

A new look at the relationship between diversity and stability

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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 Levin (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.

coolly mathematical models factor in compensation?

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 predictable aggregate community or ecosystem properties (Patten 1975; McNaughton 1977). In the insurance 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; Rastek *et al.* 1999; Tilman 1999a; Walker *et al.* 1999; Lehman and Tilman 2000).

Although the assumptions, degree of generalization 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 is the rule rather than the exception in many natural communities (Paine 1992; Raffaelli and Hall 1996). 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 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 10) 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 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.	n; -R	Neg.	1y	256	1,40,50,60	Resistance	r. of fine-root bm	None
Joshi et al. 2000 ¹	Exp., F	rr	Grassland	bi	Neg.	4m (3y)	0.25	1-32	Resistance	r. to loss of above-ground bm	↑ with funct. group no.
Leps et al. 1982	Succ., F	nr	Grassland	n; -R	Neg.	4y	no inf	4-20	Resistance	Comparison with pre- and post drought y	↑
Melinger and McNaughton 1975	Succ., F	nr	Old field	e; +N	Pos.	1y	1500	~35/~50	Resistance	r. in bm to N-pulse	↑
Mulder et al. 2001	Exp., F	rr	Bryophyte community	e; -R; +L	Neg.	5d (15m)	0.24	1-32	Resistance/Resilience compared to control	Decrease of bm after drought	↑
Pfisterer et al. (submitted) ¹	Exp., F	rr	Grassland	e; +Hi	Neg.	2w (5y)	0.09	1-32	Resistance	r. to loss of above-ground bm	↑
Tilman and Downing 1994	Nutr., F	nr	Grassland	n; -R	Neg.	2y	16	1-26	Resistance	Decrease of bm in drought rel. to normal y	↑
Tilman 1996	Nutr., F	nr	Grassland	n; -R	Neg.	2y	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.	2y	256	1,40,50,60	Variability	v. of herbivory	↓
Dodd et al. 1994	Nutr., F	nr	Grassland	n	—	42y	1000-2000	8-45	Variability	v. in bm	↓ (tendency)
Emmerson et al. 2001	Exp., M	nr	Marine benthic invertebrates	—	—	15d	41	1-3	Variability	v. in nutrient flux	↓
Tilman 1996	Nutr., F	nr	Grassland	n; -R	Neg.	8y	16	1-26	Variability	v. in bm in non-drought ys	↓
Leps et al. 1982	Succ., F	nr	Grassland	n; -R	Neg.	2y	no inf.	4-20	Resilience	Prop. return during 2y following drought	↓
Tilman and Downing 1994	Nutr., F	nr	Grassland	n; -R	Neg.	2y	16	1-26	Resilience	Deviation 4/ 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 Schläpfer 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 Béhera 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 Béhera 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 Schläpfer 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	300 l	p/c1/c2	1-5/1-5/1-5	3	All	Resistance	r. in resp. rates after pH-pulse perturbation.	—	—
Griffiths et al. 2000	Rem., M	—	Pasture soil	1 y	—	c1/c2/dec/b/f	—	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 et al. 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.)	—
Smedes 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 et al. 2000	Exp., M	n	Grassland	14 m	0.0006 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	300 l	p/c1/c2	1-5/1-5/1-5	3	All	Resilience	r. in resp. rates after pH pulse-pert.	↑	↑
Griffiths et al. 2000	Rem., M	—	Pasture soil	1 y	—	c1/c2/dec/b/f	—	5	All	Resilience	r. in decomposition after heat pulse-pert.	↑
Smedes 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 et al. 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; r: 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	rr	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> 2001 ^a	F	rr	Grassland	bi	4 y	4.0	1–11	47	Resistance	Weed invasion resistance	↑
Ioshi <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.
Knops <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)	↑
Levine 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>Euploea</i> sp. (protozoa))	↑ (id.)
Naem <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: phytometer; 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-mixture 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 had the highest diversity level with c mixtures. Another limitation of these studies is that they have typically used 'invaders' regional flora which have coevolved with species that constitute 'invaded' communities. The impact of 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 diversity-stability debate, we now have the ingredients for scientific progress: a conceptual framework that is sufficiently clear—albeit certainly improvable—to allow fusion and sweeping generalizations, a convergence of observational, experimental and theoretical approaches towards common 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 is no guarantee of clarity and relevance. Experimental and observational evidence account for the weaknesses of past, abstract theories and become more apparent. Theory needs to provide better guidance for experiments, for example, the classical equilibrium approaches based on numerous 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 the potential compensations in ecosystems, new approaches should be developed that take into account the dynamics of diversity and the potential for large 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 Odum (1986) and Levin (1999). Most of the current theory is also borrowed from community ecology.

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 environmental factors that drive natural diversity and of diversity itself, and new theory that integrates the mutualism among biodiversity changes, ecosystems and abiotic factors into a single, unified theory (Loreau *et al.* 2001).

7.6 Implications for policy and management

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

Society depends on the steady and reliable inputs of ecosystem services (Daily 1997). Evidence suggests that higher diversity leads to greater reliability in the production of services such as food and fibre production levels, and nutrient cycling. Diversification decreases the probability of successful invasions by non-native species, many of which have substantial economic, conservation, and social consequences (Mooney and Drake 1986; Mooney 1989). Extinctions of native species lead to a further decrease in stability through cascades of other extinctions, accelerating community change (Pimm *et al.* 1988; Bazelet *et al.* 2000). Finally, declines in ecosystem stability reduce our ability to predict or detect environmental changes in a background of system variability, including the influence of processes such as climate change (Cottam 2000). Thus, the impact of biodiversity on ecosystem stability appears to be a relevant consideration in policy and management decisions.

We have shown, however, that there are components to stability, and that diversity may alter ecosystem stability in ways. Stability at one level may require stability at another level; for instance, we have shown how increased average magnitude and variability of ecosystem processes can

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.

Do species interactions buffer environmental variation (in theory)

J. B. Hughes, A. R. Ives, and J. Norberg

8.1 Introduction

The interconnectedness of species within ecosystems underlies the popular notion that biodiversity contributes to a balance of nature. Species interactions are also fundamental to ecologists' formulations of how biodiversity and the stability of ecosystem functioning are related. Many have reviewed how the intricacies of stability definitions affect these relationships (e.g. McCann 2000; Pimm 1984). Fewer have examined how the varied aspects of species interactions, such as strength and number, affect diversity–stability relationships in models (e.g. Benedetti-Cecchi 2000; May 1973) and experiments (e.g. Aoki and Mizushima 2001; Mulder *et al.* 2001).

In this chapter, we investigate the role of species interactions in the buffering (dampening variation) of aggregate community biomass against environmental variation. Thus, we consider only one aspect of ecosystem stability, the variability of aggregate community biomass as measured by the coefficient of variation of total community biomass, or the CV of the sum of the abundances of all species in a community (CV_{sum}) (see Loreau *et al.*, Chapter 7 for other definitions of stability). Community stability is inversely related to CV_{sum} ; the lower the CV_{sum} , the greater the stability. This type of stability is of particular interest because of its potential to reflect the variability of primary production, which in turn is related to a variety of ecosystem processes. A caveat of this measure, however, is that biomass is the end product of many processes and does not necessarily reflect the

stability of the processes themselves (Naeem Chapter 1).

In the first part of the chapter, we discuss the connection between a number of recent models and then give a general formula for the relationship between diversity and stability that incorporates these models and discuss how different aspects of interactions affect the diversity–stability relationship. We limit our scope to communities of coexisting species that compete for common resources. In other words, the models represent communities with only one trophic level and do not address the issue of species coexistence and extinction. Furthermore, we examine communities that are subjected to repeated, stochastic fluctuations, as opposed to perturbations such as press disturbances (Ives or species removals (Naeem 1998; Petchey 2001)).

We then discuss how interaction strength, number of interactions, asymmetries among interactions, and interaction strength variability influence the relationship between diversity and stability. We conclude that the role of competition in stabilizing communities against environmental variation may be minor. In light of this, we consider the importance of species–environment interactions relative to species–species interactions.

8.2 How species interactions are incorporated

In the models considered below, the communities are made up of species that are assumed to compete for shared resources, although these resource

not explicitly included in the models. Instead, competition enters in two manners: directly, through per capita effects represented by interaction coefficients, and indirectly, through assumptions about the relationship between diversity and total community biomass. In the next sections, we discuss statistical models that incorporate interactions indirectly and dynamic models that incorporate interactions directly. These approaches are related, however, even if only conceptually.

Direct competitive effects can be conceptualized by considering the overlap of species along a resource axis, as in the classic literature on resource apportionment (e.g. MacArthur 1960; May 1975; Pielou 1975). At one extreme, species use exactly the same resources; they completely overlap on the resource axis (the left-hand side of Fig. 8.1(a)). At the other extreme, no species interact, as they all use unique segments of a resource axis (Fig. 8.1(b)). In the intermediate case, species partially compete with one another (Fig. 8.1(c)). The value of pairwise competition coefficients reflect

the degree to which the species' resource utilization curves overlap.

Interactions can also be included (or excluded) indirectly by assumptions about the relationship between diversity and total community biomass. Consider again the three cases in Fig. 8.1. If every new species added to a community uses the same resources as in case (a), total biomass should be independent of species richness (the right-hand side of Fig. 8.1). As a result, as diversity increases, each species has access to a smaller share of resources. In a community where species do not interact (case (b)), the length of the resource axis used increases with diversity, and total biomass increases linearly with species richness. In the case of partial competition (case (c)), each species added extends the resources axis (i.e. resource complementarity occurs), and biomass increases at a decreasing rate with richness. Thus, even without explicitly defining the amount of competitive overlap among species, models that assume diversity–total biomass relationships make implicit assumptions about species interactions.

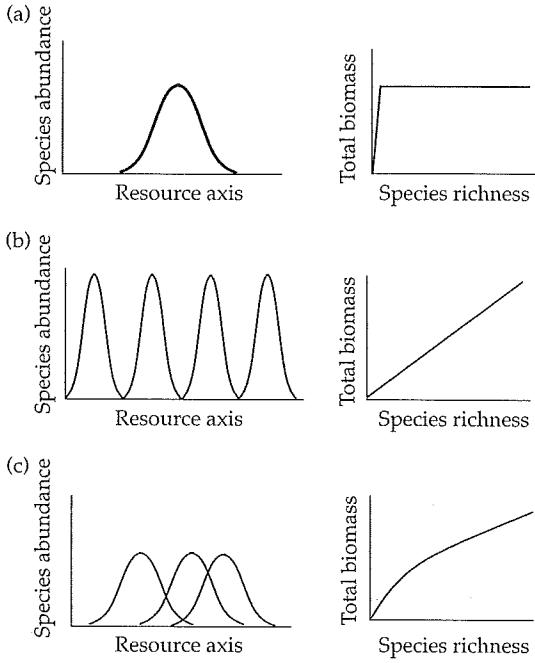


Figure 8.1 A schematic of three levels of resource competition and the parallel relationships between number of species and community biomass. (a) Complete competition, (b) No interactions and (c) Partial competition.

8.3 Statistical models with all or nothing interactions

Recently, Doak *et al.* (1998) formalized the idea that diversity may buffer environmental variation through a statistical averaging effect, even without interactions between species. They described a community where every species has the same mean abundance and variance, and total community biomass (T , the sum of species' abundances) is constant regardless of how many species (m) are present. Thus, the mean abundance of every species is T/m . They also assumed that the variance of a species' density (σ_n^2) scales with the square of its mean abundance, so that $\sigma_n^2 = c(T/m)^2$, where c is a constant. If species fluctuations are assumed to be independent of the fluctuations of other species, the CV of total biomass (CV_{sum}) is simply

$$CV_{\text{sum}} = \frac{\sqrt{m\sigma_n^2}}{T} = c^{1/2} m^{-1/2} \quad (8.1)$$

Thus, CV_{sum} decreases and stability increases with increasing species richness. More generally, if we allow the correlation between the fluctuations

among all pairs of species to be ρ , then (Doak *et al.* 1998, eqn (5))

$$\begin{aligned} CV_{\text{sum}} &= \frac{\sqrt{m\sigma_n^2 + \rho m(m-1)\sigma_n^2}}{T} \\ &= c^{1/2} m^{-1/2} (1 + (m-1)\rho)^{1/2} \end{aligned} \quad (8.2)$$

(The constraint that $\rho \geq -1/(m-1)$ is simply the constraint on any covariance matrix, that it must be positive definite. For example, you cannot have the pairwise correlations between three species all equal to -1 .)

Tilman *et al.* (1998) noted that the relationship between stability and species richness changes if one relaxes the assumption that the variance of a species' density scales with the square of its mean. Specifically, they let $\sigma_n^2 = c(T/m)^x$, where x is a constant that is not necessarily equal to 2. Under this assumption, eqn (8.2) becomes

$$CV_{\text{sum}} = c^{1/2} T^{(x-2)/2} m^{(1-x)/2} (1 + (m-1)\rho)^{1/2} \quad (8.3)$$

Thus, stability increases with increasing diversity when $x > 1$, but decreases with diversity when $x < 1$. Tilman *et al.* (1998) and Tilman (1999a) argue from field studies of prairie plant communities that x usually falls between 1 and 2.

Although competition is not included in these models directly, competition is included indirectly through the diversity–total biomass relationship. These models assume a fixed community biomass (T), regardless of the number of species added or subtracted to the community. Thus, the mean abundance of a species (k) depends on the number of other species present. This assumption is similar to the case depicted in Fig. 8.1(a), where all species compete for the same section along a resource axis.

What happens if these implied interactions are removed? If the species do not interact with one another, then k should be independent of species richness and total biomass should increase linearly as each species is added, i.e. $T = mk$ (the case in Fig. 8.1(b)). Equation (8.3) then becomes

$$CV_{\text{sum}} = c^{1/2} k^{(x-2)/2} m^{-1/2} (1 + (m-1)\rho)^{1/2} \quad (8.4)$$

Thus, without species interactions, stability always increases with diversity whenever $\rho \neq 1$,

regardless of how variance scales with abundance (see Appendix of Hughes and I 2000).

Yachi and Loreau (1999) show that averaging can also produce a positive stability relationship when species overlap in resource use. In their abundance of each species is specified variable, and the variances of the species. Competitive interactions are reflected in the diversity–biomass relationship. For a system with extreme interspecific competition, biomass is defined as the most produced at any given time. As long as the community species fluctuations is less than the variance of total biomass decreases with increasing species richness. Because total biomass increases and then levels off with increasing diversity, the CV of total biomass also decreases and then increases.

In sum, statistical averaging can alter community stability with or without species interactions. Furthermore, species interactions are incorporated indirectly through the diversity–biomass relationship can alter the stability relationship.

8.4 Dynamic models with part interactions

Ives *et al.* (1999), Lehman and Tilman (1999), Hughes and Roughgarden (2000) (hereafter L&T, and H&R models a and b) investigate the relationship between diversity and stability. Lotka–Volterra derived models incorporate competitive interactions directly through a competition coefficient α . Although these models incorporate species interactions differently than the statistical models, as discussed above, the addition in these models can be considered similarly (Fig. 8.1).

In these dynamic models, population growth rates are affected by environmental variation, and this variation is reflected in population growth rates. Two forms of these models are presented. The linear approximation of all the models and the difference in density from

Table 8.1 The difference equations of four dynamic models that track changes in the population density of species i at time t , $N_i(t)$, where ε is a random variable with mean zero and variance σ_ε^2 . In all models, species have carrying capacities K and intrinsic rates of increase r ; and α is the competition coefficient measuring the effect of one species on another. H&R model (a) is the diffuse competition case and model (b) is the limiting similarity case in Hughes and Roughgarden (2000)

Model	$N_i(t+1) =$	Diversity–stability relationship
IG&K	$N_i(t)\exp\left[r\left(1 - \frac{N_i(t)+\alpha\sum_{j\neq i}^m N_j(t)}{K}\right)\right]\exp[\varepsilon_i(t)]$	Positive, independent of K
L&T	$N_i(t) + rN_i(t)\left[1 - \frac{N_i(t)+\alpha\sum_{j\neq i}^m N_j(t)}{K+\varepsilon_i(t)}\right]$	Positive, dependent on K
H&R (a)	$N_i(t) + rN_i(t)\left[1 - \frac{N_i(t)+\alpha\sum_{j\neq i}^m N_j(t)}{K}\right] + \varepsilon_i(t)$	Negative or positive, dependent on α and K
H&R (b)	$N_i(t) + rN_i(t)\left[1 - \frac{N_i(t)+\alpha(N_{i-1}(t)+N_{i+1}(t))}{K}\right] + \varepsilon_i(t)$	Positive, dependent on α and K

$(N^* - N_i(t+1))$ of species i at time $t+1$ is (Ives and Hughes, in press)

$$\begin{aligned} n_i(t+1) &= \left(1 - r\frac{N^*}{K}\right)n_i(t) \\ &\quad - r\alpha\frac{N^*}{K}\sum_{j\neq i}^m n_j(t) + z_i(t) \end{aligned} \quad (8.5)$$

for IG&K, T&L, and H&R(a), and

$$\begin{aligned} n_i(t+1) &= \left(1 - r\frac{N^*}{K}\right)n_i(t) - r\alpha\frac{N^*}{K}(n_{i-1}(t) \\ &\quad + n_{i+1}(t)) + z_i(t) \end{aligned} \quad (8.6)$$

for H&R(b), where K is the carrying capacity of a species, r is the intrinsic rate of increase, and $z_i(t)$ gives the environmentally driven variability in the population growth rate with standard deviation σ_z (the value of $z_i(t)$ is discussed below). When $0 < r < 2$ and $0 < \alpha < 1$, the equilibrium is positive and stable.

The CV_{sum} of all models can be summarized by the general equation

$$CV_{\text{sum}} = \sigma_p \left(\frac{1 + (m-1)\rho}{m(1 - (1-r)^2)} \right)^{1/2} \quad (8.7)$$

where σ_p is the standard deviation of the environmental fluctuations measured as the change in per capita population growth rates from time t to $t+1$ (see derivation in Ives and Hughes 2002). The standard deviation of the per capita population

growth rates are related to the standard deviation of $z(t)$ by $\sigma_p = \sigma_z/N^*$. The difference between σ_p and σ_n from the statistical models in the preceding section highlights an important distinction between these two types of models. In the models in Table 8.1, environmental fluctuations are added to species' population growth rates. In contrast, the statistical models introduce environmental fluctuations as variation to species' densities. These terms are related, in the sense that increasing the environmentally driven fluctuations in population growth rates, σ_p , will increase the variation in population densities, σ_n . (Note, however, that an increase in σ_n does not necessarily indicate an increase in σ_p .) Nonetheless, for models explicitly including species interactions, the variation in population densities (σ_n) depends not only on how environmental fluctuations change growth rates (σ_p) but also on how these environmental fluctuations are perpetuated through species interactions (Ives *et al.* 1999).

The disparate diversity–stability relationships among models in Table 8.1 arise from differences in the relationship between σ_p and m , which result from three assumptions that differ among the models. First, the point-of-entry of an environmental perturbation ($\varepsilon(t)$) differs among the models. In IG&K the perturbations are multiplicative. In T&L the perturbations are added to the carrying capacity, and in the H&R models the perturbations are additive (Table 8.1). An environmentally driven fluctuation in a population's growth rate is given

by z (the final term in eqs (8.5) and (8.6)) and is a function of an environmental perturbation ε . Specifically, $z_i(t) = gN^*\varepsilon_i(t)$, and it can be shown that the value of g depends on the placement of $\varepsilon_i(t)$ (Table 8.2; Ives and Hughes 2002).

Second, how the variance in population growth rates scales with the mean abundance of a species is important. In general terms, the variance of z can be written as a function of the mean abundance of the population as $\sigma_z^2 = \sigma_\varepsilon^2(gN^*)^x$, where as before, x scales the rate at which the variance in z increases with the mean density.

Third, the mean abundance of a species (its equilibrium value, N^*) may depend on the relationship between diversity and total biomass. As a general case, we let $N^* = T/m^y$, where y is a constant.

We can incorporate all three assumptions, which leads to the relationship

$$\sigma_p = \sigma_\varepsilon g^{x/2} \left(\frac{T}{m^y} \right)^{x-2/2}$$

Substituting σ_p into eqn (8.7),

$$CV_{\text{sum}} = \sigma_\varepsilon g^{x/2} \times \left(\frac{T}{m^y} \right)^{(x-2)/2} \left(\frac{1 + (m-1)\rho}{m(1 - (1-r)^2)} \right)^{1/2} \quad (8.8)$$

where g is given in Table 8.2. This equation is a general form that includes all of the above models as special cases, including the models without interactions. For instance, if $r=1$ and T/m^y is given by a constant k , then eqn (8.8) reduces to eqn (8.4).

Table 8.2 The values of g , x , and y (eqn (8.8)) for the models in Table 8.1. The three models assume different values of g and x , and thereby result in a different relationship between the per capita environmentally driven variation (σ_p) and the mean abundance of a species (N^*). The value of y does not affect the IG&K and L&T models

Model	g	x	y	σ_p
IG&K	1	2	—	σ_ε
L&T	$\frac{r}{K}$	2	—	$\sigma_\varepsilon \frac{r}{K}$
H&R(a)	$\frac{1}{N^*}$	0	> 0	$\sigma_\varepsilon N^*$
H&R(b)	$\frac{1}{N^*}$	0	0	$\sigma_\varepsilon N^*$

How do interspecific interactions affect in this most general case? The interaction α is missing from eqn (8.8). Therefore, interactions only enter the equation in their influence on mean abundances. Exact interactions influence stability depends or bination of the diversity–biomass relation, point-of-entry of the perturbations, and the variance scaling constant. Table 8.2 summarizes three differences among the models presented in Table 8.1. Both IG&K and L&T assume that therefore, the mean abundance of a species, affect the diversity–stability relationship. In contrast, H&R assume $x=0$, and the effect of interactions on mean abundance explains different diversity–stability relationships predicted by their models (a) and (b) (Fig. 8.3).

8.5 Which aspects of species interactions influence stability?

The above models give some insight in how species interactions might buffer or predict environmental variation through the dynamics of a community; in particular, they suggest what is important to distinguish between different aspects of species interactions when determining whether interactions influence the diversity–stability relationship. There are at least four types of species interactions that can be distinguished: interaction strength, the number of interactions, asymmetries among interactions, and interaction variability.

8.5.1 Interaction strength

The strength of interspecific interactions (the magnitude of α) does not affect the direction of the diversity–stability relationship for competitive communities with symmetrical interaction strengths (Ives *et al.* 1999, 2000). In fact, as Doak *et al.* demonstrated, the occurrence of species interactions is not required for a positive diversity–stability relationship. Thus, in this sense, a community of strongly interacting species is not necessarily more stable than a community of weakly interacting species.

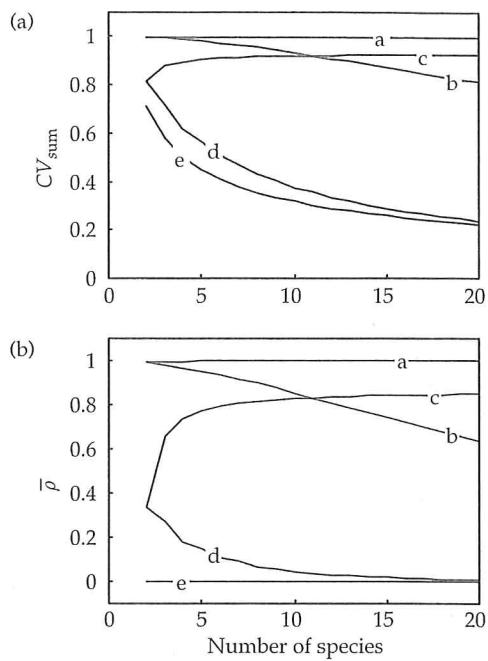


Figure 8.2 The change in (a) CV_{sum} and (b) $\bar{p}[m]$ with increasing numbers of species in competitive communities. Equation (8.10) was used to calculate each pairwise correlation between species, and (b) gives the average of these values. Values of $\bar{p}[m]$ from (b) were then used in eqn (8.11) to compute CV_{sum} and are plotted in (a), with $\sigma_p = 1$ and $r = 1$. See text for explanation of cases a–e.

8.5.2 Number of interactions

Interactions may influence stability indirectly through the relationship between diversity and the biomass of individual species. The shape of the diversity–biomass relationship will be determined in large part by the number of non-zero interactions or the connectance (Gardner and Ashby 1970; May 1973) of a community. For instance, in the H&R model (a), every species interacts with every other species, and therefore total biomass generally increases at a decelerating rate with diversity. At the other end of the spectrum, in the H&R model (b), each species interacts with two species, regardless of community diversity, and total biomass increases linearly with diversity.

The shape of the diversity–biomass relationship, however, only affects the diversity–stability relationship if the per capita effect of environmental

fluctuations on individuals of a species changes with the mean density of the species (i.e. when σ_p is a function of N^*). Recognizing the independence of the diversity–stability and the diversity–biomass relationships is important for disentangling the effects that diversity has on ecosystems.

8.5.3 Asymmetries among interactions

We have only considered models in which species interactions are symmetric ($\alpha_{ij} = \alpha_{ji}$) and equal for all species. Simulations of communities with moderate asymmetries among interactions suggest that the general conclusions still hold (e.g. Hughes and Roughgarden 1998; Ives *et al.* 1999). In the case of extreme asymmetries, however, the community will be dominated by one or a few species, and accordingly the community should have the dynamics corresponding to these few dominant species rather than the dynamics of an equally diverse community with a more even distribution of species abundances.

8.5.4 Interaction strength variability

Environmental fluctuations could affect the strength or presence of interactions and thereby affect the diversity–stability relationship. The models we have analysed examine stability in the face of environmental fluctuations that affect population growth rates. However, environmental fluctuations may also vary interspecific interaction strengths, particularly by altering the abundance and quality of different resources. For example, a resource may or may not be shared between species, depending on other resources available to each species. Thus, as resource availability fluctuates, the amount of resource overlap between species may vary. Benedetti-Cecchi (2000) constructed a conceptual model to examine the importance of variability in the strength of interactions between consumers and resources. Although this model is not directly comparable to competition models, it demonstrated that variance in interaction strength affects the variability of species abundances. This same idea deserves further attention in other models.

In sum, interspecific competitive interactions do not necessarily buffer community biomass against

environmental variation (eqn (8.7)). Moreover, diversity may increase stability in the absence of competitive interactions (eqn (8.4)). Thus, we suggest that the role of competition in stabilizing some aggregate measure of a community (such as biomass) against environmental variability may be relatively minor, particularly in comparison to species–environment interactions discussed in the next section. This conclusion does not exclude the possibility that other types of interspecific interactions such as predation and mutualism play a larger role in community stability (Aoki and Mizushima 2001; Mulder *et al.* 2001).

each species has expectation r and follows a 'bell-shaped' curve with respect to environmental variable $E(t)$, reaching a sharp maximum when $E(t)$ equals u_i . The difference among species in their values is greater than the differences in their optimal conditions.

The covariance between $\gamma_i(t)$ and $\gamma_j(t)$ for two species can be derived from property distributions and is given by $1 + 2u_i u_j$ the correlation ρ_{ij} between $\gamma_i(t)$ and $\gamma_j(t)$

$$\frac{(1 + 2u_i u_j)}{((1 + 2u_i^2)(1 + 2u_j^2))^{1/2}}$$

The closer the values of u_i and u_j are to each other, the higher the correlation between the two species i and j to environmental fluctuations. This is not surprising; if, e.g. two species have similar optimal temperatures, both should respond in a highly correlated way to fluctuations in temperature.

Table 8.3 gives two examples of correlation matrices for five species, with the values of u_i equally spaced and with u_3 for the mid-value located at zero, the mean value of the environmental variable $E(t)$. In the first example (Table 8.3(a)), the species phenotypes are closely spaced, and are similar in how they respond to $E(t)$. The species growth rates are highly positively correlated (Table 8.3(b)). In the second case,

Table 8.3 Correlation matrices for the effects of environmental fluctuations $E(t)$ on the intrinsic rates of increase, $\gamma_i(t)$, for five species with values of u_i equaling (a) $-0.2, -0.1, 0, 0.1$ and 0.2 and (b) $-2, -1, 0, 1$, and 2

Species	1	2	3	4
(a)				
1	1	0.99	0.96	0.91
2		1	0.99	0.96
3			1	0.99
4				1
5				
(b)				
1	1	0.96	0.33	-0.58
2		1	0.58	-0.33
3			1	0.58
4				1
5				

8.6 Species–environment interactions

Given the indirect role played by competition in the diversity–stability relationship, the importance of how a species responds to environmental fluctuations, rather than to other species, emerges. The correlated responses of species growth rates (ρ) gives a measure of species–environment interactions for the community as a whole, and this term appears in the stability equations above (Eqs (8.4), (8.7), and (8.8)).

To demonstrate the importance of species–environment interactions for the diversity–stability relationship, we developed a stochastic model inspired by the deterministic model analysed by Norberg *et al.* (2001). Consider a community of species that compete for the same set of resources. The growth rate R of species i is $\exp[r + \gamma_i(t)]$, where r is a constant and

$$\gamma_i(t) = -(u_i - E(t))^2 + u_i^2 + 1. \quad (8.9)$$

$E(t)$ is a time-varying environmental variable such as rainfall or predator abundances that affects all species in the community, and u_i is the species' phenotype, the position along the environmental spectrum where the species reaches its maximum growth rate. We assume that $E(t)$ follows a normal distribution, and that there is no serial correlation. Without loss of generality, we can also assume $E(t)$ follows a $N(0, 1)$ normal distribution.

In eqn (8.9), $\gamma_i(t)$ has an expectation of zero and reaches a maximum value when $E(t)$ equals u_i . Thus, the log per capita population growth rate of

phenotypes are dissimilar with values of u_i spaced far apart. Their growth rates are less positively correlated than in the first case, and some species are negatively correlated. Thus, if two species have optima that are very different and are on opposite sides of the mean of the environmental variable, environmental fluctuations can drive negative correlations in population growth rates.

This simple example demonstrates that a single environmental factor can generate a range of positive and negative correlations among species responses to environmental fluctuations, even in the absence of interspecific competition. Moreover, the model suggests that environmentally driven correlations are probably not independent of species diversity, because the distribution of phenotypes in a community may depend on the number of species in that community. Thus, when correlations between species are not identical, eqn (8.7) becomes

$$CV_{\text{sum}} = \sigma_p \left(\frac{1 + (m - 1)\bar{\rho}[m]}{m(1 - (1 - r)^2)} \right)^{1/2} \quad (8.11)$$

where $\bar{\rho}[m]$ is the average of the pairwise correlations between species responses to environmental fluctuations. We have written $\bar{\rho}[m]$ as a function of m to emphasize that this average correlation could depend on the number of species in a community.

To demonstrate how assumptions about species–environment interactions may influence the diversity–stability relationship, consider five cases of the above model (Fig. 8.2). Each case differs in its assumption about how the added species differ in their responses to $E(t)$. In case (a) there are initially two species ($m=2$) and the difference between species' optima ($u_1 - u_2$) equals 0.1. Species are then added such that the maximum difference between the optima of the species remains 0.1. In other words, the range of responses to $E(t)$ does not change with increasing numbers of species. In case (b), the difference between the optima of the two initial species ($u_1 - u_2$) also equals 0.1, but each additional species is added so that the spacing between all adjacent species ($u_i - u_{i+1}$) equals 0.1. In other words, each new species increases the total optima range by 0.1. Cases (c) and (d) are similar to (a) and (b), respectively, except that the initial difference between species is 1.0 rather than 0.1; therefore,

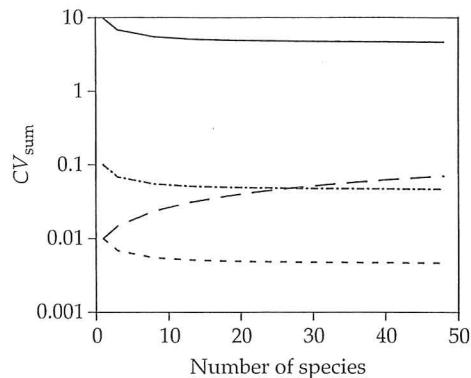


Figure 8.3 The diversity–stability relationship for the four models (IG&K, —; L&T, - - -; H&R(a), - - ; H&R(b), - - -) using the eqn (8.8) and the parameter constraints given in Table 8.2. The remaining parameters used are $\rho_e = 10$, $T = 1000$, $\rho = 0.2$, $r = 1$, and $K = 100$.

species are more dissimilar in their responses to the environment. Finally, case (e) gives the situation in which there is no correlation in species responses to environmental fluctuations ($\rho = 0$), i.e. when each species is influenced by different, independent environmental factors, rather than the single factor $E(t)$.

Figure 8.2(a) reveals that when increasing the number of species in a community does not increase the range of species' environmental optima, increasing the number of species either has little effect on CV_{sum} (case a) or actually increases CV_{sum} (case c). This pattern results because the average correlation between species' responses to environmental fluctuations ($\bar{\rho}[m]$) remains constant (case a) or increases with m (case c) when the range of species' optima remains fixed (Fig. 8.2(b)). Conversely, when the difference between adjacent species' optima remains fixed (cases b and d) so that the range of species' optima broadens with higher species diversity, increasing m decreases the average correlation between species' responses to environmental fluctuations. As a result, CV_{sum} decreases with increasing numbers of species in the community.

In sum, species diversity only increases stability (i.e. decreases CV_{sum}) if the additional species are different in how they respond to environmental fluctuations from those already present. The diversity of responses to environmental perturbations, rather than simply the number of species, influences

community stability. Thus, an important empirical question is whether diverse communities exhibit a greater range of species responses to environmental fluctuations than depauperate communities and therefore have a lower average correlation between species' responses to environmental fluctuations.

8.7 Reconsidering the questions

Much of the interest in diversity–stability relationships seems to be motivated by a desire to predict how biodiversity loss and human-driven disturbances affect ecosystems. Our ability to apply theoretical results to natural communities rests on how well model assumptions reflect reality. Even if these models reflected reality perfectly, however, do they involve the type of stability, disturbance, and biodiversity in which we are interested? More specifically, do any of the models we have discussed actually address how changes in biodiversity and the rate of human-driven disturbance will affect the stability of ecosystem functioning in a manner that is ecologically or economically significant?

Earlier results demonstrated that similar studies could reach 'opposite' conclusions based on different definitions of stability (McCann 2000; Pimm 1984; Loreau *et al.*, Chapter 7). For instance, the Lotka–Volterra models above predict that, in general, stability of community biomass increases with diversity, but that the stability of individual species decreases with diversity.

The question of which aspect of ecosystem stability is most relevant to understanding the consequences of biodiversity loss is inextricably linked to the question of whether current studies examine appropriate types of disturbances. It has long been established that the point of entry of random fluctuations influences the results of stochasticity on population growth models (e.g. Levins 1969; May 1973), and this conclusion is upheld for the diversity–stability models here. This result suggests that it matters if environmental fluctuations more directly affect a species' growth rate or its carrying capacity. In fact, the appropriate way to model environmental variability may be different for different types of disturbances. For instance, in some species, fluctuations in the availability of nesting sites might be best modelled as variation in carrying

capacity, whereas fluctuations in might be best modelled as variation

Similarly, the models in this community responses to continuous but serially uncorrelated fluctuations change and widespread pollution, perhaps it would be more appropriate effects of long-term unidirectional temperature increases (Petchey *et al.* 2000) abrupt disturbances such as fire (Cottingham and Schindler 2000; 1981). In these cases, one might be interested in the magnitude of change of species' property rather than variability of the time. In sum, much remains to be understood about the nature of environmental variation species' experience this variation.

It is also not clear that using species richness as a measure of diversity is appropriate for understanding how biodiversity loss affects community stability. For instance, biomass variability is often measured as the number of species weighted by the biomass of an individual of that species. Their degree of independence in response to environmental fluctuations. The models I have presented assume that all species in a community in which biomass is evenly distributed among species. Losing a species in a community of 100 species that is dominated by one species is the same as losing a species in a community of 100 species that are evenly abundant. Thus, an evenness measure would be a more appropriate measure of species richness. The situation in natural communities may be particularly important for understanding how invasive species affect community stability. Although the addition of new species may increase species richness, it may alter the relative composition of the community (Hobbs and Mooney 1998).

Measuring diversity as species richness ignores the reality that species loss is not equivalent in all species. Some species are more susceptible to extinction and may have differentially affected stability. For instance, species with slow growth rates may be more susceptible to extinction; therefore, decreased diversity will affect the distribution of growth rates. The models demonstrated that variability in species' responses to environmental perturbations influence community stability.

stability. How the community responds to species extinction will depend in part on how the remaining species respond to environmental fluctuations compared to the species lost (e.g. whether the species lost was in the centre or on the extreme of the range of species' phenotypes).

Finally, feedbacks between diversity and ecosystem function are notably absent from most diversity-stability theory. Most models change diversity, holding 'all else equal.' Yet environmental disturbances will directly affect the ecosystem properties that maintain community diversity. For example, nitrogen deposition will not only affect relative abundances of species, but also nutrient availability and the number of species that can coexist. To investigate these types of links, mechanistically based models are needed. Loreau (1998a) modelled how species richness was affected by the mobility of nutrients in a community of spatially separated plants. The mobility rate of the nutrient determined the degree of interaction between adjacent plants and thus also the number of species maintained in the community. Moreover,

environmental disturbances themselves may maintain species diversity and in turn, affect ecosystem functioning. For instance, Norberg *et al.* (2001) investigated the relationship between phenotypic diversity and community biomass in a community where all species compete equally for the same resource. In this study, the environmental fluctuations themselves allow phenotypic diversity to persist, and this diversity affects the average and variance of community biomass.

In conclusion, only through better understanding of the nature of disturbances that natural ecosystems face and the mechanisms that control the feedbacks between diversity and ecosystem function will we be able to predict the response of a natural community to disturbance. At this point, we cannot yet be complacent in the mathematical result that species diversity and stability are positively related.

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Biodiversity and stability in soil ecosystems: patterns, processes and the effects of disturbance

P. C. de Ruiter, B. Griffiths, and J. C. Moore

9.1 Soil biodiversity and soil processes

Soil harbours a large part of the world's biodiversity and governs processes that are regarded as globally important components in the cycling of materials, energy and nutrients (Wolters 1997; Griffiths *et al.* 2000). The taxonomy of soil organisms is however relatively poorly known and possibly the majority of the species is still to be identified (Mikola *et al.*, Chapter 15). Precise taxonomical descriptions of the soil biodiversity are hampered by technical difficulties in extracting and identifying the soil organisms and by the large variation in species richness among soil ecosystems (Lawton *et al.* 1996; Wall and Virginia 1999; Mikola *et al.*, Chapter 15). By far the most dominant groups of soil organisms, in terms of numbers and biomass, are the microbial organisms, i.e. bacteria and fungi (Andrén *et al.* 1990; Bloem *et al.* 1994). Besides the microbial organisms, soil ecosystems generally contain a large variety of faunal organisms, like protzoa (amoebae, flagellates, ciliates), nematodes (bacterivores, fungivores, omnivores, herbivores and predators), micro-arthropods such as mites (bacterivores, fungivores, predators) and collembola (fungivores and predators), enchytraeids and earthworms (Fig. 9.1).

Soil organisms are assumed to be directly responsible for soil ecosystem processes, especially the decomposition of soil organic matter and the cycling of nutrients (Wardle and Giller 1997). These processes are regarded as major components in the global cycling of materials, energy and nutrients. For

example, most arable soils harbour approximately 2500 kg C in living biomass in the top (25 cm) per hectare. This is equivalent to dry matter and 50,000 kg fresh material. Estimates of a biomass turn-over rate of one year and an energy conversion efficiency (Hunt *et al.* 1987; de Ruiter *et al.* 1993b), then mass processes 1,00,000 kg of fresh organic matter each year. This processing includes the digestion of dead organic matter by the microbes, as the consumption and production rates in the community food web (Hunt *et al.* 1987; McIntyre 1988; de Ruiter *et al.* 1994). With its large size and complexity the soil community has a major influence on soil processes, and the way in which these processes may vary in time and space. As these processes also determine nutrient availability for plants to take up, the below-ground decomposer interactions also influence above-ground plant productivity and carbon sequestration (Wardle and Moore 1999).

Several field and laboratory studies have been carried out to establish the role of the different groups of soil organisms in soil processes (Elliott *et al.* 1986; Hunt *et al.* 1987; Brussaard *et al.* 1990; Moore *et al.* 1988; Andrén *et al.* 1990; Van der Valk and Brussaard 1990; de Ruiter *et al.* 1993b) showing that microbes, because of their abundance, are the most important contributors to the soil processes. The faunal groups of organisms, however, are considered to contribute considerably to the soil processes, despite their relatively low densities.

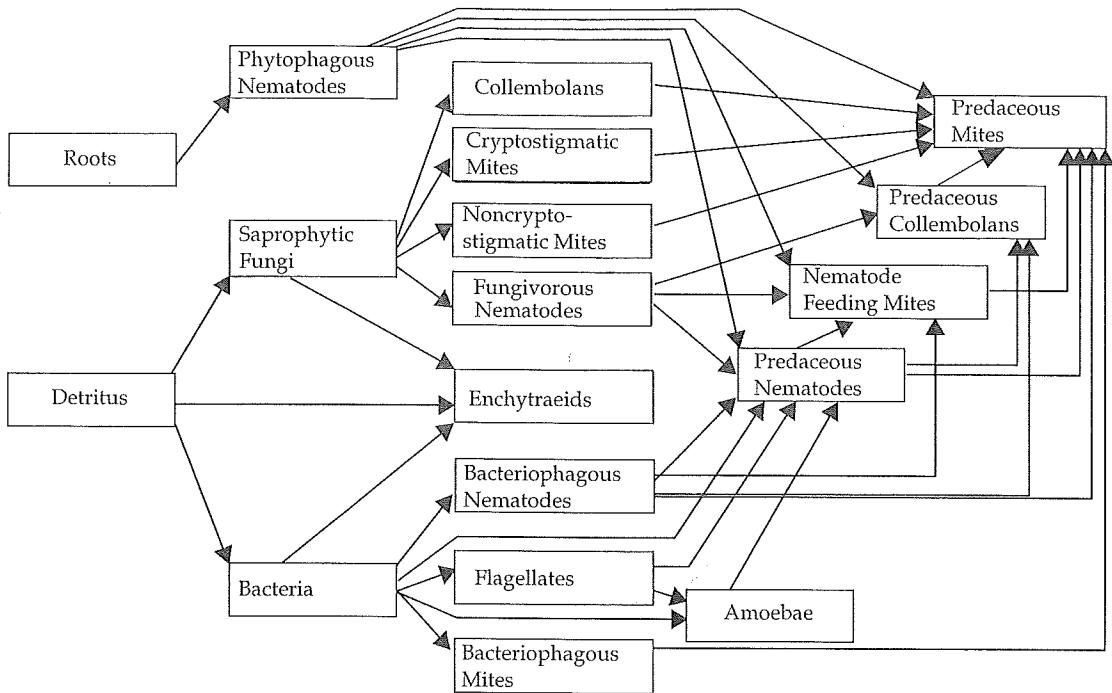


Figure 9.1 Diagram of the below-ground food web from the conventional farming system of the Lovinkhoeve experimental farm (de Ruiter *et al.* 1993a). Species are aggregated into functional groups, i.e. based on food choice and life-history parameters groups (Moore *et al.* 1988). Detritus refers to all dead organic material. Material flows to the detrital pool through the death rates and the excretion of waste products are not represented in the diagrams, but are taken into account in the material flow calculations and stability analyses.

example, in many soils microbes constituted more than 90% of the total soil biomass, while the contribution of the soil fauna to mineralization processes was estimated to be higher than 30%. Apart from their direct contributions, higher trophic level organisms may also indirectly contribute to soil processes by stimulating microbial activity, e.g. through reducing the microbial population sizes and hence enhancing the relative and absolute microbial growth rates (Coleman *et al.* 1978, 1983; Woods *et al.* 1982; Verhoef and Brussaard 1990), or through increasing the availability of limiting resources like oxygen or nutrients (Woods *et al.* 1982; Coleman *et al.* 1983; Mikola and Setälä 1998a; Scheu and Setälä 2001). Stimulation of microbial growth through increasing nutrient availability by the soil fauna links the above-ground and below-ground ecosystem compartments. The higher trophic levels in the below-ground decomposer food web enhance the availability of nutrients for microbial activity

and the decomposition of soil organic matter, as well as for plants, enhancing above-ground primary productivity and primary producer based food chain processes (Wall and Moore 1999; Hooper *et al.* 2000).

The range of biological soil processes depends on the activity of a variety of soil organisms. Some groups are exclusively responsible for particular processes in the N-cycle like nitrification and denitrification (Swift *et al.* 1998). Other processes such as the decomposition of soil organic matter depend on a large variety of soil organisms, as the ability to decompose the various organic compounds is related to the genetic properties and variation in the soil microbial community (Griffiths *et al.* 2000). A recent review on the possible relationship between soil biodiversity and soil ecosystem functioning has, however, not provided clear and unambiguous patterns (Mikola *et al.*, Chapter 15). In fact, experimental evidence indicates that soil ecosystems have

a high level of functional 'redundancy' (Andrén *et al.* 1995), and hence traits involving the transfer of materials, energy and nutrients through the soil community food web seem broadly distributed, so that changes in the food web diversity have little effect on ecosystem processes (Wolters 1997; Wolters *et al.* 2000).

In this chapter, we will focus on the relationship between soil biodiversity and soil ecosystem functioning in terms of ecosystem stability. Ecosystem stability here includes *qualitative stability* of the soil community (the ability of the community to withstand disturbance in a way that all species return to their original equilibrium state), as well as *resistance* (sensitivity to disturbance in terms of relative change) and *resilience* (speed with which the changed variable returns to its original level) of the soil ecosystem processes (Loreau *et al.*, Chapter 7). The idea behind a biodiversity–stability relationship is that in soils the communities are highly diverse, and that this diversity is maintained through the energetic organization of the communities, e.g. in terms of pools and flows of energy, compartmentation in energy channels or patterned interaction strengths among the populations (Moore and Hunt 1988; de Ruiter *et al.* 1995; Moore and de Ruiter 1997). Disturbance is thought to affect this organization leading to reduced community stability and diversity and in consequence reduced stability of soil ecosystem processes. First, we will summarize observed patterns in soil community structure, and how these patterns relate to community stability. Then we highlight food web analyses as a way to connect soil community structure to community stability and present experimental evidence of disturbance effects on soil biodiversity and the stability of soil processes. Finally, we discuss these findings in the context of the relationship between biodiversity and stability in ecosystems (Loreau *et al.*, Chapter 7).

9.2 Patterns in community structure, community stability, and the effects of disturbance

The increasing awareness of environmental problems has directed much ecological research

towards the question of how environmental stress-factors that are caused by human activities alter the structure of ecological communities and the functioning of ecosystems. Examples of environmental issues that inspired ecologists are climate change, land-use change, environmental pollution, acidification and enrichment. This has generated an impressive amount of knowledge and understanding about the way ecosystems function under different disturbance regimes and how community populations are able to survive stress events. A central concept in these studies is stability, which is often measured by various properties, such as qualitative stability, resistance and resilience (Loreau *et al.*, Chapter 7; McCann 2000). A classical contribution to this field was the work by May (May 1972, 1973) who encouraged ecologists to rethink relationships between complexity and stability, as his models indicated a negative relationship between complexity and stability rather than the positive relationship assumed by many ecologists at that time (MacArthur 1955; Elton 1927). The work of May encouraged many theoretical and empirical studies on complexity, patterns in community structure and stability (Pimm and Lawton 1978; Paine 1980, 1992; Pimm *et al.* 1980; Yodzis 1981; McCann *et al.* 1988; Moore and Paine 1988; Polis 1991; DeAngelis 1992; de Ruiter 1995; Neutel *et al.* 2002). All these studies provided indications that in real ecosystems the structure of communities is organised in patterns that are important to community stability. These patterns may refer to properties of food web structure such as the rarity of omnivory and detritivory (Pimm *et al.* 1981), the lengths of food chains (Lawton 1977) and compartmentation (Pimm and Lawton 1977; Moore *et al.* 1993), as well as patterns in the interaction strengths among populations such as a few strong links embedded in a majority of weak links (Paine 1992) and specific organization of interaction strengths across trophic levels and trophic loops (McCann 1988; de Ruiter *et al.* 1995; Neutel *et al.* 2002). This has led to the argument that patterns in natural communities are critical to the sustainable conservation of biological diversity (Pimm and Polis 1998).

9.3 Food web analysis as a way to connect community structure to processes and community stability

While in the above-ground ecosystem compartment biodiversity and ecosystem processes are importantly influenced by intraspecific and interspecific competition and habitat exploitation (Naeem *et al.* 1994a; Tilman *et al.* 1996), in soils the relationship between biodiversity and soil processes is thought to be primarily controlled by dynamics and interactions in the soil community food web (Moore and de Ruiter 1997; de Ruiter *et al.* 1998; Wall and Moore 1999). Food web (i.e. trophic) interactions affect the distribution and abundance of organisms in fundamental ways, since the dynamics of populations are largely a function of energy gains and losses derived from predation by and on other populations. Food webs therefore provide a way to analyse the dynamics of populations in the context of the community structure as a whole. Since trophic interactions represent transfer rates of energy and matter, overall processes, such as the cycling of energy and nutrients, and food web structure are deeply interrelated (Hunt *et al.* 1987; Moore *et al.* 1988, 1993; DeAngelis 1992; Hairston and Hairston 1993; de Ruiter *et al.* 1994, 1995). Food webs therefore also provide a way to connect the dynamics of populations to the dynamics in pathways within the cycling of matter, energy and nutrients (DeAngelis 1992; de Ruiter *et al.* 1994). Hence, by means of the population dynamical descriptions of the trophic interactions in food webs, we can analyse the stability and disturbance effects on community structure as on ecosystem processes.

The aim to connect community structure to ecosystem processes, and the incomplete taxonomic descriptions of the soil biodiversity, has led to the functional group approach in soil food web research (Moore *et al.* 1988). Within broad taxonomical units (bacteria, fungi, protozoa, nematodes, micro-arthropods), functional groups are defined on the basis of similar food choice, predators, and physiological properties such as energy conversion efficiencies, and specific growth and death rates. The functional groups approach therefore implicitly assumes that species within groups respond

similarly to changes in community structure and environmental conditions. The functional group approach aims to describe community and processes in the same 'currencies', i.e. in terms of material pools (e.g. population sizes in kg C ha^{-1}) and material flows (e.g. feeding rates in $\text{kg C ha}^{-1} \text{ yr}^{-1}$). Each functional group then represents a specific component in the cycling of materials, energy and nutrients. Effects of disturbances on particular groups can then be translated into effects in terms of altered contributions to ecosystem processes. This approach implies that diversity is defined 'functionally', in terms of the diversity in functional groups and the diversity in pathways in the cycling of materials, energy or nutrients.

9.4 Patterns and stability in soil food webs

During the last decades several large multidisciplinary research programs have been carried out directed to the development of sustainable agricultural management practices (Hendrix *et al.* 1986; Hunt *et al.* 1987; Brussaard *et al.* 1988, 1990; Moore *et al.* 1988; Andrén *et al.* 1990; de Ruiter *et al.* 1993b; Zwart *et al.* 1994). The outcome of these field programmes provided estimates of the population sizes for all functional groups, making it possible to construct qualitative (Fig. 9.1) and quantitative (Table 9.1) descriptions of the soil food web structures and relate these structures to soil organic matter decomposition and the mineralization of nutrients.

Based on observed population sizes (Table 9.1) and on literature values regarding death rates and energy conversion efficiencies, the feeding rates among the functional groups in the soil food webs were estimated through food web modelling (O'Neill 1969; Hunt *et al.* 1987; de Ruiter *et al.* 1993b), (Box 9.1(a)). The outcome of these calculations indicated that the feeding rates in the food webs show similar patterns as the population sizes (Table 9.1) in the form of trophic pyramids, i.e. decreasing population sizes and feeding rates with increasing trophic level (Fig. 9.2(a)). The modelled feeding rates have been verified at the level of overall carbon mineralization, indicating that the calculated rates were close to the observations

Table 9.1 Biomass estimates (kg C ha^{-1}) for the functional groups in the different food webs. Values refer to the 0–25 cm depth layer, except for the Horseshoe Bend webs (0–15 cm). CPER: a short grass prairie from the Central Plains Experimental Range, Colorado, USA (Hunt *et al.* 1987; Moore *et al.* 1988). LH: Lovinkhoeve Experimental Farm (Marknesse, The Netherlands); CF: conventional farming; IF: integrated farming; integrated farming differs from conventional farming with respect to the more frequent use of organic manure instead of inorganic fertilizer, reduced use of pesticides and reduced soil tillage (Brussaard *et al.* 1988, 1990; de Ruiter *et al.* 1993; Zwart *et al.* 1994). HSB: Horseshoe Bend Research Site, Georgia, USA; CT: conventional tillage; NT: no tillage (Hendrix *et al.* 1986, 1987). KS: Kjettlsinge Experimental Field, Uppsala, Sweden; BO: barley without nitrogen fertilizer; B120: barley with fertilizer (Andrén *et al.* 1990)

	CPER	LH-IF	LH-CF	HSB-NT	HSB-CT	KS-BO	KS-B120
<i>Microbes</i>							
Bacteria	304	245	228	440	690	740	900
Fungi	63	3.27	2.12	160	150	1500	2300
VAM	7						
<i>Protozoa</i>							
Amoebae	3.78	18.9	11.5	40 ²	50 ²	110 ²	34 ²
Flagellates	0.16	0.63	0.53				
<i>Nematodes</i>							
Herbivores	2.90	0.35	0.19	0.40	0.50	0.18	0.29
Bacteriovores	5.80	0.36	0.30	0.46	1.40	0.45	0.50
Fungivores	0.41	0.13	0.08	0.12	0.08	0.20	0.12
Predators ¹	1.08	0.06	0.06			0.44	0.44
<i>Arthropods</i>							
Herbivorous Herbage Arthropods						0.10	0.14
Predatory Herbage Arthropods						0.15	0.19
Herbivorous Macro-arthropods						0.19	0.19
Micropredatory Macro-arthropods						0.25	0.25
Predatory Macro-arthropods						0.49	0.49
Predatory Mites	0.16	0.08	0.06	0.20 ³	0.04 ³	0.18 ⁴	0.28 ⁴
Nematophagous Mites	0.16	0.006	0.004				
Cryptostigmatic Mites	1.68	0.003	0.007	0.80	0.22		
Non-Cryptostigmatic Mites	1.36	0.04	0.02	0.90	0.39		
Bacteriovorous Mites	0.0003	0.001					
Fungivorous Collembola	0.46	0.38	0.47	0.30	0.09	0.17 ⁵	0.17 ⁵
Predatory Collembola	0.008	0.03					
<i>Annelids</i>							
Enchytraeids	0.21	0.43	0.10	0.30	4.20	3.40	
Earthworms	63.5	—	100	20	13	13	

¹ Including predators and omnivores.

² including amoebae and flagellates.

³ including all predatory arthropods.

⁴ including all predatory micro-arthropods.

⁵ including all microbial feeding micro-arthropods.

(de Ruiter *et al.* 1993b). Hence, the structure of the soil food webs includes patterns that are common to most ecosystems: energy pools (population sizes) and the energy flows (feeding rates) form a pyramidal structure along trophic level (Odum 1963).

The strengths of the interactions, i.e. the effect the populations upon each other, are regarded as central importance to food web stability (May 1973; Yodzis 1981; McCann *et al.* 1988; Paine 1980; de Ruiter *et al.* 1995). Interaction strengths can be mathematically defined as the entries of

Box 9.1 Methods of calculation

(a) Modelling energy flow rates: feeding rates

Feeding rates are derived from population sizes and data on death rates and energy conversion efficiencies. The basic assumption underlying the calculation of feeding rates is that the annual (equilibrium) feeding rates should balance the annual death rate through natural death and predation (Hunt *et al.* 1987; O'Neill 1969):

$$F_j = \frac{d_j B_j + M_j}{a_j p_j} \quad (9.1)$$

where F_j is the feeding rate ($\text{kg C ha}^{-1} \text{yr}^{-1}$), d_j is the specific death rate (yr^{-1}), B_j is the average annual (equilibrium) population size ($\text{kg C ha}^{-1} \text{yr}^{-1}$), M_j is the death rate due to predation ($\text{kg C ha}^{-1} \text{yr}^{-1}$), a_j is the assimilation efficiency, and p_j is the production efficiency.

For polyphagous predators, the feeding rate per prey type (F_{ij}) is based on the relative abundances of the prey types and on prey preference:

$$F_{ij} = \frac{w_{ij} B_i}{\sum_{k=1}^n w_{ik} B_k} F_j \quad (9.2)$$

where F_{ij} is the feeding rate by predator j on prey i , w_{ij} is the preference of predator j for prey i over its other prey types. The calculations of feeding rates start with the top predators, which suffer only from natural death, and proceeded working backwards to the lowest trophic levels.

(b) Modelling interaction strengths and stability

Interaction strengths are the entries of the community matrices (May 1972, 1973), referring to the per capita—in this case per biomass—effects upon one another in equilibrium. The interaction strengths are derived from the population sizes and energy flow rates by assuming Lotka–Volterra equations for the dynamics of the functional groups:

$$\dot{X}_i = X_i \left[b_i + \sum_{j=1}^n c_{ij} X_j \right] \quad (9.3)$$

where X_i and X_j represent the population sizes of group i and j , respectively, b_i is specific rate of increase or

community matrices (May 1973), to be derived from population sizes and feeding rates (Box 9.1(b)). Estimates of the interaction strengths obtained this way for the soil food webs also revealed patterns along trophic position (Fig. 9.2(b)), but different from the population sizes and feeding rates, as the

decrease of group i , and c_{ij} is the coefficient of interaction between group i and group j . The matrix elements (α_{ij}) are defined as the partial derivatives near equilibrium: $\alpha_{ij} = (\partial \dot{X}_i / \partial X_j)^*$. Values for the interaction strengths are derived from the equilibrium descriptions by equating the death rate of group i due to predation by group j in equilibrium, $c_{ij} X_i^* X_j^*$, to the average annual feeding rate, F_{ij} (eqn 9.1) and the production rate of group j due to feeding on group i , $c_{ij} X_i^* X_j^*$, to $a_j p_j F_{ij}$ (de Ruiter *et al.* 1995). With equilibrium population sizes, X_i^* , X_j^* , assumed to be equal to the observed annual average population sizes, B_i , B_j , the effect of predator j on prey i is

$$\alpha_{ij} = c_{ij} X_i^* = -\frac{F_{ij}}{B_j} \quad (9.4)$$

and the effect of prey i on predator j is

$$\alpha_{ji} = c_{ji} X_j^* = \frac{a_j p_j F_{ij}}{B_i} \quad (9.5)$$

(c) Evaluating community stability

The stability of the matrices is established by evaluating the eigenvalues of the community matrices; when all real parts are negative the matrix is stable, and the food web is considered to be locally stable (May 1973).

In the stability analysis of the seven soil food webs (Fig. 9.3), the matrix element values in the ‘real’ matrices are sampled randomly from the uniform distribution with intervals $[0, 2\alpha_{ij}]$, in which α_{ij} is the value as derived from the observations (eqs (9.4) and (9.5)). Elements referring to the feedbacks to detritus are derived in the same way as the trophic interactions. The diagonal matrix elements referring to intragroup interference are set at three levels of magnitudes (s_i) proportional to the specific death rates (d_i) with $s_i = 1.0, 0.1$ and 0.01 for all groups equally (de Ruiter *et al.* 1995). In the disturbed matrices, the non-zero pairs of values of the matrix elements are randomly permuted (Yodzis 1981). This method leaves food web structure (placing of the non-zero terms) and the logical pairing of the elements unchanged. The comparison is based on 1000 runs.

patterning is characterized by relatively strong top-down effects at the lower trophic levels and relatively strong bottom-up effects at the higher trophic levels (Fig. 9.2(b)).

The patterns of interaction strengths in the soil food webs were found to be important to the

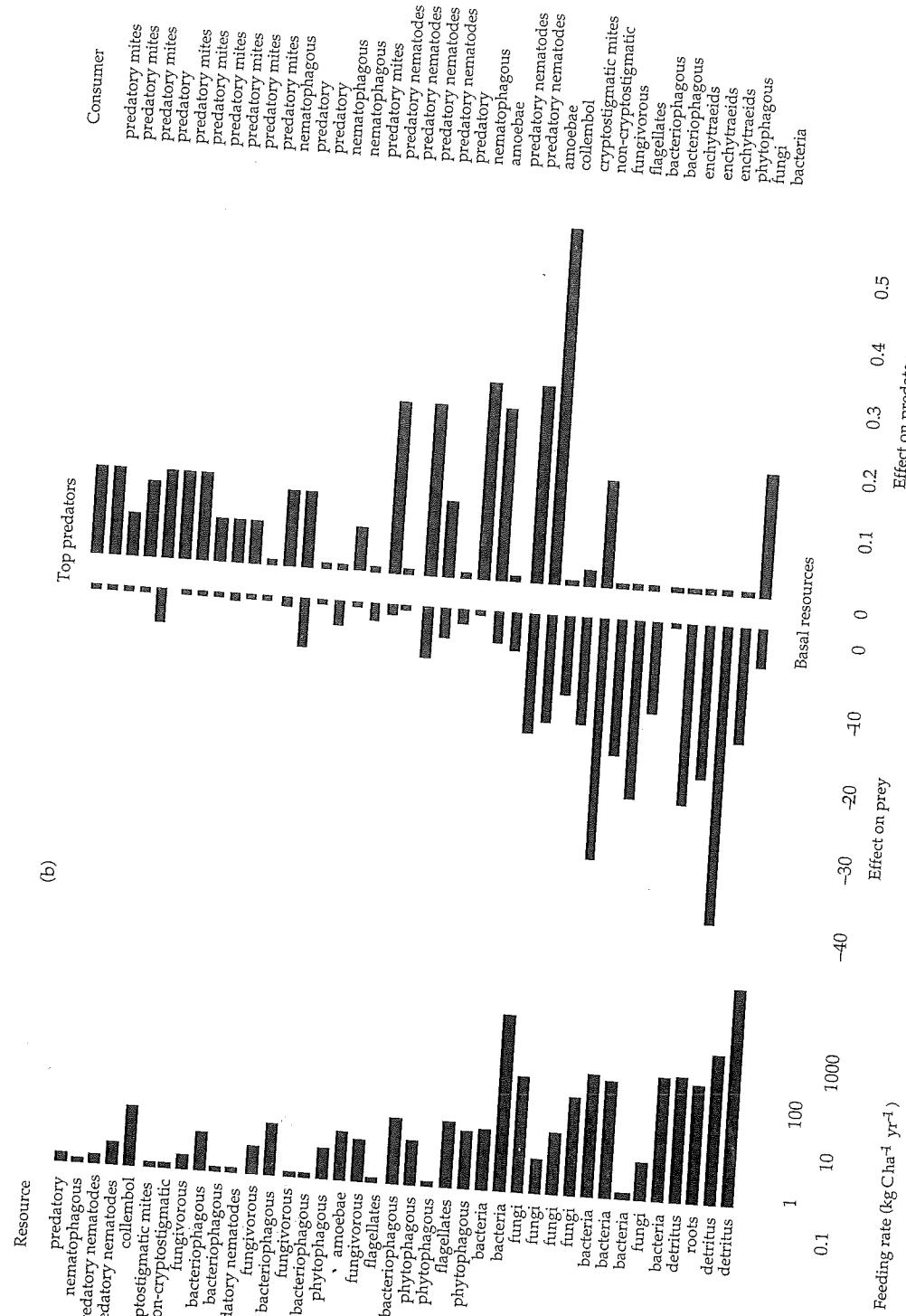


Figure 9.2 Pattern in feeding rates and interaction strengths along trophic level in the food web of the Lovinkhoeve experiments. (a) Feeding rates. (b) Interaction strengths (yr^{-1})

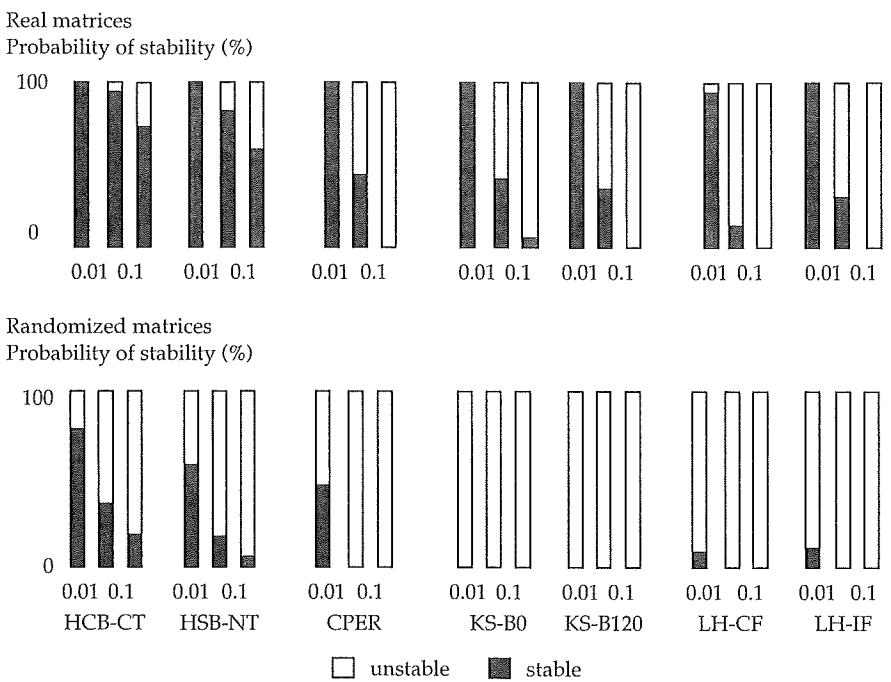


Figure 9.3 The effect of disturbing the patterning of interaction strength on the stability of seven food webs (de Ruiter *et al.* 1995). The black fraction in the bars denotes the percentage of stable matrices based on 1000 runs (Box 9.1(c)). In the real matrices, the element values are sampled randomly from the uniform distributions $[0, 2\alpha_{ij}]$, in which α_{ij} is the value as derived from the observations (Box 9.1(b)). The diagonal matrix elements referring to intragroup interference are set at three levels of magnitudes (s_i) proportional to the specific death rates (d_i) with $s_i = 1.0, 0.1$ and 0.01 for all groups equally. In the disturbed matrices, the non-zero pairs of values of the matrix elements are randomly permuted (Yodzis 1981). Abbreviations denoting the different soil ecosystems are given in the legend of Table 9.1. A sensitivity analysis (Neutel 2001) showed that variation in the parameter values within intervals between half and twice the observed value (Table 9.1) led to variation in interaction strengths and in the probability of matrix stability, but this variation was relatively small compared to the difference in stability probability between the real and the random matrices, indicating the robustness of the stability analyses (Neutel *et al.* 2002).

community stability. A comparison was made between the stability of community matrix representations of the soil food webs using the empirically based values of interaction strengths ('real' matrices) and that of matrices in which these values were randomized (Yodzis 1981), (Box 9.1(c)). Stability of the community matrices was established by evaluating the signs of eigenvalues of the matrices; when all real parts were negative the matrix is stable, and the food web was considered to be locally stable (Box 9.1(c)). This approach follows the definition of local stability analysis (May 1973). The comparison showed that matrices including the realistic patterns of interaction strengths were far more likely to be stable than their randomized counterparts (Fig. 9.3). This result indicates that energetic organization and community stability

are inextricably interrelated, as the stabilizing patterns of the interaction strengths were the direct results of patterns in population sizes and feeding rates (Box 9.1(a)). Disturbing the patterning of interaction strengths (Fig. 9.3) or the energetic properties of the functional groups such as population size distributions (de Ruiter *et al.* 1995) caused a loss in community stability.

9.5 Experimental evidence of environmental effects on soil biodiversity and process stability

To obtain empirical information of the relationship between disturbance, biodiversity and stability in soils ecosystems, a European consortium (MICRODIVERS) carried out laboratory experiments

in which soils were submitted to repeated stress regimes (Griffiths *et al.* 2000, 2001b). The stress-on-stress experiments were designed to test whether a (first) disturbance affects the way in which a community or a process responds to a next disturbance (Griffiths *et al.* 2000). In the first experiment, a first stress was applied by exposing the soil to chloroform vapour (fumigation) for 0 h (unfumigated control), 0.5, 2, or 24 h (Fig. 9.4(a)). Following the fumigation, soils were incubated for 5 months to allow the surviving organisms to grow and for the overall biomasses within the different treatments to equilibrate. No recolonization was possible during this incubation. When measured after this incubation, the first stress was found to reduce the diversity of the soil community progressively as fumigation time increased, leading to the disappearance of much functional, species and genetic variation, especially in the soils fumigated for 2 and 24 h (Griffiths *et al.* 2000). The genetic (measured through DNA-fingerprinting), phenotypic (from colony morphology) and functional (measured as ability to utilize sole carbon sources) diversity of the bacterial community decreased, as did the biodiversity (number of trophic groups, phyla within trophic groups, and taxa within phyla) of the microfauna (protozoa and nematodes; micro-arthropods not measured). Overall there was a 60% reduction in biodiversity. The fumigation also affected soil ecosystem processes, but to a more limited degree: many species disappeared but no ecosystem process was eliminated. Some process rates increased, e.g. microbial growth with a 30% increase in thymidine incorporation and a 10% increase in the decomposition rate of added plant residues, while other process rates decreased, e.g. nitrification by 90%, denitrification by 70% and methane oxidation by 95%. The results of the first stress therefore indicate a level of functional redundancy: although many groups of organisms disappeared, ecosystem processes were still able to continue, especially the process of soil organic matter decomposition in which a high diversity of decomposers is involved (Griffiths *et al.* 2000).

The second stress was applied as either a persistent disturbance by adding a heavy metal (copper in the form of CuSO_4), which reduced growth rates, or a transient disturbance, by applying a

temperature shock (brief heating to 40°) population sizes. The effects of the second stress were measured as changes in respiration with decomposition of freshly added organic matter. Respiration in the most diverse soils (fumigation) was hardly affected by the temperature shock, while respiration in the disturbed soils (fumigation) decreased by more than 70%. Soils given the transient heat stress showed resilience, with the least diverse soil recovering within 57 days, while in the most diverse soils recovery was complete within 15 days, with the lowest diversity even showing an 'overshoot-response', in that respiration rapidly exceeded the rate before the disturbance. The results of this experiment agreed with the notion that the relationship between diversity, soil biodiversity and ecosystem function is not direct (Mikola *et al.*, Chapter 15; M. Setälä 1998a): while the effects of the first stress indicated functional redundancy for soil matter decomposition and respiration, the second stress showed that the stability of these processes was reduced. Hence, there was redundancy after the first stress; such loss of redundancy may be highly relevant for ecosystem recovery in the course of multiple stress events.

These experimental results cannot be interpreted as direct effects of reduced biodiversity on ecosystem stability, however, as it might have been the disturbance that reduced both biodiversity and stability. A second experiment was carried out to separate disturbance effects from biodiversity effects (Griffiths *et al.* 2001b). Basically, the experimental set-up was the same as the first experiment (Fig. 9.4(a)), but the first stress was now applied by inoculating sterile soils with serially diluted suspensions prepared from the parent soil (Griffiths *et al.* 2001b). Dilution factors were 10^0 (control), 10^4 , and 10^6 and there was a similar period for populations to recover from the first stress as in the first experiment. Hence, a comparison could be made among soils that were all disturbed, but differed with respect to biodiversity depending on the dilution factor. A possible 'hidden treatment' in such a dilution approach might be that different dilutions had differential effects on body size, because

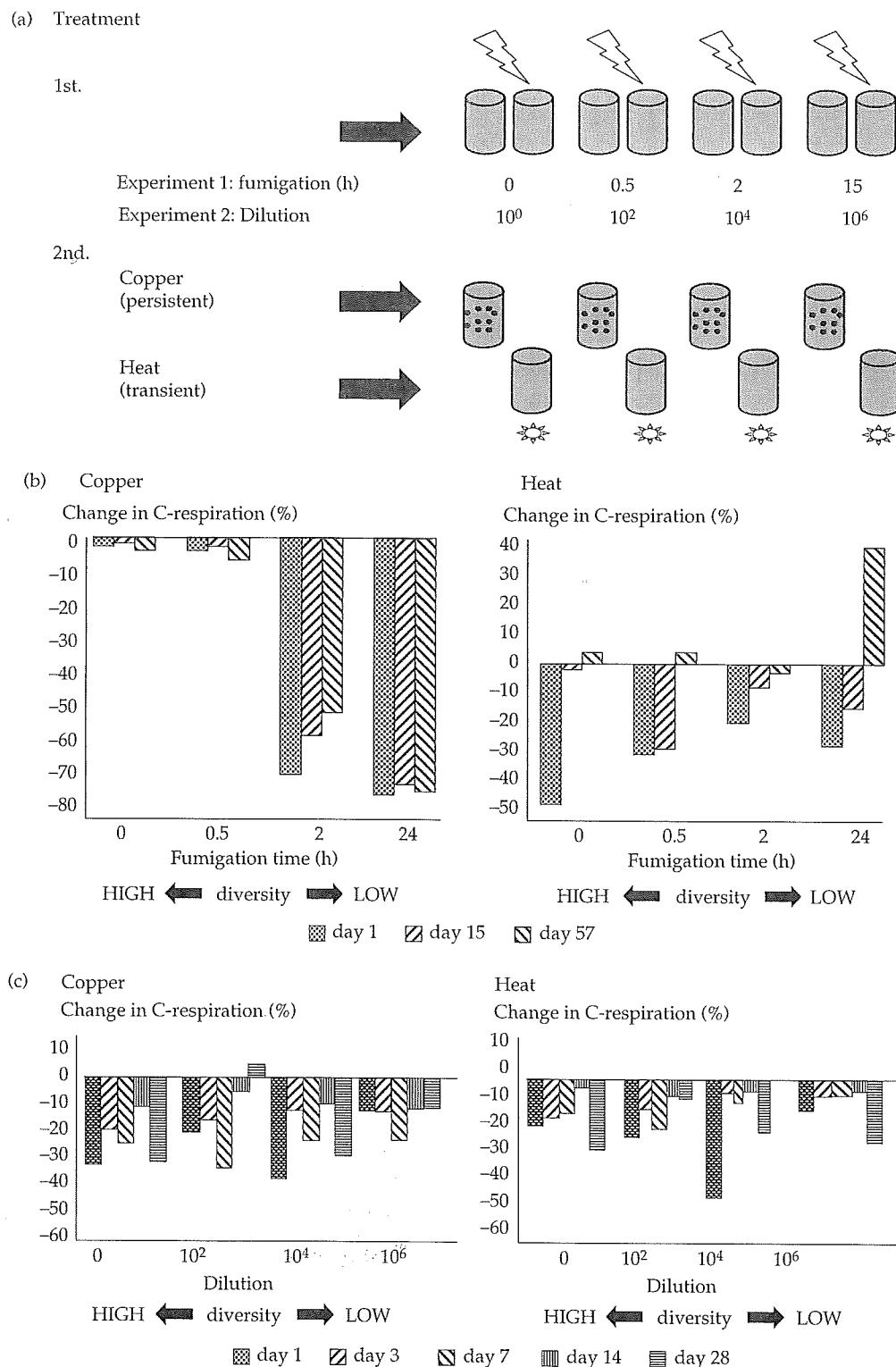


Figure 9.4 Design (a) and results (b, c) of two stress-on-stress experiments (Griffiths *et al.* 2000, 2001b). In the first experiment, the first stressor is soil fumigation of various duration, and in the second experiment it is inoculating sterile soils with serially diluted soil suspensions from the parent soil. In both experiments, the second stressors are a persistent (Cu addition) or a transient (heat-shock) disturbance. (b) and (c) the effects are measured in terms of relative change in carbon respiration measured 1, 15 and 57 days (experiment 1) or after 1, 3, 7, 14 and 28 days (experiment 2).

species are less common than smaller species, and that the variance between treatment replicates would be expected to be higher at higher dilutions. In practice, this did not occur as there were no trends observed of body size or variability with dilution factor. The results of this experiment showed that the first stress led to similar effects as in the first experiment, with progressively decreasing biodiversity (bacterial, fungal and protozoan) with increasing dilution factor, while process rates were less affected (Griffiths *et al.* 2001b). The second stress factors were the same as in the first experiment: either a copper treatment or a heat shock. The effects of the second stressors in this experiment showed similar responses in all dilution treatments, with the strengths of the responses comparable to those in the least diverse soils (2 and 24 h fumigation) in the first experiment. These results therefore indicate that in the first experiment it might have been the stress itself (the initial fumigation) that reduced process stability, not necessarily changes in biodiversity. The hypothesis that disturbance affects stability has further been tested experimentally by subjecting soils to combinations of the persistent (copper) and transient (heat) stresses as used above. In this case, soils from two management regimes, intensive or organic horticulture as described by (Griffiths *et al.* 2001a), were subjected to a copper or heat stress followed a week later by the other type of stress.

Table 9.2 The decomposition of grass residues added to intensively or organically managed soils receiving combinations of persistent (copper) and transient (heat) stresses. Decomposition was measured as the liberation of CO₂ over 24 h following addition

Soil management	Pre-stress	Stress	μgCO ₂ -C g ⁻¹ d ⁻¹	Standard error	% change from unstressed
Intensive	None	None	45.6	0.68	
	None	Cu	41.5	1.69	-9
	Heat	Cu	38.4	0.97	-16
	None	Heat	46.4	1.36	2
	Cu	Heat	36.1	1.08	-20
	None	None	50.2	1.01	
	None	Cu	51.6	1.01	3
	Heat	Cu	49.4	1.03	-5
	None	Heat	53.8	1.26	7
	Cu	Heat	53.6	3.32	7

The results of this experiment decomposition of organic matter w. soils that had been previously str destabilization depended on manag the organically managed soil was m the intensively managed soil (Griffit

These experimental findings all disturbance affects the structure and l soil communities and the stability processes. The first stress-on-stress showed effects on process stability t caused by disturbance, by reduced bi by both disturbance and biodiversity and third experiment indicated the of disturbance. To establish a biodiv separated from any disturbance effect, are required on a series of undisturbe vary (strongly) in biodiversity. It has hc difficult to find suitable series, as n that differ in biodiversity are to be ex to differ in organic matter richness, hel soil structure and texture and humidity all interfere with the analyses of biodiv stability.

9.6 Conclusions: biodiversity, sta and the effects of disturbance

Food webs provide a way to explicitly re munity structure to ecosystem process

food web interactions represent transfer rates that participate in the cycling of materials, energy and nutrients. Such a direct relation is important for untangling and understanding the complex relationship between biodiversity and ecosystem functioning. This is especially the case when looking at properties such as community stability and ecosystem process stability (Loreau *et al.*, Chapter 7). The results show that in soils, communities are energetically organized in a way that is important to stability, since energetic properties, such as population size distributions, energy conversion efficiencies and growth and death rates (Table 9.1), determined the stabilising patterns of the interaction strengths (Fig. 9.2(b)). The results also indicate that biodiversity itself does not necessarily influence stability, but that it might also be the environmental stress and disturbance that causes this effect. The stabilizing energetic set-up of the soil communities results from properties that seem common to many ecosystems, such as the trophic biomass pyramids in combination with omnivorous interactions (Neutel *et al.* 2002). Therefore, the present results might also apply to other kinds of ecosystems.

Although disturbance seems to affect both community stability and process stability, we should be careful in linking these two *variables of interest* (Loreau *et al.*, Chapter 7). For the soil communities it was the qualitative stability that was assessed, while for process stability the analyses focused on resistance and resilience. Also, process stability was assessed in soils in which community structures were strongly altered and biodiversity was reduced. On the other hand, there should be some link between community stability and process stability since population dynamics and interactions in food webs represent material flow rates and hence components in ecosystem processes. Relating community stability to process stability, and identifying key-properties in natural ecosystems that are critical to both community and process stability, should be focus of future research. This may provide the necessary scientific basis for understanding biodiversity–ecosystem functioning relationships and the adverse effects and risks of human activities on natural ecosystems on which decisions can be made about how best to treat our natural environment (Polis 1998).

