

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

Contents

Contributors	x
PART I Introduction	
1 Biodiversity and ecosystem functioning: the emergence of a synthetic ecological framework	3
<i>S. Naeem, M. Loreau, and P. Inchausti</i>	
2 The debate on the role of biodiversity in ecosystem functioning	12
<i>H. A. Mooney</i>	
PART II Core areas of debate: biodiversity and ecosystem processes in grassland ecosystems	
3 Plant diversity and composition: effects on productivity and nutrient dynamics of experimental grasslands	21
<i>D. Tilman, J. Knops, D. Wedin, and P. Reich</i>	
4 Biodiversity manipulation experiments: studies replicated at multiple sites	36
<i>A. Hector, M. Loreau, B. Schmid, and the BIODEPTH project</i>	
5 Evaluating the relative strengths of biotic versus abiotic controls on ecosystem processes	47
<i>M. A. Huston and A. C. McBride</i>	
6 The design and analysis of biodiversity experiments	61
<i>B. Schmid, A. Hector, M. A. Huston, P. Inchausti, I. Nijs, P. W. Leadley, and D. Tilman</i>	
PART III New perspectives on ecosystem stability	
7 A new look at the relationship between diversity and stability	79
<i>M. Loreau, A. Downing, M. Emmerson, A. Gonzalez, J. Hughes, P. Inchausti, J. Joshi, J. Norberg, and O. Sala</i>	
8 Do species interactions buffer environmental variation (in theory)?	92
<i>J. B. Hughes, A. R. Ives, and J. Norberg</i>	

9 Biodiversity and stability in soil ecosystems: patterns, processes and the effects of disturbance	102
<i>P. C. de Ruiter, B. Griffiths, and J. C. Moore</i>	
10 Neighbourhood scale effects of species diversity on biological invasions and their relationship to community patterns	114
<i>J. M. Levine, T. Kennedy, and S. Naeem</i>	
PART IV Extending the scope to other systems	
11 Contributions of aquatic model systems to our understanding of biodiversity and ecosystem functioning	127
<i>O. L. Petchey, P. J. Morin, F. D. Hulot, M. Loreau, J. McGrady-Steed, and S. Naeem</i>	
12 How can marine ecology contribute to the biodiversity–ecosystem functioning debate?	139
<i>M. Emmerson and M. Huxham</i>	
13 Multi-trophic dynamics and ecosystem processes	147
<i>D. Raffaelli, W. H. van der Putten, L. Persson, D. A. Wardle, O. L. Petchey, J. Koricheva, M. van der Heijden, J. Mikola, and T. Kennedy</i>	
14 Biodiversity, ecosystem functioning and above-ground–below-ground linkages	155
<i>D. A. Wardle and W. H. van der Putten</i>	
15 Biodiversity, ecosystem functioning and soil decomposer food webs	169
<i>J. Mikola, R. D. Bardgett, and K. Hedlund</i>	
16 The critical role of plant–microbe interactions on biodiversity and ecosystem functioning: arbuscular mycorrhizal associations as an example	181
<i>M. G. A. van der Heijden and J. H. C. Cornelissen</i>	
PART V Extending the scope to other dimensions	
17 Species diversity, functional diversity, and ecosystem functioning	195
<i>D. U. Hooper, M. Solan, A. Symstad, S. Díaz, M. O. Gessner, N. Buchmann, V. Degrange, P. Grime, F. Hulot, F. Mermillod-Blondin, J. Roy, E. Spehn, and L. van Peer</i>	
18 Slippin' and slidin' between the scales: the scaling components of biodiversity–ecosystem functioning relations	209
<i>J. Bengtsson, K. Engelhardt, P. Giller, S. Hobbie, D. Lawrence, J. Levine, M. Vilà, and V. Wolters</i>	
19 Effect of biodiversity on ecosystem functioning in managed ecosystems	221
<i>J. Vandermeer, D. Lawrence, A. Symstad, and S. Hobbie</i>	

PART VI Synthesis

20 Perspectives and challenges	237
<i>M. Loreau, S. Naeem, and P. Inchausti</i>	
Bibliography	243
Index	283

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PART III

**New perspectives on ecosystem
stability**

A new look at the relationship between diversity and stability

M. Loreau, A. Downing, M. Emmerson, A. Gonzalez, J. Hughes, P. Inchausti, J. Joshi, J. Norberg, and O. Sala

7.1 Introduction

The relationship between biodiversity and ecosystem functioning has emerged as one of the most exciting and controversial research areas in ecology over the last decade. Faced with the prospect of a massive, irreversible loss of biodiversity, ecologists have begun investigating the potential consequences of these dramatic changes in biodiversity for the functioning of natural and managed ecosystems. These investigations have been motivated by both the scientific challenge and the need to understand better the role biodiversity plays in providing sustainable ecological goods and services for human societies. An increasing amount of evidence suggests that changes in biodiversity can have adverse effects on the average rates of ecosystem processes such as primary production and nutrient retention in temperate grassland ecosystems (see chapters by Hector *et al.*, Chapter 4; Tilman *et al.*, Chapter 3; Wardle and van der Putten, Chapter 14). Most of this evidence, however, comes from relatively short-term experimental studies (see, however, Petchey *et al.*, Chapter 11) under controlled experimental conditions, which are little informative about sustainable functioning.

The temporal variability of natural environments over a broad spectrum of time scales from days to centuries (Halley 1996), as well as increasing anthropogenic pressures (Sala *et al.* 2000), inevitably generate temporal changes in both population sizes and ecosystem processes. It is therefore of considerable interest to understand how biodiversity loss will affect long-term temporal patterns in

ecosystem functioning. Will ecosystem functional properties and services become more variable and less predictable when species diversity is reduced? Are species-rich ecosystems more capable of buffering environmental variability and maintaining ecosystem processes within acceptable bounds than species-poor ecosystems?

To answer these questions appropriately and avoid 'reinventing the wheel', it is important to realize that they address in a new form a long-standing debate in ecology concerning the relationship between the complexity (loosely defined as a combination of species diversity and the number and strength of species interactions) and stability of ecological systems. The study of this relationship has had a long and controversial history (May 1974; Pimm 1984, 1991; McCann 2000). To delineate the differences between contemporary issues and the historical debate, we first briefly revisit the central components of this debate, and propose a new, integrated conceptual framework derived both from lessons from this debate and insights newly arising from current research on biodiversity and ecosystem functioning. We then examine, within this framework, how recent theoretical and experimental work provide new insights into the complexity–stability debate. Our treatment therefore complements some recent reviews of the topic (Loreau 2000a; McCann 2000; Schwartz *et al.* 2000; Cottingham *et al.* 2001) which have not used the framework we present. Finally, we discuss the need to develop new theoretical and methodological approaches and to strengthen

the link between theory and experiments in this area. We conclude with some implications for policy and management.

7.2 Historical and conceptual background

The early view that permeated ecology until the 1960s was that diversity (or complexity) begets stability. This view was formalized and theorized by people such as Odum (1953), MacArthur (1955) and Elton (1958) in the 1950s. Odum (1953) and Elton (1958) observed that simple communities are more easily upset than rich ones, i.e. they are more subject to destructive population oscillations and invasions. MacArthur (1955) proposed, using a heuristic model, that the more pathways there are for energy to reach a consumer, the less severe is the failure of any one pathway. These conclusions were based on either intuitive arguments or loose observations, but lacked a strong theoretical and experimental foundation. Probably because they represented the conventional wisdom ('don't put all your eggs in one basket') and the prevailing philosophical view of the 'balance of nature', they became almost universally accepted.

This 'conventional wisdom' was seriously challenged in the early 1970s by theorists such as Levins (1970), Gardner and Ashby (1970) and May (1972, 1974), who borrowed the formalism of deterministic autonomous dynamical systems from Newtonian physics and showed that, in these model systems, the more complex the system, the less likely it is to be stable. Stability here was defined qualitatively by the fact that the system returns to its equilibrium or steady state after a perturbation. The intuitive explanation for this destabilizing influence of complexity is that the more diversified and the more connected a system, the more numerous and the longer the pathways along which a perturbation can propagate within the system, leading to either its collapse or its explosion. This conclusion was further supported by analyses of one quantitative measure of stability, resilience (Table 7.1), in model food webs (Pimm and Lawton 1977; Pimm 1982). This theoretical work had a number of limitations. In particular, it

was based on randomly constructed model communities. More realistic food webs incorporating thermodynamic constraints and observed patterns of interaction strengths do not necessarily have the same properties (DeAngelis 1975; de Ruiter *et al.* 1990). Also, there have been few direct experimental tests of the theory, and many of the natural patterns that agree with theoretical predictions can be explained by more parsimonious hypotheses such as the trophic cascade model (Cohen and Newman 1985). Despite these limitations, the view that diversity and complexity beget instability, not stability, quickly became the new paradigm in the 1970s and 1980s because of the mathematical rigour of the theory.

There are other limitations in this theory which are critical for the questions that we address here. First, stability is really a meta-concept that covers a range of different properties or components. Summarizing the debate, Pimm (1984) recognized a number of these properties and concluded that the relationship between diversity and each of them need not be the same. In Table 7.1, we attempt a classification—albeit imperfect, as any classification—of the different components of stability, which includes more recent notions. Second, each of these stability properties can be applied to a number of variables of interest at different hierarchical levels, such as individual species abundance, community species composition, or ecosystem-level processes or properties (Table 7.1). Again, the relationship between diversity and any stability property may be different for different variables (Pimm 1984). This creates a large matrix of potential combinations of stability properties and variables of interest, of which the new theory concerned only a small part. Specifically, May's (1974) and Pimm's (1982) theory concerned the qualitative stability and resilience of communities as ensembles of populations, not ecosystem-level aggregate properties.

Third, the formalism of autonomous, deterministic dynamical systems, which describes a fixed set of variables with time-independent parameters, inherently excludes a number of phenomena that characterize biological and ecological systems. In particular, it does not allow for the fact that these systems are subject to continuous environmental changes at various temporal scales and have the

Table 7.1 Concepts and definitions

Stability property	Definition
<i>Components of stability</i>	
Qualitative stability	Property of a system that returns to its original state after a perturbation. Generally used for an equilibrium state, though it could also be applied to systems that return to non-equilibrium trajectories.
Resilience	A measure of the speed at which a system returns to its original state after a perturbation* (Webster <i>et al.</i> 1974). Generally used for an equilibrium state, though it could also be applied to systems that return to non-equilibrium trajectories.
Resistance	A measure of the ability of a system to maintain its original state in the face of an external disruptive force (Harrison 1979). Generally used for an equilibrium state.
Robustness	A measure of the amount of perturbation that a system can tolerate before switching to another state. Closely related to the concept of ecological resilience <i>sensu</i> Holling* (1973). Can be applied to both equilibrium and non-equilibrium states.
Amplification envelope	Describes how an initial perturbation from an equilibrium state is amplified within a system (Neubert and Caswell 1997).
Variability	A measure of the magnitude of temporal changes in a system property. A phenomenological measure which does not make any assumption about the existence of an equilibrium or other asymptotic trajectories.
Persistence	A measure of the ability of a system to maintain itself through time. Generally used for non-equilibrium or unstable systems before extinction occurs.
<i>Variables of interest</i>	
Individual species abundances	
Species composition	
Ecosystem processes or properties	
<i>Sources of stability/instability</i>	
Internal: species interactions, demographic stochasticity	
External: environmental changes, biological invasions, extirpations	

* Some confusion surrounds the term resilience in the ecological literature. Though the term was first introduced into ecology by Holling (1973), it has most often been used in the sense defined by Webster *et al.* (1974). We follow here the common usage without any judgement on the relative merits of the two definitions.

ability to react or adapt to these changes through asynchronous population fluctuations, species replacement, phenotypic plasticity and evolutionary changes. By ignoring these features, most of the theory on the complexity and stability of ecological systems has focused on deterministic equilibria and ignored much of the potential for functional compensation, both within and between species, which is the basis for the stabilization of aggregate ecosystem properties. Functional compensation between species or types occurs when changes in the level of functioning contributed by one type are associated with opposite changes in the level of functioning contributed by another, whether these changes be of a dynamical, phenotypic or genetic nature.

During the golden period of the new paradigm (the 1970s and 1980s), few dissenting voices were heard. Those proposing an alternative viewpoint were ecosystem ecologists emphasizing functional compensation between species as the mechanism that stabilizes ecosystem processes against a background of wider variability of individual populations (Patten 1975; McNaughton 1977, 1993). Though often ignored, these ideas are the basis of the new wave of theoretical, experimental, and observational work that developed in the late 1990s. The new interest in the functional consequences of biodiversity changes in the 1990s has moved the focus from populations, communities and food webs to ecosystems and the interplay between community-level dynamical processes and ecosystem-level

functional processes (DeAngelis 1992; Jones and Lawton 1995; Loreau 2000a). This shift is particularly clear in the recent development of theory, which requires formalization of concepts and hypotheses. New approaches explicitly address the link between the variability of individual species and that of aggregate ecosystem properties, and explicitly incorporate population dynamical responses to environmental fluctuations, and even evolutionary adjustments (Ives 1995; Doak *et al.* 1998; Yachi and Loreau 1999; Lehman and Tilman 2000; Norberg *et al.* 2001).

These new approaches have generally emphasized the potential stabilizing influence of diversity on ecosystem properties, in agreement with the conventional wisdom of early ecologists. This refocusing of the diversity–stability debate does not contradict the previous findings of May (1974) and others, but it does considerably restrict their generality. Previous work focused on qualitative stability and resilience as the stability properties, on species-level population abundances as the variables of interest, and on deterministic autonomous systems at equilibrium, in which only the internal forces of species interactions came into play. In contrast, new work is focusing on variability as the main stability property, on ecosystem-level properties as the variables of interest, and on systems subject to environmental fluctuations, in which the species' responses to these external fluctuations interact with the internal forces of species interactions. The two perspectives are not necessarily contradictory (Tilman 1996; Ives *et al.* 2000). Another avenue of research which has received renewed interest concerns the invasibility or invasion resistance of communities or ecosystems (see Levine *et al.*, Chapter 10), which can be interpreted within our conceptual framework (Table 7.1) as the resistance (stability property) of species composition (variable of interest).

7.3 What we have learned from theory

The insurance hypothesis (Yachi and Loreau 1999) proposes that biodiversity buffers ecosystem processes against environmental changes because different species or phenotypes respond differently to these changes, leading to functional compensations

among species or phenotypes, and hence more predictable aggregate community or ecosystem properties (Patten 1975; McNaughton 1977). In this hypothesis, species that are functionally redundant for an ecosystem process at a given time show temporal complementarity (Loreau 2000a). There have been a number of variations on this theme during the last years (Doak *et al.* 1998; Naeem 1998; Tilman *et al.* 1998; Ives *et al.* 1999, 2000; Rastetter *et al.* 1999; Tilman 1999a; Walker *et al.* 1999; Lehman and Tilman 2000).

Although the assumptions, degree of generality and technical approaches differ considerably among models, a few generalities do emerge from this recent theoretical work. There is often a tension between the destabilizing influence of strong species interactions within the system and the stabilizing influence of asynchronous species responses to external forcing on ecosystem properties. As diversity increases, the number of interactions may increase, leading to the classical result of decreased resilience and increased variability of individual populations (May 1974; Tilman 1996). This destabilizing effect, however, may be reduced for aggregate ecosystem properties (May 1974; Tilman 1996; Hughes and Roughgarden 1998, 2000; Yachi and Loreau 1999; Ives *et al.* 1999, 2000; Lehman and Tilman 2000), and counteracted by decreased mean interaction strength or presence of weak interactions (McCann *et al.* 1998; Ives *et al.* 2000), which are the rule rather than the exception in many natural communities (Paine 1992; Raffaelli and Hall 1994). In contrast, variability of ecosystem processes driven by external environmental factors generally decreases as diversity increases because of the buffering effect of asynchronous species responses (Yachi and Loreau 1999; Ives *et al.* 1999). The net result is generally a smaller variability of aggregate ecosystem properties at a higher diversity (Ives *et al.* 1999; Lehman and Tilman 2000), in agreement with the insurance hypothesis. Hughes *et al.* (Chapter 8) discuss further how variability driven internally by species interactions and variability driven externally by environmental fluctuations interact to determine ecosystem-level stability. Although most of this new theory has been developed for competitive communities, the same conclusions seem to hold for multi-trophic systems (Ives *et al.* 2000).

Differences among species or phenotypes in their responses to environmental changes can not only lead to decreased variability, but also to increased average magnitude of ecosystem processes. When selection processes such as competition favour species or phenotypes within a functional group that are better adapted to current environmental conditions, a higher diversity of types permits a greater adaptability of the system, and hence an enhanced performance, at the functional group level (Yachi and Loreau 1999; Norberg *et al.* 2001). Although a high phenotypic trait diversity can lead to a lower instantaneous productivity because many sub-optimal types are present, a diverse system can have a higher long-term productivity than any single type because better adapted types tend to replace less adapted ones. It can even be shown quantitatively that the rate at which succession towards the current optimal type proceeds is proportional to phenotypic diversity (Norberg *et al.* 2001), which provides an ecological analogue to the fundamental theorem of natural selection, and a potential approach to defining and measuring the ability of ecosystems to adapt to the environment. Given this analogy with evolutionary selection, Loreau (2000a) and Loreau and Hector (2001) have coined the term ‘ecological selection’ to describe changes in dominance and species composition driven by differences in species traits. This analogy allows for employing theoretical approaches developed in evolutionary genetics for disentangling selection from complementarity effects (Loreau and Hector 2001; Hector *et al.*, Chapter 4). The ecological processes that generate adaptability at the ecosystem level also emphasize the importance of regional species richness for ecosystem functioning since external inputs, such as immigration of individuals or propagules, are essential to maintain a wide range of phenotypic traits within an ecosystem, and it is this phenotypic diversity that provides adaptability.

In contrast to studies on variability, theoretical studies on resilience and resistance of ecosystem processes after a perturbation have been scarcer. The results of Hughes and Roughgarden (1998, 2000) and Ives *et al.* (1999, 2000) imply that the resilience of some ecosystem properties may be independent of species richness in systems with special

symmetries amongst species interactions, but Loreau and Behera (1999) found that phenotypic trait diversity generally tends to decrease resilience at both the population and ecosystem levels. Loreau and Behera (1999) also showed that phenotypic diversity can have a variety of effects on the resistance of ecosystem properties. They suggested, however, that positive ecological selection, by which species with favourable traits become dominant, should generally yield a positive effect of diversity on the resistance of ecosystem processes at the primary producer level in the case of ‘negative’ perturbations (i.e. perturbations, such as drought, that have an intrinsically negative effect on the production of most species), while the opposite should be true for ‘positive perturbations’ (i.e. perturbations, such as nitrogen addition, that have an intrinsically positive effect on the production of most species).

The effect of species diversity on invasion resistance is another area that has received increased attention recently, although there have been very few theoretical studies on this issue. It is commonly hypothesized that species-rich communities are more resistant to invasion than species-poor communities because they use resources more completely (Elton 1958; MacArthur 1970; Levine and D’Antonio 1999; Tilman 1999). This pattern may be expected when reduced species richness is indeed accompanied by reduced saturation of niche space—a hypothesis for which there is some experimental evidence (see below). Otherwise, theory is mixed in its conclusions about species richness as a predictor of invasion resistance. The nature of the relationship between species richness and invasion resistance is expected to depend critically on the coexistence mechanisms that cause variation in species richness (Moore *et al.* 2001).

7.4 What we have learned from experiments

A number of recent experimental studies have investigated the relationship between species diversity and various stability properties. Experimental manipulations of diversity within a single trophic level have mostly concerned plants in grassland ecosystems (Table 7.2). The studies reviewed in

Table 7.2 Effects of experimental manipulations of species diversity within a single trophic level on ecosystem stability properties

Reference	Diversity gradient ^a	Species comp. ^b	Ecosystem type	External drivers ^c	Disturbance direction	Time scale	Plot size (m ²)	Diversity levels	Stability property	Specifications to stability property	Type of diversity effect ^d
Berish and Ewel 1988	Succ., F	nr	Plantation, forest succ.	ni; -R	Neg.	1 y	256	1,40,50,60	Resistance	r. of fine-root bm	None
Joshi <i>et al.</i> 2000 ¹	Exp., F	rr	Grassland	bi	Neg.	4 m (3 y)	0.25	1-32	Resistance	r. to loss of above-ground bm	↑ with funct. group no.
Leps <i>et al.</i> 1982	Succ., F	nr	Grassland	ni; -R	Neg.	4 y	no inf	4-20	Resistance	Comparison with pre- and post drought y	↑
Mellinger and McNaughton 1975	Succ., F	nr	Old field	e; +N	Pos.	1 y	1500	~35/~50	Resistance	r. in bm to N-pulse	↑
Mulder <i>et al.</i> 2001	Exp., F	rr	Bryophyte community	e; -R; +L	Neg.	5 d (15 m)	0.24	1-32	Resistance/Resilience	Decrease of bm after drought compared to control	↑
Pfisterer <i>et al.</i> (submitted) ¹	Exp., F	rr	Grassland	e; +Hi	Neg.	2 w (5 y)	0.09	1-32	Resistance	r. to loss of above-ground bm	↑
Tilman and Downing 1994	Nutr., F	nr	Grassland	ni; -R	Neg.	2 y	16	1-26	Resistance	Decrease of bm in drought rel. to normal y	↑
Tilman 1996	Nutr., F	nr	Grassland	ni; -R	Neg.	2 y	16	1-26	Resistance	Decrease of bm in drought rel. to normal y	↑
Brown and Ewel 1987	Succ., F	nr	Plantation, forest succ.	n	Neg.	2 y	256	1,40,50,60	Variability	v. of herbivory	↓
Dodd <i>et al.</i> 1994	Nutr., F	nr	Grassland	n	—	42 y	1000-2000	8-45	Variability	v. in bm	↓ (tendency)
Emmerson <i>et al.</i> 2001	Exp., M	nr	Marine benthic invertebrates	—	—	15 d	41	1-3	Variability	v. in nutrient flux	↓
Tilman 1996	Nutr., F	nr	Grassland	ni; -R	Neg.	8 y	16	1-26	Variability	v. in bm in non-drought ys	↓
Leps <i>et al.</i> 1982	Succ., F	nr	Grassland	ni; -R	Neg.	2 y	no inf.	4-20	Resistance	Prop. return during 2 y following drought	↓
Tilman and Downing 1994	Nutr., F	nr	Grassland	ni; -R	Neg.	2 y	16	1-26	Resistance	Deviation 4 y after drought from pre-d. bm.	↑ (optimum)

^a Exp.: experimentally newly created diversity gradient; Nutr.: gradients created by different nutrient levels; Succ.: gradients created by different successional stages; F: field study; M: microcosm/mesocosm study.

^b r: random mixture; rr: random mixture with restrictions; n: nested design; nr: other non-random mixture.

^c n: natural perturbation; e: experimental perturbation; bi: biological invasion; +Hi: addition of an insect herbivore; +N: increased N-supply; -R: drought. Time scale refers to either the duration of the perturbation (in the case of experimental perturbations—duration of study in brackets) or the duration of the study (in the case of natural perturbations).

^d Presence/absence and direction of the observed ecosystem process. ↑: positive relationship between diversity and stability property; ↓: relationship negative; none: no significant relationship; id.: identity (species identity or species-mixture identity most important).

¹ Studies were conducted in the same experimental system.

Table 7.2 were selected as described in Schlöpfer and Schmid (1999) and Schmid *et al.* (2002); they are restricted to those studies that observed effects of either experimentally or naturally imposed disturbances on the stability properties of communities differing in diversity within a single trophic level. These studies have provided some evidence that the temporal variability of various ecosystem properties decreases with increasing diversity, in agreement with the insurance hypothesis (Brown and Ewel 1987; Dodd *et al.* 1994; Tilman 1996; Emmerson *et al.* 2001; see also Schmid *et al.* 2002). When external perturbations were imposed on the system, plant species diversity had a positive effect on the resistance of above-ground biomass in all the studies listed (Leps *et al.* 1982; Tilman and Downing 1994; Tilman 1996; Mulder *et al.* 2001). The one study that measured the resistance of fine-root biomass, however, did not find a diversity effect (Berish and Ewel 1988). The evidence provided by most of these experiments, however (with the exception of Mulder *et al.* 2001), is inconclusive because of the presence of potential confounding factors (Givnish 1994; Huston 1997). For example, in Tilman and Downing's (1994) study, variations in diversity resulted from a fertilization gradient with plots receiving the highest fertilization having the lowest diversity. Fertilization itself could have resulted in the larger response to drought that was observed in the low-diversity treatments, although reanalysis by Tilman (1996) suggests that the effect of diversity was significant even after controlling for fertilization.

All but one study that tested the effects of external perturbations used negative perturbations (*sensu* Loreau and Behera 1999), mainly drought. The impact of positive perturbations such as nitrogen addition was only studied in Mellinger and McNaughton (1975). Given the anthropogenically induced global change in atmospheric nitrogen deposition (Vitousek *et al.* 1997) the effect of species diversity on the resistance of ecosystem and community properties under positive perturbations would merit more attention. There have been few studies on the influence of species diversity on the resilience of ecosystem processes (Leps *et al.* 1982; Tilman and Downing 1994). The one study that found a positive effect of species diversity on

resilience (Tilman and Downing 1994) used an inadequate measure of resilience (it incorporated resistance by ignoring differences in the magnitude of the initial effect of the perturbation). The effect disappeared after accounting for confounding factors (Tilman 1996). Thus, overall, the experiments performed so far provide results that do not contradict theory (Loreau and Behera 1999).

Experiments that test the effect of species diversity at multiple trophic levels on ecosystem stability properties (Table 7.3) might reflect realistic extinction scenarios of complex, highly connected ecosystems which have to face direct but also secondary extinctions (Williams and Martinez 2000). The studies reviewed in Table 7.3 are restricted to experiments in which species diversity at multiple trophic levels were manipulated and ecosystem stability properties were measured (see also Schlöpfer and Schmid 1999; Schmid *et al.* 2002). Two such experiments found decreasing variability of ecosystem properties with increasing diversity (McGrady-Steed *et al.* 1997; Naeem and Li 1997), in agreement with theory. The interpretation of these experiments, however, has been debated because of the presence of confounding factors: in one study (McGrady-Steed *et al.* 1997), ecosystem variability was confounded with variability among replicates; in the other (Naeem and Li 1997), variation in species diversity was confounded with variation in similarity among replicates (Wardle 1998).

Resistance of ecosystem processes after a press perturbation increased with diversity in one study only (Griffiths *et al.* 2000). Studies that measured resistance of community (Petchey *et al.* 1999) or ecosystem properties after pulse perturbations found either no (Downing, submitted; Petchey *et al.* 1999) or a negative (Hurd and Wolf 1974) relationship with increasing diversity. There is no appropriate theory, however, with which these results can be compared.

Lastly, a number of experiments have recently been performed on the effects of species diversity within a single trophic level on invasion resistance. Studies reviewed in Table 7.4 were selected based on a search on ISI web of science (1988–2001) in June 2001 using 'biodiversity' and 'invasion' as search terms (see also Hector *et al.* 2001a; Levine *et al.*, Chapter 10, for reviews). The majority of these

Table 7.3 Effects of experimental manipulations of species diversity at multiple trophic levels on ecosystem stability properties

Reference	Diversity gradient ^a	Species comp. ^b	Ecosystem type	Time scale	Plot size	Groups with diversity ^c	Diversity levels	Number troph. gr. ^d	Level of effect	Stability property	Specifications to observed variable	Type of effect ^e
Downing submitted	Exp., M	r	Aquatic		300l	p/c1/c2	1–5/1–5/1–5	3	All	Resistance	r. in resp. rates after pH-pulse perturbation.	—
Griffiths <i>et al.</i> 2000	Rem., M	—	Pasture soil	1 y	—	c1/c2/dec/bf	—	5	All	Resistance	r. in decomposition after heavy metal press-pert.	↑
Hurd and Wolf 1974	Succ. F	nr	Old field	6 m	1500 m ²	p/c1	~35, ~50 (p)	2	c2	Resistance	r. to N pulse-pert.	↓
Petchey <i>et al.</i> 1999	Exp., M	n	Aquatic	7 w	100 ml	p/c1/c2/b	1–5/1,3/0–3/1,3	4	All	Resistance	Extinction risk due to temperature elevation (press-pert.)	—
Snedes and Hurd 1981	Succ. F	nr	Marine benthic	2 y	0.01 m ²	c1/c2/dec	~30, ~35 (total)	3	Several	Resistance	r. to predation	↓
Wardle <i>et al.</i> 2000	Exp., M	n	Grassland	14 m	0.006 m ³	p/c1/c2	1–4/1–2/0–1	3	All	Resistance	r. to biomass loss and decomposition after drought press-pert.	—
Downing submitted	Exp., M	r	Aquatic		300l	p/c1/c2	1–5/1–5/1–5	3	All	Resilience	r. in resp. rates after pH pulse-pert.	↑
Griffiths <i>et al.</i> 2000	Rem., M	—	Pasture soil	1 y	—	c1/c2/dec/bf	—	5	All	Resilience	r. in decomposition after heat pulse-pert.	↑
Snedes and Hurd 1981	Succ., F	nr	Marine benthic	2 y	0.01 m ²	c1/c2/dec	~30, ~35 (total)	3	Several	Resilience	r. after predation	↓
McGrady-Steed <i>et al.</i> 1997	Exp., M	rr	Aquatic	42 d	100 ml	p/c1/c2	3–31	4	Several	Variability	v. in ecosystem respiration	↓
Naeem and Li 1997	Exp., M	r	Aquatic	57 d	50 ml	p/c1/c2	1–3/1–3/1–3	5	All	Variability	v. of biomass per trophic group	↓

^a Exp.: experimentally newly created diversity gradient; Rem.: diversity gradient created by selective removing of species from existing ecosystems; Nutr.: gradients created by different nutrient levels; Succ.: gradients created by different successional stages; F: field study; M: microcosm/mesocosm study.

^b r: random mixture; nr: random mixture with restrictions; n: nested design; nr: other non-random mixture.

^c p: primary producer; c1: primary consumer; c2: secondary consumer; dec: decomposer; f: fungivore; b: bacterivore.

^d Number of trophic groups varied.

^e Presence/absence and direction of the observed ecosystem process. ↑: positive relationship between diversity and stability property, ↓: relationship negative; none: no significant relationship.

Table 7.4 Effects of experimental manipulations of species diversity within a single trophic level on invasion resistance

Reference	Type of exp. ^a	Species comp. ^b	Ecosystem type	External drivers ^c	Time scale	Plot size (m ²)	Diversity levels	Species pool	Stability property	Specifications to stability property	Type of diversity effect ^d
Crawley <i>et al.</i> 1999	F	nr	Grassland	bi	7 y (8 y)	9.0	1–4, 80	4, 80	Resistance	Weed invasion resistance	None/identity
Dukes 2001	M	rr	Med. grassl.	bi	1 y	0.03	1–16	16	Resistance	Weed invasion resistance	↑ with funct. group no.
Hector <i>et al.</i> 2001a	F	rr	Grassland	bi	4 y	4.0	1–11	47	Resistance	Weed invasion resistance	↑
Joshi <i>et al.</i> 2000 ¹	F	rr	Grassland	bi	1 y (3 y)	0.25	1–32	48	Resistance	Weed invasion resistance	↑ with funct. group no.
Knopf <i>et al.</i> 1999 ²	F	r	Grassland	bi	2 y (4 y)	9.0	1–24	24	Resistance	Weed invasion resistance	↑
Lavorel <i>et al.</i> 1999 ³	F	nr	Med. grassl.	bi	1 m (8 m)	4.0	3,6,18	18	Resistance	Weed invasion resistance	None
Palmer and Maurer 1997	F	nr	Crops	bi	4 m	5.0	1,5	5	Resistance	Weed invasion resistance	↓/none
van der Putten <i>et al.</i> 2000	F	rr/n	Grassland	bi	2 y	100	4,15	37	Resistance	Weed invasion resistance	↑ (id.)
Troumbis <i>et al.</i> submitted	F	rr	Med. grassl.	bi	1 y (4 y)	1.0	1–18	23	Resistance	Weed invasion resistance	↑
Diemer and Schmid 2001 ¹	F	rr	Grassland	bi	2 y (4 y)	4.0	1–32	48	Resistance	Weed invasion resistance (phytometer study)	↑
Lévine 2000	F	r	Med. riparian primary succ.	bi	1 y (2 y)	0.04	1–9	9	Resistance	(sown) Weed invasion resistance	↑ (id.)
McGrady-Steed <i>et al.</i> 1997	M	rr	Aquatic	bi	2 w (8 w)	100 ml	3–16	27	Resistance	Invasion resistance (controlled addition of <i>Euplates</i> sp. (protozoa))	↑ (id.)
Naeem <i>et al.</i> 2000 ²	F	r	Grassland	bi	1 y (3 y)	9.0	1–24	24	Resistance	Weed invasion resistance (phytometer study)	↑
Prieur-Richard <i>et al.</i> 2000 ³	F	nr	Med. grassl.	bi	7 m (1 y)	4.0	3,6,18	18	Resistance	Weed invasion resistance (phytometer study)	(↑) /funct. gr. identity.
Stachowicz <i>et al.</i> 1999	F	r	Marine benthic	bi	65 d (—)	0.01	1–4	4	Resistance	Invasion resistance (controlled addition of an exotic ascidian species)	↑
Symstad 2000	F	n	Grassland	bi	2 y (4 y)	32	1–3 funct. groups	—	Resistance	(sown) Weed invasion resistance	↑ with funct. group no.

^a Exp.: experimentally newly created diversity gradient; rem.: diversity gradient created by selective removing of species from existing ecosystems; nutr.: gradients created by different nutrient levels; succ.: gradients created by different successional stages; P: phytotron; F: field study; M: microcosm/mesocosm study.

^b r: random mixture; rr: random mixture with restrictions; n: nested design; nr: other non-random mixture.

^c bi: biological invasion. Time scale refers to either the duration of the perturbation (in the case of experimental perturbations—duration of study in brackets) or the duration of the study (in the case of natural perturbations).

^d Presence/absence and direction of the observed ecosystem process. ↑: positive relationship between diversity and stability property; ↓: relationship negative; none: no significant relationship; id.: identity (species identity or species-identity most important).

^{1,2,3} Studies were conducted in the same experimental system.

studies showed a positive relationship between plant species or functional-group richness and resistance against naturally invading weeds. In addition, all studies investigating the impact of diversity within a trophic level on the performance of experimentally added invaders showed increased invasion resistance with community diversity. Only one experiment found the opposite effect (Palmer and Maurer 1997); this experiment investigated weed invasion in crop monocultures and five-species mixtures and found that the more diverse crop mixtures harboured a more species-rich (mostly annual) weed community. Weed invasion resistance in terms of weed biomass, however, was not affected by diversity. Another work by Lavorel *et al.* (1999) found no diversity effect on invasion resistance in Mediterranean grassland communities. In contrast to the other studies in Table 7.4, these two studies were relatively short-term experiments in which weed species were established at the same time as target communities. No predictable effect of diversity on invasion resistance was found either in an experiment by Crawley *et al.* (1999), in which species composition was non-random, just as in Palmer and Maurer (1997) and Lavorel *et al.* (1999). From the currently available evidence, it seems that more diverse communities are harder to invade in fully established communities with random, restricted random, or nested (one study) designs, with true replication of diversity levels and experimental introduction of invading species.

The mechanisms behind the positive relationship between diversity and invasion resistance in these small-scale experiments probably involve both better resource utilization in more diverse communities (Hector *et al.* 2001a; Levine *et al.*, Chapter 10) and selection processes since more diverse communities have a higher chance to contain species that benefit from altered environmental conditions (Schmid *et al.* 2002). Strong effects of species identity or species composition were detected in four of the 13 studies that found a positive effect of diversity on invasion resistance. Disentangling species diversity and species identity effects, however, requires true replication of diversity treatments with different species assemblages (Allison 1999), a requirement which was not fulfilled in all

experiments. For example, few studies replicated the highest diversity level with different species mixtures. Another limitation of these studies is that they have typically used 'invaders' from the extant regional flora which have coevolved with those species that constitute 'invaded' communities. Invasion by new exotic species is likely to follow different dynamics.

7.5 Strengthening the link between theory and experiments

Perhaps for the first time in the history of the diversity–stability debate, we now have two essential ingredients for scientific progress: first, a conceptual framework that is sufficiently broad and clear—albeit certainly improvable—to avoid confusion and sweeping generalizations, and, second, a convergence of observational, experimental and theoretical approaches towards common objectives and questions. It must be borne in mind, however, that the current work focused on biodiversity and ecosystem functioning is addressing only part of the original debate, several aspects of which remain untested.

Theory has historically been prominent in the diversity–stability debate. But profusion of theory is no guarantee of clarity and relevance. As experimental and observational evidence accumulates, the weaknesses of past, abstract theories have become more apparent. Theory needs to evolve to provide better guidance for experiments. Most of the classical equilibrium approaches based on autonomous dynamical systems may be inadequate to understand stability properties such as variability, resilience and resistance at the ecosystem level.

Here, we have argued that, to understand functional compensations in ecosystems, new approaches should be developed that take into account the dynamics of diversity and the potential for adaptive changes through asynchronous species fluctuations, species replacement, phenotypic plasticity and evolutionary change. In other words, ecosystems must be fully treated as complex adaptive systems, as proposed by such scientists as Holling (1986) and Levin (1999). Most of the current theory is also borrowed from community ecology, with

an emphasis on total plant biomass or primary production as the ecosystem properties investigated. Total plant biomass and primary production are easily related to individual plant or population-level properties by simple aggregation, but this might be less straightforward for other ecosystem processes. The historical separation between community ecology, which is demography oriented, and ecosystem ecology, which focuses on whole-ecosystem functional processes, demands new approaches to lay a bridge between these different perspectives (Loreau 2000a). There have been very few attempts to explore the effects of biodiversity on the functioning of full ecosystems comprising higher trophic levels, decomposers and nutrient cycling (Loreau 1996, 2001), and none as yet has considered stability explicitly.

It is very encouraging that experiments have started to test new ideas on the relationships between the diversity and various aspects of stability of ecosystems. A number of these experiments, however, have been debated because of the potential presence of confounding factors, which now need to be addressed by new experimental designs. To date, no experimental studies have directly manipulated long-term environmental variability 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. Several empirical studies suggest that this may be so. Some microcosm studies have demonstrated that certain types and frequency of environmental fluctuation may set levels of species richness and affect community stability (Eddison and Ollason 1978; Ollason 1977; Rashit and Bazin 1987). More directly, the work reported by Frost *et al.* (1995) and Klug *et al.* (2000) provides some short-term evidence demonstrating the operation of compensatory dynamics in lake communities in response to pH perturbations, and Morgan-Ernest and Brown (2001) provide long-term evidence for the existence of similar compensatory dynamics in arid grassland communities.

Establishing the general importance of the insurance hypothesis would require the demonstration of the assembly or evolution of an ecosystem functioning in this manner under controlled environmental fluctuations. Experiments of this kind would

define the subset of environmental and ecological conditions conducive to the establishment of such a mode of ecosystem functioning. Perhaps the main difficulty here is the production under experimental conditions of realistic environmental fluctuations with a controlled frequency structure. Methodological advances in this direction have been made (Cohen *et al.* 1998) and key microcosm experiments are starting to be conducted. Clearly, there is still scope for many innovative ideas in the design of experiments in this area.

To strengthen the link between theory and experiments, theoretical and experimental studies should attempt to adopt similar measurements of stability. Many past theoretical developments and predictions are difficult to directly test experimentally because equivalent measures of stability often do not exist in experimental systems. For example, there is not a straightforward experimental equivalent to an eigenvalue. Experimental approaches, in turn, must consider relevant theoretical work when designing and interpreting results. Experimental response variables could be chosen to correspond more closely to theoretical stability estimates. In addition, care must be taken to not misapply theoretical results to experimental results, particularly when the definitions of stability differ.

One of the difficulties of measuring stability in natural ecosystems is that natural ecosystems show a variety of complex dynamics. Many ecosystems experience predictable variations, such as the seasonal changes in the pelagic community of temperate lakes or succession in forests, or react to disturbance in a fairly predictable manner; algal blooms following eutrophication or re-establishment of forests after local clear-cuts are examples. Under normal environmental fluctuations, ecosystems often develop along a trajectory that is an environmentally determined dynamical attractor; systems starting out with different initial conditions then converge over time. Such non-equilibrium systems are stable and return to their attractor following a perturbation. In this case, tests of stability properties following perturbation could use the deviation between a perturbed system and a control system as a measure (e.g. Wardle *et al.* 2000a) or, alternatively, the relative difference in disturbance effects along a gradient of diversity

(e.g. van der Putten *et al.* 2000). A caveat, however, is that perturbations may be initially amplified before returning to the original state (Neubert and Caswell 1997), in which case a sufficiently long experimental time period is necessary to ensure that the system does converge.

Ecosystems that exhibit more complex dynamics or flip between alternative stable states (Scheffer *et al.* 2001) will be harder to analyse because there is no single reference system. A disturbance can switch a system into a different configuration such that the 'recovered' system is vastly different than the unperturbed control. Such systems require a focus on what Holling (1973) termed 'ecological resilience', or what we here call 'robustness' (Table 7.1). An appropriate experimental design would employ a range of disturbance magnitudes, which allows defining the domain within which disturbed systems will not lose critical functional groups or processes. Complete similarity with the undisturbed system may not be necessary as a criterion for recovery; one might be interested in maintaining the same ecological processes, such as top-down or bottom-up control. Thus, different types of systems may require different kinds of concepts, measures and experimental design.

A future challenge will be to recognize various types of complex dynamics in natural ecosystems, and to incorporate them in theoretical work attempting to study the relationship between stability and diversity. Such theory would hopefully produce realistic patterns of diversity–stability relationships, provide testable mechanisms, and help to sharpen and focus experiments designed to explore diversity–stability relationships. As theoretical and experimental foundations become more solid, there will also be an increasing need for long-term empirical data in the field. Long-term monitoring of both biodiversity and ecosystem processes is critical to apply our basic scientific understanding to real ecosystems, both natural and managed. Such data will need to be scaled to the turnover time of the ecosystem processes being considered if we are to understand their implications and relevance in the context of the natural functioning of ecosystems. This means that in some ecosystems, such as forests, very long time series will be necessary. The critical challenges with nat-

ural ecosystems will be to untangle the effects of environmental factors that drive natural variations in diversity and of diversity itself, and to develop new theory that integrates the mutual interactions among biodiversity changes, ecosystem functioning and abiotic factors into a single, unified picture (Loreau *et al.* 2001).

7.6 Implications for policy and management

As human impact on ecological systems increases, scientists are increasingly challenged to communicate new knowledge to policy- and decision-makers (Lubchenco 1998). Does our current state of knowledge of diversity–stability relationships provide specific information for policy and management decisions?

Society depends on the steady and predictable inputs of ecosystem services (Daily 1997). Current evidence suggests that higher diversity may provide greater reliability in the production of ecosystem services such as food and fibre production, pollination levels, and nutrient cycling. Diversity may also decrease the probability of successful invasions of non-native species, many of which have had substantial economic, conservation, and societal consequences (Mooney and Drake 1986; Drake and Mooney 1989). Extinctions of native species may lead to a further decrease in stability that causes a cascade of other extinctions, accelerating the rate of community change (Pimm *et al.* 1988; Borrvall *et al.* 2000). Finally, declines in ecosystem stability may reduce our ability to predict or detect future environmental changes in a background of higher ecosystem variability, including the influence of slow processes such as climate change (Cottingham *et al.* 2000). Thus, the impact of biodiversity on ecosystem stability appears to be a relevant feature to consider in policy and management decisions.

We have shown, however, that there are a number of components to stability, and that changes in diversity may alter ecosystem stability in a variety of ways. Stability at one level may require change at another level; for instance, we have discussed how increased average magnitude and decreased variability of ecosystem processes come about

through changes at the species level. Despite progress in our understanding of diversity–stability relationships, current research is still largely unable to provide specific policy recommendations due to the lack of abundant, consistent, and relevant long-term data on ecosystem processes for most biomes (Schwartz *et al.* 2000; Cottingham *et al.* 2001; Hector *et al.* 2001b; Lawler *et al.* 2002). Diversity appears to play some role in maintaining stability of certain processes in a handful of ecosystems, but more research is needed before we can confidently justify biodiversity conservation on the basis of its ability to enhance or protect ecosystem stability. Future work should begin to focus on scenarios that are immediately relevant to human society. For example, human impact causes non-random changes in diversity or composition (Petchey *et al.* 1999). Exploring the consequences of these non-random diversity changes for stability will become important. Research could also be

profitably focused on economically important ecosystems, such as agricultural ecosystems, and on ecosystem goods and services of importance to society, including reliable supplies of clean fresh water, and crop and fisheries production.

Given what we currently understand about the potential of diversity to buffer ecosystems against environmental fluctuations, future management efforts should look towards preserving the already ‘built-in’ capacity of ecosystems to adapt to environmental perturbations. This approach would require an emphasis on preserving regional species diversity and the necessary habitat connectivity required for the assembly of local communities in order to maintain the potential for high local diversity. Until we have a better understanding of how diversity relates to stability, management strategies aimed at preserving diversity will at the very least increase the potential for ecosystems to respond to future, changing environments.