Functional diversity revealed by removal experiments

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The dominant protocol to study the effects of plant diversity on ecosystem functioning has involved synthetically assembled communities, in which the experimental design determines species composition. By contrast, the composition of naturally assembled communities is determined by environmental filters, species recruitment and dispersal, and other assembly processes. Consequently, natural communities and ecosystems can differ from synthetic systems in their reaction to changes in diversity. Removal experiments, in which the diversity of naturally assembled communities is manipulated by removing various components, complement synthetic-assemblage experiments in exploring the relationship between diversity and ecosystem functioning. Results of recent removal experiments suggest that they are more useful for understanding the ecosystem effects of local, nonrandom extinctions, changes in the natural abundance of species, and complex interspecific interactions. This makes removal experiments a promising avenue for progress in ecological theory and an important source of information for those involved in making land-use and conservation decisions.

Current extinction rates caused by human activities are orders of magnitude higher than natural background levels [1], and it is crucial that we understand the functional consequences of such extinctions. Terrestrial plants provide the basis for many fundamental ecosystem processes and services; therefore, many initiatives have been launched in the past decade to address this issue by documenting the possible effects of terrestrial plant diversity on ecosystem processes. Most of these studies are based on experiments using synthetic communities, in which different combinations of species or functional types are artificially assembled to represent different diversity levels or species assemblages decided by the investigator [2–6]. Synthetic-assemblage experiments (SAEs) have stimulated much critical thought about the mechanistic links between diversity and ecosystem function. However, they are technically feasible only in certain ecosystem types, such as semi-natural and early-successional grasslands, and their interpretation and relevance to real ecosystems continues to be intensely debated (e.g. [7–9]). Also, components of diversity other than species and functional-type richness, such as the diversity of traits represented by the species and the relative abundance of species have rarely been addressed in SAEs [10], even though they all play a key role in ecosystem functioning [11]. These limitations call for a variety of complementary research approaches to investigate the issue of accelerated diversity loss [12]. One such approach is the removal of species or functional types from established, natural or semi-natural communities. Experimental manipulations involving the exclusion of plants [13], intertidal invertebrates [14], large ungulates [15,16], soil fauna and microbiota [17] have long been used to gain insight into fundamental community and ecosystem processes. Here, we provide a critical evaluation of the potential of removal experiments (REs) for testing the role of diversity, species traits and interactions in ecosystem functioning, with a focus on terrestrial plants.

The functional role of diversity: a need for multiple research strategies

Understanding the relationship between diversity and ecosystem processes requires a broad array of approaches, including monitoring patterns in nature, manipulating natural communities in the field, and assembling synthetic communities in controlled environments. There is no single best protocol (Fig. 1). REs and SAEs differ in several issues of experimental design (Table 1), although these are not their most crucial differences. Some differences between REs and SAEs have significant consequences for the interpretation of their results and their applicability to real ecosystems. As a result, not all questions are addressed equally well by the two approaches. Questions about species richness *per se* (i.e. the general effect of the number of species) might be better answered by SAEs because of their greater control of species richness and composition within and across

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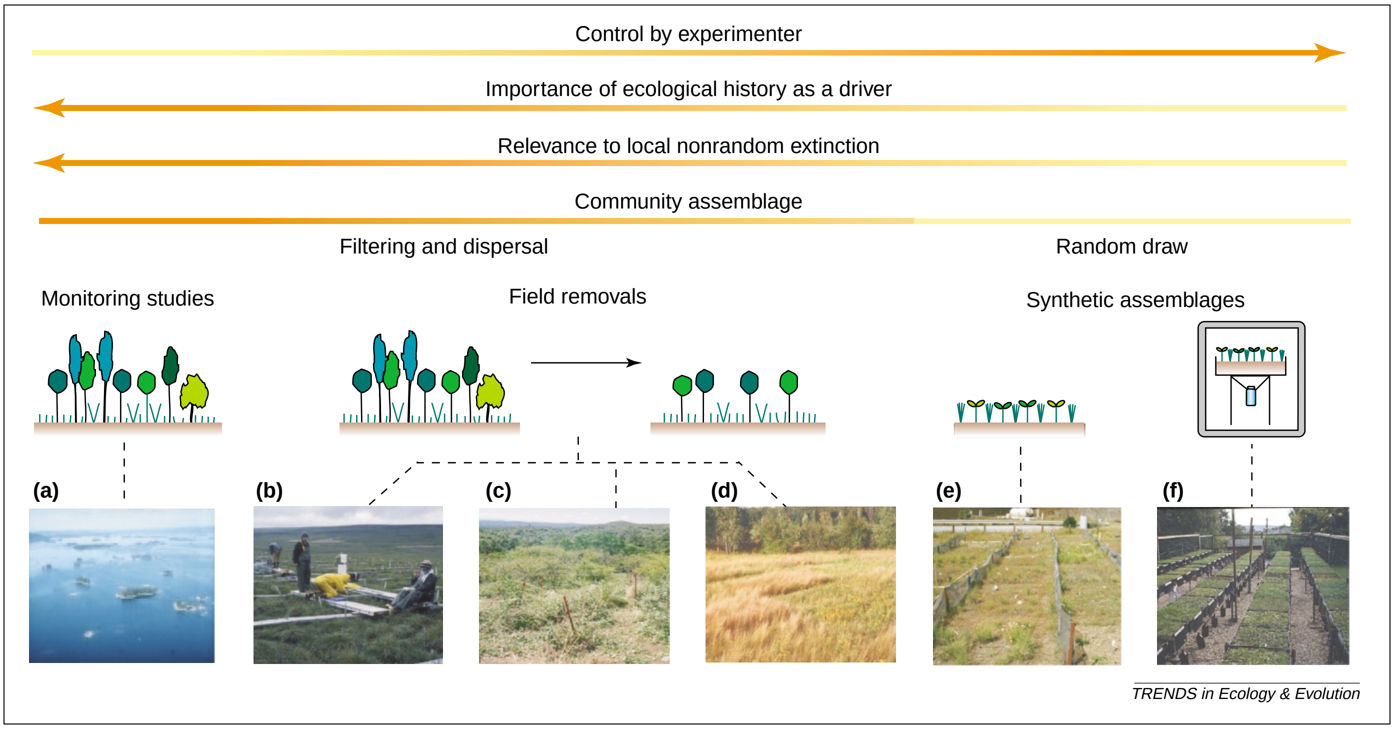

Fig. 1. Comparison of different approaches to the study of diversity–ecosystem functioning linkages (modified, with permission, from [55]). (a) Monitoring studies of boreal vegetation in islands (Sweden) [56]; field removal experiments in (b) the tussock tundra (AL, USA) [44], (c) a mountain shrubland (Córdoba, Argentina) ([43]; and (d) an old field-sand prairie (MN, USA) [36]; synthetic-assemblage experiments in (e) the field (CA, USA [2]; and (f) in microcosms (Sheffield, UK) [52]. Images reproduced with permission from O. Zackrisson (a), S. Díaz (b,f), D.E. Gurvich (c), A.J. Symstad (d) and D.U. Hooper (e)

replicates. Some questions can be addressed by both SAEs and REs, such as: (1) what is the overall ecosystem-level effect of losing different species or functional types?; (2) is the effect of losing different species of the same functional type similar?; and (3) what is the role of resource-use complementarity? Finally, there are questions that are better addressed by REs (Box 1). The major differences between REs and SAEs that determine which questions are best answered by a specific approach stem from the different assembly processes that the manipulated communities have gone through. This difference in assembly not only creates a difference in the diversity reduction scenario simulated by the experiment, but also affects composition and interaction components of the community that ultimately cause diversity effects (Table 1).

Naturally versus synthetically assembled communities

Monitoring studies and REs are based on naturally assembled communities and thus incorporate important natural processes that might be underestimated by SAEs. In experiments operating on naturally assembled communities, the local set of species and their relative abundances are the result of filtering processes exerted by the long-term operation of climate, disturbance regime, landscape processes and biotic interactions on a large regional species pool [18–22]. These processes can yield naturally

Box 1. Key questions in understanding links between diversity and ecosystem functioning that can be addressed by the use of removal experiments

- What is the role of the amount of plant biomass versus the identity of that biomass in ecosystem functioning? Is the ecosystem effect simply a function of the amount of biomass lost, or is it determined by the species composition or richness of the biomass lost?
- Following the loss of species or functional types, do the same or different species or functional types take over? Is the final result of the loss of species or functional types a more or a less diverse system?
- Is the effect of losing the same functional type similar in different ecosystems? Do naturally species-poor systems react to the same loss in consistently different ways from naturally species-rich systems? Do resource-rich systems react to the same loss in consistently different ways from resource-poor systems?
- Do remaining species compensate for the loss of one species? Is there any evidence for functional redundancy between species belonging to the same functional type?
- What is the relative importance of indirect versus direct effects of losing one species or functional group?
- Are there substantially different responses, in terms of occupation by neighbouring, already existing, species versus invasion by new species, in the face of loss of similar functional types in different systems?
- How do the components of the removal effect (Box 2) contribute to the ecosystem-function effects of the loss of a species or functional group?
- What are the ecosystem-function effects of common management practices that involve removal of species groups?
- What are the management and/or conservation implications of the loss or removal of different species or groups? (e.g. increased or decreased productivity, flammability, carrying capacity for animals, habitat structure, or balance between native and exotic species).

Table 1. Comparison between different experimental approaches to the investigation of the role of diversity in ecosystem functioning

	Synthetic-assemblage experiments (SAE)	Removal experiments (RE)[a]
Experimental design and setting		
Artifactual effects of experimental procedures	Mostly related to altered soil properties from preparation, unnatural combinations of species and Relative abundances [52], and random selection of elements within diversity treatments [53,54]	Mostly related to the disturbance effect procedures (effect 3 in Box 2)
Species number	Low (usually <40)	Potentially very high, determined by existing vegetation
Kind and range of functional types involved	Often very limited range, restricted to small, relatively fast-growing herbaceous plants	Can include organisms with contrasting sizes and resource-use strategies (e.g. several species of long-lived trees, epiphytes and annual herbs in the same experiment)
Control of external variables	Higher than in REs	Lower than in SAEs
Variability among replicates	Typically lower than in REs	Typically higher than in SAEs
Community assembly		
Initial assemblage process	Random draw from a subset of local species pool	Abiotic and biotic filtering of regional species pool
Disturbance and landscape processes	Disturbance tends to be minimized, so its effects are often not realized in the community Often cannot capture patch dynamics (e.g. influx and efflux of materials between different patches in a heterogeneous landscape)	Historical and/or present-day effects of disturbance and patch dynamics produce variation
Dispersal and recruitment	Natural dispersal of some species into the system is not allowed (composition of assemblage is usually kept fixed); dispersal and recruitment of naturally rare species are artificially favoured Can create communities with unrealistically equitable abundances across species and distort abundance-mediated compositional effects	Differential dispersal and recruitment from regional species pool occurs. Rate, magnitude and limitations of dispersal and recruitment of different members of natural regional species pool thus maintained Natural facilitation and suppression effects of established vegetation on recruiting seedlings occur
Founder effect	Eliminated or strongly reduced, because initial composition of community is decided by researcher and all species start at the same stage	Differences in species composition and relative abundance can result from stochastic variation in the order of species recruitment
Compositional effects		
Effects derived from relative abundances of species in natural systems, from ecosystem engineers and from other complex and indirect interactions	Less likely to be incorporated than in REs; effects linked to relative abundance can be either under- or overestimated	More likely to be captured than in SAEs
Interpretation of results		
Main natural process tested	Colonization by species pools of different sizes	Local nonrandom extinction

[a] All considerations made for removal experiments also apply to other naturally assembled communities, with the exception of artifactual effects of experimental procedures.

low-diversity communities because the filtering factors are so strong that only a few species can thrive. Under these circumstances, the local community niche space is 'saturated' [23] even when diversity is low because any 'unused' portion of niche space is eventually occupied by dispersal and local recruitment. By contrast, SAEs start with a list of species comprising a subset of the local species pool that are often chosen for their ease of propagation. Subsets of this list are used to create different levels of species richness, within which the species composition is often chosen randomly, and these combinations of richness and composition are artificially maintained. This hindrance of natural assembly processes (Table 1) could prevent the local community niche space from being fully exploited. Thus, although community- and ecosystem-level effects of low diversity documented in SAEs, such as higher loss of soil resources [24], lower biomass production [5], or higher invasibility [25] can demonstrate the importance of niche complementarity, they cannot be applied directly to naturally species-poor systems.

SAEs instead test the effect of occupation of bare ground by different numbers of species or functional types, simulating the impoverishment of regional species pools available for recolonization of severely disturbed ground. This might be a reasonable representation of some situations, such as in regions where ancient and intensive land use has already resulted in local extinction that is too widespread to enable spontaneous recolonization (e.g. within the context of extensification schemes in northern and central Europe, in which land formerly subjected to intensive agricultural use is set aside in the hope that species-rich seminatural communities, such as calcareous grasslands and hay meadows, will recover [26]). However, it does not capture the full range of processes that produce natural assemblages and that occur in other diversity-loss situations. For example, effects of disturbance, landscape processes and asynchronous biotic interactions (e.g. founder effect, facilitation and/or inhibition of seedling growth by adults of another species) on the biota are minimal in synthetically assembled communities of SAEs compared with the naturally assembled ones of REs (Table 1).

Compositional effects in naturally assembled communities

REs enable assessment of the direct effects of local extinctions on ecosystem functioning in a way that SAEs cannot [27]. This is because REs simulate local extinctions from an already established 'saturated' community in which species interactions working over long timescales and at large spatial extents have influenced the composition and relative abundance of species in the community. Interactions that operate at small spatial and temporal scales, such as competition and some forms of predation and facilitation, should occur in synthetically assembled communities much as they would in naturally assembled ones. However, the following examples illustrate how some interactions and compositional effects are better captured by REs.

Species abundance versus presence

The impact of a species or functional group on ecosystem functioning depends not only on whether that component is present in an ecosystem, but also how abundant it is. Some of the positive effects of diversity on grassland productivity detected in two SAEs can be attributed to the high productivity of legumes and/or their facilitative interaction with other functional types, presumably because of the nitrogen that they contribute to the ecosystem [4,5,28]. The abundance of legumes in these SAEs might be unnaturally high, however, because initial planting densities released them from dispersal limitation and many herbivores were excluded (e.g. through fencing). When fences excluded deer from a natural grassland similar to that simulated by the SAE of Tilman and colleagues [3,4], the proportion of plant biomass comprised by a native legume increased fivefold. This led to higher total plant biomass and, after 13 years, higher total soil nitrogen [29]. Thus, the importance of the facilitative effect of legumes on other species might be overestimated by SAEs in which the abundance of legumes in the synthetically assembled communities is abnormally high.

Species interactions affected by life stages of the organisms involved

In a Patagonian shrub steppe dominated by shallow-rooted tussock grasses and deep-rooted shrubs, a long-term RE showed that the type of interaction between these two functional types depends on their life stages [30]. Shrubs trap the wind-dispersed seeds of grasses and shelter their seedlings, leading to a higher seedling density of grasses below the shrubs. This facilitative interaction shifts to a competitive one when the grasses reach the adult stage and intercept water in the upper soil layers, decreasing the amount that percolates into deep layers from which the shrubs obtain water. At this stage, the removal of grasses leads to increased shrub production; however, removal of shrubs does not affect the remaining adult grass production. Consequences of the loss of one of these functional types on ecosystem productivity or water use would therefore depend upon at which stage of development the group was lost.

Indirect interactions mediated by highly mobile organisms and/or ecosystem engineers

Indirect interactions that are mediated by highly mobile organisms and/or ecosystem engineers include interactions that typically involve medium- to large-sized organisms (e.g. trees or vertebrates), but also large, long-lasting structures built by smaller organisms; interactions that are difficult to include in SAEs. For example, harvester ants *Messor* spp. have a strong influence on desert communities and ecosystems. As shown in a removal experiment performed by Wilby *et al.* in the Negev desert [31], this is mostly through ecosystem engineering. The ants construct long-lived nest mounds that intercept the flow of organic matter, water and seeds, and thus have a strong impact on plant community biomass production.

Other complex interactions

REs are very suitable for investigating the ecosystem consequences of complex cascading and/or ramifying interactions, such as those involving keystone species [32]. One research area in which REs can make a substantial contribution is the assessment of the whole-ecosystem effects of species invasions [33]. SAEs can readily simulate some of the effects of invasive species (e.g. competition, especially that involving seedlings or adults of small plants). However, REs, without the risks involved in the introduction of invasive species into an uninvaded area, are in a much better position to capture the real dimension of the impact of invasions than are SAEs. For example, some of the strongest ecosystems consequences of invasion by exotic grasses in Hawaii involve invader-mediated changes in fire regime and modulation of resource supply through facilitative interactions, processes that have been adequately captured by REs [34,35].

What can be learnt from REs? Challenges and perspectives

The interpretation of REs

The nature of SAEs creates specific effects that need explicit consideration both in their design and in the interpretation of their results. This is also true of REs. The effect of removing one or more species or functional type from a community is the final outcome of at least three different components: (1) the loss of a certain organism; (2) the response of other organisms to that loss; and (3) the act of removal itself (Box 2). Most removal studies are primarily interested in the first component, but the importance of the other two, which varies with the system and organism involved, should not be underestimated. The response of other organisms is a crucial component of system response and is itself of great interest [36], although it has so far received little attention. The act of removal itself can potentially result in misleading conclusions if it is not evaluated explicitly and if adequate controls are not included in the experimental design.

Rather than insurmountable obstacles, these are factors that should be considered when interpreting results, and the comparison of their relative magnitude in different systems is a legitimate topic of investigation in its own right. For example, REs used in the study of competition have been criticized for their potential for confounding effects stemming from apparent competition (e.g. third-species interactions, microhabitat changes) and the influence of changing abiotic conditions in the field [13,37,38]. In addition, high variability among replicates in REs makes statistical tests less powerful. However, in trying to understand the

Box 2. What happens in a removal experiment?

The removal effect (i.e. the effect on ecosystem functioning directly measured by a researcher after removing certain organisms from a natural community) is the result of at least three components.

(1) The effect of the loss of a certain organism, or how the system works when the organism is absent.

(2) The effect mediated by the response of other remaining organisms, or new organisms that colonize the system. This effect depends on which species occupies the space and/or resources released by the removed organism and on the recruiting and/or spreading ability of the colonizing organisms. For example, Symstad and Tilman [36] removed forbs, cool-season C3 graminoids and warm-season C4 graminoids from a sand prairie-old field in Minnesota, USA, and found that the removal of different functional types affected plant biomass production, nitrogen dynamics in the soil and community drought resistance. However, these effects were attributed to the differential recruiting abilities of the remaining groups rather than to the loss of certain groups. Specifically, C4 graminoids filled gaps, and therefore took up available resources, more slowly than did the other groups.

(3) The disturbance effect, or effect of the act of removal itself, including changes in resource supply or physical interference with the habitat structure for remaining organisms. For example, the disturbance caused by mechanical or chemical removal of vegetation can lead to physical, chemical or biotic alteration of the soil [13,57]. The disturbance effect tends initially to predominate over the effects of the absence of the removed organisms, particularly in later successional communities. Its importance in determining responses to removal can decrease after a few years, or its legacy can still be detected after several years or decades, depending on the ecosystem and kind of manipulation performed. This effect is greatly reduced, however, in removal experiments involving early successional communities, which might have naturally small biomass and ground cover, and high natural rates of disturbance [27]. Physical barriers built to exclude small vertebrates can act as obstacles that intercept debris and plant propagules, potentially leading to altered spatial patterns of dispersal [58]. The breakdown products of biocides applied to remove some components of the soil microbiota can alter nutrient availability to plants [59].

functional role of diversity in ecosystems, these indirect and cascading interactions, and their interplay with high spatial and temporal heterogeneity, are increasingly becoming a target of research, rather than a source of unwanted variance [11,39,40]. Because these complications and the three components of removal can also occur when species are removed or go extinct from real ecosystems, REs are particularly relevant for understanding the implications of nonrandom extinctions (Box 3), which are representative of what happens during real extinction events [41,42]. Also, REs can be directly related to management in many situations, because many land-use practices involve the selective extraction of species or whole functional types, and key conservation issues often relate to the gain or loss of particular species from natural communities [11,33].

REs in different contexts: obstacle or opportunity?

REs offer different insights and pose different challenges in different ecosystems, even within the context of terrestrial vegetation. For example, the importance of the three components of the removal effect (Box 2) varies between systems. In an old field-sand prairie manipulated by Symstad and Tilman [36] (Box 2), the dominant C4 grass is a poor recruiter, so gaps created by experimental removals of other functional types were occupied by elements previously rare in the assemblage, such as annual or short-lived perennial grasses and sedges. In other systems, such as seasonally dry forests [34], subtropical shrublands [43] and arctic tussock tundra [44], recruitment limitations seem to play a much less important role. In these circumstances, empty space left by removals tends to be occupied by species that are already dominant in the assemblage, which often expand through vegetative growth. The space released by the removal of different functional types in an ecotone between shortgrass steppe and Chihuahuan Desert ecosystems is always occupied by the same remaining functional type (annual forbs) [45], whereas in a subtropical shrubland, the space is occupied by different

Box 3. Exploring the ecosystem effects of nonrandom extinctions

The most widespread diversity–ecosystem functioning conceptual models [60] assume that all species contribute in a more or less similar way to ecosystem functioning, and that what matters is mainly the number, rather than the characteristics, of species added or lost from a system. There is mounting evidence, however, that the traits and abundance of species lost or added are crucially important. Rank-abundance curves and inequitable abundances among species in communities [61] have frequently been used as a basis for recognizing that some species are likely to have greater effects than others when lost from the ecosystem, solely on the basis of their dominance of total community biomass [19,62]. Sala *et al.* [63] have therefore proposed a framework in which greater ecosystem effects should occur when abundant, rather than rare, species are lost first; when the same amount of biomass is removed from the most abundant species versus from all species in proportion to their abundance; and when an entire functional group is lost versus the loss of the same number of species drawn from a variety of functional types. REs are highly appropriate for empirical testing of these ideas.

Although intuition suggests that the loss of the most abundant species would have a strong ecosystem effect, there are relatively few published studies that test this prediction (e.g. [27]). However, there is an indication that the loss of rare species can sometimes have significant ecosystem impacts. For example, Lyons and Schwartz [64] found that removing the least common species from a mountain meadow increased the susceptibility of the community to invasion by an exotic more so than did removing an equal amount of biomass of the most abundant species.

Removal experiments support the prediction that the loss of entire functional types has strong effects on ecosystem functioning, but they illustrate simultaneously how the nature and magnitude of these effects depends on the identity of the functional type lost. For example, plant abundance responded differently to the removal of similar amounts of grass biomass in savannah depending on whether the most palatable species were removed first or the removal was made in a completely nonselective way [65]. In a perennial grassland [27], the effects of removing functional types strongly depended on the identity of the plant functional types removed and the traits of their component species, rather than on the number of species lost.

These examples highlight the importance of species identity in determining the ecosystem consequences of local extinctions. They also suggest, however, that the consequences of a local extinction cannot always be directly predicted from the relative abundance of that species in the community.

Box 4. Recommendations and future developments for removal experiments

- Consider the three components of the removal effect (Box 2) and their relative importance in the experiment in question.
- Consider the benefits and disadvantages of standardizing the key measurements to be performed in different removal experiments (REs) (e.g. http://gcte.org/RemovalExperiments.htm). Because REs are usually long-term experiments, coordination of actions between different research groups worldwide can maximize the insight to be gained from these efforts.
- Consider questions that have received little attention (http://gcte.org/RemovalExperiments.htm) (Box 1) and information gaps concerning organisms and ecosystems.
- Secure long-term funding for REs and environmental monitoring. Changes in experimental ecosystems are the result of historical trends or regional patterns as well as of the manipulation, therefore long-term monitoring is needed to understand how environmental trends and focal organisms interact [39,46,48].
- Complement long-term removal experiments with screening for species traits, behaviour and natural history in general. One important lesson from the few decades-long experiments available [32,39,49] is that trait variation within communities is crucial for ecosystem processes, and indirect interactions among diverse taxa and trophic levels, far from being exceptions, have prevailing importance in determining ecosystem-level dynamics.

remaining functional types depending on the functional type that is removed [43].

These variations, together with the fact that the distinction of the three components of the removal effect (Box 2) is sometimes overlooked, have led to concerns over the lack of comparability between experiments in different regions and ecosystems. In our view, however, these differences actually create opportunities for comparative studies between different systems (e.g. low versus high-diversity systems, productive versus unproductive systems), with the potential of gaining insight into the main factors driving the diversity–ecosystem functioning relationship by contrasting natural situations. The usefulness of such comparisons can be maximized by the application of common conceptual frameworks and methodological protocols (Box 4) [46].

Making the most of natural, accidental and forgotten experiments

Ad hoc REs on the role of diversity in ecosystem functioning are much less common than those based on synthetic communities, although REs that were originally set up for other purposes are not uncommon in the literature, having already been mentioned in the literature at the beginning of the 19th century and being commonly used during the 1950s. They include many experiments that explored competition between pairs of species (see [13] for a review) and a few examples of the role of removal of a community component on landscape-scale biogeochemical processes (see [46] for a review). Large-scale, long-term REs have become more common since the 1980s [39], and there are also many experiments in forestry and range ecology, as well as many unintended removal 'experiments' in systems around the world (e.g. [47]). These include the application of management practices, such as selective logging or tree or shrub removal in rangelands, in which certain functional types are removed or reduced in diversity. The ecosystem consequences of these practices are often not measured, but the practices represent a rich source of information for both theoretical and practical reasons.

Prospects

REs offer a promising venue for research about the role of diversity in ecosystem processes. They are also more directly relevant than are SAEs in interpreting and ameliorating some of the impacts of land use in natural and semi-natural ecosystems. REs are most appropriate for testing: (1) the role of natural abundance differences among species; (2) the role of indirect, shifting, and/or unexpected interactions among species; (3) the ecosystem- and community-level impact of nonrandom local extinctions; and (4) the factors constraining the response of natural systems to species removals by natural or anthropogenic factors. In addition, several authors [9,47–50] have stressed the need for considering links between diversity and ecosystem functioning at different spatial scales. REs are a crucial link between the scales studied with SAEs and field observations.

SAEs and REs should complement, rather than replace each other in the quest for understanding diversity–ecosystem-functioning links and their application to management and conservation. SAEs appear most suitable for understanding the consequences of having increasingly few potential colonizer species, whereas REs are best used to investigate the ecosystem impacts of local nonrandom extinctions. As highlighted recently [40,51] there is an urgent need to translate the findings of fundamental research on diversity–ecosystem functioning into management and conservation tools. In this process, it is crucial to understand that different approaches to the diversity–ecosystem functioning relationship often give different answers because they are posing different questions. Identifying which diversity–ecosystem functioning questions should be applied to specific land management and conservation issues is one of the largest challenges ahead.

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