

MINI- REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

Biodiversity and ecosystem functioning: recent theoretical advances

Michel Loreau

Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. – *Oikos* 91: 3–17.

The relationship between biodiversity and ecosystem functioning has emerged as a major scientific issue today. As experiments progress, there is a growing need for adequate theories and models to provide robust interpretations and generalisations of experimental results, and to formulate new hypotheses. This paper provides an overview of recent theoretical advances that have been made on the two major questions in this area: (1) How does biodiversity affect the magnitude of ecosystem processes (short-term effects of biodiversity)? (2) How does biodiversity contribute to the stability and maintenance of ecosystem processes in the face of perturbations (long-term effects of biodiversity)?

Positive short-term effects of species diversity on ecosystem processes, such as primary productivity and nutrient retention, have been explained by two major types of mechanisms: (1) functional niche complementarity (the complementarity effect), and (2) selection of extreme trait values (the selection effect). In both cases, biodiversity provides a range of phenotypic trait variation. In the complementarity effect, trait variation then forms the basis for a permanent association of species that enhances collective performance. In the selection effect, trait variation comes into play only as an initial condition, and a selective process then promotes dominance by species with extreme trait values. Major differences between within-site effects of biodiversity and across-site productivity–diversity patterns have also been clarified. The local effects of diversity on ecosystem processes are expected to be masked by the effects of varying environmental parameters in across-site comparisons.

A major reappraisal of the paradigm that has dominated during the last decades seems necessary if we are to account for long-term effects of biodiversity on ecosystem functioning. The classical deterministic, equilibrium approaches to stability do not explain the reduced temporal variability of aggregate ecosystem properties that has been observed in more diverse systems. On the other hand, stochastic, nonequilibrium approaches do show two types of biodiversity effects on ecosystem productivity in a fluctuating environment: (1) a buffering effect, i.e., a reduction in the temporal variance; and (2) a performance-enhancing effect, i.e., an increase in the temporal mean. The basic mechanisms involved in these long-term insurance effects are very similar to those that operate in short-term biodiversity effects: temporal niche complementarity, and selection of extreme trait values. The ability of species diversity to provide an insurance against environmental fluctuations and a reservoir of variation allowing adaptation to changing conditions may be critical in a long-term perspective.

These recent theoretical developments in the area of biodiversity and ecosystem functioning suggest that linking community and ecosystem ecology is a fruitful avenue, which paves the way for a new ecological synthesis.

M. Loreau, Laboratoire d'Ecologie, UMR 7625, Ecole Normale Supérieure, 46 rue d'Ulm, F-75230 Paris Cedex 05, France (loreau@ens.fr).

Accepted 26 May 2000

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ISSN 0030-1299

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The relationship between biodiversity and ecosystem functioning has emerged as a major scientific issue today. Although the idea that greater plant diversity allows greater biomass production dates back to Darwin (McNaughton 1993), it is only in recent years that the interest in the effects of biological diversity on ecosystem processes has penetrated experimental and theoretical ecology, where it is now spreading rapidly. The interest in this issue has grown from concerns about the potential ecological consequences of the present and future loss of biodiversity caused by the increased impact of human activities on natural and managed ecosystems. There has been growing recognition that ecosystems operate in a manner that provides ecological services to humans, the economic significance of which might be considerable (Costanza et al. 1997). These services are derived from the normal functioning of ecosystems, raising the important question whether depauperate ecosystems perform differently or less efficiently than the more species-rich systems from which they are derived (Ehrlich and Wilson 1991, Schulze and Mooney 1993, UNEP 1995, Chapin et al. 1998). A number of major experiments have been devoted to this issue recently, some of them involving considerable means in terms of equipment and personnel (Naeem et al. 1994a, 1995, Tilman et al. 1996, 1997a, Hooper and Vitousek 1997, Hector et al. 1999).

These experiments have tested the short-term effects of species diversity on ecosystem processes. But biodiversity might also be important, perhaps even more important, in the long term. Even when high species richness is not critical for maintaining ecosystem processes under constant or benign environmental conditions, it might nevertheless be important for maintaining them under changing environmental conditions. Species that are functionally redundant (i.e., that perform the same function, and thus whose diversity is not critical for maintaining the function) for an ecosystem process at a given time may no longer be redundant with respect to future environmental fluctuations. This idea is the basis for the 'insurance hypothesis' (Walker 1992, Lawton and Brown 1993, Yachi and Loreau 1999). Several recent experiments have also partially explored this issue (Tilman and Downing 1994, Tilman 1996, McGrady-Steed et al. 1997, Naeem and Li 1997, Petchey et al. 1999). In a way, this is the old stability–complexity debate resurfacing in a new form. The classical view that the complexity and diversity of ecological systems make for their stability (Odum 1953, MacArthur 1955, Elton 1958) seemed to be almost dead and buried after the mathematical demonstrations of May (1972, 1973) and others (though never completely: Patten 1975, McNaughton 1977, 1993). It is essentially this view that is coming back to life following the recent work, but with new arguments and a new rigour.

It is remarkable that this new interest in the effects of biodiversity on ecosystem functioning has risen from some intuitive hypotheses with little theoretical and modelling support. This is fundamentally a sign of vitality. In the long term, however, it may also become a fatal weakness. Theory provides a framework for interpreting and generalising otherwise isolated empirical observations, and for formulating new hypotheses. The lack of such a theoretical framework may well be one of the reasons for the renewed debates about the interpretation of recent experiments (André et al. 1994, Givnish 1994, Naeem et al. 1994b, Tilman et al. 1994, Aarssen 1997, Grime 1997, Huston 1997, Tilman 1997, Naeem and Li 1998, Wardle 1998, 1999, van der Heijden et al. 1999). Furthermore, experimental results have not all been convergent. While most experiments have supported (or at least have been interpreted as supporting) the hypothesis that loss of plant or mycorrhizal diversity impairs plant biomass production and nutrient retention (Naeem et al. 1994a, 1995, Tilman et al. 1996, 1997a, van der Heijden et al. 1998, Hector et al. 1999), some experiments have suggested that other ecosystem processes, such as decomposition, might be little affected by species diversity (Naeem et al. 1994a, 1995, Wardle et al. 1997a, Mikola and Setälä 1998, Hector et al. 2000), or that the response may differ in different systems (see Schläpfer and Schmid 1999 for a review). To what extent are the observed effects of biodiversity general? How can they be understood? What are the processes that generate them? What are their implications? These are some of the questions that quickly come to mind, and answering these questions calls for new concepts, theories and models. Thus, as experiments progress, there is a growing need for adequate theories and models to provide robust interpretations, generalisations, and predictions of experimental results.

Building such theories and models, however, is not straightforward. Linking the perspectives of community ecology and ecosystem ecology is hampered by the increasing separation of the two subdisciplines that has prevailed during decades. These grew largely independently, each having its own concepts, theories and methodologies. Population and community ecology is mainly concerned with the dynamics, evolution, diversity and complexity of the biological components of ecosystems; its starting point is the population and its interactions with other populations. Ecosystem ecology is mainly concerned with the functioning of the overall system composed of biological organisms and their abiotic environment; its starting point is the flow of matter or energy among functional compartments. Between the two subdisciplines, communication has been difficult, sometimes non-existent. The need to understand the relationship between biodiversity and ecosystem processes is one of the factors that are pushing towards greater integration again (Jones and Lawton 1995). The theoretical studies devoted specifically to

this issue have been few so far, but they are stimulating the development of a new area at the interface of community, ecosystem and evolutionary ecology.

This paper provides an overview of recent advances that have been made possible by these theoretical studies on the effects of biodiversity on ecosystem functioning. Tilman (1999) recently reviewed some of the insights gained from experimental and theoretical work in this field. This review differs from his in two respects: (1) it focuses specifically on theory and models, and (2) it covers other, more recent work.

I examine the two major questions in this area:

- (1) How does biodiversity affect the magnitude of ecosystem processes? This question deals with short-term effects of biodiversity.
- (2) How does biodiversity contribute to the stability and maintenance of ecosystem processes in the face of perturbations? This question deals with long-term effects of biodiversity.

Although these two questions are related, they may lead to different answers, as explained above, and therefore should be distinguished. An additional question which takes on increasing importance concerns mechanisms of biodiversity effects on ecosystem processes. Different mechanisms may have different implications. This is another lesson from theoretical considerations, which I shall discuss for each of the above-mentioned questions.

Short-term effects of biodiversity on ecosystem processes

How does biodiversity affect the magnitude of ecosystem processes in the relatively short term, or in a constant environment? This is the simplest question that can be asked. It is also the first question that has been tested in controlled experiments. Yet, paradoxically, there have been very few formal theoretical treatments of this question because this lacks a previous history.

Tilman et al. (1997b) proposed three simple models to explain the asymptotic relationship between biomass production and initial species diversity that was observed in some experiments with plant communities (Naeem et al. 1994a, 1995, Tilman et al. 1996, 1997a). Two different basic mechanisms were involved: a *sampling effect*, and *niche differentiation*.

Their model for the sampling effect assumes competition between all species for a single limiting nutrient, such that a single species eventually outcompetes all the others – the species that has the highest resource-use intensity, thus driving down the nutrient level most. This species also has the highest biomass, the highest productivity and best conserves the nutrient within the

ecosystem because less inorganic nutrient is left for leaching. In each plot, then, primary productivity is determined by the productivity of the competitively dominant species. Now suppose that species are drawn randomly from a pool to assemble communities in each plot, as in several field experiments (Tilman et al. 1996, 1997a, Hector et al. 1999). The probability of sampling a highly productive species from the pool increases as the number of species sampled to assemble a community increases. As a result, primary productivity is expected to increase, on average, asymptotically with initial species richness, the asymptote being determined by the productivity of the most competitive species in the pool. The same pattern holds for total plant biomass and nutrient retention. Note that, in this scenario, all communities eventually become monocultures; hence species diversity is not maintained through time, but only determines the initial range of trait variation from which the competitively dominant species is drawn.

The same effect was proposed simultaneously by Huston (1997), who called it a *selection probability effect*. But he and others (Aarssen 1997, Wardle 1999) interpreted it as a statistical artefact or hidden treatment invalidating recent experiments, contrary to Tilman (1997, Tilman et al. 1997b) who interpreted it as a valid biodiversity effect. Another difference is that Huston (1997) did not make strong assumptions about the mechanism that is responsible for the effect. Nijs and Roy (2000) showed that dominance also builds up through time in a community of exponentially growing plant populations in an unlimited environment. They used exponential growth as an approximation for the seasonal growth of annual plants in Mediterranean communities. This generates an effect akin to the sampling or selection probability effect, in which the initial range of trait variation has a major effect on primary productivity. Thus, this type of effect does not hinge on strong competitive interactions. Its two basic ingredients are (1) an initial trait variation causing interspecific differences in productivity, and (2) a selective process that promotes dominance by the most productive species.

The other two models of Tilman et al. (1997b) involve niche differentiation among species, either in the form of an interspecific trade-off between the competitive abilities for two essential resources, or in the form of niche differences along two resource gradients. They also predict an asymptotically increasing productivity at a higher diversity, with the rate of approach to the asymptote depending on the amount of heterogeneity along the two niche axes: productivity increases more steadily with species diversity in more heterogeneous, and hence also in larger-sized, habitats. The cause and consequences, however, are very different from those of the sampling effect. Niche differentiation implies both the maintenance of species coexistence and complemen-

tarity in resource use by the various species, which results in a better collective resource use by the community as a whole (MacArthur 1972). The resulting increase in productivity is directly related to the realised species diversity in a community and goes beyond the productivity of any species alone; it is also predictable from the biological properties of the interacting species.

These models allowed identification of two different basic factors leading to a positive effect of biodiversity on ecosystem processes. But how do these factors interact? Does biodiversity necessarily lead to increased productivity? And, if not, under what circumstances? To answer these and other questions, I built a mechanistic ecosystem model based on plant competition for a limiting soil nutrient in a spatially structured environment (Loreau 1996, 1998a). In this model, plant nutrient uptake is considered to decrease the soil concentration of a limiting nutrient in the immediate vicinity of the rooting system, thus creating a local resource depletion zone around each plant (Huston and DeAngelis 1994). Variation in the rate of nutrient physical transport between these and the general soil nutrient pool determines the degree to which plants interact competitively through their indirect effect on the shared nutrient pool. The advantages of this model are that (1) it is both simple enough to be tractable analytically, and realistic enough to be applicable to actual experiments; (2) it allows a variety of different scenarios and relationships between biodiversity and ecosystem processes to be explored. Species richness was chosen as a measure of biodiversity to mimic experiments, but it is really phenotypic diversity as determined by intra- or interspecific differences in plant traits that matters in this model, because its approach is fundamentally individual-based. Two plant traits turned out to play a critical role: (1) the potential overlap between their local resource depletion zones, which determines niche differences in space occupation among species, and (2) their resource-use intensity, i.e., their ability to depress the resource level locally, which determines their competitive ability.

I explored two limiting cases of potential niche overlap in space occupation. One limiting case occurs when plants from all species have the same root geometry and potentially occupy identical resource depletion zones. I called such species *redundant*, because they occupy the same spatial niche and thus fulfil the same functional role, even though their resource-use intensity may differ. The other limiting case occurs when plants from different species have very different root geometries and occupy completely non-overlapping spaces. I called such species *complementary*, because they occupy distinct spatial niches and thereby fulfil complementary functional roles.

In the case of redundant species (Fig. 1A), the effect of biodiversity on either primary productivity, total plant biomass or nutrient retention (these are again

correlated because of the assumption of a single limiting nutrient) is further sensitive to the way the average resource-use intensity varies with diversity. A 'null' scenario of no response of primary productivity to species diversity is obtained, logically, when species are redundant and average resource-use intensity does not change with diversity. But primary productivity is expected to change with diversity when the latter covaries with average resource-use intensity. In Fig. 1, I have considered two scenarios where species are added to the community sequentially, in either increasing or decreasing order of competitive ability. Productivity then either increases or decreases with diversity (Fig. 1A). These particular scenarios may be interpreted as different selective increases in the available range of trait variation as diversity increases. In general, however, co-variation between diversity and average re-

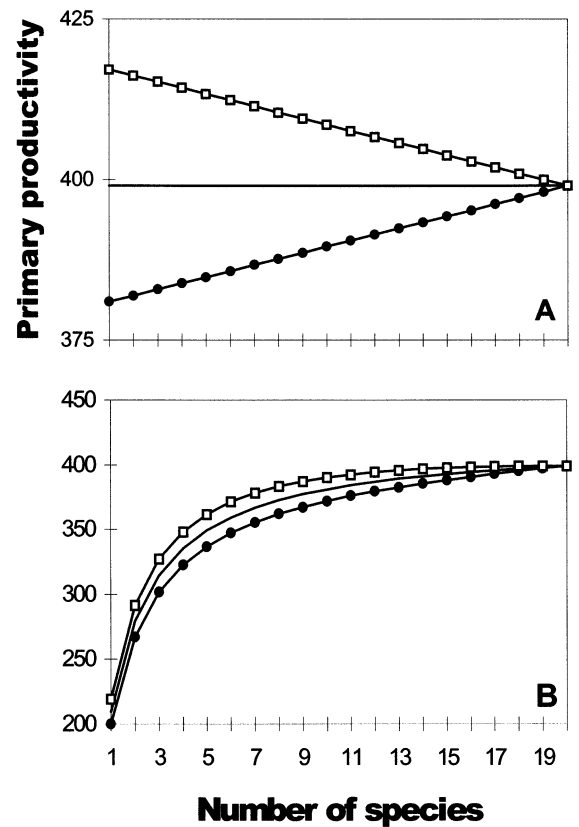


Fig. 1. Primary productivity as a function of plant species richness, in the two cases of 'redundant' (A) and 'complementary' (B) species in the mechanistic model of plant competition for a limiting nutrient (Loreau 1998a). Continuous line: 'null' scenario in which average resource-use intensity is independent of species richness. Filled circles: scenario in which species are added in increasing order of resource-use intensity. Open squares: scenario in which species are added in decreasing order of resource-use intensity. Resource-use intensities are assumed to follow a regular distribution, $L_{i*} = iL_{1*}$, where i is the species competitive rank and L_{i*} is the equilibrium nutrient concentration in the local resource depletion zones of species i . Adapted from Loreau (1998a).

source-use intensity is likely to operate in two steps: first species diversity increases the available range of trait variation, and then a selective process favours species with either a higher or a lower resource-use intensity. Any such process would have effects similar to those showed in Fig. 1: productivity should increase with diversity when species with a higher resource-use intensity are selectively favoured, and decrease when species with a lower resource-use intensity are selectively favoured. The sampling effect as proposed originally may thus be viewed as a special case of this general mechanism, in which selection is so strong as to eliminate all species but the highest yielding competitor. But my model shows, first, that the effect need not be as extreme, and, second, that it can also operate in the opposite direction. Complete dominance of the highest yielding competitor leading to the virtual elimination of inferior competitors is not required for a positive selection effect in which higher yielding species are favoured. And an *inverse sampling effect* or *negative selection effect* is also possible if competitive ability is correlated negatively with biomass production because, for instance, of trade-offs between resource acquisition and interference competition, or between resource acquisition and resource-use efficiency. This would generate a negative correlation between average resource-use intensity and diversity, and hence a decrease of primary productivity with diversity. Although they may seem unlikely at first sight, such trade-offs may be more common than previously believed. A negative selection effect might be operating in Hooper and Vitousek's (1997) experiment, and negative selection seems to be as frequent as positive selection in the BIODDEPTH experiment (Loreau, Hector, Yachi and Lawton unpubl.).

In the case of complementary species (Fig. 1B), primary productivity (as well as total plant biomass and nutrient retention) is always expected to increase asymptotically with diversity, changes in the mean competitive ability only affecting the steepness of the response. This shows that resource-use complementarity through niche differentiation, when it occurs, can have a much stronger effect than the selection effect. This seems consistent with the results of recent experiments, which suggest that the selection effect is not enough to explain the positive responses of primary productivity to diversity and that some form of complementarity among species should drive these responses, in particular among plants from different functional groups (Tilman et al. 1997a, Hector et al. 1999, Spehn et al. 2000, Loreau, Hector, Yachi and Lawton unpubl.).

Overall, the insights from these theoretical studies may be summarised as follows. Two major types of mechanisms by which biodiversity influences productivity or other ecosystem processes have been recognised, leading to two types of biodiversity effects: (1) *functional niche complementarity* (the *complementarity effect*) and (2) *selection of extreme trait values* (the

selection effect). In both cases, biodiversity provides a range of trait variation which is the raw material for the operation of these effects. In the complementarity effect, trait variation forms the basis for a permanent association of species that enhances collective performance. In the selection effect, trait variation comes into play as an initial condition, and a selective process then promotes dominance by species with particular trait values. I suggest using the term *selection effect* instead of the previous terms 'sampling effect' and 'selection probability effect' because it is both more precise and more general. It is more precise because there is a sampling component in both the complementarity and the selection effect: in both cases, a higher diversity allows sampling of a wider trait range. It is more general because it does not require complete dominance of the best performing species and can also operate in the opposite direction. Finally, there is an obvious analogy between this effect and the evolutionary process by natural selection.

This may help to clarify several aspects of the current debate. Firstly, species diversity, or biodiversity at large, matters only to the extent that it provides phenotypic variation related to the particular function considered. Recent experiments have used species richness as a surrogate for phenotypic diversity, which is much more difficult to measure a priori, especially when different ecosystem processes are studied simultaneously. The need to separate the effect of species diversity from that of species identity or community composition (Tilman 1997) has led to some confused discussions about the effect of species number per se, a meaningless concept since what is aimed at behind species richness in these experiments is really the effect of phenotypic diversity. Thus, distinguishing the effects of functional-type diversity from species diversity within functional types is useful to assess whether it is possible to identify more precisely the kind of functional differences that are critical to explain biodiversity effects on ecosystem processes (Tilman et al. 1997a, Hector et al. 1999). Within- and between-functional-type diversity, however, are two components of the same functional phenotypic diversity, and should not be opposed.

Secondly, the analogy between the selection effect in biodiversity experiments and natural selection in evolutionary biology strongly suggests that this type of effect should not be discarded as purely non-biological and artefactual. It is true that the two types of mechanisms identified above have different implications for the significance of biodiversity for ecosystem functioning. Functional complementarity is permanent, is predictable from the individual species' biological traits, and has a consistent, positive effect on several ecosystem processes, such as total plant biomass, primary production and nutrient retention. Selection effects – at least as short-term effects – are linked to the processes

of community assembly or disassembly, they are likely to be more variable (in particular, they can be positive or negative), and their short-term significance may vary depending on a number of factors, including the kind of systems, the kind of organisms, the spatial and temporal scale considered, as well as the scientist's or the manager's objectives. Managed or agricultural ecosystems, for instance, experience artificial selection by man, and accordingly natural selection effects may have little relevance for those who manage them in the short term. But the assembly (species gain) or disassembly (species loss) of natural ecosystems has a component of chance or historical contingency. The predicted global changes in climate, land use and biological invasions will likely have huge effects on the local dominance and proneness to extinction of species, and greatly increase this component of contingency. Also, many systems in the world are harvested rather than managed. Harvesting often selectively removes species with dominant or key roles and may drive them to extinction – fisheries provide a good example of this threat. Thus, the performance of species and the order in which they are likely to be lost in the future might be highly variable and unpredictable. All this argues for considering the selection effect as a relevant biological effect. Finally, this type of mechanism may play a critical role in the long term in changing environments (see below).

Another implication of the selection effect is that factors that contribute to maintain species diversity by counteracting it may lead to opposite productivity–diversity relationships. As an example, we recently explored the potential consequences of recurrent immigration on the properties of local plant communities using a model describing the dynamics of space occupation (Loreau and Mouquet 1999). Immigration contributes to maintain local diversity through the continuous supply of inferior competitors. This increases the total space occupation by the community, but also dilutes the competitively dominant species into a mass of species that are less adapted to the local environment, thus decreasing the average competitive ability. As a result, productivity often decreases as diversity increases. The mechanism here is opposite to the selection effect: local diversity maintained by non-local processes counteracts local selective processes that promote dominance by the most productive species.

Given the potential differences between the two types of mechanisms underlying the response of ecosystem processes to biodiversity, it seems desirable to separate them in biodiversity experiments as far as possible. This has sparked new interest in methods borrowed from agricultural sciences (Garnier et al. 1997, Jolliffe 1997, Hector 1998, Loreau 1998b). The general principle of these methods is to compare the yield of a mixed culture with its expected yield based on the yields of the monocultures of the same species and the abundance of

species in the mixture. This comparison aims to remove the effects of species composition and changes in dominance. We are currently developing a more powerful method that allows separation of the complementarity and selection effects by additive partition (Loreau, Hector, Yachi and Lawton unpubl.). These methods have seldom been used in the analysis of experimental data (Wardle et al. 1997a, Hooper 1998, Hector et al. 1999), yet their contribution may be valuable for interpreting and understanding experimental results.

The two types of mechanisms identified in the existing theoretical models, however, surely do not exhaust the range of possibilities. Firstly, attention has been concentrated almost exclusively on plants so far. It is very likely that animals and micro-organisms will reveal other biodiversity effects, such as effects mediated by the chemical quality of food and substrates or by modification of the physical structure of the environment. In a recent experiment, Naeem et al. (2000) manipulated the diversity of algae and bacteria simultaneously in aquatic microcosms, and found complex interactive effects of algal and bacterial diversity on algal and bacterial biomass production. Both algal and bacterial diversity had significant effects on the number of carbon sources used by bacteria, suggesting nutrient cycling associated with microbial exploitation of organic carbon sources as the link between bacterial diversity and algal production. Theory also predicts that selection effects at higher trophic levels should be more complex than at the plant trophic level (Holt and Loreau 2000). Experimental tests of the effect of diversity at the herbivore and other trophic levels on ecosystem processes are only just starting (Norberg 2000). Secondly, even in plants, all mechanisms have not yet been explored. At least a third type of mechanism is likely to be involved in the effects of plant diversity on ecosystem processes: *direct interactions between species*, either negative (interference) or positive (facilitation). It is not obvious, however, that this type of mechanism generates effects that can be separated from the other two. If species interact positively, the stimulation of growth induced by the presence of other plants should translate into a better collective exploitation of resources equivalent to a form of functional complementarity, and/or into a competitive advantage in resource exploitation leading to increased dominance, hence to a selection effect. Opposite effects should result from interference competition. Therefore, instead of generating distinct effects, direct interactions are probably intimately involved in both the complementarity effect and the selection effect.

We have recently developed an analytical model for a light-limited grassland ecosystem which supports this idea (Yachi and Loreau unpubl.). Light differs from other resources in that it is directional, and hence generates asymmetrical interspecific competition. Therefore competition for light may be viewed as in-

volving both exploitation and interference competition. We found, as expected, that light-use complementarity among plant species contributes to increase total biomass production. But we also found that, if the various species experience different intensities of light competition, this imbalance between species promotes competitive dominance, which can have a negative effect, not only on the biomass production of inferior competitors, but also on that of the community as a whole. The imbalance in species' competitive abilities may be viewed as generating a selection effect. This effect can be so strong as to surpass the complementarity effect and result in the total biomass production in mixed communities falling below the mean biomass production of monocultures. Thus, the dynamics of light competition appears to generate both a complementarity effect and a selection effect simultaneously.

Within-site versus across-site relationships between productivity and diversity

Recent experiments and theories have focused on the local effect of biodiversity on ecosystem processes. But there is a long tradition in ecology of considering the opposite effect, i.e., how species diversity is affected by abiotic factors, hence indirectly by ecosystem processes, in particular productivity (Briand and Cohen 1987, Rosenzweig and Abramsky 1993, Tilman and Pacala 1993, Huston 1994, Abrams 1995). To investigate this issue, ecologists have usually correlated diversity with productivity – or, more exactly, with factors (such as soil fertility) that determine productivity – across sites with different characteristics. It is tempting to use these comparisons across sites to reverse the question, and ask how productivity is influenced by diversity, as for instance Wardle et al. (1997b) did. But, is this justified theoretically? Can across-site comparisons be used to detect the effect of biodiversity on productivity? How do environmental factors, biodiversity and productivity interact? To answer these questions, I have used the same mechanistic model of plant competition for a limiting nutrient as above (Loreau 1998a), and analysed how variations in environmental factors simultaneously affect plant diversity and primary productivity.

Assume that, in each site, species diversity reaches an equilibrium level determined by local environmental constraints and the distribution of traits available in the regional species pool. Further assume that species are complementary, in which case the effect of diversity on productivity is positive at each site (see above). Variations in abiotic factors among sites then have two effects on productivity: a direct effect, and an indirect effect through changes in species diversity (Fig. 2). The analysis of my model showed that the direct effect always prevails over the indirect effect. When the two

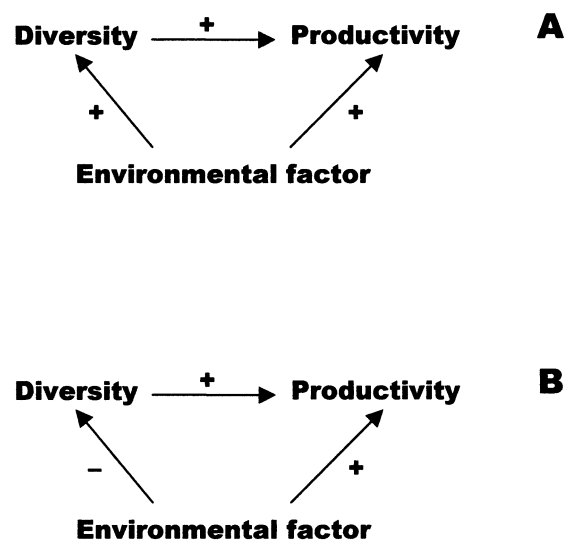


Fig. 2. Causal relations between changes in environmental factors, plant species diversity and primary productivity that generate across-site relationships between productivity and diversity. Species are assumed to be complementary; therefore species diversity has a positive effect on primary productivity. In A, sites differ in an environmental parameter, such as the inflowing nutrient concentration in the soil, that has direct positive effects on both diversity and productivity. This generates a positive correlation between productivity and diversity across sites (Fig. 3A). In B, sites differ in an environmental parameter, such as the rate of nutrient transport between local resource depletion zones and the general soil nutrient pool, that has a direct positive effect on productivity but a negative effect on diversity. Since the direct positive effect of the environmental factor on productivity prevails over the indirect negative effect through changes in diversity, this generates a negative correlation between productivity and diversity across sites (Fig. 3B).

effects are convergent, as is the case when the inflowing nutrient concentration in the soil varies, a positive correlation between productivity and diversity emerges across sites (Figs 2A and 3A). But when the two effects are contradictory, as is the case when the rate of nutrient transport between local resource depletion zones and the general soil nutrient pool varies, a negative correlation emerges across sites (Figs 2B and 3B). When several abiotic parameters vary simultaneously (here, both the inflowing nutrient concentration and the rate of nutrient transport in the soil), the correlation between productivity and diversity across sites tends to disappear (Fig. 3C), or can be combined to produce a hump. Yet in all cases controlled experiments would reveal that diversity is intrinsically beneficial to productivity at each site (Fig. 3A, B, C). The same conclusions hold for total plant biomass and nutrient retention. This shows that the local effect of diversity on ecosystem processes should be masked systematically by the effects of environmental parameters on these processes in across-site comparisons.

This is an important but disturbing conclusion. Its 'negative' side is that comparisons across sites cannot

reveal the short-term effect of diversity on ecosystem processes unless abiotic conditions are very tightly controlled, which severely restricts the use of such comparisons. Note that the problem is not simply one of spatial scale. Generally speaking, one should expect that the

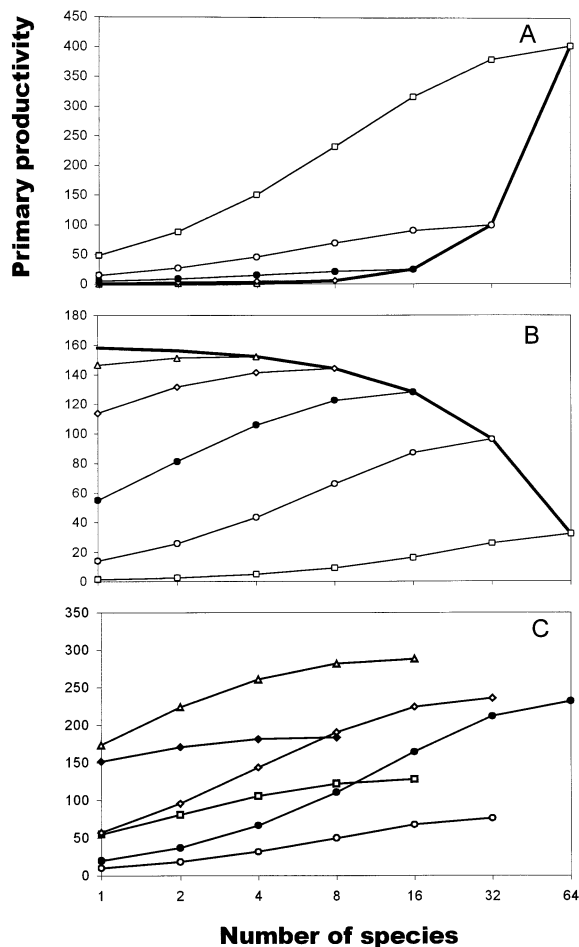


Fig. 3. Within-site versus across-site relationships between primary productivity and plant species richness, in the case of complementary species, obtained using the mechanistic model of plant competition for a limiting nutrient (Loreau 1998a). The thin lines show the positive effect of species richness on primary productivity within each site (i.e., holding environmental parameters constant), as controlled experiments would reveal it. The various lines correspond to different sites defined by different sets of environmental parameters. The right endpoint along each line corresponds to the maximum number of species that can coexist at equilibrium in each site, given the same regular distribution of resource-use intensities as in Fig. 1; this is assumed to be the 'natural' situation in each site. Across-site comparisons would reveal either a positive (A, thick line), a negative (B, thick line), or no (C) relationship between productivity and species diversity, depending on the environmental parameters that vary among sites, and regardless of the positive effect of species diversity on primary productivity within each site. The environmental parameters that vary among sites are the inflowing nutrient concentration in the soil in A, the rate of nutrient transport between local resource depletion zones and the general soil nutrient pool in B, and both parameters in C.

larger the scale at which a site is defined, the more each site incorporates environmental heterogeneity and the more difficult the detection of significant biodiversity effects. But here the problem is also one of operation of different causal pathways at different scales: species diversity is driven by changes in environmental conditions in comparisons across sites, whereas it can be manipulated experimentally within each site. One implication is that, when species diversity has the time to adjust to changes in the environment, the impact of changes in diversity on ecosystem functioning is expected to be secondary compared with the direct impact of environmental changes. In the case of gradual environmental changes such as changes in climate, for instance, their impact on ecosystem functioning might be approximately predicted by ignoring the dynamics of species diversity. This should not be true, however, for massive species losses as they are predicted in the near future. In the latter case, changes in biodiversity may play a significant independent role, which cannot be ignored.

On the 'positive side', documented cases of negative or absent relationships between productivity and diversity across sites are compatible with positive local effects of diversity on productivity, which may reconcile apparent contradictions in the literature. The BIODEPTH experiment, performed in eight sites across Europe, provided results that strongly support this theoretical conclusion. Despite large differences in primary productivity between locations and no apparent relationship between productivity and maximum within-site species richness, productivity generally declined as species were lost within a site, generating a pattern that looks very much like Fig. 3C (Hector et al. 1999).

Long-term effects of biodiversity in a fluctuating environment

How does biodiversity contribute to the long-term stability and maintenance of ecosystem processes in the face of environmental changes or perturbations? As mentioned in the Introduction, this question is part of an old debate on the relationship between the stability and the complexity or diversity of ecological systems. One major lesson from this debate was that the concept of 'stability' was too broad and fuzzy to allow robust generalisations. Summarising the debate, Pimm (1984) identified a number of different properties commonly included under the concept of 'stability', in particular mathematical stability, resilience, resistance, persistence, and temporal variability. These properties all contribute to stability and yet may have very different relationships with diversity. He also stressed that these properties may be very different depending on the

variable under consideration. In particular, the stability properties of individual populations may differ from those of aggregate variables such as total biomass or production at the community or ecosystem level (Micheli et al. 1999).

The results from recent (Tilman and Downing 1994, Tilman 1996, McGrady-Steed et al. 1997, Naeem and Li 1997) as well as older (McNaughton 1977) experiments have suggested that biodiversity increases the resilience and resistance of ecosystem processes and decreases their variability, all properties pointing to greater stability. Note that some of these authors have used new terms to describe stability properties of ecosystem processes, such as 'reliability' (Naeem 1998) and 'predictability' (McGrady-Steed et al. 1997), but these terms can be subsumed under the classical concepts of persistence and variability. These results seem to contradict the theory that has prevailed for more than 20 years, which predicts lower stability in more diverse and more complex systems (May 1972, 1973). There are two ways to resolve this apparent contradiction: either the experiments are flawed, or the theory is inadequate to explain such results. There are problems with the experiments (Givnish 1994, Huston 1997, Wardle 1998). In particular, no experiment so far has controlled temporal variability or perturbations directly. However, Tilman (1996) found a significant positive effect of species diversity on the resistance of total plant biomass to drought in a multiple regression that included potentially confounding factors in the previous analysis of Tilman and Downing (1994). On the other hand, the effect of species diversity on the resilience of total plant biomass after drought disappeared when potentially confounding factors were taken into account. Tilman (1996) also found a significantly lower year-to-year variability in total plant biomass in plots with greater species richness, a pattern that was also found in aquatic microcosms by McGrady-Steed et al. (1997) and Naeem and Li (1997). Thus, although the experiments performed so far are insufficient to unambiguously demonstrate positive effects of diversity on the stability of aggregate ecosystem properties, they strongly suggest such effects on temporal variability and resistance.

So to the theory. May's (1972, 1973) theory essentially concerned the demographic mathematical stability of the populations that compose the ecosystem, not the stability of processes at the ecosystem level. Based on his empirical data on temporal fluctuations of plant populations, Tilman (1996) suggested a resolution of the apparent contradiction between the theory and the experiments: a greater diversity would destabilise individual populations but stabilise aggregate community or ecosystem properties. What is the theoretical support for this hypothesis?

We first investigated this hypothesis following the classical approaches for the analysis of the local stabil-

ity of an equilibrium (Loreau and Behera 1999). Again we used the mechanistic model of plant competition for a limiting nutrient presented above (Loreau 1996, 1998a), but in its simplest possible configuration, i.e., with only two plant species. Two plant traits were allowed to vary: nutrient uptake rate and mortality rate. Phenotypic diversity was measured by the difference between the trait values of the two species while the average trait value was kept constant. Resilience, which quantifies the speed of return to equilibrium after a pulse perturbation, was measured by the absolute value of the dominant eigenvalue of the Jacobian matrix evaluated at equilibrium. Resistance of an ecosystem stock or process was measured by its ultimate displacement from its equilibrium value following a press perturbation of the trait values. We showed that, except in very special cases, resilience characterises the system as a whole, and thus applies to aggregate ecosystem processes as well as to individual populations. As a rule, this tends to decrease with increased phenotypic diversity. On the other hand, resistance is a property that characterises each system component and process separately. But the resistance of ecosystem stocks and processes either monotonically decreases or increases over part of the parameter range with increased diversity. Furthermore, it is very sensitive to parameter values. Thus, these results support the view that there is no simple relationship between diversity and stability in equilibrium deterministic systems, whether at the level of populations or aggregate ecosystem processes.

There are probably two critical factors that explain the difference between this theoretical approach and previous experiments. First, in our model, the effect of phenotypic diversity was studied per se, while keeping average parameter values constant. In Tilman and Downing's (1994, Tilman 1996) experiment, drought was a 'negative' perturbation overall, which had a negative effect on most species simultaneously. This amounts to changing both the difference and the average of trait values simultaneously. There are good reasons to believe that diversity should have a positive effect on the resistance of total plant biomass in the case of a 'negative' perturbation. Increasing phenotypic diversity increases the probability of having species that are less negatively affected by the perturbation, and these species should tend to become dominant in the community because they are best adapted to the conditions prevailing during the perturbation. But the same argument suggests that the resistance of plant biomass should also be lower in the case of a 'positive' perturbation, i.e., a perturbation that has an intrinsically positive effect on the biomass of most species (before competition has taken place), such as might be the case with nitrogen addition for instance. In this case indeed, increasing phenotypic diversity increases the probability to have species that are more positively affected by the perturbation, and these species should tend to become

dominant in the community. Thus, resistance of ecosystem processes may still either increase or decrease depending on the type of perturbation. It is interesting to note, however, that in both cases, diversity should have a positive effect on ecosystem processes through the same selection mechanism discussed in the first section: biodiversity increases the range of trait variation, and a selective process promotes dominance by species with extreme trait values.

The second critical factor that may explain the discrepancy between theory and experiments is a fundamental limitation in the classical theoretical approaches to stability, which are based on a deterministic, equilibrium view of ecological systems. The equilibrium concept may be a valid approximation for some processes on some scales, but nonequilibrium processes generally abound (DeAngelis and Waterhouse 1987). Most empirical work has studied a stability property – temporal variability – that does not lend itself to an equilibrium analysis (Tilman 1996, McGrady-Steed et al. 1997, Naeem and Li 1997, Petchey et al. 1999). And the cause of the stabilising influence of diversity on ecosystem processes may lie precisely in fluctuations away from equilibrium from the component populations (Walker 1992, Lawton and Brown 1993, Yachi and Loreau 1999). Several authors have proposed different theoretical treatments of this issue independently (Doak et al. 1998, Naeem 1998, Yachi and Loreau 1999).

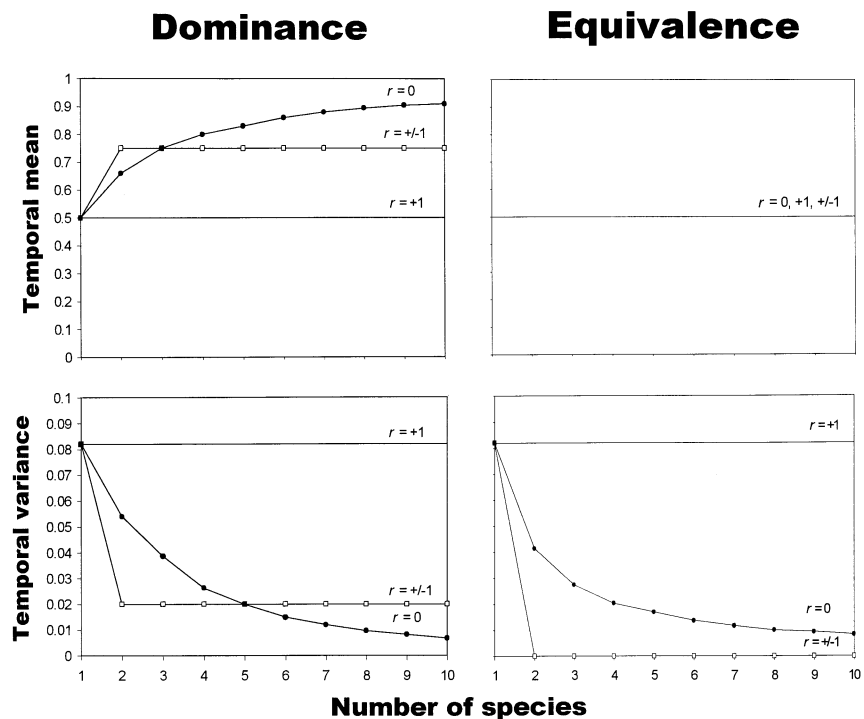
The basic idea behind this theoretical approach was already expressed clearly by Patten (1975) in a provocative contribution 25 years ago: “The aggregate of large numbers of individual events gives a smooth result. In general, ecosystem complexity confers behavioral regularity. With so many cross-currents of interaction occurring simultaneously in the interconnection network, behavioral details in microscale tend to smooth out at the whole-system level. Different spatial and temporal scales of processes, and statistical variability in their operation, also tend to average out in their net system effects” (p. 531). Doak et al. (1998) re-discovered this general idea and applied it concretely to the effect of species richness on variability of total community biomass. They made a simple but cogent point: in communities with independently fluctuating populations and the same average total biomass, the temporal variation in total biomass is expected to decrease, and thus stability is expected to increase, as species diversity increases because of the statistical averaging of the fluctuations in species abundances. This elementary statistical effect is sufficient to explain the positive effect of diversity on community stability (assessed by some inverse measure of temporal variability) irrespective of species interactions, although its actual strength is determined by the relative abundances of species, as well as by the existence of positive or negative correlations in the fluctuations of species abundances. These results

led Doak et al. (1998) to conclude “the statistical inevitability of stability–diversity relationships in community ecology”.

The phrase ‘statistical inevitability’ was unfortunate because nothing is inevitable in a probabilistic world; any statistical effect ultimately requires an explanation in ecological terms. In particular, Tilman et al. (1998) showed that Doak et al.’s (1998) demonstration rested on the implicit assumption that the temporal variance in the abundance of each species scaled with the square of the mean, and extended their results to arbitrary power-law relationships between the variance and the mean. Applying their more general formula to Tilman’s (1996) empirical data, they found that statistical averaging was likely to contribute to stability, though to a lesser extent than Doak et al. (1998) suggested. They also stressed the potential importance of negative covariances between fluctuations of species abundances driven by competitive interactions between species. This argument was further elaborated by Tilman (1999) using a model of resource competition in a habitat that experiences temperature fluctuations, with each species having its maximal competitive ability at a different temperature. It is still unclear, however, to what extent species interactions are important in driving stability–diversity relationships. Hughes and Roughgarden (1998) and Ives et al. (1999) used first-order autoregression models to approximate the temporal variances in species abundances in competitive systems, and showed that the strength of interspecific competitive interactions has little effect on the stability–diversity relationship. On the other hand, the degree of asymmetry of competitive interactions appears to be important (Hughes and Roughgarden 1998). I believe that this debate over the role of species interactions, interesting as it is in its own right, should not obscure the fundamental conclusion that greater diversity is expected to reduce the variability of aggregate ecosystem processes.

This fundamental conclusion was emphasised in our work on the same issue (Yachi and Loreau 1999). We followed a slightly different approach. Instead of starting from given statistical relationships between the variance and the mean or from models of species interactions, we started from a description of the way individual species respond to environmental fluctuations. We built a stochastic dynamical model based on two assumptions only: (1) the productivity of each species obeys a stochastic process in response to environmental fluctuations, and (2) it fluctuates within the same range for all species (although this second assumption was chosen for convenience and can be relaxed easily). There was no restriction either on the probability density distributions of species responses or on within- and between-species temporal correlations in responses. Total productivity at the ecosystem level at each time was then determined according to one of two rules: (1) determination by equivalence, in which inter-

Fig. 4. Effects of species richness on the expected temporal mean (top) and variance (bottom) of ecosystem productivity in a fluctuating environment, in the two cases of determination by dominance (left) and determination by equivalence (right). r is the correlation coefficient of species responses; $r = 0$, $+1$, and $+/-1$ correspond to the cases of independent responses, perfect positive correlation, and perfect correlation (including negative correlation), respectively. The probability density distribution is here assumed to be a uniform distribution on $[0, 1]$. Adapted from Yachi and Loreau (1999).



specific competitive interactions are negligible, so that all species contribute equally to ecosystem productivity and the latter is simply the average of the various species' productivities; (2) determination by dominance, in which interspecific competition is strong and ecosystem productivity is approximated by the productivity of the most productive species, as in the sampling effect. These two rules can be thought of as two limiting cases, between which reality should generally lie.

The analysis of this model has both generalised and clarified the results obtained in other studies in several respects. First, it showed two types of biodiversity effects on ecosystem productivity in a fluctuating environment (Fig. 4): (1) the stabilising effect also found by the other authors, which we preferred to call more precisely a *buffering effect*, i.e., a reduction in the temporal variance (or other measures of variability) of ecosystem productivity; but also (2) a *performance-enhancing effect*, i.e., an increase in the temporal mean of ecosystem productivity. Because, through both these effects, species diversity contributes to maintain or enhance ecosystem functioning in the face of environmental fluctuations, we called them *insurance effects* of biodiversity. Second, our model identified the mechanisms involved in these two effects. The buffering effect generally occurs under both determination rules, but disappears when there is perfect positive correlation between the various species' responses (Fig. 4). Thus its fundamental basis lies in the *asynchrony of species responses* rather than in the absolute strength of competitive interactions. This asynchrony can be inter-

preted as a form of *temporal niche differentiation* between species, which shows that its stochastic nature does not make it 'statistically inevitable': it has a biological basis. Note that temporal niche differentiation, just as functional niche differentiation, promotes species coexistence (Chesson 1991, Chesson and Huntly 1997). Thus, here again, the conditions that promote coexistence within communities are involved in biodiversity effects on community-level properties. The performance-enhancing effect is an additional effect that occurs under the rule of determination by dominance (Fig. 4). Its basis is that of the selection effect: biodiversity increases the range of trait variation available at any time, and a *selective process* such as interspecific competition promotes dominance by species that perform best under the current environmental conditions. This effect does not require complete dominance by the best performing species; a slight selective advantage may suffice to generate it. Note that negative selection effects are also theoretically possible, just as in the short term, a possibility that has not been explored so far. It is likely, however, that on a long enough time scale or with large enough environmental variations, the mere persistence of species able to perform an ecosystem process will have more significant effects than any possible trade-off between traits, and thus positive selection effects will outweigh negative selection effects.

Together these studies provide a strong theoretical foundation for the idea that biodiversity acts as a 'biological insurance' against the disruptive effects of environmental fluctuations on ecosystem functioning.

The basic mechanisms involved in these long-term insurance effects are very similar to those that operate in short-term biodiversity effects: temporal niche complementarity, and selection of extreme trait values. The selection effect is likely to be important in a long-term perspective. In the long term, neither the environmental changes nor the responses of species to them are completely predictable. Therefore, the ability of species diversity to provide a reservoir of variation allowing adaptation to changing conditions may be critical, and parallels the importance of genetic diversity in the evolutionary process. Minor or transient species in a community may substitute for dominant species and maintain ecosystem processes under changing conditions (Grime 1998, Walker et al. 1999). This conclusion is supported by recent experimental evidence (Petchey et al. 1999). Therefore Sankaran and McNaughton's (1999) warning that species-rich ecosystems may not cope better than species-poor ones in the face of perturbations because of greater changes in species composition and relative abundances is inopportune. It is precisely this compositional variability that provides the basis for the maintenance of ecosystem processes in a changing environment.

An important limitation of these studies, however, is that they have considered a single trophic level, usually plants. Ives et al. (2000) recently generalised the insurance hypothesis to model communities constructed from modular multi-trophic-level subcommunities. Naeem (1998) proposed another approach taken from engineering to investigate the reliability (i.e., the probability of persistence) of multi-trophic-level ecosystems, which suggests similar patterns, that is, the higher the number of species within a trophic level, the lower the probability that a particular ecosystem process will fail, and hence the higher ecosystem reliability. Although his approach had some technical weaknesses (Rastetter et al. 1999) and is based on a special food-web structure in which species within a trophic level behave like parallel elements, his overall conclusions are likely to be relatively robust. Borrvall et al. (2000) have recently revisited classical Lotka–Volterra models of food webs studied by Pimm (1979), and found that increasing the number of species within a trophic level decreases the risk of losing additional species after an extinction event, thus increasing resistance to further extinctions. In a slightly different vein, using more complex nonlinear models, McCann et al. (1998) suggested that greater food-web complexity could dampen population oscillations through the addition of weak trophic links. Thus, recent studies point to stabilising influences of diversity and complexity on ecological systems even at the level of individual component populations in fluctuating environments, although there is as yet no experimental evidence for this hypothesis (Petchey et al. 1999). It may be too early to draw general conclusions from this scattered work, but it is becoming clearer and clearer

that a major reappraisal of the paradigm that has dominated during the last decades, based on an equilibrium analysis, is inevitable if we are to account for nonequilibrium processes and compensations among species.

Conclusions and perspectives

Lawton (1999) recently drew a dark picture of the current situation of community ecology, “where there are a large number of case histories, and very little other than weak, fuzzy generalisations”. The community is indeed the hierarchical level where the basic characteristics of life – its diversity, complexity, and historical nature – are perhaps the most daunting and challenging. Community ecology has had difficulties in developing new perspectives in recent years. Paradoxically, however, most of the theoretical insights that have been gained about the effects of biodiversity on ecosystem functioning come from approaches developed in community ecology. By linking itself to ecosystem ecology and focusing on questions that need urgent answers, community ecology may find a new impetus and renew itself. The same message also holds for the other partner in this association, i.e., ecosystem ecology. It is high time that the approaches of community and ecosystem ecology, which are actually two different perspectives on the same material reality, be merged into a new ecological synthesis.

The recent theoretical developments in the area of biodiversity and ecosystem functioning do suggest that this interface between community and ecosystem ecology is a fruitful avenue. Although studies in this area are new and still limited in number, significant advances have been made. Different types of mechanisms that may drive the short-term effects of biodiversity on ecosystem processes have been identified, methods to separate them have been proposed, major differences between within-site effects of biodiversity and across-site productivity–diversity patterns have been clarified, different long-term effects of biodiversity on ecosystem processes and their temporal variability in fluctuating environments have been demonstrated, and their mechanisms have been analysed. Finally, new perspectives are suggested on the long-standing problem of the relationship between the stability and diversity of ecological systems. It is encouraging that these results have come from work conducted over the last three years.

This is only the beginning, however, not the end. None of the questions can be considered to have received a definitive answer (as far as this can exist at all). One of the urgent needs now is to extend theories and models to full ecosystems with multiple trophic levels and functional groups, including microbial and animal biodiversity. Another critical issue that needs to be

addressed is the spatial dimension of the relationship between biodiversity and functional processes: how to scale up from a small patch, to which most of recent experimental and theoretical studies apply, to the landscape scale, at which most management issues are dealt with? A third problem that would merit exploration in the future concerns the ecosystem consequences of the evolutionary processes that are involved in the origin, maintenance and dynamics of biodiversity. Attempts to approach the evolutionary dimension of ecosystem functioning have been very few so far (Loreau 1998c), and yet might yield important insights into the present relationship between biodiversity and ecosystem processes. Lastly, more effort could be profitably devoted to the definition and application of the concepts of functional groups and functional diversity. Hulot et al. (2000) recently showed that the identification of appropriate functional groups within trophic levels significantly improved the prediction of the response of lake ecosystems to nutrient enrichment compared with the predictions of classical linear food-chain models. Functional groups are simply a convenient way of categorising phenotypic or functional diversity, and thus should depend on the type of ecosystem process considered. In particular, they are likely to differ for short-term and long-term biodiversity effects. Objective identification of functional groups is therefore of great potential interest (MacGillivray et al. 1995, Lavorel et al. 1997, Hulot et al. 2000).

A striking feature of all the questions evoked here and earlier is that they are important both to progress in basic science and to provide guidance in the management and conservation of our planet. This is another example showing that academic interest can go hand in hand with the search for answers to societal concerns on questions of general interest. Theoretical ecology, and ecology in general, can, and should, also be a guide for action. There are plenty of exciting challenges ahead of us, only awaiting our enthusiasm, earnestness and creativity.

Acknowledgements – I thank Andy Gonzalez, Andy Hector, Pablo Inchausti, Hal Mooney, Jacques Roy, David Wardle and Shigeo Yachi for helpful comments on the manuscript. This work was supported by CNRS GDR 1936 DIV-ECO.

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