaf area index, N, nitrogen.

[c]In the case of species and functional richness, only positive effects were considered: No, either no effect or negative effect; in the case of functional composition: Yes, any significant (positive or negative) effect; NA, not assessed.

[d]Species: vole, *Arvicola terrestris*; earthworms, *Octolasion synaeum, Nicodrilus longus, Allolobophora rosea, A. chloroitica, Lumbricus terrestris* and *L. castaneum*.

[e]Species richness effect obvious only when annuals were included in analysis.

[f]Effect of increasing litter diversity on soil microbial biomass was not unidirectional: two- and four-species litter treatments decreased it, whereas five- and six-species treatments increased it.

[g]Shannon Diversity Index.

Box 1. Is species richness a good surrogate for functional richness?

Many authors assume that plant species richness is a surrogate for functional richness[a–c]. In addition to practical considerations, this also rests on the assumption that higher species richness leads to higher functional richness. Although there is often a positive relationship between them (especially if random assemblage is assumed), it is not sufficiently universal to justify using species richness as a reliable surrogate for functional richness.

Species richness should be an adequate surrogate for functional richness only if there is a linear increase in niche space 'coverage' as species richness increases. Theoretically, this can happen in only two situations. The first is random occupation of niche space (Fig. Ia), such as in the 'snowballs on the barn roof' effect[b,c], in which species ('snowballs') are drawn at random during community assemblage, thus increasing the coverage of niche space (the 'barn roof'). Another theoretical case in which a linear increase should be expected is uniform occupation of the niche space (Fig. Ib). In Fig. Ia,b, species richness is a good surrogate for functional richness. However, neither of these cases is common in nature, in which aggregation or 'lumpiness' in plant species occupation of niche space[d] and nonrandom assemblage of communities from the regional species pool[e] seem to be the norm rather than the exception. Aggregated occupation of niche space might be related to strong convergence of different species into contrasting functional types (Fig. Ic), or to strong differentiation in niche space among different genotypes, phenotypes, or ontogenetic stages within a single species (Fig. Id). There are many empirical examples in which variations in species diversity do not match variations in functional diversity[f–h].

In Fig. Ic, species richness overestimates functional richness: species impoverishment can affect different functional types in an equitable way, or it can differentially affect certain functional types and not others. Given a reduction of a certain number of species, in the second case, the impoverishment in functional richness will be much more dramatic than in the first case. Although species impoverishment can equally affect all functional types, differential species reduction at the expense of some functional types is more common. This occurs, for example, in vegetation shifts along altitudinal gradients[g], or in management practices involving selective clearing[h]. In Fig. Id, species richness underestimates functional richness: shifts or reductions of genotypes within a species (functional reduction) will not be reflected in a reduction of species richness[h].

Biotic interactions, such as competition or facilitation, can modify the niche of populations. They can also alter the local biotope space: for example, in the case of ecosystem engineers.
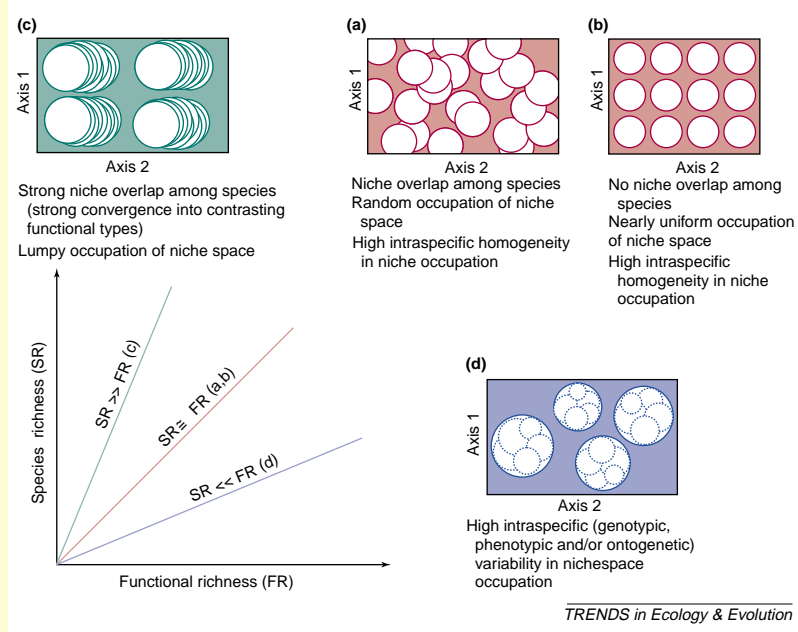

Fig. I. Extreme cases of links between plant species richness and functional richness (partially based on Refs b,c,f). Axes 1 and 2 in the shaded rectangles represent different resource or disturbance axes. Solid-line circles represent the fundamental niche space of different species; dashed-line circles represent the niche of different genotypes, phenotypes or ontogenetic stages within a single species. Whereas uniform and random occupation of niche space (a,b) are mostly theoretical or experimental scenarios, aggregated occupation of niche space (c,d) is closer to the situation of natural communities, although wide gaps in occupation of niche space (exaggerated and simplified in this illustration for the sake of clarity) are unlikely to occur in nature.

References
a Lawton, J.H. *et al.* (1998) Biodiversity and ecosystem function: getting the Ecotron experiment in its correct context. *Funct. Ecol.* 12, 848–852
b Tilman, D. (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80, 1455–1474
c Tilman, D. (2001) Functional diversity. In *Encyclopedia of Biodiversity* (Vol. 3) (Levin, S.A., ed.), pp. 109–120, Academic Press
d Holling, C.S. *et al.* (1996) Self-organization in ecosystems: lumpy geometries, periodicities and morphologies. In *Global Change and Terrestrial Ecosystems* (Walker, B. and Steffen, W., eds), pp. 346–384, Cambridge University Press
e Zobel, M. (1997) The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends Ecol. Evol.* 12, 266–269
f Cowling, R.M. *et al.* (1994) Species diversity; functional diversity and functional redundancy in fynbos communities. *S. Afr. J. Sci.* 90, 333–337
g Vázquez, J.A. and Givnish, T.J. (1998) Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlán. *J. Ecol.* 86, 999–1020
h Díaz, S. *et al.* (1999) Plant functional traits, ecosystem structure, and land-use history along a climatic gradient in central-western Argentina. *J. Veg. Sci.* 10, 651–660

However, this knowledge has rarely been incorporated into diversity studies, in which species richness continues to be the main (and often only) measure of diversity. This reflects the existence of two parallel lines of enquiry in ecology during most of the 20th century. One of these (the 'species-based' approach) stressed the unique role of every species in a community, and has influenced the design of many studies on the role of diversity in ecosystem functioning, especially during the early 1990s. The other (the 'functional-type' approach) focused on the common solutions of many species to the same

environmental challenges irrespective of their ancestry[45]. This lack of crossfertilization might partly explain the current controversies and also that, although functional diversity is acknowledged as the key mechanism by which diversity affects ecosystem functioning, there is still no satisfactory standardized way of quantifying it. As a consequence, species richness is often used as a surrogate of functional richness, despite its inadequacy (Box 1).

Both the species-based and the functional type-based approaches gained renewed momentum in the early 1990s as a result of the challenges posed by global environmental change. There exists a wealth of literature on the links between diversity and ecosystem functioning[2,20,21,25], and the relationships between plant functional traits and types and ecosystem processes[10,36–44] (Box 2). However, these fields have remained mostly isolated from each other. A few conceptual, empirical and modelling contributions have been made with an integrated perspective (e.g. Refs 1,11,24,40,46), providing a foundation from which to explain why and how different components of diversity might influence ecosystem processes.

How can functional diversity affect resource dynamics?
Two main mechanistic explanations have been proposed to explain the role of plant diversity in ecosystem resource dynamics[4,5,7,11–13]. One is the 'selection effect': the higher the species richness in a community, the higher the probability of the presence of species with particularly important traits, which can dominate ecosystem functioning (an analytical explanation is given in Refs 12,13). The other mechanism is the 'niche complementarity effect': at higher diversity, a greater range of functional traits will be represented, providing opportunities for more efficient resource use in a spatially or temporally variable environment[11,13]. Although there is continuing debate on whether the 'selection effect' is either an important biological mechanism or a sampling artifact[5,7,11,13,15], most authors recognize that COMPLEMENTARITY OF RESOURCE USE should increase the magnitude and/or rate of short-term resource use[21]. Trait differences among species, a major component of functional diversity, are crucial for both mechanisms, as shown by theoretical and modelling work (e.g. Refs 7,11,13). The selection effect stresses the presence of certain key trait values, whereas the niche complementarity effect stresses the presence of a range of different traits.

Different functional types can be seen as cases of complementarity of resource use, with members of different functional types showing a higher degree of complementarity than do members of the same functional type. The more complementary niches are with one another, the stronger the effects of diversity on ecosystem functioning should be. Only when all species have equally complementary niches (i.e. each species contributes uniquely and strongly to ecosystem functioning) the rate of ecosystem processes should be expected to increase linearly with species richness. If differences in responses to the environment and effects on ecosystem processes are greater among some species than among others (i.e. if niche space occupation is aggregated, or 'lumpy'[47]) the relationship will not be linear. Most often, species are not equally important in their contributions to ecosystem processes, and a few key species can account for a large fraction of ecosystem functioning[2,37,40,46]. These trait and abundance differences should lead to non-linear responses to species additions or deletions (conceptual models and examples are given in Ref. 48). The loss of an entire functional type (e.g. because of climatic or disturbance factors, which tend to affect certain types differentially; Box 1) could therefore have a larger impact on ecosystem functioning than would deleting the same number of species drawn from a variety of functional types. The same is valid for species additions: the incorporation of a species representing a new functional type could dramatically change ecosystem functioning. Empirical support for these theoretical predictions can be found in 'natural experiments' related to land use. Species invasions illustrate how a minimal increase in species richness (usually by one species) can drastically change ecosystem processes, including water and nutrient dynamics, disturbance regime, or trophic transfers. For example, invasion by the nitrogen-fixing tree *Myrica faya* leads to dramatic functional and structural changes in Hawaiian forests, and dominance by invasive tussock grasses increases fire frequency in the Americas, Oceania and Mediterranean Europe[1].

How can functional diversity affect ecosystem stability?
There is continuing debate about whether all plant species or just a few representatives of each general functional type are needed at any one time to maintain major resource dynamics. However, theoretical developments and empirical results suggest that different responses by different species to environmental factors (e.g. extreme climatic or disturbance events such as frosts, fires or prolonged droughts) contribute to the maintenance of long-term ecosystem functioning, particularly in a changing environmental context[23]. This has been explained using the concepts of functional redundancy and functional insurance, which can be viewed as two sides of the same coin, and have been at the hub of the diversity/ecosystem functioning debate.

Functional redundancy
Two or more species are considered redundant with respect to an ecosystem process when the

---

Box 2. Plant functional types: responses to the environment and effects on ecosystem processes

Plant functional types are sets of species showing similar responses to the environment and similar effects on ecosystem functioning[a]. These groupings tend to be based on common attributes rather than on phylogenetic relationships[b,c]. Plant functional types can be viewed from two different angles[d]: functional response types and functional effect types.

Functional response types

Functional response types are groups of plant species that respond to the abiotic and biotic environment, such as resource availability, climatic conditions, or disturbance regime, in similar ways. Examples of response functional type classifications are xerophytic versus mesophytic species, gap versus understorey species, fire tolerant versus fire intolerant, drought or frost resistant and grazing tolerant versus grazing intolerant.

Functional effect types

Functional effect types are groups of plants that have similar effects on the dominant ecosystem processes, such as primary productivity, nutrient cycling and trophic transfer. Examples include nitrogen fixers, ecosystem engineers, nurse species and fire-promoting species. Functional response and effect types often coincide, particularly in the case of resource use; for example, traits that confer high resistance to environmental stress and herbivory (i.e. response) also determine slow decomposition and slow down nutrient cycling (i.e. effect)[e].

There is no universal functional type classification. Rather, the classification depends on the aim of the study, its scale (from local to global), and the ecosystem process or environmental factor of interest[a,c]. Therefore, functional types are, like most categories used to simplify the natural world, arbitrary divisions of a relatively continuous trait space.

Most of the literature on functional types refers to functional response types[a,c]. However, studies of the links between diversity and ecosystem functioning tend to focus on functional effect types. The consideration of functional response types (often nested within functional effect types) seems important, especially in relation to the long-term persistence of ecosystem function.

References

a Gitay, H. and Noble, I.R. (1997) What are plant functional types and how should we seek them? In *Plant Functional Types* (Smith, T.M. *et al.*, eds), pp. 3–19, Cambridge University Press
b Díaz, S. and Cabido, M. (1997) Plant functional types and ecosystem function in relation to global change. *J. Veg. Sci.* 8, 463–474
c Lavorel, S. *et al.* (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends Ecol. Evol.* 12, 474–478
d Walker, B.H. *et al.* (1999) Ecosystem function and plant attribute diversity: the nature and significance of dominant and minor species. *Ecosystems* 2, 95–113
e Aerts, R. (1995) The advantages of being evergreen. *Trends Ecol. Evol.* 10, 402–407

---

disappearance of one or more of those species does not affect that ecosystem process in a significant way, because the remaining species can compensate for it (i.e. the species removed represents 'redundant information' with respect to that particular process)[24,49]. This concept has sometimes been taken beyond its original context, acquiring some negative connotations of superfluousness[50]. However, its original sense is one of redundancy as a way of increasing a reliability of a system[49,51]. In engineering, reliability increases when redundant components are added to a system: the more components performing the same function, the smaller the probability of that function being disrupted owing to the failure of a given component. In this context, rather than superfluous repetition, redundancy is an insurance policy against the loss of function in the event that species are lost. The larger the number of functionally similar species in a community, the greater the probability that at least some of these species will survive changes in the environment and maintain the properties of the ecosystem[46].

Functional insurance
Strongly linked to the concept of functional redundancy is the 'insurance hypothesis'[11]. The greater the variation in responses among species in a community, the lower the species richness required to buffer an ecosystem. In this way, functional richness (in this context, referring to interspecific variation in response) is expected to contribute to the insurance effect because greater functional richness increases the odds that at least some species will respond differentially to variable conditions and perturbations.

The distinction between functional effect and functional response types (Box 2) has radical implications for the links among functional diversity, insurance and redundancy. Although by definition the members of a given functional effect type should show at least some degree of redundancy with respect to a given ecosystem process, and thus the loss of one of them should not produce major shifts in short-term ecosystem functioning, they might respond differently to changes in the environment, acting to buffer it against dramatic ecosystem change. Thus, different functional response types nested within a functional effect type might play an important role in sustaining the long-term functioning of ecosystems[1,40,46,49,51]. It has been suggested that, although most of an ecosystem's resource dynamics at any given time depends on a few dominant species, the presence of minor species within each functional type, performing similar roles in terms of resource dynamics, but with different responses to climatic and disturbance factors (e.g. fire, grazing, frosts or pathogens) might have important implications for ecosystem stability[24,40] (Box 3).

Conclusions and prospects

There is now general agreement based on both theory and empirical evidence that plant functional

---

Box 3. Plant functional types, redundancy and insurance

Within the same functional effect type (Box 2), species with different requirements and tolerances (i.e. belonging to different functional response types) contribute to the redundancy of important ecosystem functions. They therefore provide insurance to the system, in the form of long-term resilience against changes in environmental factors such as climate, disturbance regime, or pathogens. Empirical examples of this can be found for several different ecosystems:

- Species belonging to a same functional effect type in an Australian savannah exhibited different degrees of grazing resistance: this was found to buffer carbon and nitrogen cycling and water budget in the face of heavy grazing[a].
- Species belonging to the same functional effect type (such as evergreen or deciduous shrub, graminoid, or moss) showed individualistic responses to experimental warming of the air temperature in the Arctic tundra[b] of Alaska.
- Pairs of species of sedges, grasses, and rosette forbs with highly similar resource dynamics showed widely differing tolerances to an extreme drought event in British calcareous grasslands[c].
- Members of the same functional effect type (such as deciduous or evergreen shrub, graminoid, forb, or bromeliad) from a regional climatic gradient in central Argentina exhibited widely differing degrees of frost tolerance when subjected to an experimental frost treatment[d].

References

a Walker, B.H. *et al.* (1999) Ecosystem function and plant attribute diversity: the nature and significance of dominant and minor species. *Ecosystems* 2, 95–113

b Chapin, F.S., III *et al.* (1996) The functional role of species in terrestrial systems. In *Global Change and Terrestrial Ecosystems* (Walker, B. and Steffen, W., eds), pp. 403–428, Cambridge University Press

c Buckland, S.M. *et al.* (1997) A comparison of plant responses to the extreme drought of 1995 in northern England. *J. Ecol.* 85, 875–882

d Díaz, S. *et al.* (1999) Plant traits as links between ecosystem structure and functioning. In *Proceedings of the VIth International Rangeland Congress – Townsville, Australia* (Eldridge, D. and Freudenberger, D., eds), pp. 896–901, VI International Rangeland Congress, Inc.

diversity, including both functional richness and composition, is important in determining ecosystem functioning. The values and range of functional traits, or the kinds and number of functional types, present in an ecosystem strongly influence its short-term fluxes of matter and energy. However, species diversity within functional types seems to play an essential role in long-term ecosystem stability in the face of environmental change.

For many philosophical, cultural and practical reasons, the conservation of species richness deserves the highest priority in ecological agendas. The preservation of key ecosystem processes, and the services derived from them, represents only one aspect of diversity conservation. That said, information on species richness is unlikely to be sufficient to maximize the long-term persistence of key ecosystem processes in the context of a changing environment. This is because plant species vary strongly in both their responses to the environment and their effects on ecosystem processes: therefore, the effects of the recruitment or loss of the same number of plant species can have rather different effects on ecosystem functioning, depending on the identity of the species. As an obvious consequence, functional richness and composition, and especially the traits of the dominant plant species, deserve particular attention.

Although they are not independent, species richness seems an inadequate surrogate for functional diversity in many cases. The distinction between species richness, functional richness and functional composition can seem elusive[16], and does pose statistical and experimental design difficulties[19,21,26]. However, the distinction provides an insight into ecosystem processes that would not be allowed by an approach based solely on species richness. Two steps are important in this sense. First, explicit tests of the effect of functional richness need to be built more often into the design of microcosms and field experiments. Experiments considering both mixtures of species and species growing in monoculture should provide invaluable information on how the functional traits of different species in the mixture influence ecosystem processes. Ideally, trait differences among different genotypes or ontogenetic stages within the same species should be considered, as well as trait differences among species.

Second, it is imperative to find more standardized ways of quantifying functional richness and composition. Several methods of identifying functional types and measuring trait distances among plants have been proposed[24,39,45]. The traits to focus on depend on the objective of the study, namely what ecosystem processes or environmental factors are considered to be relevant. Several compilations of traits linked to different ecosystem processes and responses to climatic and disturbance factors have been published in the past few years (e.g. Refs 44,46,52). Although widely used, functional type richness and composition have strong limitations as indicators of functional diversity. The development of standard measurements of functional trait distance[21,24] will certainly accelerate progress in this field of research.

There is also a need for better links between research questions and results at different spatial scales. This includes findings from synthetic assemblages and those from field monitoring and manipulation studies, which allow for more contrasting functional types, and more realistic abundance distributions and assemblage and extinction processes. Some aspects of the diversity–ecosystem functioning relationship are

Glossary

Complementarity of resource use: spatial or temporal partitioning of resources such as water, soil nutrients, pollinators or food, among organisms that coexist at a given site. Examples are plants that grow at the same site but use different resources, or the same resources at different times, such as shallow-rooted grasses and deep-rooted shrubs in cold steppes, cool-season and warm-season grasses in prairies, or nitrogen-fixing beans and nitrogen-demanding maize in mixed crops.

Ecosystem functioning: the flow of energy and materials through the arrangement of biotic and abiotic components of an ecosystem. It includes many ecosystem processes, such as primary production, trophic transfer from plants to animals, nutrient cycling, water dynamics and heat transfer. In a broad sense, ecosystem functioning includes two components, ecosystem resource dynamics and ecosystem stability.

Ecosystem resource dynamics: the magnitude (how much) and rate (how fast) of inputs, outputs, and internal cycling of key resources, such as carbon, water and mineral nutrients, in an ecosystem at a particular time.

Ecosystem services: goods and services provided by ecosystem processes to humans. Examples are food, fibre, fodder, fuel, water provision, control and detoxification, amelioration of weather, soil formation, carbon sequestration, medicinal resources, and recreation.

Ecosystem stability: capacity of an ecosystem to persist in the same state. It has two components, ecosystem resistance, the ability to persist in the same state in the face of a perturbation, and ecosystem resilience, the ability to return to its former state following a perturbation.

Functional components of diversity: aspects of diversity related to functional traits, as opposed to species richness. One of these components is functional richness, the 'functional trait distance', or difference in terms of one or more functionally relevant traits, between organisms. For practical reasons, functional richness is often measured as the number of functional types. The other component is functional composition, the presence and relative abundance of certain functional traits. Functional composition is commonly expressed as the presence of certain functional types, such as legumes or tussock grasses. Functional diversity includes these two components.

Functional diversity: the value and range of functional traits of the organisms present in a given ecosystem. The value of traits refers to the presence and relative abundance of certain values (or kinds) of leaf size, nitrogen content, canopy heights, seed dispersal and dormancy characteristics, vegetative and reproductive phenology, etc. The range of traits refers to the difference between extreme values of functional traits, for example, the range of leaf sizes, canopy heights, or rooting depths deployed by different plants in an ecosystem.

Functional traits: the characteristics of an organism that are considered relevant to its response to the environment and/or its effects on ecosystem functioning. Examples of functional traits are leaf size, toughness and longevity, seed size and dispersal mode, canopy height and structure, ability to resprout, and capacity for symbiotic fixation of nitrogen.

Functional type: the set of organisms sharing similar responses to the environment (e.g. temperature, water availability, nutrients, fire and grazing) and similar effects on ecosystem functioning (e.g. productivity, nutrient cycling, flammability and resilience).

Species richness: the number of different species in a given system.

---

harder to document in the field than are others. For example, the 'insurance' effect of diversity is harder to test than its short-term effects on matter and energy fluxes. However, natural and seminatural systems are the obvious target for conservation and sustainable management initiatives, and thus deserve increased research effort.

The links between local and regional diversity, and the factors influencing them, represent a relatively unexplored area in which exciting ideas have started to emerge. Local assemblages can be interpreted as the result of successive 'filters' on the regional species pool. These filters, represented by climatic conditions, disturbance regime and biotic interactions, typically operate at different spatial scales, with the end result being a non-random local assemblage[21,44], which might be a biased sample of the functional diversity present in the regional species pool. It has been suggested that, at a given site, species richness is limited by the regional species pool, whereas functional diversity is limited by the local availability of niches, or biotope space[21].

Finally, comparatively little progress has been made in empirically documenting the role of interactions between species and functional types in ecosystem functioning. Ecosystem processes tend to be non-additive functions of the traits of interacting species. The traits of the organisms in a given ecosystem strongly influence mutualistic, competitive, trophic, and ecosystem-engineering[41] interactions, and these interactions can in turn modify the local value, range, and abundance of traits[1]. For example, interactions can determine whether herbivores increase or reduce plant diversity, whether invasive species thrive in an area or not, whether most of the primary production is cycled through the herbivore compartment or directly through the decomposer compartment. The ways in which the links between diversity and ecosystem functioning are modulated by direct and indirect interactions represent an extremely promising area for future research.

Perhaps the most substantial contribution of the plant functional trait approach to ecosystem and community studies is that it provides a much stronger insight into the links between community structure and ecosystem functioning than does the consideration of species richness alone. A novel approach, resulting from crossfertilization between the species-based and the functional type-based approaches, has the potential to contribute to practical management for the conservation of diversity and ecosystem services. This approach can also help in the construction of models of how changes in biome distributions resulting from global environmental change could affect the circulation of energy and materials at the ecosystem level.

References

1 Chapin, F.S., III *et al.* (2000) Consequences of changing biodiversity. *Nature* 405, 234–242
2 Schulze, E-D. and Mooney, H.A. (1994) *Biodiversity and Ecosystem Function*, Springer-Verlag
3 Grime, J.P. (1997) Biodiversity and ecosystem function: the debate deepens. *Science* 277, 1260–1261
4 Hooper, D.U. and Vitousek, P.M. (1997) The effects of plant composition and diversity on ecosystem processes. *Science* 277, 1302–1305
5 Huston, M.A. (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110, 449–460

6 Tilman, D. *et al.* (1997) The influence of functional diversity and composition on ecosystem processes. *Science* 277, 1300–1302
7 Tilman, D. (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80, 1455–1474
8 Wardle, D.A. *et al.* (1997) Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos* 79, 247–258
9 Hector, A. *et al.* (1999) Plant diversity and productivity experiments in European grasslands. *Science* 286, 1123–1127

10 Grime, J.P. *et al.* (2000) The response of two contrasting limestone grasslands to simulated climate change. *Science* 289, 762–765
11 Loreau, M. (2000) Biodiversity and ecosystem functioning: recent theoretical developments. *Oikos* 91, 3–17
12 Crawley, M.J. *et al.* (1999) Invasion-resistance in experimental grassland communities: species richness or species identity? *Ecol. Lett.* 2, 140–148
13 Loreau, M. (1998) Biodiversity and ecosystem functioning: a mechanistic model. *Proc. Natl. Acad. Sci. U. S. A.* 95, 5632–5636
14 Tilman, D. (2001) Functional diversity. In *Encyclopedia of Biodiversity* (Vol. 3) (Levin, S.A., ed.), pp. 109–120, Academic Press

15 Hodgson, J.G. *et al.* (1998) Does biodiversity determine ecosystem function? The Ecotron experiment reconsidered. *Funct. Ecol.* 12, 843–856

16 Lawton, J.H. *et al.* (1998) Biodiversity and ecosystem function: getting the Ecotron experiment in its correct context. *Funct. Ecol.* 12, 848–852

17 Huston, M.A. *et al.* (2000) No consistent effect of plant diversity on productivity. *Science* 289, 1255a

18 Hector, A. *et al.* (2000) Response to Huston *et al. Science* 289, 1255a

19 Allison, G.W. (1999) The implications of experimental design for biodiversity manipulations. *Am. Nat.* 153, 26–45

20 Schwartz, M.W. *et al.* (2000) Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* 122, 297–305

21 Schmid, B. *et al.* Empirical evidence for biodiversity–ecosystem functioning relationships. In *Functional Consequences of Biodiversity: Experimental Progress and Theoretical Extensions* (Kinzig, A.P. *et al.*, eds), Princeton University Press (in press)

22 Sankaran, M. and McNaughton, S.J. (1999) Determinants of biodiversity regulate compositional stability of communities. *Nature* 401, 691–693

23 Johnson, K.H. *et al.* (1996) Biodiversity and the productivity and stability of ecosystems. *Trends Ecol. Evol.* 11, 372–377

24 Walker, B.H. *et al.* (1999) Ecosystem function and plant attribute diversity: the nature and significance of dominant and minor species. *Ecosystems* 2, 95–113

25 Schläpfer, F. and Schmid, B. (1999) Ecosystem effects of biodiversity: a classification of hypotheses and exploration of empirical results. *Ecol. Appl.* 9, 893–912

26 Naeem, S. *et al.* (1999) Plant neighborhood diversity and production. *Ecoscience* 6, 355–365

27 Hector, A. *et al.* (2000) Consequences of the reduction of plant diversity for litter decomposition: effects through litter quality and microenvironment. *Oikos* 90, 357–371

28 Lavorel, S. *et al.* (1999) Invasibility and diversity of plant communities: from patterns to processes. *Div. Distrib.* 5, 41–49

29 Koricheva, J. *et al.* (2000) Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grasslands. *Oecologia* 125, 271–282

30 Spehn, E.M. *et al.* (2000) Above-ground resource use increases with plant species richness in experimental grassland ecosystems. *Funct. Ecol.* 14, 326–337

31 Spehn, E.M. *et al.* (2000) Plant diversity effects on soil heterotrophic activity in experimental grassland ecosystems. *Plant Soil* 224, 217–230

32 Troumbis, A.Y. *et al.* (2000) Hidden diversity and productivity patterns in mixed Mediterranean grasslands. *Oikos* 90, 549–559

33 Dukes, J.S. (2001) Biodiversity and invisibility in grassland microcosms. *Oecologia* 126, 563–568

34 Lepš, J. *et al.* (2001) Separating the chance effect from other diversity effects in the functioning of plant communities. *Oikos* 92, 123–134

35 Naeem, S. *et al.* (2000) Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91, 97–108

36 Aerts, R. (1995) The advantages of being evergreen. *Trends Ecol. Evol.* 10, 402–407

37 Wilson, J.B. and Agnew, A.D.Q. (1992) Positive-feedback switches in plant communities. *Adv. Ecol. Res.* 23, 263–336

38 Hobbie, S.E. (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecol. Monogr.* 66, 503–522

39 Díaz, S. and Cabido, M. (1997) Plant functional types and ecosystem function in relation to global change. *J. Veg. Sci.* 8, 463–474

40 Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86, 901–910

41 Jones, C.G. *et al.* (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78, 1946–1957

42 Lepš, J. *et al.* (1982) Community stability, complexity and species life-history strategies. *Vegetatio* 50, 53–63

43 MacGillivray, C.W. *et al.* (1995) Testing predictions of the resistance and resilience of vegetation subjected to extreme events. *Funct. Ecol.* 9, 640–649

44 Díaz, S. *et al.* (1999) Functional implications of trait-environment linkages in plant communities. In *The Search for Assembly Rules in Ecological Communities* (Weiher, E. and Keddy, P.A., eds), pp. 338–362, Cambridge University Press

45 Lavorel, S. *et al.* (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends Ecol. Evol.* 12, 474–478

46 Chapin, F.S., III *et al.* (1996) The functional role of species in terrestrial systems. In *Global Change and Terrestrial Ecosystems* (Walker, B. and Steffen, W., eds), pp. 403–428, Cambridge University Press

47 Holling, C.S. *et al.* (1996) Self-organization in ecosystems: lumpy geometries, periodicities and morphologies. In *Global Change and Terrestrial Ecosystems* (Walker, B. and Steffen, W., eds), pp. 346–384, Cambridge University Press

48 Sala, O.E. *et al.* (1996) Biodiversity and ecosystem functioning in grasslands. In *Functional Roles of Biodiversity* (Mooney, H.A. *et al.*, eds), pp. 129–150, John Wiley & Sons

49 Walker, B.H. (1995) Conserving biological diversity through ecosystem resilience. *Conserv. Biol.* 9, 747–752

50 Gitay, H. *et al.* (1996) Species redundancy: a redundant concept? *J. Ecol.* 84, 121–124

51 Naeem, S. (1998) Species redundancy and ecosystem reliability. *Conserv. Biol.* 12, 39–45

52 Weiher, E. *et al.* (1999) Challenging Theophrastus: a common core list of plant traits for functional ecology. *J. Veg. Sci.* 10, 609–620

53 Symstad, A.J. *et al.* (1998) Species loss and ecosystem functioning: effects of species identity and community composition. *Oikos* 81, 389–397

54 Bardgett, R.D. and Shine, A. (1999) Linkages between plant litter diversity, soil microbial biomass and ecosystem function in temperate grasslands. *Soil Biol. Biochem.* 31, 317–321

55 Rusch, G.M. and Oesterheld, M. (1997) Relationship between productivity and species and functional group diversity in grazed and non-grazed Pampas grassland. *Oikos* 78, 519–526

56 Wardle, D.A. *et al.* (1997) The influence of island area on ecosystem properties. *Science* 277, 1296–1305

57 Troumbis, A.Y. and Memtsas, D. (2000) Observational evidence that diversity may increase productivity in Mediterranean shrublands. *Oecologia* 125, 101–108

58 Symstad, A.J. (2000) A test of the effects of functional group richness and composition on grassland invasibility. *Ecology* 81, 99–109

59 White, T.A. *et al.* (2000) Sensitivity of three grassland communities to simulated extreme temperature and rainfall events. *Glob. Change Biol.* 6, 671–684

60 Symstad, A.J. and Tilman, D. (2001) Diversity loss, recruitment limitation, and ecosystem functioning: lessons learned from a removal experiment. *Oikos* 82, 424–435