

Biodiversity and Ecosystem Functioning

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Synthesis and Perspectives

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Preface

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

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

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

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

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

Michel Loreau, Shahid Naeem and Pablo Inchausti
14 January 2002

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PART IV

Extending the scope to other systems

Contributions of aquatic model systems to our understanding of biodiversity and ecosystem functioning

O. L. Petchey, P. J. Morin, F. D. Hulot, M. Loreau, J. McGrady-Steed, and S. Naeem

11.1 Introduction

Biodiversity has been shown to affect ecosystem functioning in an assortment of ecosystems (McGrady-Steed *et al.* 1997; Naeem and Li 1997; van der Heijden *et al.* 1998b; Hector *et al.* 1999; Petchey *et al.* 1999; Hulot *et al.* 2000; Naeem *et al.* 2000a; Norberg 2000; Emmerson *et al.* 2001; Ruesink and Srivastava 2001). These studies continue to guide the development of theories that relate diversity to the magnitude and stability of ecosystem functioning (Loreau 2000a). In a simple world, the existence of comparable findings from a wide range of systems would suggest a general relationship between biodiversity and ecosystem functioning. However, reviews show that effects of diversity vary widely among systems (Schlöpfer and Schmid 1999; Schwartz *et al.* 2000; Loreau *et al.* 2001). For example, increasing plant diversity increases grassland primary productivity across Europe (Hector *et al.* 1999), while the diversity of soil microbes has affected functioning in some experiments (van der Heijden *et al.* 1998b) but not in others (Mikola and Setälä 1998a).

Key differences between experiments include the kinds of ecosystems considered, the levels of biological complexity (numbers and types of interactions among species), degree of experimenter control over environmental conditions, and the

different kinds of manipulations (direct or indirect, random or non-random) of biodiversity used. Here we show that differences in (1) duration, (2) trophic complexity, and (3) links with theory separate experiments with aquatic model systems from biodiversity–ecosystem functioning experiments in many terrestrial model systems (e.g. growth chamber, pot, greenhouse, and plot experiments). To make general points we primarily use examples of our own research because of our familiarity with it.

11.2 What are aquatic micro and mesocosms?

Microcosms and mesocosms are spatially delimited artificially constructed model ecosystems. They have enjoyed a long history of use in ecology (Byers and Odum 1993). These aquatic systems, which range in scale from bottles and beakers to tanks and artificial ponds (Lawler 1998; Morin 1998), are less complex than natural systems, a situation that poses special advantages and interpretive challenges (Peterson and Hastings 2001). Such systems may contain fewer species and trophic levels than their most complex natural counterparts, but nonetheless preserve key features of interest. That simplicity, combined with opportunities for replication and experimental manipulation, provides an important

rationale for their use. Distinctions between microcosms and mesocosms are necessarily relative and somewhat arbitrary (Lawler 1998). Although the smallest microcosms are easily housed in laboratories and mesocosms are often placed in the field, larger size and greater biological and spatial complexity distinguish mesocosms from microcosms. The greater complexity of mesocosms can include greater environmental variability as well as greater total diversity when, for example, plankton communities are samples of natural communities (Hulot *et al.* 2000). The varying complexity of micro and mesocosm experiments, with mesocosms often reflecting natural systems more closely than microcosms do, is analogous to the range of realism present in theoretical models.

For many ecological issues, aquatic microcosms are ideal experimental systems. Initial composition can be controlled, processes can be manipulated, and many replicates can be readily constructed. Microcosms complement field and observational studies of natural systems. Skeptics, however, view them as unsatisfactory simplifications of the full biological and physical complexities of nature (Carpenter 1996). We note a continuum between microcosm and field studies in which the former represent controlled examinations of theory and mechanism while the latter represent closer approximations to natural systems (Lawton 1995). Observational studies of natural systems remain crucial for formulating hypotheses, but observations and correlations alone cannot unambiguously sort causes from effects (Manly 1992; Naeem 2001). That is where experiments play an essential role.

Aquatic microcosm studies differ from other studies in several respects. Here, we focus on three of their most important differences (duration, trophic complexity, links to theory). These attributes of aquatic microcosm studies offer a unique insight into the functional role of biodiversity that might not be obtained from terrestrial experiments using communities that are dominated by long-lived organisms. Obviously, ecologists need to use the full range of systems and approaches at their disposal to understand how ecosystems work (Lawton 2000). Progress in ecology is made by integrating results from theoretical, microcosm, field, and observational studies.

11.3 Duration

Although aquatic microcosm studies have a shorter absolute duration (weeks/months) than many studies conducted in the field (years), they typically last for tens to hundreds of generations of the organisms involved. This means that populations can grow (or decline) to levels determined by resources and interactions with other species (Fig. 11.1). The average number of generations that elapse during an experiment provides a dimensionless scaling factor that can be used to evaluate whether patterns represent transient or long-term dynamics (Peterson and Hastings 2001).

A survey of 35 recent biodiversity–ecosystem functioning experiments (similar to the survey in Ives *et al.* (1996) and found by searching the literature manually) illustrates the contrast in duration, measured in number of generations of the manipulated organisms, between experiments in artificial terrestrial and aquatic ecosystems. The duration of each study was scored as less than five generations (21 studies), between five and twenty generations (nine studies), or more than twenty generations (five studies) of the manipulated organisms. These broad categories make differences between generation times of different organisms within a single experiment less influential, although the range of generation times within a single study may, in itself, be important. Where the generation times of organisms within an experiment differed greatly we used the longest generation time. The majority of terrestrial experiments lasted less than five generations, whereas the aquatic experiments most commonly lasted more than 20 generations (Fig. 11.2(a)). Indeed, with generation times often as short as 3–12 h (e.g. for ciliates in aquatic microcosms), a six week long experimental study of aquatic microbes provides the population dynamic equivalent of a study of annual plants running for 84–336 years!

These very different durations make integrating results across experiments problematic. Results of longer-term experiments reflect population dynamics, including differential population growth (Hulot *et al.* 2000), density compensation (McGrady-Steed and Morin 2000), and complex interactions within the food web (Naeem and

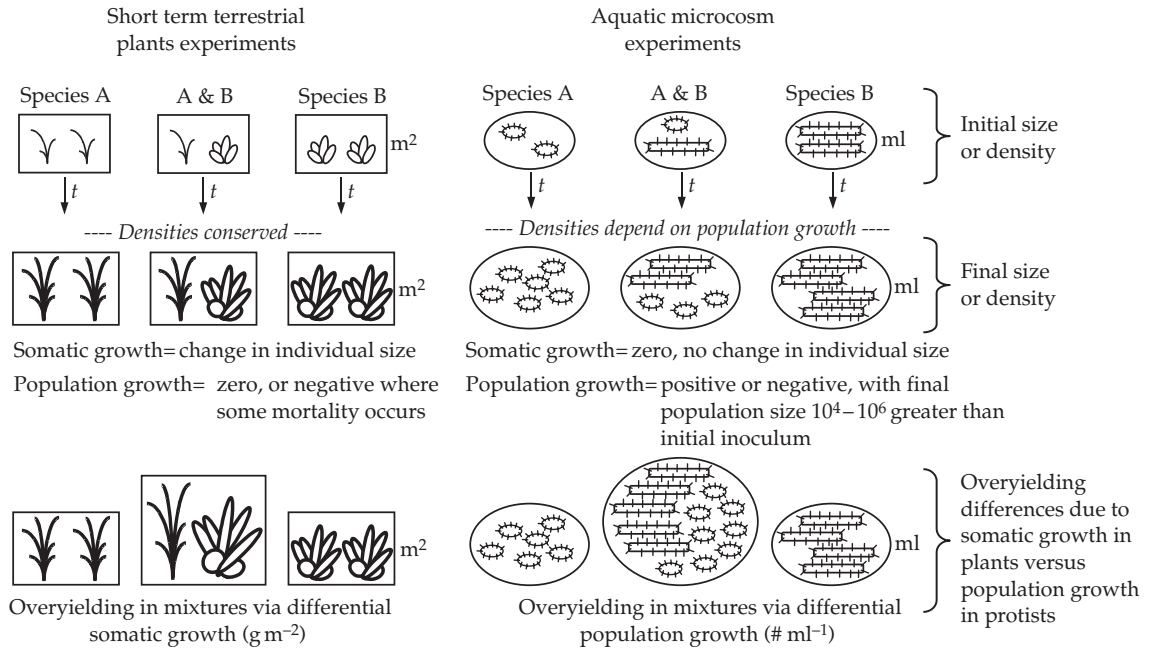


Figure 11.1 Differences between terrestrial plant experiments and aquatic microbe experiments involve the extent to which initial planting/seeding densities or population growth determine results. Planting densities matter in terrestrial plant experiments because results are dominated by changes in the size of individuals. Population growth determines results and initial densities matter less in the longer-term aquatic microbe experiments. Recent experiments in terrestrial plant communities (e.g. Hector *et al.* 1999; Tilman *et al.* 2001) may not fit neatly into this dichotomy as they include several generations and some population growth.

Li 1997; Petchey *et al.* 1999; Naeem *et al.* 2000a). Results in shorter terrestrial experiments that run for one to several generations may be coloured by transient effects of initial species composition and organism densities. (Note that aquatic mesocosm (i.e. large microcosm) experiments often contain longer-lived organisms without concurrent increases in absolute duration. Therefore, micro and mesocosms may also be separated along a continuum of generational duration).

11.3.1 Design issues in long-term experiments

Different durations of experiments pose challenges for optimal experimental design, in particular regarding the choice of initial conditions. Diversity manipulations use either a substitutive or additive design to determine initial density/abundance (Harper 1977; Naeem *et al.* 1994a; Hooper and Vitousek 1997; Symstad *et al.* 1998; Jolliffe 2000; Levine 2000a). Implicit in both designs is the

assumption that the density of organisms set at the beginning of the experiment will influence the results, as happens in most experiments with vascular plants. Initial density is less relevant to microcosm experiments, where densities are low to start (e.g. tens of individual ciliates per 100 ml), but over the many generations of a microcosm experiment, can increase by several orders of magnitude, remain unchanged, or go extinct. Densities and population dynamics are not constrained by the initial densities of species added to the systems, except for the obvious situation where species initially absent remain so (unless contamination or deliberate invasion comes into play, e.g. McGrady-Steed *et al.* (1997)). Population densities therefore reflect the consequences of many generations of interactions within and between species, resource levels, and nutrient cycling.

These differences in sensitivity to initial densities between field experiments and aquatic microcosms reflect differences in the number of generations

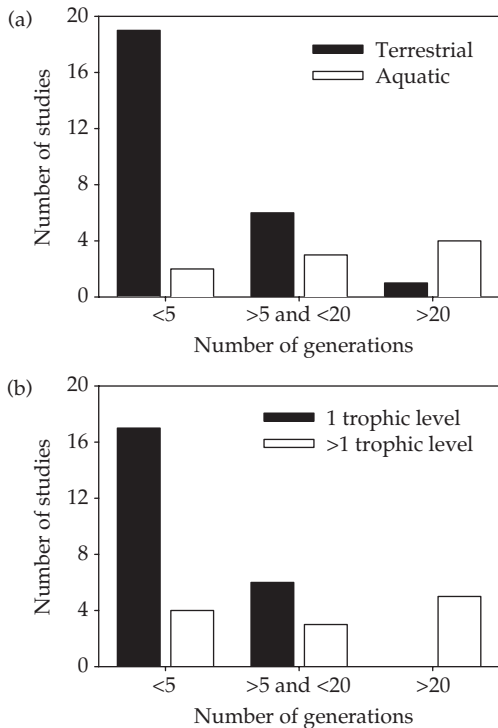


Figure 11.2 The distribution of biodiversity–ecosystem functioning experiments by their duration, (a) the type of ecosystem, and (b) the number of trophic levels that were manipulated. The survey was limited to direct and indirect experimental manipulations of diversity and excluded observational studies of relations between biodiversity and ecosystem functioning because it is difficult to define their duration. Using broad categories of experimental durations, less than five generations, between five and 20 generations, or more than 20 generations, made the results less sensitive to imperfect knowledge of the generation times of organisms.

these experiments typically cover rather than fundamental ecological differences (but see Hairston 1989). The duration of an experiment in generations is important because it measures the effective temporal scale of experiments, and changing temporal scales (as well as spatial scales) can change the dominant ecological processes and patterns (Levin 1992; Levin and Pacala 1997; Peterson and Hastings 2001). For example, relations between biodiversity–ecosystem functioning in microcosm experiments can be caused by changes in population size that result from intra- and inter-specific competition, predation, indirect interactions, and extinctions. A different set of processes and properties

determine relations between biodiversity–ecosystem functioning in very short-term experiments (e.g. initial densities of each species, growth of individuals, and short-term competition and survival).

11.3.2 Long-term ecosystem dynamics

The long-term dynamics of ecosystem functioning are arguably more important than the magnitude of ecosystem functioning at any particular time (Loreau 2000a; Cottingham *et al.* 2001) (Loreau *et al.*, Chapter 7). Theory predicts lower long-term variability of ecosystem functioning in more diverse communities, in part because more diverse communities contain species that can either respond to or tolerate a greater range of environmental variation (Ives *et al.* 1999). Testing these theories (McNaughton 1977; Tilman *et al.* 1997b; Yachi and Loreau 1999; Hughes and Roughgarden 2000; Ives *et al.* 2000) therefore requires long-term experiments, for which microcosms are ideal (e.g. McGrady-Steed *et al.* 1997; Naeem and Li 1997).

Studies of microcosms show that ecosystem-level predictability increases with increasing diversity. Here, predictability measures both temporal variation and between-replicate (spatial) variation in ecosystem processes (temporal variation is equivalent to the ‘variability’ defined in Loreau *et al.*, Chapter 7). Total autotroph biomass (Naeem and Li 1997) and carbon dioxide flux (McGrady-Steed *et al.* 1997) have been found to be more predictable in more diverse communities. These experiments used microbial communities containing algae, bacteria, protists, and (in the case of McGrady-Steed *et al.* 1997) micro-metazoans, and communities differed in species richness within and across functional groups.

Both approaches indicated that ecosystem functioning was more predictable in more diverse communities (Fig. 11.3(a)). Subsequent analysis showed that the temporal variability of biomass within functional groups usually decreased with diversity, while the temporal variability of individual population sizes was unrelated to diversity (McGrady-Steed and Morin 2000). These results mirror patterns seen in terrestrial systems, where temporal variability in total plant biomass

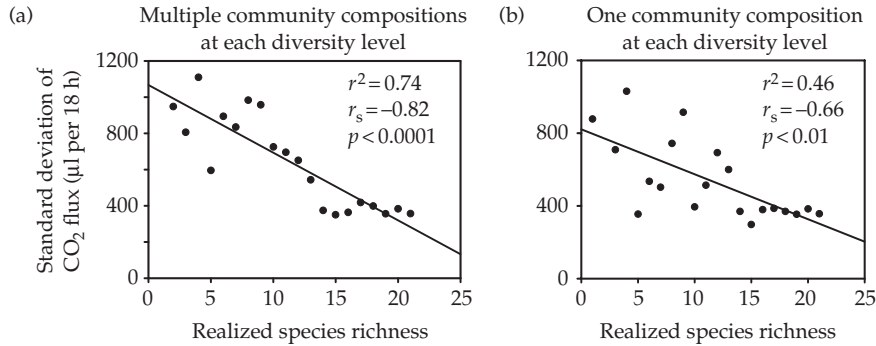


Figure 11.3 Effects of species richness on predictability of the magnitude of an ecosystem-level process. (a) Each data point represents a mean calculated across time, replicates, and different communities at each diversity level. Here, greater compositional similarity at high diversity levels compared to low diversity levels could contribute to the negative relation, in addition to mechanisms that act through time. (b) Each data point represents a mean calculated across only time and replicates of the same community composition. Here, differences in compositional similarity across the diversity gradient cannot influence the negative relation. Only mechanisms that act through time or across replicates of the same community composition can cause the negative relation.

decreased as diversity increased, while temporal variability in the biomass of individual species increased as diversity increased (Tilman 1996). This supports the idea that diversity affects stability (of which variability is a measure; Loreau *et al.* Chapter 7) differently at different levels of ecological organization (McNaughton 1977; King and Pimm 1983; Tilman 1999a). In addition, these results also support the idea that high biodiversity insures against future environmental changes (Frost *et al.* 1995; Walker 1995; Ives *et al.* 1999; Walker *et al.* 1999; Yachi and Loreau 1999) (Loreau *et al.* Chapter 7).

Many uncertainties remain about the links between population and ecosystem-level dynamics. Theory shows that a suite of statistical effects and deterministic mechanisms either create or modify the links between population and ecosystem level dynamics (Cottingham *et al.* 2001). One effect concerns the smaller differences in composition that high diversity treatments exhibit (Fukami *et al.*). That is, when diversity of replicate communities begin to approach the full diversity possible (the species pool available for experimentation), they all begin to have similar compositions. It is possible that such similarity in composition results in greater predictability among microcosms, though this cannot completely explain the greater predictability at higher diversities in McGrady-Steed *et al.* (1997). An existing analysis (McGrady-Steed *et al.* 1997) that includes only a single community com-

position at each diversity level preserves the stabilizing influence of diversity on ecosystem level predictability (Fig. 11.3(b)).

Changes in species composition and diversity can also influence long-term ecosystem dynamics. Low ecosystem level variability can arise from unchanging population abundances and constant community composition or from compensatory changes in abundance and species composition (Micheli *et al.* 1999). A relatively constant trophic structure observed along productivity gradients can result from species turnover (Leibold *et al.* 1997), and suggests an important role for immigration in maintaining ecosystem functioning. Some microbes used in some aquatic microcosm experiments (e.g. Petchey *et al.* 1999) may have wide, often cosmopolitan distributions (because of extremely high dispersal rates), so that local diversity is a relatively large fraction of regional diversity (Fenchel *et al.* 1997; Finlay and Clarke 1999a,b; Finlay and Fenchel 1999) (though see Foissner 1999). Aquatic microcosm experiments with different dispersal treatments provide one route for investigating if regional scale dispersal can maintain maximal microbial functioning across sites (Finlay *et al.* 1997).

Effects of habitat isolation and fragmentation on immigration rates may threaten long-term ecosystem functioning. Experiments clearly show that dispersal or immigration affect population variability

and food web structure (e.g. Luckinbill 1974; Holyoak and Lawler 1996a,b; Spencer and Warren 1996; Holyoak 2000). Similar experiments focusing on ecosystem-level properties are needed.

11.4 Diversity across multiple trophic levels

Recent experiments differ in whether diversity was manipulated within a single trophic level (e.g. Tilman *et al.* 1997a; Hobbie and Chapin 1998; Hector *et al.* 1999; Stocker *et al.* 1999) or across multiple trophic levels (e.g. McGrady-Steed *et al.* 1997; Naeem and Li 1997; Petchey *et al.* 1999; Hulot *et al.* 2000; Naeem *et al.* 2000a; Wardle *et al.* 2000a; Downing 2001). Of the 36 recent biodiversity–ecosystem functioning experiments that we surveyed, 23 manipulated diversity in a single trophic level, while 12 manipulated diversity within multiple trophic levels (Fig. 11.2(b)). Manipulating diversity across multiple trophic levels is relatively common in closed systems like microcosms where assembly and invasion is under tight control. In contrast, experiments in terrestrial systems tend to manipulate diversity in one trophic group, often plants or fungi, while higher trophic levels remain uncontrolled (often for logistic reasons) or manipulated by the addition or exclusion of multiple higher trophic groups, such as the use of pesticides to remove insects (e.g. Mulder *et al.* 1999). Consequently, in comparison to aquatic microcosms, such terrestrial experiments effectively ignore trophic diversity. Two studies illustrate how biodiversity can interact with trophic structure to determine ecosystem functioning.

11.4.1 Producer and decomposer interactions

Producers and decomposers form the base of food webs, where patterns of nutrient cycling can profoundly influence the rest of the web (e.g. Cole 1982; Vitousek and Walker 1989). Interactions between producers and decomposers can range from competition for nutrients to a mutualism based on exchange of inorganic nutrients for photosynthate (Cole 1982; Harte and Kinzig 1993; Daufresne and Loreau 2001). Naeem *et al.* (2000a) simultaneously

manipulated the number of producers and decomposer species in aquatic microbial microcosms. Each combination of 0, 1, 2, 4, or 8 species of green algae and 0, 1, 2, 4, or 8 additional species of bacteria was maintained for four weeks, sufficient time to include at least 20 generations of the manipulated organisms.

After four weeks of growth, treatments showed a positive relationship between algal diversity and algal biomass (Fig. 11.4(a)), similar to results from experiments with assembled plant communities in grasslands (Tilman *et al.* 1997a; Hector *et al.* 1999). Simultaneous variation in algal and bacterial diversity, however, caused complex changes in algal biomass, where interactions between algal and bacterial richness influenced biomass production (Fig. 11.4(a)). Thus, knowledge about diversity within a single trophic group did not adequately explain ecosystem functioning.

This co-dependency between producer and decomposer diversity raises questions about the interpretation of diversity manipulations focused within single trophic levels. Certainly, experimental manipulations of diversity within trophic levels provide useful information about how that targeted trophic level affects ecosystem functioning. Terrestrial plants may also be the dominant drivers of ecosystem functioning in their communities. Studies show, however, that below-ground community composition and diversity significantly affects above-ground processes (Laakso and Setälä 1999b; Griffiths *et al.* 2000) and that mycorrhizal diversity affects plant communities (van der Heijden *et al.* 1998b) (Raffaelli *et al.* Chapter 13). Focusing only on above-ground plant diversity may miss important complications when biodiversity changes simultaneously on several interacting trophic levels.

11.4.2 Direct and indirect effects of disturbance

A second example considers how environmental change can have both direct and indirect effects on ecosystem functioning. The direct effects results from changing metabolic rates or resource supply rates. Indirect effects of the environment on ecosystem functioning can occur through changes in the diversity, composition, and structure of interactions of a community. Petchey *et al.* (1999)

investigated direct and indirect effects by gradually warming four different microbial communities. Gradual warming had two interrelated effects on the food webs: a reduction in species richness and modified interactions between species associated with loss of higher trophic levels. Both of these changes could conceivably affect ecosystem functioning. Partitioning the net effect of warming on primary production into direct and indirect effects showed that indirect effects were consistently and logically associated with changes in community structure. Warming decreased consumer diversity, increased producer biomass, and increased primary production beyond levels expected from direct metabolic effects of temperature. The magnitude of the indirect effect peaked during the sixth week of the experiment and approached the magnitude of the direct effect (Fig. 11.4(b)) suggesting that indirect effects of warming caused by changes in trophic structure could be as important as direct effects.

These results and other lines of evidence (Raffaelli *et al.*, Chapter 13) clearly indicate that trophic structure modulates effects of diversity on ecosystem functioning (though see Downing 2001). Recent emphasis on the role of niche complementarity, selection probability, and facilitation surely

stem in part from a focus on short-term experiments using a single trophic level, plants (e.g. Loreau and Hector 2001; Mulder *et al.* 2001). There are many ways that changes in trophic structure can affect ecosystem functioning, including trophic cascades, destabilizing effects of extra trophic levels, and loss or addition of keystone species (Bengtsson 1998).

11.4.3 Design issues in multi-trophic level experiments

Ideally, a factorial manipulation of diversity per trophic group and number of trophic groups could be designed. Analysis of factorial manipulations of diversity per trophic group and number of trophic groups require random assignment of species to treatments (Allison 1999). Common sense and studies of community assembly both indicate that this type of design is difficult to arrange. Obviously, treatments with predators and without prey will fail, as would treatments with herbivores and without producers. Weatherby *et al.* (1998) showed, furthermore, that only eight of the 63 possible combinations of six protist species persisted in the long-term. The inability to assemble some communities and the long-term instability of many communities

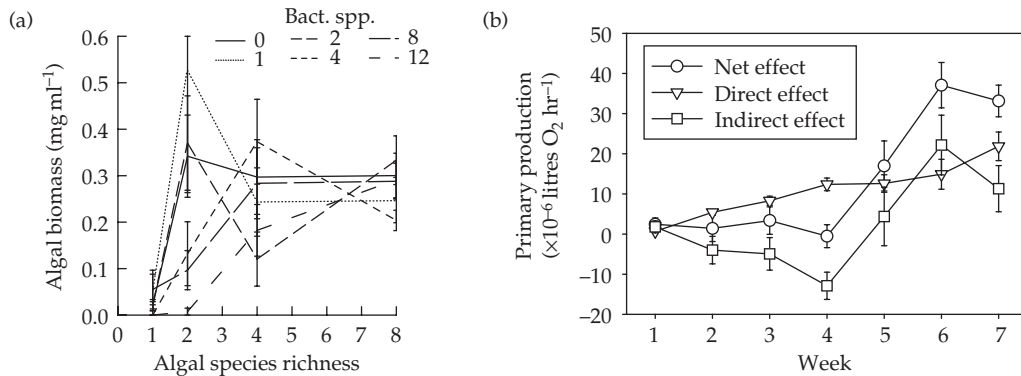


Figure 11.4 (a) Algal biomass response in microbial microcosms to variation in bacterial decomposer diversity (error bars are $\pm 1SE$). Although a generally positive relationship is observed between algal production and algal species richness, as observed in other experiments, the shape of the response curve is sensitive to decomposer diversity (see Naeem *et al.* 2000 for details of experiment). (b) Net, direct, and indirect effects of temperature on primary production during gradual warming of microbial microcosm communities (error bars are $\pm 1SE$). Changes in physiological process rates are assumed to cause direct effects of warming and were calculated by assuming a Q_{10} of 2. Indirect effects were the difference between the direct effect and the observed primary production in warmed communities and were significantly associated with changes in food-web structure.

precludes the completely random assembly of food webs (Drake 1990; Law and Blackford 1992; Holt *et al.* 1994; Leibold 1996). Designing appropriate multi-trophic level biodiversity–ecosystem functioning experiments remains challenging.

Fortunately, experiments in microcosms and lakes that do not explicitly examine biodiversity–ecosystem functioning have been common. For example, considerable effort has focused on the effects of number of trophic levels and prey heterogeneity on population, community, and ecosystem dynamics (e.g. Briand and McCauley 1978; Persson *et al.* 1992, 2001; Lawler and Morin 1993; Leibold *et al.* 1997; Kaunzinger and Morin 1998; McCann *et al.* 1998a; Bohannan and Lenski 1999; Steiner 2001). These commonplace effects of food web structure on community and ecosystem dynamics (Raffaelli *et al.*, Chapter 13) suggest that changes in diversity may affect ecosystem functioning mostly through changes in the distribution of species among trophic groups. The trophic position in a food web that species are lost from may influence ecosystem functioning more than the total number of species present. Furthermore, species from some trophic, functional, and taxonomic groups suffer a greater extinction risk than others (Pimm *et al.* 1988; Cutler 1991; Tracy and George 1992; Wright and Coleman 1993; Gilbert *et al.* 1998; Petchey *et al.* 1999), suggesting that extinctions from natural communities will change the distribution of species among the trophic and functional groups. This argues for a better theoretical (Naeem 1998; Ives *et al.* 2000; Loreau 2001) and experimental understanding of how trophic structure influences ecosystem functioning (Lawton 2000).

11.5 Links with theory

Close coupling of theory, experimentation, and observation can result in well-directed and efficient ecological research programmes (Levin 1981; Kareiva 1989; Werner 1998). We have already mentioned that microcosm experiments, given their long generational duration, can test theoretical predictions about long-term dynamics. Here we show how microcosms can directly address questions raised by ecological theory. Two experiments

that focus on the influence of diversity on ecosystem level processes illustrate particularly tight links with theory (Hulot *et al.* 2000; Naeem *et al.* 2000a).

11.5.1 Producer and decomposer interactions

The first example shows that iterative feedback between experiments and theory can rapidly advance understanding. Simple models of producer–decomposer interactions describe nutrient cycling between four compartments (Harte and Kinzig 1993): primary producers (plants, algae), decomposers (bacteria, eukaryotic microorganisms), dead organic matter (litter, dead producers), and a pool of inorganic nutrients. The two living compartments, the producers and the decomposers, simultaneously compete for nutrients and exchange other nutrients in a mutualistic nature. This model makes a number of explicit assumptions: (i) The system is closed, so that rates of nutrient cycling within the system dominate dynamics. (ii) Environmental conditions are constant unless explicitly modelled otherwise. (iii) There are no other organisms to interact with; e.g., there is no predation. (iv) Steady state, long-term dynamics are considered. (v) All organisms within a trophic group are identical. The congruence between theoretical assumptions and conditions in aquatic microcosm here is considerable. Microcosms: (i) can be closed systems, (ii) are typically run in controlled environments, (iii) contain only the desired organisms, (iv) display long-term dynamics, and (v) can be engineered so that the decomposer and producer groups each contain only a single species. The model also implicitly assumes a lack of spatial structure, which can match the conditions in aquatic microcosms well (e.g. Buckling *et al.* 2000; Kassen *et al.* 2000) compared to terrestrial systems. A lack of spatial variation in environmental conditions and relatively mobile individuals should limit the extent of spatial aggregation in aquatic microcosms and result in dynamics that approximate mean field situations (Tilman and Kareiva 1997). This contrasts with terrestrial plant communities, with sedentary individual plants and greater spatial environmental heterogeneity. The six assumptions outlined above are not peculiar to Harte and

Kinzig's (1993) model; they permeate ecological theory. Consequently, conditions in microcosms often correspond well to the assumptions of simple theory.

Naeem *et al.* (2000a) examined the fifth assumption in Harte and Kinzig's (1993) model and showed the distribution of biomass between producers and decomposers depended on the number and identity of producers and decomposers (Fig. 11.4(a)). Obviously, the assumption of functionally identical producers and decomposers is unrealistic. Accordingly, Loreau (2001) developed a model including a diversity of decomposer species that differentially exploit a diversity of organic compounds derived from producers. Increasing producer diversity could reduce ecosystem process rates if it increased the likelihood that some organic compounds could not be utilized by a given set of decomposers. In contrast, increased decomposer diversity could increase ecosystem process rates if more organic compounds could be utilized. These predictions match the significant positive correlation between microbial diversity and the diversity of carbon sources decomposed described by Naeem *et al.* (2000a), but differ in other respects, such as interactions between decomposer and producer diversity. It is possible that the experiment, even though long by ecological standards, remained far from equilibrium. Consortia of microbial species may break down organic compounds in ways that are not predicted by their individual effects. These possibilities suggest that research considering transient dynamics and resource driven interactions between decomposer species would be particularly worthwhile (Loreau 2001).

11.5.2 Functional diversity and nutrient enrichment

Models of how aquatic ecosystems respond to enrichment are important because of deleterious consequences of phytoplankton blooms caused by eutrophication (Briand and McCauley 1978). Early models used many of the same assumptions as Harte and Kinzig (1993), in particular that discrete trophic levels contained functionally identical species (Oksanen *et al.* 1981). In such models, and

in experiments that strictly adhered to these assumptions (Kaunzinger and Morin 1998), enrichment increases the abundance of the highest trophic level and trophic levels located an even number of levels below the top level. The considerable natural diversity within trophic levels, however, raised questions about whether that diversity would lead to different predictions (Leibold 1989; Hunter and Price 1992; Leibold and Wilbur 1992; Hairston and Hairston 1993). Abrams (1993) predicted that multiple functional groups within trophic levels could produce very different responses than those predicted by models of simple linear food chains.

Hulot *et al.* (2000) tested this prediction by manipulating nutrient levels and fish densities in aquatic mesocosms (we use the term mesocosm only to follow Hulot *et al.* (2000) and Lacroix and Lescher-Moutoué (1991)). The mesocosms were large plastic bags suspended in a shallow lake that initially contained many different organisms. With respect to the assumptions of Harte and Kinzig (1993) this experimental system (i) is closed, (ii) is in a naturally varying environment, (iii) mostly contains only the organisms of interest, (iv) is not strongly influenced by initial conditions, and (v) contains a diversity of organisms in each trophic group. We also might expect lower levels of spatial heterogeneity than in other systems, although enclosure walls introduce some spatial heterogeneity.

Hulot *et al.* (2000) examined the importance of diversity within trophic levels for ecosystem responses to enrichment by comparing their experimental results to predictions of linear food chain models (Oksanen *et al.* 1981; Arditi and Ginzburg 1989) and a model that included functional diversity within trophic levels (as did Abrams 1993). Phytoplankton, herbivorous zooplankton, and carnivorous zooplankton were modelled either as identical species (a linear food chain), or by dividing these trophic levels into functional groups based on the size and the diet of organisms (a simplified food web). Responses of each trophic level to enrichment without and with fish were inconsistent with the linear food chain model (Fig. 11.5). For example, enrichment decreased the abundance of top trophic level, invertebrate carnivores! The more complex food-web model, however, matched experimental results in nine of ten instances, including a negative

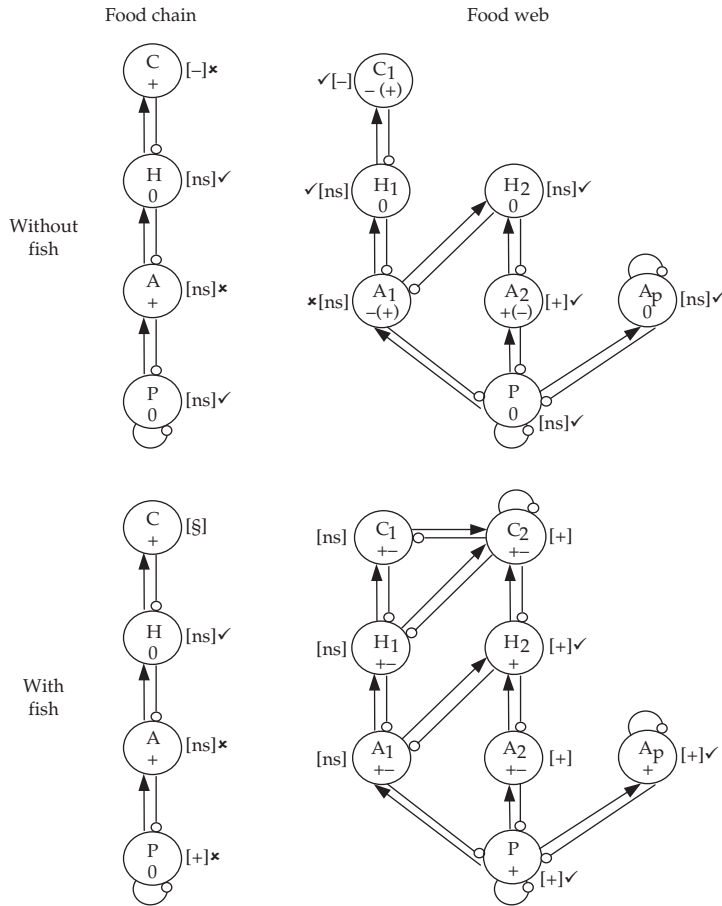


Figure 11.5 Contrasts between observed (in square brackets) and predicted (inside the circles/nodes) effects of nutrient enrichment in mesocosms without fish and with fish. Ticks indicate correct predictions and crosses indicate incorrect predictions. No tick or cross indicates when comparisons were not possible because theory made undetermined predictions or because the sum of invertebrate carnivores density and fish biomass is senseless (§). (Food chain predictions are according to a prey-dependent model.) The nodes of the food chains/webs correspond to the trophic groups. P: mineral phosphorus; A: algae; A₁: edible algae; A₂: protected algae; A_p: periphyton; H: herbivores; H₁: small herbivores; H₂: large herbivores; C: carnivores; C₁: invertebrate carnivores; C₂: fish. Links between nodes correspond to direct effects between trophic groups, determined by the coefficients of the Jacobian matrix for the dynamical system at equilibrium (Levins 1974). An arrow or a line ending with a circle from node *i* to node *j* corresponds to a positive or a negative direct effect, respectively, of trophic group *i* on trophic group *j*. Predictions and empirical results (significant at $\alpha=0.05$ or not significant ns) are indicated by their sign: +, 0, and -, denoting a positive effect, no effect and a negative effect, respectively, of nutrient enrichment on biomass. Additional predictions were +- for undetermined outcome and +(-) or -(-) indicating a very likely positive or negative outcome, respectively. Modified from Hulot *et al.* (2000).

effect of enrichment on invertebrate carnivore abundance (Fig. 11.5). This level of agreement could not be ascribed to chance alone (sign test, $P < 0.025$). Thus, integrated use of models and experimentation showed that functional diversity within trophic levels was important in understanding the full range of ecosystem responses to nutrient enrichment and top predators.

The two studies discussed here (Hulot *et al.* 2000; Naeem *et al.* 2000a) provided data to test and modify existing theory. The microcosms conformed closely enough to model assumptions that even small increases in model complexity, which result from relaxing a particular assumption (for example, by including functional diversity) significantly increased predictive power. The mesocosm

experiment (Hulot *et al.* 2000) likely meets model assumptions less well, but sufficiently so that linking the experiment to theory was profitable. The resulting models of intermediate complexity (such as in Hulot *et al.* 2000; Loreau 2001) are an important middle ground between very simple and very complex models. They contain considerable information on natural history, but are not so complex that they are completely intractable (Briggs and Godfray 1995). Combining tractable models and experimental systems that meet many model assumptions is a powerful approach for advancing ecological understanding.

11.6 Future directions

Of course, microcosms are useful model systems in their own right, and they offer important insights into the workings of well-defined ecosystems of low to moderate complexity. Whether we can extrapolate results from aquatic microcosms to other ecological situations requires an understanding of the spatial and temporal scaling of ecological processes (Lawton 1999; Peterson and Hastings 2001). The first step in solving this problem is to identify and quantify changes in scale, as we have done for the temporal scale of recent biodiversity–ecosystem functioning experiments, using non-dimensional parameters (Peterson and Hastings 2001), such as the generational duration of experiments. Changes in biological complexity also represent changes in scale, from single populations, to simple community modules in isolation, to entire communities. We have shown how the differences in trophic complexity between ecosystem-functioning experiments might explain the qualitative range of results (also see Schwartz *et al.* 2000).

An implication of the difference in duration and complexity between microcosms and many other experiments is that cross-system comparisons become difficult. Such comparisons cannot easily separate system-specific consequences (e.g. aquatic versus terrestrial), from temporal differences, from trophic complexity differences. Biodiversity manipulations of species across multiple trophic levels predominantly occur in experiments lasting more than 20 generations (Fig. 11.2(b)). Quantifying scale

at least helps us understand that any of several differences between experiments could explain the difference in the results. The next step is to record how and why the relative strength of processes changes with scale. Biodiversity–ecosystem functioning research provides an example of how the relative strength of processes change across scales. Opposite relationships between biodiversity and ecosystem functioning can occur at local and regional scales because the processes that determine functioning also change (Loreau 1998a; Lawton 2000; Levine 2000a). It should be possible to develop models of biodiversity and ecosystem functioning that include scale as an explicit parameter, rather than an implicit assumption. Similar experiments across a range of several scales (e.g. Warren 1996; Bertolo *et al.* 1999) and approaches (microcosms, mesocosms, field settings) might then parameterize the models and provide a scale-free framework for both extrapolating from small-scale experiments to larger scales, and more generally for understanding and predicting effects of scale on ecological patterns and processes.

In the rapidly expanding field of biodiversity–ecosystem functioning research, microcosms are likely to remain a principle means for exploratory research and the first proving grounds for theoretical models. There are several important directions this research can move into. Long-term experiments could reveal the effects of genetic processes on ecosystem functioning. The manipulation of immigration and emigration rates, the manipulation of volume or spatial heterogeneity to test coherency of results across different scales, longer experiments to examine long-term dynamics, and the incorporation of modern molecular methods to examine bacterial and viral community structure will permit examining pathogen/parasite and decomposer diversity at a level of detail unimaginable in larger systems. The very different spatial and temporal scales that organisms at different trophic levels operate at is currently missing from theoretical and experimental investigation. Crossing biodiversity manipulations with other co-varying global change factors, such as UV-B radiation, eutrophication, species invasions, and habitat fragmentation also represent new directions. In all cases, microcosms will help to test and guide

theory, as well as provide insights into conducting more effective large-scale field experiments (e.g. whole ecosystem manipulations) and perhaps reducing the costs of such experiments by providing guidelines for effective and economic design.

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