
Biodiversity and Ecosystem Functioning

Synthesis and Perspectives

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OXFORD
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Great Clarendon Street, Oxford OX2 6DP

Oxford University Press is a department of the University of Oxford.
It furthers the University's objective of excellence in research, scholarship,
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Oxford New York

Auckland Bangkok Buenos Aires Cape Town Chennai
Dar es Salaam Delhi Hong Kong Istanbul Karachi Kolkata
Kuala Lumpur Madrid Melbourne Mexico City Mumbai Nairobi
Sao Paulo Shanghai Taipei Tokyo Toronto
with an associated company in Berlin

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Published in the United States
by Oxford University Press Inc., New York

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First published 2002

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A Catalogue record for this title is available from the British Library

Library of Congress Cataloging in Publication Data
(Data available)

ISBN 0 19 851570 7 (Hbk)

ISBN 0 19 851571 5 (Pbk)

10 9 8 7 6 5 4 3 2 1

Typeset by Newgen Imaging Systems (P) Ltd, Chennai, India
Printed in Great Britain
on acid-free paper by The Bath Press, Avon

Perspectives and challenges

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Few areas of ecology have expanded as fast as biodiversity and ecosystem functioning research during the last few years. Starting from simple intuitive hypotheses, this scientific area has generated a new wave of ambitious experiments using synthesized model ecosystems in both terrestrial and aquatic environments, it has stimulated the emergence of new theoretical approaches linking concepts and perspectives from community ecology and ecosystem ecology, and it has more broadly renewed interest in synthetic approaches in ecology, cutting across increasingly specialized ecological sub-disciplines.

These exciting scientific developments have also been accompanied by an animated debate over the interpretation and implications of recent experiments, as is almost inevitable in any new area (Naeem *et al.*, Chapter 1; Mooney, Chapter 2). This volume, as well as the review paper that we have recently co-authored with the main protagonists in the debate (Loreau *et al.* 2001), are testimony to the fact that such scientific debates can be resolved with three main ingredients: an open mind, an appropriate conceptual and theoretical framework, and strong data. Although the debate is not over, we believe that the work performed during and around the Synthesis Conference does provide the bases for its resolution.

In this concluding chapter, we offer some reflections on where we stand today and how the biodiversity and ecosystem functioning area can profitably be developed in the future.

20.1 Resolving the debate over biodiversity effects in small-scale experiments

The controversy over the interpretation of the biodiversity experiments started with the

realization that their results can be generated by different mechanisms. The mechanisms discussed so far may be grouped into two main classes. First are local deterministic processes, such as niche differentiation and facilitation, which increase the performance of communities above that expected from the performance of individual species grown alone, and which we subsume here under the term 'complementarity' for convenience. Second are local and regional stochastic processes involved in community assembly, which are mimicked in recent experiments by random sampling from a species pool. Random sampling coupled with ecological 'selection' of highly productive species can also lead to increased average primary production with diversity because plots that include many species have a higher probability of containing highly productive species (Huston 1997; Aarssen 1997; Tilman *et al.* 1997b). Two major issues are involved in this controversy: (i) are stochastic community assembly processes relevant? (ii) what is the relative importance of the two classes of mechanisms? A third, related issue concerns the extent to which such mechanisms can be detected in observational studies or in natural systems where extrinsic factors, such as site fertility, disturbance, or climate, covary with biodiversity (see below).

There have been diverging views on the relevance of the sampling component of biodiversity effects. As sampling processes were not an explicit part of the initial hypotheses, they have been viewed by some as 'hidden treatments' (Huston 1997), whereas others have viewed them as the simplest possible mechanism linking diversity and ecosystem functioning (Tilman *et al.* 1997b). Resolving this part of the debate requires increasing knowledge about the patterns and processes of biodiversity loss in nature, which are still poorly known overall. If dominant species control

ecosystem processes and mostly rare species go extinct, the vagaries of community assembly or disassembly may have little relevance for the impact of biodiversity loss on natural ecosystems. But environmental changes and landscape fragmentation could prevent recruitment of appropriate dominants (Grime 1998). Also, climate change could lead to gradual losses of species as abiotic conditions begin to exceed species' tolerance limits. Such losses could be random with respect to species effects on any given ecosystem process, leading to patterns of process response to changes in diversity similar to those observed in randomly assembled communities. It should be recalled here that recent experiments were not intended to reproduce any particular sequence of species loss. They were designed to test theoretical hypotheses (Naeem *et al.*, Chapter 1), and thus reflect potential patterns, unaffected by correlations between diversity loss and compositional changes, rather than actual predictions of functional consequences of biodiversity loss under specific global change scenarios.

Recent experiments were also not designed to directly test underlying biological mechanisms. Assessing the relative importance of complementarity and sampling or selection effects has so far been done indirectly, using comparisons between

the performances of mixtures and monocultures (Tilman *et al.*, Chapter 3; Hector *et al.*, Chapter 4). Furthermore, it is becoming clear that complementarity and sampling are not mutually exclusive mechanisms as previously thought. Communities with more species have a greater probability of containing a higher phenotypic trait diversity. Ecological 'selection' that leads to dominance of species with particular traits, and complementarity among species with different traits are two ways by which this phenotypic diversity maps onto ecosystem processes. These two mechanisms, however, may be viewed as two poles on a continuum from pure selection to pure complementarity. Intermediate scenarios involve complementarity among particular sets of species or functional groups, or selection of particular subsets of complementary species (Fig. 20.1). Any bias in community assembly that leads to correlations between diversity and community composition may involve both selection and complementarity effects.

Rigorously testing the hypothesis that there is a minimum subset of complementary species that is sufficient to explain diversity effects will often be difficult because it would ideally require testing, with replication, the performance of all species combinations at all diversity levels. Analysis of data from both the Cedar Creek and BIODEPTH

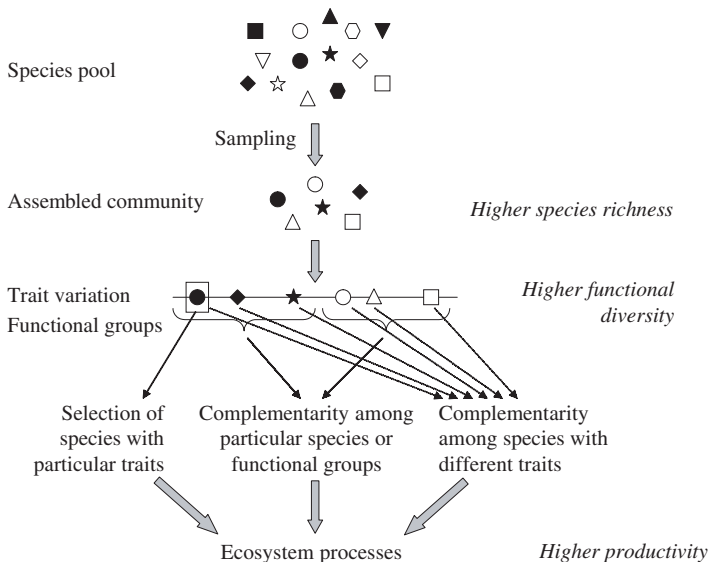


Figure 20.1 Hypothesized mechanisms involved in biodiversity experiments using synthetic communities. Sampling effects are involved in community assembly, such that communities that have more species have a greater probability of containing a higher phenotypic trait diversity. Phenotypic diversity then maps onto ecosystem processes through two main mechanisms: selection of species with particular traits, and complementarity among species with different traits. Intermediate scenarios involve complementarity among particular species or functional groups or, equivalently, selection of particular subsets of complementary species. Modified from Loreau *et al.* (2001).

experiments shows significant effects of species richness on plant biomass even after controlling for the strong effects of certain species, such as legumes (Tilman *et al.*, Chapter 3; Hector *et al.*, Chapter 4). Thus, these results imply that complementarity does occur among at least several species belonging to different functional groups in these experiments. Huston and McBride (Chapter 5) challenge these results, and propose a new hypothesis which combines two-species selection, 'variance reduction' and 'quasi-replication' effects to account for the observed effects. We emphasize, however, that the nature of the debate has changed qualitatively in the process. Previous debate focused on whether single-species selection effects driven by dominant species are sufficient to explain results from biodiversity experiments. Now that the initial hypothesis of single-species selection effects has been rejected in several experiments (Tilman *et al.*, Chapter 3; Hector *et al.*, Chapter 4), the debate is moving to multiple-species selection effects, which, as we discussed above, necessarily involve complementarity. Thus, the borderline between selection and complementarity is vanishing, which, in principle, should facilitate resolution of the debate.

New tests of multiple-species selection effects would be useful to reach the final resolution of this debate. As the many contributions in this volume suggest, however, this debate will no longer be as prominent as it once was. We are reaching a point where it is becoming fruitful to turn to other issues and new experiments. Future experiments should strive to overcome the limitations that led to the recent controversy. Schmid *et al.* (Chapter 6) provide several recommendations and suggestions along this line. Testing biological mechanisms directly and testing more realistic species loss scenarios are two obvious ways to progress in this area.

20.2 Generalizing across ecosystems and trophic levels

Most of the recent experiments that found significant effects of species diversity (Tilman *et al.*, Chapter 3; Hector *et al.*, Chapter 4) have concerned effects of plant diversity on primary production

and nutrient retention in temperate grasslands, both of which are under direct plant control. These experiments have often failed to detect significant effects on below-ground decomposition processes (Naeem *et al.* 1994a; Hector *et al.* 2000a; Knops *et al.* 2001), perhaps because these processes are under microbial control. This questions whether results obtained on primary production in grasslands can be generalized to other processes and ecosystems.

Wardle and van der Putten (Chapter 14) and Mikola *et al.* (Chapter 15) review a large number of studies that addressed effects of species or functional diversity on below-ground soil processes and linkages between above-ground and below-ground processes. The overall conclusion that seems to emerge from this overview is that the complexity of soil biodiversity and the processes they govern defy generality. In contrast, van der Heijden and Cornelissen (Chapter 16) suggest that the diversity of symbiotic mycorrhizal microorganisms is critical for the maintenance of both plant diversity and plant-based ecosystem processes. It would therefore be of interest to revisit the functional role of soil biodiversity using new experiments and new hypotheses based on more solid theory. Of particular importance are the vast areas of biodiversity that involve small organisms such as viruses, bacteria, archaea, protists, microarthropods and nematodes that drive the bulk of ecosystem processes. Modern molecular tools are beginning to make possible the integration of microbial diversity into studies of ecosystem processes (Øvreås 2000).

There have been remarkably few theoretical and experimental investigations into the functional impacts of diversity at higher trophic levels. Yet interesting complex biodiversity effects on ecosystem processes may be expected at these levels. Complementarity and selection effects should tend to improve resource exploitation just as in plants. This should lead to higher secondary productivity if bottom-up control prevails, as in plant-decomposer interactions. But enhanced resource exploitation can also lead to overexploitation, and thus decreased productivity, if top-down control is important, as might be the case with herbivores and predators. Raffaelli *et al.* (Chapter 13) review

our current level of knowledge—and ignorance—in this area, and plea eloquently for the establishment of a link between classical food-web theory and modern biodiversity–ecosystem functioning research.

There is also a need to extend our current knowledge to ecosystem types other than temperate grasslands. Aquatic microcosms have proved a particularly valuable tool to test theoretical hypotheses in the biodiversity–ecosystem functioning area (Petchey *et al.*, Chapter 11). But field experimental studies in freshwater and marine ecosystems have been scarce (Emmerson and Huxham, Chapter 12). Forests constitute other important biomes that have been neglected so far. Generalizing across ecosystems is not simply useful for the sake of accumulating knowledge: differences in coexistence mechanisms may lead to differences in biodiversity effects on ecosystem functioning, and thus significant differences may be expected between ecosystem types just as between trophic levels (Bengtsson *et al.*, Chapter 18).

20.3 Scaling-up in space and time

Experiments performed at small spatial and temporal scales are likely to underestimate the functional role of biodiversity because different species have different requirements and typically replace each other along spatial and temporal gradients. Even when high diversity is not critical for maintaining ecosystem processes under constant or benign environmental conditions, it might nevertheless be important for maintaining them under changing conditions. The insurance hypothesis and related hypotheses propose that biodiversity provides a buffer against environmental fluctuations because different species respond differently to these fluctuations, leading to more predictable aggregate community or ecosystem properties (Loreau *et al.*, Chapter 7).

Recent theoretical developments on these issues are relatively solid, and provide new perspectives on the long-standing debate on the relationship between stability and diversity (Loreau *et al.*, Chapter 7; Hughes *et al.*, Chapter 8). The experimental

evidence for these hypotheses, however, is still comparatively thin (Loreau *et al.*, Chapter 7; de Ruiter *et al.*, Chapter 9). An important step forward on this issue would be to design experiments in which long-term environmental variability is directly manipulated to test the potentially important role that environmental fluctuations may play as both the creator and driver of the conditions necessary for the existence of compensatory dynamics among species. Another issue on which greater understanding would be desirable concerns the mechanisms that govern the effects of species diversity on community invasion resistance (Levine *et al.*, Chapter 10). Few theoretical studies have addressed this issue, and explanations are still largely intuitive.

Just as diversity allows functional compensations between species through time, it allows functional compensations through space. The larger the spatial scale, the greater the environmental heterogeneity, and the higher the biological diversity that should be needed to take full advantage of these environmental differences. One of the most potent effects of declining diversity, however, could be the decline in the rate at which appropriate dominant species or combinations of species are recruited during ecosystem assembly. Diversity loss at regional scales and dispersal limitations due to landscape fragmentation may reduce the pool of potential colonists at local scales, and hence the potential for local compositional adjustments to environmental changes. Functional effects of biodiversity changes at landscape to regional scales have been virtually ignored so far, and yet may be particularly important and complex (Bengtsson *et al.*, Chapter 18). These larger scales are all the more critical to investigate since it is at these scales that management and policy decisions usually take place.

20.4 Linking biodiversity dynamics and ecosystem functioning

As one turns to larger spatial and temporal scales, the processes that are responsible for the generation, maintenance and loss of biodiversity are likely to be increasingly important in determining the

relationship between diversity and ecosystem functioning. Recent experiments have examined whether diversity alone has a local effect on productivity when all other environmental factors are held constant. This was a historically necessary step to assess and understand the direct causal effect of diversity on ecosystem functioning, which is otherwise hidden by variation in a host of other environmental factors (Lawton *et al.* 1998; Loreau 1998a). Once this causal relationship has been established, we are in a position to return to natural and managed ecosystems, and ask how environmental changes, such as changes in soil, climate and land use, or management regimes affect biodiversity, ecosystem functioning, and the interaction between them. This important step is not only necessary from an applied or management perspective, it also raises new and interesting questions from a basic science perspective. In particular, it allows us to re-establish a much needed link between controlled experiments and natural patterns. Natural patterns of both diversity and ecosystem processes such as productivity and nutrient cycling indicate a variety of relationships between these factors (Bengtsson *et al.*, Chapter 18). What are the respective effects of abiotic factors, such as soil and climate, on diversity, of abiotic factors on productivity, and of diversity on productivity in these patterns? Separation of these effects should become possible, and would allow us to develop a more predictive ecological science. Prediction of future impacts of global change scenarios is another obvious area in which this approach should deliver important results. Experiments have begun to investigate interactions between changes in biodiversity and other components of global change, such as warming, increase in CO₂ concentration and nitrogen deposition (Petchev *et al.* 1999; Reich *et al.* 2001). Understanding the nature of these interactions will be increasingly important in the future.

To understand and predict changes in biodiversity and ecosystem processes at large scales, therefore, we need to move beyond unidirectional causality approaches in which diversity is either cause or effect, and address feedbacks among biodiversity dynamics, ecosystem functioning and environmental factors (Loreau *et al.* 2001). This is a fundamental shift which requires new theoretical, experimental and observational approaches. In

recent experimental and theoretical studies, diversity has been manipulated as an independent variable. In reality, biodiversity is itself a dynamic variable, which depends on both extrinsic and intrinsic, abiotic and biotic factors, including the complex interactions which develop among the organisms that make up this biodiversity. Different kinds of interactions between species, and between species and their environment, are known to produce different levels of species diversity, and are equally likely to impose different constraints on the relationship between diversity and ecosystem processes. This simple theoretical observation has far-reaching consequences. Community ecology has been traditionally concerned with the factors that generate and maintain diversity. Merging this perspective with the new perspective on the functional role of biodiversity has the potential to further promote the integration of community ecology and ecosystem ecology, which has already been greatly stimulated by the emergence of the biodiversity–ecosystem functioning area.

In fact, its integration potential goes beyond the borders of ecology, and includes evolutionary biology. Evolutionary constraints have been recognized for a long time in community ecology, but have often been ignored in ecosystem ecology. Yet current ecosystems are the product of past evolution, and ecosystem processes impose constraints on the natural selection of species traits (Loreau 2002). New theoretical and experimental approaches are beginning to tackle the natural selection of ecosystem properties, such as primary productivity, secondary productivity and nutrient cycling efficiency, as the result of evolution of species traits, such as plant and decomposer resource competitive abilities (Loreau 1998b; Swenson *et al.* 2000; de Mazancourt *et al.* 2001; Yamamura *et al.* in press). Incorporating evolutionary constraints and trade-offs responsible for the maintenance of species diversity into such approaches would be an exciting development, which would help bring about a broader synthesis of community, evolutionary and ecosystem ecology. Interestingly, evolutionary concepts, theories, and even equations are already finding striking ecological analogues in the biodiversity–ecosystem functioning area (Loreau and Hector 2001; Norberg *et al.* 2001).

20.5 Conclusion

The biodiversity–ecosystem functioning research programme has been extremely successful in recent years. It has attracted a lot of interest, has made major advances in our understanding of ecological systems, and has pushed towards integration across ecological subdisciplines. The challenges that lie ahead of us, which we have tried to identify in this chapter, are equally exciting from a basic science perspective.

The emergence of this new scientific interface was motivated by a simple but pressing question: Can the current decline in biodiversity alter the functioning and stability of ecosystems and of the Earth system? As evidenced throughout this volume, the answer to this question is ‘yes’, but there are many intricacies, uncertainties and questioning behind this deceptively simple answer. This answer nevertheless urges adoption of a precautionary approach to biodiversity management and conservation, but we still have some way to go before it can be translated into more concrete, practical recommendations for policy and management decisions from local to global scales.

Despite our current limited ability to deliver quantitative predictions, the social and economic implications of biodiversity–ecosystem functioning research should not be lost from sight. More efforts should be devoted to effects of biodiversity on ecosystem processes that generate ‘ecosystem services’ of relevance to human societies. The

relationship between biodiversity and ecosystem processes and ‘services’ in managed ecosystems deserves greater attention—a call which seems particularly appropriate since agro-ecology was in several ways a predecessor of the current interest in the productivity of diverse assemblages (Vandermeer *et al.*, Chapter 19). It is perhaps in a management perspective that functional classifications of biodiversity are most important. Specific knowledge of functional types may be critical to predict ecosystem responses under different global change scenarios, or where management priorities seek to manipulate species composition directly, for example in complex agro-ecosystems, forestry, or ecosystem restoration with particular functional goals in mind (Hooper *et al.*, Chapter 17). We have, however, to keep in mind that the predictability of ecological systems is intrinsically limited, and that no functional classification will spare us the need to be prepared to expect the unexpected (Holling 1986).

After nearly a decade of research, it is becoming clear that biodiversity can no longer be regarded as a passive reflection of static abiotic constraints and biotic interactions within communities, but is itself a dynamic component of local and global environmental changes. We are confident that the closer integration of ecological subdisciplines fostered by the biodiversity–ecosystem functioning research programme will help science and society to meet the challenges of human-induced global change.