



LARGE-SCALE BIODIVERSITY EXPERIMENTS

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- I. Biodiversity Experiments
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-

functional group A group of species thought to have similar impacts on ecosystem functioning (functional effect groups).

GLOSSARY

biodiversity A contraction of biological diversity that encompasses all biological variation from the level of genes, through populations, species, and functional groups (and sometimes higher levels such as landscape units).

ecosystem functioning An umbrella term for the processes operating in an ecosystem.

ecosystem processes The biogeochemical flows of energy and matter within and between ecosystems, for example, primary production and nutrient cycling.

ecosystem services An ecosystem process that is beneficial for human beings, for example, the provision of foods and materials, sequestration of carbon dioxide, and stabilization of soils.

factorial design Involves all possible combinations of the levels of the crossed experimental factors (fully factorial) or an incomplete but informative combination of levels (fractional factorial).

BIODIVERSITY EXPERIMENTS are designed to identify how ecosystem functioning is affected by changes in diversity that can occur due to the decline, extinction, or invasion of species. Biodiversity experiments are a recent complement to observational studies, which examine the correlation between biodiversity and ecosystem processes across landscapes. There are two main ways to manipulate biodiversity: through the removal of species or by the assembly of experimental ecosystems of varying diversities. The richness of diversity in most ecosystems, and the wide range of ecosystem services that they provide have meant that a key feature of biodiversity experiments is their large scale.

I. BIODIVERSITY EXPERIMENTS

Biodiversity experiments aim to identify the consequences of changes in diversity for ecosystem functioning and services (as opposed to looking at the covariation of these two factors in comparative

analyses of observational datasets). In the early 1990s, ecologists began formulating a set of hypothetical relationships between biodiversity and ecosystem functioning. These hypotheses ranged from those that implied a strong relationship in which the species are complementary and all play an important role, to those that include differing degrees of functional redundancy (species that overlap in functional role) to a null hypothesis of no link. In the early 1990s, these hypotheses were untested and the relationship between biodiversity and ecosystem functioning unknown. The subsequent years have seen a succession of experiments designed to test the effect of biodiversity on ecosystem functioning (Hooper *et al.*, 2005; Kinzig *et al.*, 2002; Loreau *et al.*, 2001, 2002). These experiments have revealed significant effects of biodiversity on ecosystem processes likely to affect the delivery of ecosystem services to human societies.

There are two main ways to manipulate biodiversity. One is by the assembly of synthesized model communities, either in laboratory cultures or in the field using artificial ponds or streams, forest plantations, plots in grasslands and similar experimental systems. An alternative approach is to remove species from natural communities, through weeding and herbiciding of plant species for example (Wardle *et al.*, 1999; Wardle and Zackrisson, 2005). Both approaches have strengths and weaknesses but both approaches attempt to hold other factors as constant as possible while manipulating the diversity of the experimental systems. A third nonmanipulative approach is to infer the relationship between biodiversity and ecosystem functioning by seeing how they are correlated across habitats.

Removal experiments are more familiar as they have a history of use in community ecology to examine interactions between species (principally competition). They are more realistic than assembly experiments in that they are based in real ecosystems. However, increased realism comes at the price of a loss of control through potential unknown confounding factors. The approach also has its own potential limitations through the disturbance involved in species removal and other effects like fertilization through the decay of roots left behind after species removal.

The design and analysis of biodiversity experiments is not straightforward (Schmid *et al.*, 2002). One problem is the substantial levels of diversity present in most systems, which means that the number of possible experimental combinations soon exceeds what is logistically possible and fully factorial designs are only feasible when dealing with very small numbers of species. One way around this is to combine species

into a small number of functional groups—species that are expected to have similar effects on ecosystem functioning. However, functional diversity may not fall into discrete groups and objectively identifying these groups is also not straightforward, leading to the development of approaches for looking at continuous measures of functional diversity (Petchey and Gaston, 2006). A second problem is that different aspects of diversity, such as numbers of species and functional groups, are often confounded. The combination of confounded explanatory variables and nonorthogonal designs has made it hard to definitively identify the importance of different aspects of diversity and the mechanisms by which they affect ecosystem functioning.

A further issue for community assembly experiments is how communities should be put together since the diversity gradient formed by the synthesized communities effectively simulates the assumed order of species loss. One approach is to assemble a full community and depauperate versions that simulate a single order of species loss. An alternative approach that provides a more general result is to replicate multiple communities of a given diversity by random selection of species from the pool available. However, species are not usually lost from ecosystems in random order (although random loss may approximate some real-world cases). Instead, when a given extinction scenario can be predicted, communities can be assembled to simulate it. Alternatively, a fully factorial approach simulates all possible combinations of species but is limited by logistics to small numbers of species (or more often functional groups). Community assembly experiments should give a high level of experimental control but with the usual trade-off with realism. For example, establishment of the assembled communities usually involves removing any existing vegetation and surviving propagules and the disturbance that involves, e.g., soil fumigation. Homogenization of the underlying substrate should reduce the experimental noise, but may also remove environmental heterogeneity that affects the relationship between diversity and functioning.

To date, no one had conducted the same biodiversity manipulation in a given system using both species removal and the assembly of experimental communities and compared the results of the two alternative approaches. Similar results would provide strong support for general effects regardless of experimental methodology. Differences in results could be due to artifacts of the methodology but could also reflect important biological processes. For example, in removal

experiments species compensation depends in part on natural levels of colonization of the newly free space, whereas community assembly experiments usually introduce equal numbers of propagules of all species as part of the method.

Ecological experiments can be large scale in different ways as this article illustrates specifically for biodiversity manipulations. Natural experiments may use only a single experimental unit but of a very large size: whole lakes or forest catchments for example. Alternatively, experiments may use a level of replication which is not especially large (a sample size of 30 for example) but where individual experimental units are of a size large for the study system (e.g., fields-scale trials with genetically modified crop species). Other large-scale projects use experimental units of conventional size but in complex and highly replicated designs. Multisite studies can be large if they combine experiments from several locations into a single coordinated project. Long-term studies are relatively unusual but can be of great value, and are large scale in a temporal context.

A. Mechanisms

Ecological theory identifies two classes of underlying mechanism that can generate impacts on ecosystem processes when diversity changes. Species influence ecosystem processes partly through their intrinsic properties. Whether a species with relatively extreme traits is present or absent from a system is one simple mechanism for impacts of biodiversity change. When species overlap in their ecological traits they are said to be redundant. When redundant species can compensate for the loss of similar species within the same group there will be little if any change in functioning. The redundancy can nevertheless be seen to have value as an ecological insurance. Conversely, when species occupy clearly distinct and complementary niches it will be impossible for full compensation to occur. The degree of niche overlap should control the shape of the relationship between increasing diversity and ecosystem processes; low niche overlap will produce linear patterns while high overlap will lead to saturating curves as the addition of new species increases redundancy.

The interpretation of biodiversity experiments is complicated by these alternative classes of mechanism. Selection effects (Loreau and Hector, 2001) occur when communities become dominated by particular species and if dominant species occur more frequently in high-diversity communities then the traits of these species may drive ecosystem functioning. Alternatively,

complementary or positive interactions may allow diverse systems to utilize more resources or to suffer lower levels of pests and diseases. An additive partitioning method (Loreau and Hector, 2001) was developed as part of the BIODEPTH project (see below) to distinguish between these alternative mechanisms. The additive partitioning method (Loreau and Hector, 2001) defines a net effect of biodiversity which is the difference between the observed yield of a mixture and that of the average monoculture yield. This net effect is then partitioned into two additive components: the selection and complementarity effects. The selection effect is the standard statistical measure of covariance applied to the relationship between yield in monoculture and the change in relative yield in mixture. Selection effects will be positive when species with higher-than-average yield dominate communities and negative when species with lower-than-average yield dominate. The complementarity effect uses relative yields to ask whether increases in the abundance of some species exactly cancel with declines in others. When this is the case, resource partitioning is a zero-sum game with some species taking more of a fixed total pool of resources and others taking less. Positive complementarity effects occur when decreases in the abundances of some species do not compensate for the increases in the abundance of other species, which could result from facilitation, resource partitioning, or decreased impact of natural enemies in more diverse communities. The additive partitioning method has revealed widespread complementarity contributing to most published results. However, unanticipated negative selection effects have also emerged as a widespread result. One consequence is that complementarity effects are often masked by the negative selection.

II. COMMUNITY ASSEMBLY

A. Historical Precedents

The intellectual linkage of biodiversity with ecosystem functioning can be traced back to the *Origin of Species* where Darwin describes what is arguably one of the first ecological experiments: a large-scale experimental garden comparing the properties of plant monocultures and mixtures (Hector and Hooper, 2002). Interestingly, the results prefigure those of recent experiments in associating higher levels of diversity with higher levels of biomass production (Fig. 1). However, this early work inevitably lacks features of modern experimental design such as replication (in this experiment diversity

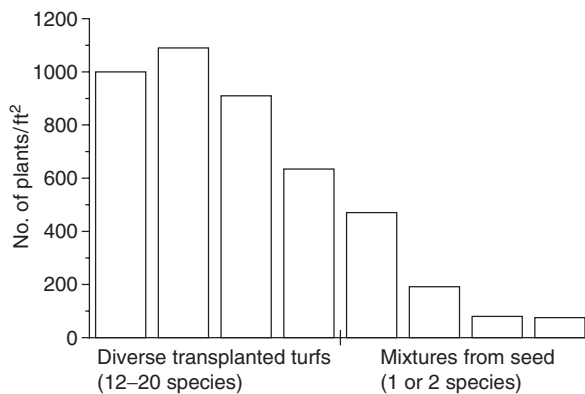


FIGURE 1 Recently rediscovered data dating to the early nineteenth century which was collected from a large-scale experimental garden at Woburn Abbey, UK has many similarities to modern biodiversity experiments and is arguably some of the earliest experimental work conducted in ecology. Graph by A. Hector.

was confounded with the origin of the experimental communities; that is whether they were transplanted natural turfs or established from seed).

B. The Ecotron Large-Scale Controlled Environment Facility

The first modern biodiversity experiment was carried out with model communities based on annual plant species grown in the Ecotron large-scale controlled environment facility (Naeem *et al.*, 1994). Most first-generation biodiversity experiments concentrated on a single trophic level. The Ecotron experiment was unusual in taking a single intact community and simultaneously reducing diversity at four trophic levels to produce two increasingly depauperate versions from which species had been omitted at random. The key result of this experiment was that the impoverished communities were progressively less productive. However, because all replicates at each diversity level were identical in composition, the effects of numbers and types of species were confounded and the results may be specific to the particular order of species extinction examined in this experiment and not general across a wider range of possible extinction scenarios.

C. Large-Scale Field Experiments

The first large-scale biodiversity experiments performed under field conditions were a series of studies by Tilman and colleagues working at Cedar Creek, Minnesota prairie grassland. A pair of biodiversity experiments concentrated on species (Tilman *et al.*,

1996) and functional group effects (Tilman *et al.*, 1997, 2001, 2006), respectively while the Biocon experiment (Reich *et al.*, 2001, 2004) looks at the interactions between biodiversity loss and elevated CO₂ and nitrogen. In contrast to the Ecotron experiment, more extensive diversity gradients were established where each level of diversity (a given number of species) was replicated with different mixtures of species selected at random from the species pool. Biodiversity effects could then be quantified with linear regression and tested against the residual differences between different composition communities within diversity levels. Productivity was positively related to numbers of species and functional groups in the communities with relationships growing stronger over several years. Levels of unconsumed soil nitrate and (potentially leachable) nitrate below the rooting zone were both reduced at higher diversity levels. Detecting how many species contribute to biodiversity relationships has proved one of the most contentious issues in interpreting biodiversity experiments. Tilman *et al.* (2001) used a diversity index approach to see how many of the most productive species in a plot had to be present to best explain their aboveground and total biomass production. For these two ecosystem processes between one quarter and three quarters, respectively, of the species in the high-diversity treatment were needed to best explain the productivity of a plot. Additional analyses of species-specific contributions suggest that much of the biodiversity effects can be explained by legumes and C₄ grasses but with additional species coexisting alongside them and contributing to total productivity (Lambers *et al.*, 2004). In contrast, in the Biocon experiment, which examined a biodiversity gradient under different conditions of elevated CO₂ and N enrichment, species and functional group richness had largely independent effects across the whole range of conditions such that species within groups were not functionally redundant but made separate contributions (Reich *et al.*, 2004).

A decade of monitoring of the Cedar Creek species and functional group diversity experiment confirmed the insurance hypothesis which predicts that biodiversity promotes greater temporal stability of ecosystem functioning (Fig. 2). The highest diversity plots had a temporal stability measure (mean/standard deviation for a given time period) for biomass production that was 70% greater than the average of the monocultures. Greater temporal stability was generated by the portfolio effect (statistical averaging of asynchronous population fluctuations) andoveryielding (where the yield of a mixture exceeds the weighted average of the

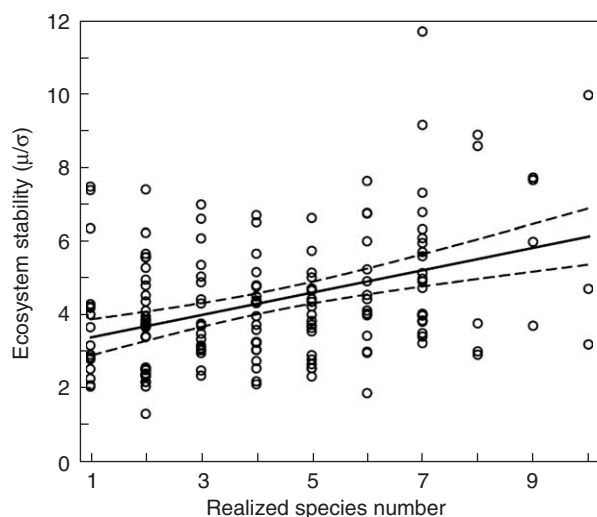


FIGURE 2 Greater temporal stability of biomass production in higher diversity communities from the first decade of the Cedar Creek prairie grassland experiment. Reproduced from [Tilman *et al.* \(2006\)](#), with permission from Nature Publishing Group.

constituent monocultures). Temporal stability at the ecosystem level was positively correlated with high root biomass but, interestingly, negatively correlated with the presence of legumes (even though they promoteoveryielding in this system).

The Jena Biodiversity Experiment ([Roscher *et al.*, 2004](#)) simultaneously manipulates numbers of both species and functional groups in a randomized design but in a more balanced way than earlier experiments and in small (3.5 × 3.5 m) and large (20 × 20 m) plots ([Fig. 3](#)). The project also contains a dominance experiment comprising plots composed only from a reduced pool of nine species predicted to be dominant (high relative abundance) in the full community.

Initial results from the Jena main experiment show that relationships from small plots can be scaled up to the large plots: results from the small and large plots were statistically indistinguishable. Productivity was positively linearly related to the log of the number of plant species. The slope of the relationship between diversity and productivity in the dominance experiment was statistically parallel to that from the fully randomized experiment but with a higher elevation ([Fig. 4](#)). This results presumably because the average biomass production per species in the dominance experiment is higher than in the main experiment where species were chosen at random from the species pool which contains many species with low maximum aboveground biomass. Comprehensive results on the role of plant functional groups are yet to be published at the time of writing (summer 2006).



FIGURE 3 The Jena Biodiversity Experiment manipulates numbers of species and functional groups in small (3.5 × 3.5 m) and large (20 × 20 m) plots. Photo by A. Klein.

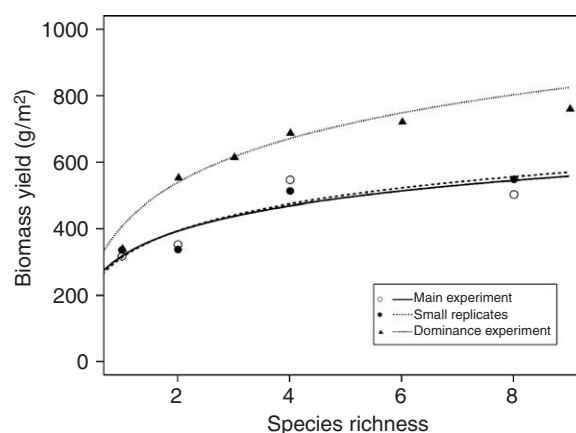


FIGURE 4 The relationship between diversity and biomass production in the second year of the Jena Biodiversity Experiment. Results from the small and large plots are statistically indistinguishable and the relationship in the dominance experiment has the same slope but with a higher elevation. Graph by J. Schumacher.

D. Multisite Biodiversity Experiments

The European BIODEPTH project ([Hector *et al.*, 1999](#); [Spehn *et al.*, 2005](#)) added two new features to the single-site experiments described above. First, in addition to replicating diversity levels with different species compositions, each composition was itself replicated which allowed the effects of both diversity and composition to be quantified. Second, the same biodiversity experiment was replicated at eight different grassland sites using standardized methodologies. Individual site analyses illustrate the broader range of responses seen in the literature—from null to positive—and the combined multisite analysis revealed an overall log-linear (asymptotic with increasing

diversity) relationship that was statistically common to all sites. Reconciling the results of the individual site analyses with the general outcome of the overall analysis has been a point of both confusion and contention. The results of the BIODEPTH project also revealed that productivity could be well explained in terms of the multiple influences of location ($\sim 30\%$ of the total sums of squares), the diversity of both species and functional groups ($\sim 20\%$), and composition ($\sim 40\%$). Later results revealed that the effects of biodiversity were not limited only to aboveground biomass production but extended to a wider suite of ecosystem processes and properties including root biomass, levels of intercepted light, nitrogen pools in aboveground vegetation, and available soil nitrogen as well as the decomposition of various substrates. However, the relationship of some of these variables to biodiversity was often more complex and less clear than that of aboveground biomass production (Spehn *et al.*, 2005).

Other multisite experiments have been performed in terrestrial systems (e.g., Van der Putten *et al.*, 2000) but relatively few in aquatic and marine systems. A notable exception is the study by Emmerson *et al.* (2001) who examined the relationship between biodiversity and ecosystem functioning at multiple sites in the United Kingdom, Sweden, and South Australia. They looked at the relationship between the diversity of marine benthic faunal communities (ranging between 1–4 dominant species and 1–3 functional groups) and the production of nitrogen in ammonia form ($\text{NH}_4\text{-N}$) as an indicator of ecosystem functioning. Nitrogen production increased with community total biomass but for a given biomass production varied depending on the make up of the community. However, alongside this variation there were positive trends for greater predictability in ecosystem functioning at higher levels of diversity and a greater degree of complementarity between species in more diverse mixtures. In light of this combination of species identity and species number effects Emmerson *et al.* characterized the relationship between biodiversity and ecosystem functioning in these marine systems as positive but idiosyncratic.

E. Highly Replicated Laboratory Experiments with Microbial Microcosms

In response to the complexities in the analysis and interpretation of biodiversity experiments, Bell *et al.* (2005) used a highly replicated laboratory experiment

with a novel design to test whether the relationship between biodiversity and ecosystem functioning found for terrestrial plant communities extended to microbial microcosms. They took a pool of 72 laboratory culturable bacterial species isolated from the communities that develop in tree holes (the pools of water that collect between the exposed roots of trees at the base of their trunks). They took all the factors of 72 as their diversity levels (1, 2, 3, 4, 6, 8, 9, 12, 18, 24, 36, and 72) and replicated each level by drawing species from the pool without replacement. Five independent diversity gradients were formed in this way to give five alternative partitions of the species pool. Finally, each particular partition was repeated twice to provide compositional replication (a feature first introduced by the BIODEPTH experiment; see below). In total, the experiment required 1374 microbial microcosms. This novel approach resulted in an analysis where the log-linear effect of species richness (numbers of species on a log-scale) was orthogonal to the effect of species composition (the collective effects of 72 variables coding for the presence or absence of each species in each microcosm). The main result was a log-linear relationship between diversity and community respiration (Fig. 5), which was similar to the relationship between diversity and biomass production in experiments with plants. The independence of the log-linear diversity effect from the composition effect, combined with only a small number of strong individual species effects suggests that the result was not produced by dominance of the microbial communities by species with high respiration rates but more likely resulted from complementary or facilitatory relationships or a combination of the two.

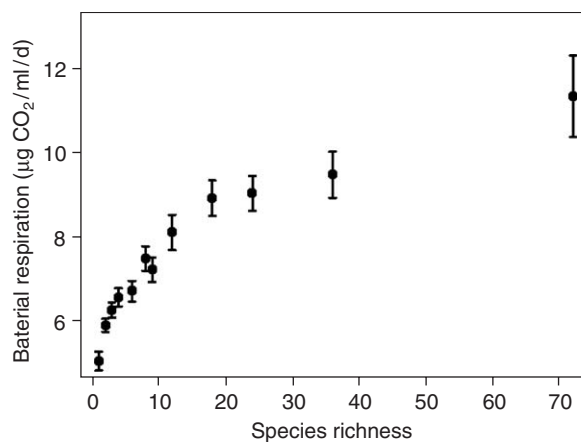


FIGURE 5 The linear relationship between the diversity of laboratory microbial microcosms and respiration rate (mean ± 1 S.E.M.). Graph by T. Bell and J. Newman.

III. SPECIES REMOVAL

Wardle and Zackrisson (2005) used a series of islands in a Swedish lake as a study system to examine influences on ecosystem functioning. The island system allowed them to look at patterns when comparing across the habitats (islands) as well as to perform removal experiments within individual systems. These islands show varying diversities and ecosystem process rates due to their size and likelihood of disturbance. Large islands are more prone to fires caused by lightning strike and therefore experience higher levels of disturbance and have lower diversity (species richness is the same on all islands but diversity varies once differences in relative abundance, or “evenness,” is taken into account). Note that this relationship is contrary to the predictions of classical island biogeographic theory, which ignores many processes like disturbance. Productivity is greatest on the large, more frequently disturbed islands, and therefore negatively related to diversity (Fig. 6a). The smaller, low-productivity islands tend to be dominated by “stress-tolerant” species (sensu Grime, 2001) and have lower levels of decomposition and related processes as well as lower productivity. Wardle and Zackrisson (2005) supplemented the across-island comparison by performing manipulative experiments to remove species and functional groups from a subset of the islands of differing sizes. Despite the negative correlation between diversity and process rates across islands, the removal experiments showed significant impacts of the removal of three species of shrub on productivity (Fig. 6b). Two of the species showed larger removal effects on islands where they were more abundant. This study demonstrates scale-dependence of the relationship between diversity and functioning and how manipulative experiments can reveal diversity effects within systems (positive in this case) which can differ from the larger-scale across-site correlation (which was negative in this study).

In an earlier removal experiment that manipulated the functional group composition of vegetation gaps in a New Zealand pasture grassland, Wardle *et al.* (1999) found some impacts on both above- and belowground processes. However, whether an effect was found and how strong it was depended on the traits of the species that were experimentally excluded. Similarly, in the same Cedar Creek prairie that hosted the community assembly experiments reported above, removal of plant functional groups also negatively affected above- and belowground biomass, soil nitrogen, and drought resistance but where the effects related to which group

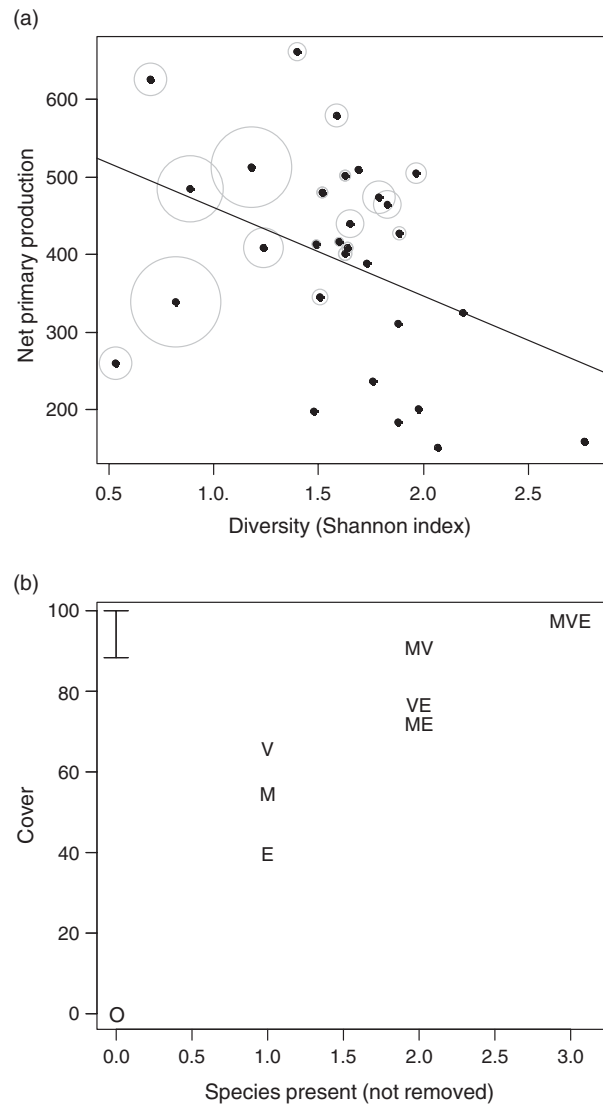


FIGURE 6 (a) Negative relationship between diversity and productivity across islands of differing sizes (island size is proportional to the size of the gray circles around each symbol). Data provided by D. Wardle. (b) Positive relationship between diversity and productivity (% cover) within islands demonstrated by the experimental removal of combinations of *Vaccinium myrtillus* (M), *V. vitis-idaea* (V), or *Empetrum hermaphroditum* (E) or all vegetation (O). After Wardle and Zackrisson (2005).

was removed and to the response of the remaining functional groups (Symstad and Tilman, 2001). Removal of plant functional groups often also facilitated invasion by other species (Symstad, 2000). Many of the results of this and other removal experiments are related to recruitment limitation, a process that is not as evident in community assembly experiments owing to the seed addition used to establish communities.

IV. UTILIZING BIODIVERSITY IN APPLIED SETTINGS

The large-scale biodiversity experiments described above all come from pure ecology and aim to identify generalities in the relationship between biodiversity and ecosystem functioning in various types of ecosystem. However, in the real world, biodiversity is lost due to specific processes (eutrophication, fragmentation, and overharvesting) and in some cases pure studies may not give general predictions which apply to particular real-world cases. A small number of applied experiments have been established to see whether biodiversity can be used in the management of habitats in a way which is beneficial to the provision of ecosystem services to humans.

A. Grassland Restoration

Bullock *et al.* (2001) performed a biodiversity experiment on the restoration of hay meadows at seven locations across southern Britain. At each site, plots were sown with “low-diversity” treatments (6–17 species depending on the site) which consisted of the seed mixtures recommended by the (then) UK Ministry for Agriculture Fisheries and Food (MAFF) for the recreation of moderately diverse grassland on land taken out of agricultural production. The recommended seed mixtures were all composed of species from the relevant regional species pool, which were also appropriate for the type of local environment to be restored. The “high-diversity” treatments (25–41 species) were supplemented with species found in diverse hay meadows typical of the region, soils, and hydrology of each site. The high-diversity mixtures therefore contained species appropriate for each site but which had been omitted from the recommended mixture and which were therefore presumably thought to be redundant for restoration purposes. The key result was a linear relationship between hay yield and the number of additional species added to the high-diversity treatments which was consistent across all sites and present for three years after the initial establishment season (Fig. 7). The selection of a wider diversity of species increased yield by up to 60%. For all the seven sites, the seed mixtures thought to be sufficient for restoration aims led to levels of hay production which were far below those achievable at the same site by more diverse mixtures that contained a wider selection of appropriate species. The increase in yield seemed not to be due to sampling or selection

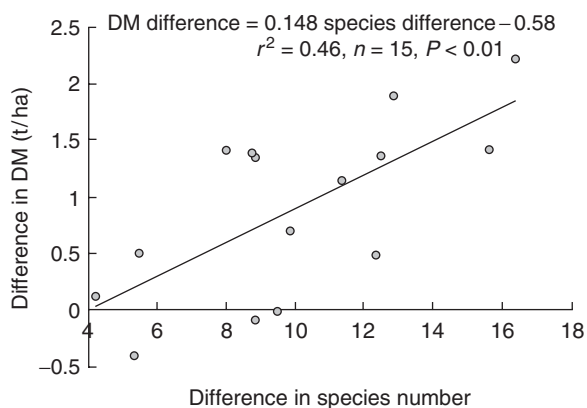


FIGURE 7 Increases in hay production through the augmentation of agriculturally recommended seed mixtures with additional species. Reproduced from Bullock *et al.* (2001), with permission from Blackwell Publishing.

effects for one or a few dominant species although rigorous testing of the underlying mechanisms was not possible without monocultures of all species involved.

B. Tree Diversity Experiments

Forest ecosystems, particularly in the tropics, are important both for the conservation of biodiversity and the provision of important ecosystem services but little is known about the relationship between forest biodiversity and ecosystem functioning. Forest ecosystems around the globe that have previously been clear felled or selectively logged are being replanted providing an opportunity to test the importance of restoring levels of biodiversity for the functioning of the rehabilitated ecosystems. There is now an informal network of forest biodiversity experiments that currently ranges from the neotropics (Panama) through Europe (Finland, Germany) to the paleotropics (Malaysian Borneo) as described by Scherer-Lorenzen *et al.* (2005). These experiments signal a new direction in research on biodiversity and ecosystem functioning which moves beyond general tests to large-scale trials in threatened ecosystems that are known to provide important ecosystem services to mankind.

See Also the Following Articles

BIODIVERSITY, DEFINITION OF • BIODIVERSITY GENERATION, OVERVIEW • BIODIVERSITY, ORIGIN OF • COMPLEMENTARITY • FUNCTIONAL DIVERSITY • FUNCTIONAL GROUPS

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