Biodiversity, Ecosystem Functioning, and Human Wellbeing

An Ecological and Economic Perspective

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CHAPTER 6

Biodiversity and the stability of ecosystem functioning

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6.1 Introduction

6.1.1 Overview

Concern that the rapid anthropogenic erosion of biodiversity (Wilson 1992) may undermine the delivery of ecosystem services (Daily 1997) has prompted a synthesis of community and ecosystem ecology over the last decade. Biodiversity-ecosystem functioning (BEF) research is central to this emerging synthesis, asking how biodiversity is related to the magnitude and stability of ecosystem processes. Isolating species richness (and diversity) effects from species composition has been a chief goal of BEF research. That species richness generally enhances the mean magnitude of a variety of ecosystem properties is now well established (Hooper *et al.* 2005; Balvanera *et al.* 2006; Cardinale *et al.* 2006a), but the effect of species richness on the stability of ecosystem properties remains equivocal (Hooper *et al.* 2005).

Early consensus (Odum 1953, MacArthur 1955, Elton 1958, Pimentel 1961) that diversity enhances various aspects of community and ecosystem stability was largely founded on qualitative observations and intuitive reasoning. This view was apparently contradicted by the results from rigorous mathematical treatments (e.g. May 1972) which showed that in a food web context stability was related to system properties, i.e. connectance, species richness, and interaction strength, and importantly, could be reduced by species richness. Recognition that stability has multiple definitions that can apply to all levels of ecological organization (Pimm 1984; see also Loreau *et al.* 2002) helped pave the way for a new, synthetic perspective that developed during the 1990s as attention to extinction's consequences for the stability of ecosystem functioning increased (Tilman and Downing 1994, Naeem and Li 1997). This BEF perspective recognized that fluctuating abundances of component species may not produce instability at the community or ecosystem level because compensatory reactions among species dampen fluctuations of aggregate abundance (Tilman 1996). The distinction between population and community-level variability was firmly drawn (Tilman 1996) and attention was focused on the latter through the BEF research agenda.

Within the BEF framework, experiments and theory explicitly relating to the effect of species richness on community-level aggregate properties (mainly biomass) have focused on variability through time in relation to background environmental variation (temporal stability) as well as on the impact (resistance) and recovery (resilience) of such properties to discrete, and often extreme, perturbations. In this chapter we review recent empirical studies examining the links between species richness and these three facets of stability (see Ives and Carpenter 2007 for a review of other types of stability). In addition, recognizing that explicit BEF experiments are limited in their spatial and temporal scope, we adopt a wider perspective by discussing how changes in biodiversity may undermine stabilizing properties of food webs and the ability of ecosystems to resist state-changes. Furthermore, using examples we emphasize that direct measurement of the stability of ecosystem services across gradients of human impacts can show how stability is influenced by human activities – both directly and indirectly via changes in diversity.

6.1.2 Theory linking biodiversity and stability

Theory has established strong links between species richness and the temporal variability of community-level properties and has provided a variety of possible explanatory mechanisms (reviewed by Cottingham *et al.* 2001, Loreau *et al.* 2002; see Box 6.2). Doak *et al.* (1998) argued that a reduction in community variability with increased diversity is an inevitable consequence of 'statistical averaging', i.e. the sum of many randomly and independently variable items is less variable than the average item. The strength of this effect depends on how the variances of populations scale with their means (Tilman *et al.* 1998), and the evenness of species' abundances and how their fluctuations are related (Doak *et al.* 1998, Tilman *et al.* 1998).

The importance of how species fluctuations are related is also reflected in another proposed stability mechanism that is closely related to the concept of statistical averaging: the 'insurance hypothesis'. This assumes that interspecific niche differentiation causes species to respond differently to the environment and that this differential response can produce compensatory dynamics among species, buffering the impact of environmental changes (McNaughton 1977, Walker 1992, Naeem and Li 1997). The insurance hypothesis depends upon functional redundancy: the concept that species within the same functional group may replace each other with no consequences for ecosystem function. The stabilizing role of this mechanism further depends upon the diversity of species' responses within functional groups (functional response diversity; Lavorel and Garnier 2002, Elmquist *et al.* 2003). Theoretical models of competitive communities formalized the insurance hypothesis and confirmed that species diversity can stabilize community properties in the face of changing environmental conditions (Yachi and Loreau 1999, Ives *et al.* 1999). This prediction also generally holds for simple, theoretical, multi-trophic systems (Ives *et al.* 2000; Thébault and Loreau 2005) and metacommunities (Loreau *et al.* 2003).

The resistance of aggregate community properties is also theoretically enhanced by diversity under the insurance hypothesis, as species tolerant to a pulse perturbation or directional change in conditions are more likely to occur in diverse communities (Walker 1992, Yachi and Loreau 1999). On the other hand, the resilience of aggregate community properties (the return rate following an equal reduction in the populations of all component species) is not incorporated under the insurance hypothesis, in which species populations are differentially affected by the environment or perturbations. The resilience of populations may in fact be reduced by high levels of diversity in competitive communities (Loreau and Behera 1999). This theory does not account for differences between species in growth rates, however, which may result in a positive relationship between species richness and return rate of community biomass (resilience) through a sampling effect (Steiner *et al.* 2005b). Theory has yet to explicitly address this possibility, however.

6.2 Empirical findings

Problems with the design and interpretation of experimental tests (Givnish 1994, Huston 1997, Fukami *et al.* 2001) together with a general shortage of such tests, have hampered the attempts of earlier reviews to assess the effect of diversity on temporal stability, resistance and resilience (Cottingham *et al.* 2001, Loreau *et al.* 2002, Hooper *et al.* 2005). Subsequent vigorous empirical research has recently been conducted in this area. This work has been generally less open to alternative interpretation, as experimental designs have evolved to limit several confounding factors previously identified (but see Wardle and Grime 2003). It has long been recognized that species composition can have strong influences on ecosystem properties. Isolating the role of species richness *per se* has been a chief goal of BEF research, and is the focus of empirical studies reviewed here.

6.2.1 Temporal stability

We first examine empirical tests of the general hypothesis that diversity enhances the temporal stability of community-level properties such as biomass or production, measured as the reciprocal of the coefficient of variation (1/CV). CV is an appropriate, and widely used, measure of variability because it is standardized to the mean, accounting for the tendency of variability to increase with the mean. Note that in the primary literature authors report either temporal variability (CV) or temporal stability (1/CV). For consistency, we interpret and discuss diversity effects from all studies in terms of temporal stability, such that positive effects are stabilizing (see Table 6.1). Eighteen separate papers published between 1994 and 2006 include a total of 22 cases in which community-level temporal stability was measured. These studies were conducted in a range of systems varying in scale from aquatic microcosms to natural forest stands. Overall, diversity stabilized community-level properties in 13 cases, had no significant effect in 8, and reduced stability in a single study.

We first deal with studies that have examined the temporal stability of community-level properties (principally biomass or its production) within a single trophic level in both manipulative and observational studies. We then consider studies that have manipulated the diversity of communities across multiple trophic levels and examined how such manipulations affect the temporal stability of biomass and ecosystem process rates.

6.2.1.1 Temporal stability of biomass within a single trophic level

Direct tests of the diversity–temporal stability hypothesis within a single trophic level have been mainly conducted within replicated grassland plots and microcosms. Recent grassland experiments in which diversity was directly manipulated show a stabilizing effect of diversity (Caldeira *et al.* 2005, Tilman *et al.* 2006b). These studies reported reduced stability of constituent populations but greater community-level stability with increased species richness, which is consistent with theory and previous experimental evidence (Tilman 1996).

Amongst the microcosm examples, only two of five studies supported the diversity–temporal stability hypothesis. Steiner *et al.* (2005a) found that the aggregate biomass of four zooplankton species in mixture exhibited greater stability than monocultures of the constituent species. Furthermore, Zhang and Zhang (2006a) found an overall stabilizing effect of algal species richness on community biomass. This effect was, however, context-dependent, in that it occurred only under conditions of low nutrient availability; no diversity effect was detectable under enriched conditions. Petchey *et al.* (2002) also did not find an effect of species richness on the temporal stability of community-level biomass, either under constant or fluctuating temperature conditions. In only a single case did diversity destabilize community biomass (Gonzalez and Descamps-Julien 2004).

The mixed outcomes of these experiments, and the lack of support for diversity–stability relationships in some cases, can be explained by a range of mechanisms that might obscure diversity effects:

1) A direct destabilizing effect of diversity on population level (growth rates: Gonzalez and Descamps-Julien 2004; biomass: Petchey *et al.* 2002) variances exists and caused some populations to vary more within diverse communities to the extent that they eclipsed the effect of stabilizing mechanisms.
2) Synchrony of species responses to environmental variability might have limited insurance effects of increased species richness.
3) Low evenness and hence high variance among population biomasses within communities could weaken the relation between species richness and community-level stability (Ives and Hughes 2002, Petchey *et al.* 2002).

A key challenge for future studies is to elucidate the source of variability among experiments and environmental contexts. Explicit consideration of the degree of functional response diversity (*sensu* Lavorel and Garnier 2002) represented by species within increasingly species-rich communities would be an important development (see e.g. Walker 1999) that could help explain effects of species richness more completely. Moreover, the degree of environmental heterogeneity through time will dictate the extent to which such functional response diversity can be realized (see Tylianakis *et al.* 2008) and should be explicitly considered in future studies.

Natural gradients in diversity are expected to be driven by external factors that may obscure the effect of diversity on stability and complicate interpretation (Ives and Carpenter 2007). However, examining natural patterns of diversity and

Table 6.1 Effect of diversity on the temporal stability of ecosystem properties.

Reference	Trophic level	Ecosystem function	Factor	Diversity gradient[a]	Ecosystem type	Time scale	Div levels	Type of div effect
Caldeira *et al.* (2005)	Primary prod	Community biomass		Exp. M	Grassland	3 yr	1 to 14	Positive
Dang *et al.* (2005)	Decomposer	Decomposition		Exp. M	Stream	28 d	1 to 16	Positive
Dodd *et al.* (1994)	Primary prod	Community biomass		Nutr. F	Grassland	42 yr	8 to 45	Positive
DeClerk *et al.* (2006)	Primary prod	Primary productivity		Nat. F	Forest	64 yr	1 to 4	None
Gonzalez and Descamps-Julien (2004)	Primary prod	Community biomass		Exp. M	Aquatic	64 d	1 to 6	Negative
Morin and McGradySteed (2004)[1]	Multi	Community CO_2 flux		Exp. M	Aquatic	42 d	3 to 9	None
Petchey *et al.* (2002)	Protists and bacteria	Community biomass	Constant temp.	Exp. M	Aquatic	6 w	2 to 8	None
Petchey *et al.* (2002)	Protists and bacteria	Community biomass	Fluctuating temp.	Exp. M	Aquatic	6 w	2 to 8	None
Romanuk *et al.* (2006)	Multi	Community biomass	Low nutrient	Exp. M (dilution)	Aquatic	5 w	1 to 8	Positive
Romanuk *et al.* (2006)	Multi	Community biomass	Med. nutrient	Exp. M (dilution)	Aquatic	5 w	1 to 8	None
Romanuk *et al.* (2006)	Multi	Community biomass	High nutrient	Exp. M (dilution)	Aquatic	5 w	1 to 8	None
Steiner (2005b)	Consumers only	Community biomass		Nat. F	Aquatic	5 m	11 to 24	Positive
Steiner *et al.* (2005a)	Consumers only	Community biomass		Exp. M	Aquatic	48 d	1 and 4	Positive
Steiner *et al.* (2005b)	Multi	Community biomass		Exp. M	Aquatic	22 d	1, 2, 4 spp (X 5 trophic groups)	Positive
Timan (1996)	Primary prod	Community biomass		Nutr. F	Grassland	8 yr	1 to 26	Positive
Tilman *et al.* (2006)	Primary prod	Community biomass		Exp. F	Grassland	10 yr	1 to 16	Positive
Tylianakis *et al.* (2006)	Multi	Parasitism		Nat. F	Agricultural	16 m	1 to 4	Positive
Valone and Hoffman (2003a,b)	Primary prod	Community biomass	Quadrat scale	Nat. F	Grassland	11 yr	1 to 16	Positive
Valone and Hoffman (2003a,b)	Primary prod	Community biomass	Plot scale	Nat. F	Grassland	11 yr	1 to 16	None
Vogt *et al.* (2006)	Multi	Community biomass		Exp. M (dilution)	Aquatic	7 w	1 to 8	Positive
Zhang and Zhang (2006a)	Primary prod	Community biomass	High nutrient	Exp. M	Aquatic	77 d	1,2,4,6	None
Zhang and Zhang (2006a)	Primary prod	Community biomass	Low nutrient	Exp. M	Aquatic	77 d	1,2,4,6	Positive

[a] Exp.: experimentally created diversity gradient; Nat.: naturally occurring diversity gradient; Nutr.: gradient produced by different nutrient levels. F.: field study; M.: mesocosm/microcosm study.

[1] Reanalysis of McGrady-Steed *et al.* (1997)

stability can reveal inter-relationships between the environment, stability and diversity. Valone and Hoffman (2003a,b) used an 11-year time series of grassland plots that varied naturally in species richness to investigate the relationship between population and community-level temporal stability. In this system, population stability increased with diversity, perhaps because the natural, productivity-driven diversity gradient resulted in larger, and thus relatively more stable, populations at higher diversity (Valone and Hoffman 2003b). At the community level, the authors found a weak stabilizing effect of diversity at the small quadrat (0.25 m^2) scale but not at the larger plot (0.25 ha) scale (Valone and Hoffman 2003a). The incongruity could be due to the scale of biological interactions, or simply due to smaller samples sizes, and thus reduced statistical power, at larger scales. At an even larger spatio-temporal scale, DeClerck *et al.*'s (2006) analysis indicates that there is no relationship between a naturally occurring gradient of conifer diversity and the temporal stability of annual biomass production in Sierra Nevada forest stands. This may be explained by a low degree of species richness and highly correlated responses of species to environmental changes. Diversity–temporal stability relationships are expected to be highly variable across natural gradients depending on the environmental driver of species diversity, the functional response range among the species, and direct environmental influences on stability.

6.2.1.2 Temporal stability in multi-trophic communities

Broadly, studies investigating the effects of diversity on temporal stability in multi-trophic systems fall into one of two categories: 1) Those that examine diversity effects on the temporal stability of community-level (and often population) biomass; 2) Those that manipulate the diversity of a non-basal species and examine effects on the stability of a non-biomass ecosystem process, e.g. decomposition. We begin by addressing the former type of multitrophic level study.

Theory developed in the context of the BEF research field predicts that, despite the complexity added when considering multi-trophic interactions, biodiversity still acts as biological insurance for ecosystem processes (Ives *et al.* 2000, Thébault and Loreau 2005). Early empirical studies (Naeem and Li 1997, McGrady-Steed *et al.* 1997) showed a stabilizing effect of diversity on community-level properties but were difficult to interpret due to confounding factors (Huston 1997, Fukami *et al.* 2001). Indeed, Morin and McGrady-Steed (2004) reanalyzed data from their earlier publication (1997) and found that the previously reported effect was due to spatial variability among replicates. Recent BEF experiments, all conducted within microcosms, have provided a further, less controvertible, glimpse at the possible effects of diversity on stability in multi-trophic systems. Steiner *et al.* (2005b) showed that diversity increased the temporal stability of community biomass, whilst species composition best explained variability in population-level abundance. They invoke the positive selection effect, suggesting that dominance of species with high population stability could underlie much of the observed influence of diversity. It would be interesting to investigate whether the populations of species that dominate mixtures are generally more stable, since if there is a trade-off between resistance and productivity (Lepš *et al.* 1982), the opposite may be true.

Other mechanisms are proposed in studies based on a microbial rock pool system. In microcosm studies, Vogt *et al.* (2006) and Romanuk *et al.* (2006) also found a stabilizing effect of diversity on the aggregate abundance of the community, but here, greater population stability at higher species richness summed to produce greater community stability. The mechanism dampening population-level variability is not clear, but Romanuk *et al.* (2006) postulate that in pools with high levels of unused resources, populations will tend to fluctuate more, because niche complementarity (at higher diversity) reduces resource levels, thus stabilizing populations. Their finding that population variability was greater in high nutrient microcosms is consistent with such a mechanism (but contrasts with the findings of single trophic level studies which showed that increased productivity led to the loss of a diversity effect (Zhang and Zhang 2006b). In an observational study Kolasa and Li (2003) found that diversity increased the temporal stability of microbial rock pool populations, but only when increasing specialization, and therefore variability, of individual species with increasing diversity was statistically controlled. This study shows that opposing forces operating in natural communities may yield no net effect of diversity on population stability.

Two notable studies have considered how species richness affects the temporal stability of ecosystem functions other than biomass or its production in multi-trophic systems. Dang *et al.* (2005) tested the effect of fungal diversity on both the mean magnitude and temporal stability of decomposition. Whilst diversity had no effect on the magnitude, temporal stability increased in close correspondence to the null-model of statistical averaging. Furthermore, the outcome was robust to a range of environmental contexts. Tylianakis *et al.* (2006) examined the effect of parasitoid diversity on the temporal stability of parasitism of wasps and bees. Again, diversity enhanced the temporal stability of this ecosystem process, indicating that diversity may play an important role in stabilizing trophic control within complex food webs. Interestingly, the effect of diversity reported by both Dang *et al.* (2005) and Tylianakis *et al.* (2006) was non-linear, producing the most rapid decrease in variability at relatively low levels of richness. This is consistent with statistical averaging models (Doak *et al.* 1998; but see Box 6.2), but more studies, as well as theory pertaining to ecosystem processes other than biomass (Box 6.1), are needed to determine the generality of these results.

Overall, the very restricted number of studies limits our ability to assess the effect of diversity on temporal stability in multi-trophic systems. However, the possibility that diversity may increase population stability in these systems is intriguing and warrants further exploration, as it is contrary to theory and experiments conducted within single-trophic level, competitive communities and May's (1972, 1973) models. Theory for multi-trophic systems (Thébault and Loreau 2005) predicts that diversity may increase population stability under some conditions, for instance, when consumers are either specialists or generalists with a trade-off between niche breadth and attack rate, and their temporal niche differentiation is low. It is difficult to assess whether these mechanisms identified by theory explain the results of recent experimental and observational studies because these studies did not test mechanisms. Other stabilizing mechanisms in food webs could be more prevalent as species richness and food web complexity increases, thus stabilizing populations (Section 6.3.1). Direct empirical evidence of such effects, and how their efficacy and prevalence varies with diversity, has yet to emerge. Detailed analyses of dynamic trophic interactions over a range of temporal and spatial scales would be necessary to demonstrate such effects in food webs.

Box 6.1 From abundance to functioning

The vast majority of diversity–temporal stability studies have used community biomass or its production as their measure of ecosystem functioning. Many of the theoretical mechanisms linking stability to diversity may equally apply to other community-aggregated properties, but this has seldom been tested. The stability of process rates represents an important divergence from recent theory; instead of variation in species' summed abundances forming the response variable, the *efficiency* of species mediating ecosystem functioning is also of interest. In this case, the density-mediated component directly linked to theory pertaining to community biomass stability remains, but a potentially density-independent 'efficiency' component is added. Furthermore, the specificity of the process measured is likely to impact results. For example, If the ecosystem function is the flux of a particular nutrient (Bracken and Stachowicz, 2006), there may be less functional redundancy than for a universal process such as primary production or decomposition. Since functional redundancy is a central tenet of the diversity–stability relationship, this suggests that, as functions become more specific, their stability will be increasingly associated with the population stability of the one or a few species mediating the function and less with the total diversity of the system. Where species vary in their contributions to multiple functions, functional redundancy will be further reduced if such multiple functions are considered concurrently (Gamfeldt *et al.* 2007).

6.2.2 The effects of discrete perturbations

6.2.2.1 *Resistance*

Tests of the insurance hypothesis could be garnered from early studies comparing stress resistance across successional diversity gradients. The findings of

Box 6.2 What causes diversity's effects on temporal stability?

Despite established theoretical mechanisms linking diversity and temporal stability, there is currently little consensus regarding the relative importance of mechanisms underpinning effects observed in empirical studies. A number of authors have examined components of temporal variability in order to gain insight into the mechanisms underlying observed effects of diversity. Temporal stability (S_T), measured as 1/CV of community biomass, can be expressed as (Lehman and Tilman 2000):

$$S_T = \frac{\sum \text{species biomasses}}{\sqrt{\sum \text{species variances} + \sum \text{species covariances}}}$$

The numerator in this equation captures the short-term or average effect of diversity on community biomass. All else being equal, an increase in average community biomass with diversity due to overyielding tends to increase community stability simply because average community biomass is used to scale the variances and covariances in the CV. Additional long-term stabilizing effects of diversity can result from reduced summed variances, reduced summed covariances, or both in the denominator. Reduction in summed variances has generally been interpreted as indicative of statistical averaging (Tilman 1999; Cottingham *et al.* 2001), whilst reduced summed covariances have generally been interpreted as indicative of compensatory dynamics owing to competitive release and/or differential response to environmental conditions (Tilman 1999; Petchey *et al.* 2002). But a fundamental problem with this statistical approach is that summed variances and summed covariances are strongly dependent on each other, and do not capture distinct biological mechanisms. Both reduced summed variances and reduced summed covariances are ultimately driven by the same mechanism, i.e. asynchronous species responses to environmental flutuactions (Loreau and de Mazancourt, unpublished manuscript).

Of the 18 studies discussed here (Table 6.1), nine included information on the statistical components of temporal stability; multiple contexts in two studies yield 13 experiments for consideration. Nine of these experiments reported a positive effect of diversity on temporal stability, whilst two did not detect an effect (Table 6.2).

Contrary to Tilman's (1996) suggestion, the negative covariance effect – the result of increasingly asynchronous population fluctuations with increasing diversity – is not a common phenomenon. Species richness resulted in increasingly negative summed covariances in just a single study (Petchey *et al.* 2002). Two experiments actually

Table 6.2 Studies reporting the statistical components of temporal stability, their reported effects of diversity on community stability (1/CV), summed covariances, summed variances, total community biomass, and the mean-variance scaling factor (*z*).

Reference	Trophic level	Stability	$\sum$Covariance	$\sum$Variance	$\sum$Biomass	z^*
Caldeira *et al.* (2005)	Single	Positive	Increased	Increased	Increased	>1
Petchey *et al.* (2002)	Single	None	Reduced	N/A	Increased	>1
Romanuk *et al.* (2006)	Multiple (low nutrient)	Positive	No effect	Increased	Increased	1
Romanuk *et al.* (2006)	Multiple (med nutrient)	Positive	No effect	Increased	Increased	0.83
Romanuk *et al.* (2006)	Multiple (high nutrient)	Positive	No effect	Increased	Increased	0.85
Steiner (2005b)	Single	Positive	No effect	Reduced	N/A	1.45
Steiner *et al.* (2005a)	Single	Positive	No effect	No effect	Increased	N/A
Steiner *et al.* (2005b)	Multiple	Positive	No effect	No effect	Increased	1.55
Tilman *et al.* (2006)	Single	Positive	No effect	Reduced	Increased	1.6
Valone and Hoffman (2003a)	Single	Positive	Increased	No effect	Increased	N/A
Vogt *et al.* (2006)	Multiple	Positive	No effect	Reduced	No effect	N/A
Zhang *and* Zhang (2006a)	Single (low nutrient)	Positive	No effect	No effect	No effect	1.74
Zhang *and* Zhang (2006a)	Single (high nutrient)	None	No effect	No effect	No effect	1.79

* z is a parameter in the equation relating CV for community biomass to total community biomass and the number of species in the community. The statistical averaging stabilizing effect only occurs when $z > 1$ (Tilman *et al.* 1998).

continues

Box 6.2 *(continued)*

revealed increasingly positive covariances with more diversity. If species are similarly influenced by environmental variability, species abundances will track environmental conditions in a correlated manner (Vasseur *et al.* 2006; Loreau and de Mazancourt 2008). Species may also respond similarly if changes in environmental conditions are extreme relative to the range of tolerances exhibited by the assemblage (see Allison 2004). Positive species covariances do not necessarily preclude positive net diversity effects on stability because any deviation from perfect correlation between species environmental responses can in principle stabilize aggregate community properties (Yachi and Loreau 1999; Ives et al. 1999).

Greater diversity yielded increased, reduced, and unaffected summed variances in four, three, and five studies, respectively. These mixed overall findings suggest that summed variances, just as summed covariances, depend on context-specific factors not universally linked to diversity, such as competitive interactions and how population abundance changes with diversity (see Valone and Hoffman 2003a), in agreement with recent theory (Loreau and de Mazancourt, unpublished manuscript).

The most consistent explanation for a positive diversity–stability effect is a combination of overyielding and asynchronous species fluctuations. Of the seven experiments that yielded a stabilizing effect of diversity and reported summed biomass with respect to diversity, overyielding (diversity and biomass were positively related) occurred in five. If overyielding occurs, variance can be smaller relative to the mean even in the absence of any changes in summed covariances or variances. Statistical averaging due to asynchronous species fluctuations most likely contributed to the temporal stability of aggregate properties in numerous studies – in fact, all seven studies that measured the scaling relationship between mean and variance reported values indicating that, even in the absence of changes in summed covariances, diversity would be expected to enhance stability (Doak *et al.* 1998; Tilman *et al.* 1998; Table 6.2).

Only two studies in multi-trophic systems measured the statistical components of temporal stability, and they found mixed results: whilst Vogt *et al.* (2006) invoke reduced population variability with diversity as a driver of community-level stability, Steiner *et al.* (2005b) found no such effect, instead crediting a form of the selection effect – the low population variability of dominant species with stabilization. With only two studies, comparisons between these and single-trophic systems are not possible. Their greater complexity allows for quite different patterns to emerge, however, as we discuss below in the context of food web ecology.

Overall, both theory and empirical data suggest that we have not yet started to disentangle the biological mechanisms that underlie the stabilizing effects of diversity on ecosystem properties. The statistical partitioning of summed species variances and summed species covariances, which was proposed for this purpose, has proved ineffective. New innovative approaches are needed to address mechanisms. One promising, but data demanding, alternative would be to test observed patterns of species temporal variations against a neutral model of community dynamics under the combined influence of density dependence, environmental forcing and demographic stochasticity (Loreau and de Mazancourt 2008).

such studies have been varied, with several suggesting positive (Hurd and Wolf 1974, Mellinger and McNaughton 1975, Lepš *et al.* 1982) and others suggesting a negative (Smedes and Hurd 1981, Berish and Ewel 1988) relationship between diversity and resistance. These studies should, however, be interpreted with caution, as species composition and life-history traits also vary during succession (Odum 1969), making the role of diversity *per se* ambiguous. Thus, a rigorous BEF experimental approach was developed during the 1990s to more explicitly test the hypothesis. Thirteen studies, including 14 experiments, three of which measured two ecosystem properties each, have used this approach (Table 6.3). Five experiments yielded a positive effect of diversity, whilst eight showed no effect and four showed a destabilizing effect.

Early empirical findings generally, but not completely, supported the supposition that diversity will increase the resistance of community-level properties to perturbation (Loreau *et al.* 2002). Diversity increased resistance to drought across a gradient of nutrient enrichment in experimental grassland plots (Tilman and Downing 1994), even after the confounding effect of fertilization was analytically controlled (Tilman 1996). Several subsequent studies also revealed a positive diversity–resistance relationship (Griffiths *et al.* 2000, Joshi *et al.* 2000, Mulder *et al.* 2001). Wardle *et al.* (2000a), however, emphasized the importance of composition, finding no effect of plant functional group richness on stability to drought in a greenhouse experiment.

Table 6.3 Effects of diversity on resistance to specific perturbations.

Reference	Stability property	Trophic level	Ecosystem property measured[a]	Diversity gradient[b]	Ecosystem type	Perturbation	Time scale	Div levels	Type of div effect
Allison (2004)	Resistance	Primary prod	Community biomass	Rem. F	Intertidal	Heating	21 m	1 to 3 FG	Negative
Caldeira *et al.* (2005)	Resistance	Primary prod	Community biomass	Exp. F	Grassland	Drought/frost	1 yr	1 to 14	None
DeClerk *et al.* (2006)	Resistance	Primary prod	Primary Productivity	Nat. F	Forest	Drought	64 yr	1 to 4	None
Griffiths *et al.* (2000)	Resistance	Multi	Decomposition rate	Rem. M	Pasture soil	Heating	1 yr	NA	Positive
Joshi *et al.* (2000)	Resistance	Primary prod	Community biomass	Exp. F	Grassland	Invasion	1 yr	1 to 32	Positive
Kahmen *et al.* (2005)	Resistance	Primary prod	AG Community biomass	Nat. F	Grassland	Drought	7 w	13 to 38	None
Kahmen *et al.* (2005)	Resistance	Primary prod	BG Community biomass	Nat. F	Grassland	Drought	7 w	13 to 38	Positive
Mulder *et al.* (2001)	Resistance	Primary prod	Community biomass	Exp. F	Bryophytes	Drought	5 d	1 to 32	Positive
Pfisterer and Schmid (2002)	Resistance	Primary prod	Community biomass	Exp. F	Grassland	Drought	8 w	1 to 32	None
Pfisterer and Schmid (2002)[1]	Resistance	Primary prod	Community biomass	Exp. F	Grassland	Drought	8 w	1 to 32	Negative
Tilman and Downing (1994)[2]	Resistance	Primary prod	Community biomass	Nutr. F	Grassland	Drought	2 yr	1 to 26	Positive
Van Peer *et al.* (2004)	Resistance	Primary prod	Community biomass	Exp. M	Grassland	Drought and heat	8 w	1 to 8	Negative
Wardle *et al.* (2000)	Resistance	Multi	Plant biomass	Exp. M	Grassland	Drought	14 m	2 to 7	None
Wardle *et al.* (2000)	Resistance	Multi	Decomposition rate	Exp. M	Grassland	Drought	14 m	2 to 7	None
Zhang and Zhang (2006a)	Resistance	Primary prod	Community biomass	Exp. M (HN)	Aquatic	Cold	6 d	1,2,4,7	none
Zhang and Zhang (2006a)	Resistance	Primary prod	Community biomass	Exp. M (LN)	Aquatic	Cold	77 d	1,2,4,8	none
Zhang and Zhang (2006b)	Resistance	Primary prod	Community biomass	Exp. M	Aquatic	Cold	105 d	1 to 5	Negative

[a] AG: above-ground; BG: below-ground

[b] Exp.: experimentally created diversity gradient; Rem.: gradient produced from selective removal of species; Nat.: naturally occurring diversity gradient; Nutr.: gradient produced by different nutrient levels. F.: field study; M.: mesocosm/microcosm study. LN: low nutrients. HN: high nutrients

[1] Resistance as measured as *absolute* biomass lost (see text)

[2] As reanalysed by Tilman (1996)

These earlier studies, as well as theory, did not consider pre-disturbance effects of diversity on resource use and community composition. Incorporating these effects yields several possible consequences stemming from selection effects and complementarity – the mechanisms that lead to positive relationships between diversity and the magnitude of ecosystem functioning. If the positive selection effect is in operation, fast-growing species, which tend to be more vulnerable to stress (Lepš *et al.* 1982), may dominate diverse mixtures, potentially producing a negative diversity–resistance relationship. Recent synthesis shows that while the positive selection effect is a common phenomenon in BEF studies, there are a substantial number of studies reporting negative selection effects (Cardinale *et al.* 2007). This raises the possibility that the above mechanism may be reversed in these cases, but empirical studies have yet to examine this possibility.

Pfisterer and Schmid (2002) postulate that complementarity indirectly rendered diverse grassland plots at the Swiss BIODEPTH site more vulnerable to experimental drought: the drought reduced the niche complementarity responsible for greater production in diverse communities. This raises the possibility that there may be a trade-off between a positive influence of diversity on the magnitude of ecosystem functioning and ecosystem stability. An important point is that Pfisterer and Schmid (2002) recorded a greater *absolute* reduction in biomass in more diverse plots, whilst there was no difference when resistance was measured *relative* to pre-drought biomass. Resistance is most meaningfully measured as a reduction in an ecosystem process relative to the pre-perturbation level; indeed, this is commonly practiced (Pimm 1984) and is consistent with measures of temporal stability.

Other experiments have revealed no effect of diversity on this metric of resistance, despite positive effects of diversity on pre-stress biomass (Wardle *et al.* 2000a, Caldeira *et al.* 2005, Zhang and Zhang 2006a). Furthermore, both Caldeira *et al.* (2005) and Zhang and Zhang (2006a) report that complementarity and selection effects were not modified by environmental stress. Finally, Van Peer *et al.* (2004) found a negative effect of diversity on resistance measured in relative terms. The positive pre-stress relationship between diversity and biomass was diminished as the demand for water exceeded acquisition in species-rich communities.

In all of these experiments the positive diversity–resistance relationship predicted by the insurance hypothesis was absent, implying that diversity may not simultaneously increase the magnitude and resistance of ecosystem functioning. High community biomass could mean that each individual within a diverse community suffers greater resource limitation, as a finite resource supply is under greater demand; in effect, the disturbance size is greater for each individual. The shortfall between resource demand and supply may outweigh the effect of the increasing range of species' tolerances with greater diversity.

The implication of this hypothesis is that in the absence of a positive diversity–biomass relationship, evidence of the insurance effect will be more likely. There are insufficient studies to assess this rigorously, but three studies provide tentative support for this hypothesis. Across a natural diversity gradient in German grasslands, Kahmen *et al.* (2005) found that the resistance of belowground biomass to an experimental drought increased with plant diversity, but no effect on aboveground biomass was observed. Reference plots showed no relationship between diversity and pre-stress biomass. Mulder *et al.* (2001) and Hughes and Stachowicz (2004) similarly reported a positive influence of diversity on stress resistance in systems without a pre-disturbance diversity–biomass relationship.

6.2.2.2 Resilience

Loreau and Behera (1999) found that diversity and resilience may be negatively related within theoretical competitive communities. Based on the very few published empirical tests (Table 6.4), no consistent influence of diversity on resilience of community properties is evident. Studies of successional diversity gradients show negative relationships between diversity and resilience (Smedes and Hurd 1981, Lepš *et al.* 1982), but species' life-history traits probably played a confounding role here. Theoretical predictions (Loreau and Behera 1999) are supported by just a single BEF experiment (Pfisterer and

Table 6.4 Effects of diversity on resilience of ecosystem properties following a perturbation.

Reference	Stability property	Trophic level	Ecosystem property measured	Diversity gradient[a]	Ecosystem type	Perturbation	Time scale	Div levels[b]	Type of div effect
Allison (2004)	Resilience	Primary prod	Community biomass	Exp. M	Intertidal	Heating	21 m	1 to 3 FG	Positive
DeClerk *et al.* (2006)	Resilience	Primary prod	Primary Productivity	Nat. F	Forest	Drought	64 yr	1 to 4	Positive
Griffiths *et al.* (2000)	Resilience	Multi	Decomposition rate	Rem. M	Pasture soil	Heating	1 yr		Positive
Pfisterer and Schmid (2002)	Resilience	Primary prod	Community biomass	Exp. M	Grassland	Drought	8 w	1 to 32	Negative
Steiner *et al.* (2006)	Resilience	Multi	Community biomass	Exp. M (HN)	Aquatic	Non-selective	53 d	1 to 4	None
Steiner *et al.* (2006)	Resilience	Multi	Community biomass	Exp. M (LN)	Aquatic	Non-selective	53 d	1 to 4	Positive
Tilman and Downing (1994)[1]	Resilience	Primary prod	Community biomass	Nutr. F	Grassland	Drought	2 yr	1 to 26	None

[a] Exp.: experimentally created diversity gradient; Rem.: gradient produced from selective removal of species; Nat.: naturally occurring diversity gradient; Nutr.: gradient produced by different nutrient levels. F.: field study; M.: mesocosm/microcosm study. LN: low nutrients. HN: high nutrients

[b] FG.: Functional groups

[1] As reanalysed by Tilman (1996)

Schmid 2002), which showed lower resilience in high-diversity grassland plots nine months after drought. Tilman (1996) found no effect of diversity on resilience after analytically removing the confounding factors present in an earlier analysis (Tilman and Downing 1994). Conversely, resilience increased with functional group richness in intertidal seaweed communities (Allison 2004), with conifer species richness in the Sierra Nevada (DeClerck *et al.* 2006), and with diversity within five trophic levels in a microcosm experiment (Steiner *et al.* 2006). DeClerck *et al.* (2006) invoke complementarity, suggesting that during community recovery, resources are abundant, thus resource partitioning is possible along several niche axes – a postulation that perhaps deserves further theoretical and empirical consideration. Steiner *et al.* (2006), on the other hand, credit their result to the sampling effect, as resilient communities exhibited a reduction in evenness over time.

It is difficult to separate resilience from resistance. Indeed, most studies have not removed the legacy of resistance from measures of community recovery (Tilman and Downing 1994, Mulder *et al.* 2001, Pfisterer and Schmid 2002, Allison 2004). To achieve this, a non-selective mortality event must occur or be experimentally applied (Steiner *et al.*, 2006). In nature, however, resistance and resilience are inextricably linked, because the community recovers with its post-perturbation composition and abundance. Thus, whilst equally reducing abundances of populations to isolate resilience *per se* from the effects of the disturbance is of considerable theoretical interest, the relevance to real systems is questionable.

6.2.3 Summary of empirical progress

Numerous diversity–stability experiments have been published in the last half-decade, substantially improving our understanding of the relationship between diversity and various facets of stability at population and community levels. Whilst diversity was commonly found to enhance community-level temporal stability, the effect of diversity on resistance and resilience is more equivocal. There is some empirical evidence to suggest that positive diversity–productivity effects may preclude a stabilizing effect of diversity in the face of extreme perturbations – a trade-off that needs further mechanistic exploration. Multi-trophic studies have been limited in number and scope, mainly being conducted in microbial rock pools or laboratory microcosms. Nevertheless, the typical result that populations are actually stabilized by diversity in these systems is intriguing and represents a major distinction from classical theory (e.g. May 1973) and findings from some grassland experiments (Tilman 1996, Tilman *et al.* 2006b).

6.3 A broadening perspective

Whilst of undoubted value, controlled experiments are logistically constrained. Isolating the role of diversity *per se* from that of species identity has proven a formidable task requiring large numbers of treatments and replicates. This has limited experiments to tractable, closed, small-scale systems–predominantly grassland plots and laboratory microcosms. Hence the degree to which the findings from these experiments are applicable to larger, landscape scales, different systems, and the delivery of important ecosystem services is questionable.

Building a more complete understanding of the role of diversity in stabilizing ecosystem functioning in these broader contexts requires approaches that trade replication and control for studies conducted over larger scales and in complete systems. In this section we outline three areas that address this link. First, we discuss several recent developments in theory that demonstrate how properties of food webs can affect aspects of population and community stability. Second, we assess possible effects of diversity on stability in systems with multiple stable states, before finally highlighting the possible role of diversity in stabilizing the delivery of two key ecosystem services: pollination and yield from fisheries.

6.3.1 Lessons from food webs

Although BEF research has begun to examine the effect of diversity on the stability of multi-trophic aquatic systems, the tie between food web theory and BEF science is not yet strong. This is unfortunate, because recent developments in food web theory illustrate several stabilizing properties of food webs that may explain the inconsistency of results in BEF-stability studies so far. Moreover, how species loss affects these properties can provide insight on diversity's effects in systems too complex for controlled experimental treatments. It must be noted that the food web literature provides definitions of stability that often vary from those in the BEF literature, they generally focus on recovery times following perturbations to the system, but also encompass measures of temporal variability among component species. Additional aspects of stability, not addressed in BEF experiments to date, may also have implications for ecosystem functioning, and as such several are outlined here.

It is now widely acknowledged that weak trophic interactions confer stability (population-level resilience) in natural food webs, and therefore that food webs with lower mean interaction strength are more stable. However, the configuration of interactions is also important, as the destabilizing effects of strong trophic links can be dampened if those strong links are coupled to weak interactions (McCann 2000). Coupled weak and strong interactions can promote asynchronous population fluctuations of prey, stabilizing aggregate prey biomass as well as resource supply to a switching predator (McCann 2000). This weak interaction effect may have marked implications for the temporal stability of community biomass in food webs. Furthermore, it has been shown that weak interactions confer local stability to food webs when they occur in omnivorous food web loops (Neutel *et al*. 2002, Emmerson and Yearsley 2004). Simulation studies have shown that an analogous effect can be scaled up to fast and slow 'energy channels' within food webs generated through alternative energy sources (Rooney *et al*. 2006). Species loss will alter the number and configuration of stabilizing weak interactions, as well as the mean interaction strength (McArthur 1955, McCann 2000), potentially destabilizing populations and ecosystem functions.

In reality, food webs are not static structures fixed in time; they are dynamic, varying in structure seasonally and from year to year. How such dynamic topologies persist is poorly understood. In this context, food webs are flexible structures, constantly changing in species composition, structure, and dynamics (de Ruiter *et al.* 2005), yet most theoretical studies of diversity–stability relationships assume static patterns of trophic linkage (May 1972, Pimm *and* Lawton 1977, 1978, de Ruiter *et al.* 1995, Neutel *et al.* 2002). Adaptation is suggested as one mechanism from which food web flexibility arises (Kondoh 2006), with adaptive defences by prey and adaptive foraging by predators influencing the strength of trophic interactions. The flexibility provided by adaptive foraging should enhance community persistence, as predators capable of a foraging shift can maximize their net energy gain by switching away from a less profitable resource. Indeed, Kondoh (2003) demonstrated that the classic negative complexity–stability relationship of many theoretical studies is inverted when the effects of adaptive foraging behaviour are incorporated. There are obvious implications of this mechanism for the diversity–stability relationship, although they have yet to be explicitly explored in the context of BEF research. A reduction of species diversity through the loss of prey species will limit the prey-switching options of adaptively foraging predators.

Primary species loss can trigger secondary extinctions, further reducing diversity and its associated stabilizing effects on ecosystem functioning. The tolerance of a food web to species loss is also an important aspect of stability in its own right: robustness (see Loreau *et al.* 2002). The traits of the deleted species markedly affect the likelihood and extent of secondary extinctions (see also Chapter 5). For example, like keystone species and ecosystem engineers, the loss of a highly connected species (species with a high proportion of total possible trophic links realized) has been shown to have disproportionate effects on food web structure (Solé and Montoya 2001).

Robustness may also depend on the characteristics of the entire food web. The amount of connectance is important, as high connectance may delay the onset of an extinction threshold (Dunne *et al.* 2002b). Whether connectance and species richness are associated in empirical (not theoretical) food webs is unresolved, however. Whilst Dunne *et al.* (2002b) report no relationship, Montoya and Solé (2003) found connectance to be lower in species-rich webs. The distribution of trophic links between species, the degree distribution, also has consequences for robustness. Food webs with skewed degree distributions, i.e. numerous poorly linked species and a few highly linked species, are robust to random species deletion but sensitive to removal of the most connected species (Solé and Montoya 2001, Dunne *et al.* 2002b). This is because randomly deleted species are likely to be poorly linked, thus having minimal knock-on effects on others. Across 12 well-described food webs, Montoya and Solè (2003) show that the degree distribution becomes progressively more skewed with increasing species richness. Consequently, species-poor webs are less robust in response to random species loss, since most species are moderately well linked. Therefore, whether species-rich food webs are likely to be more robust to species loss depends on whether species loss is random with respect to species' connectedness (see also Chapter 5). Other key factors that determine the effects of diversity on cascading species extinctions and ecosystem functioning include the strength of intraspecific density dependence (Thébault *et al.* 2007).

Although the properties that affect food web stability are critical to understanding the stability of ecosystem functioning in complex (multi-trophic) systems, it must be noted that comparisons across food webs may give results that differ from changes within a single food web. It is unknown, for example, whether the degree distribution of a species-rich web will become increasingly centralized, mirroring species-poor webs, as diversity is eroded within it. If this happens, food webs losing species will become ever more sensitive to random species deletion, yielding a positive feedback that may exacerbate system collapse. Cross-fertilization of ideas between BEF and food web science will help answer this and other unknowns. Investigating how food web properties vary concurrently with species richness in natural and manipulated food webs will help to better integrate BEF science with food web theory.

6.3.2 Diversity–stability in complex, real-world systems

6.3.2.1 Systems with multiple stable states

In all explicit diversity–stability experiments discussed here and elsewhere (Cottingham *et al.* 2001, Loreau *et al.* 2002, Hooper 2005), stability has been considered with respect to a single 'stability domain.' Both theory and observations, however, have shown that many ecosystems can exhibit non-linear dynamics, switching between multiple stable states (Scheffer and Carpenter 2003). It is thus unclear the extent to which findings from the studies discussed here (Table 6.1) can be applied to multiple equilibrium systems. Ecological resilience *sensu* Holling (1973) describes the amount of disturbance a system can absorb whilst still remaining within the same basin of attraction and can be heuristically viewed as the size of a particular stability domain. Changing environmental conditions, compounded perturbations and/or species loss can reduce ecological resilience, increasing the probability of an abrupt 'catastrophic shift' to an alternative state. The insurance hypothesis has been incorporated into this view of ecosystems (e.g. Peterson *et al.* 1998, Gunderson 2000): assuming that biodiversity increases the range of responses to the environment (functional response diversity), a more diverse system is buffered against impacts of perturbations and resultant catastrophic shifts.

Despite a dearth of experimental studies, the idea that biodiversity begets stability in systems with multiple stable states seems to be widely accepted. Reviews of regime shifts and ecosystem resilience assume a strong connection between functional response diversity and resilience (e.g. Gunderson 2000) or loss of diversity and loss of function (Briske *et al.* 2006). The diversity–stability concept even seems to have influenced environmental management in certain systems. For example, maintaining or increasing landscape diversity in pastures and rangelands is encouraged or required by many land-use agencies and programs (e.g. Mason *et al.* 2003, Mitchell *et al.* 2005), often for maintaining or increasing biodiversity itself, but also for increasing resilience in the face of disturbance (Pellant *et al.* 2004, Drever *et al.* 2006). The question is whether evidence supporting these ideas exists in the systems to which they are applied. Rangelands and coral reefs, two systems that provide a number of ecosystem services for a large part of the Earth's population and exhibit dramatic instability (undergo state changes) serve as examples.

Range and pasture lands occupy approximately 20 per cent of the land surface of the globe in areas that are particularly susceptible to drastic ecosystem changes such as desertification and grass-to-shrubland conversion (Hodgson and Illius 1996). Consequently, they have been the focus of many conceptual developments regarding ecological thresholds and alternative state theory, which are closely tied to the concept of ecological resilience (e.g. Briske *et al.* 2006). Although there is a wealth of literature on these topics, and the entire basis of rangeland management is now shifting to this paradigm in some parts of the world (USDA-NRCS 1997), there has been little research directly testing the role of biodiversity in rangeland resilience, state changes, or other aspects of stability at the scales that are applicable to range and pasture managers.

Two studies that directly address the relationship between biodiversity and stability in actual production systems had contrasting results. In Australian sheep pastures with a range of plant species richness caused by various manipulations (grazing regime, fertilization) and environmental conditions (climate, soils), variability of herbage production over 3–4 years was either not significantly related or slightly negatively related to plant diversity or species richness (Kemp *et al.* 2003). On the other hand, in dairy cattle pastures planted specifically to compare plant species richness effects on herbage production, yield did not differ significantly among treatments of 2, 3, 6, or 9 species in years with normal precipitation, but the two-species pasture did have lower production than the others in a dry year (Sanderson *et al.* 2005).

The evidence from coral reefs is equally equivocal. A biogeographical comparison can provide a tentative insight into the possible role of species diversity in providing resilience on coral reefs. In the Caribbean, eutrophication from increased nutrient inputs, disease, and over-harvesting of herbivorous fishes has resulted in a phase shift from coral- to fleshy macroalgae-dominated reef communities (Hughes 1994). Although the suite of functional groups is similar between Indo-Pacific reef systems and Caribbean reef systems, the former have much greater taxonomic diversity within most functional groups, presumably making them less susceptible to such phase-shift-causing perturbations (Bellwood *et al.* 2004). However, taxonomic richness does not guarantee functional resilience. A different single species, which is relatively rare, was responsible for reversing an experimentally induced coral–algal phase shift in the same system by high consumption on the fleshy algae (Bellwood *et al.* 2006). The effect of this single keystone species in the latter study was a complete surprise, in that it was previously unknown to consume these algae. The identity of species, rather than richness *per se*, may thus have dominant effects on the resilience of coral reefs (see also Bellwood *et al.* 2003).

That this surprise occurred in one of the better-studied systems in the world clearly supports the precautionary approach in biodiversity conservation. These results also highlight the fact that high diversity does not guarantee high redundancy and the stability often associated with it. If all the redundancy is in one functional group, then diversity will not necessarily promote stability. This is particularly relevant in light of the perturbations that afflict ecosystems today. All ecosystems evolved with a regime of disturbance, and evolutionary processes likely led to functional effect redundancy within these systems because of differences in organisms' responses to this disturbance regime (e.g. Walker *et al.* 1999). Novel individual perturbations (e.g. new diseases), as well as new combinations of disturbance events, could be tapping into functional types where that response redundancy does not yet exist.

6.3.2.2 Diversity and the stability of ecosystem services

Several empirical studies have recently emerged that bridge the gap between controlled experiments and real-world applications, demonstrating how human-impacted ecosystems can be used to examine the roles of environmental change and biodiversity in the stability of ecosystem service provision. Here we discuss two ecosystem services, first pollination and second fisheries yield, as examples. Both of these examples suggest that species diversity can influence the stability of ecosystem service provision.

Pollination is one key ecosystem service that has received attention within agricultural landscapes. Kremen *et al.* (2002, 2004) showed that intensive farming practices and a reduced proportion of natural habitats negatively affects the diversity of pollinators and temporal stability of melon pollination. Sites with high pollinator species richness provided more stable pollination services over time than sites with low species richness because of asynchronous fluctuations in the populations of pollinators from one year to the next. The role of species richness in spatial stability of pollination was demonstrated in coffee plantations: greater pollinator diversity, which is affected by local (e.g. plant diversity, light availability) and regional (e.g. isolation from natural habitat) factors, reduced spatial variation in fruit set between coffee plants (Klein *et al.* 2003a, b; Chapter 14).

Fisheries provide an important source of food for much of the world's population, underpinning the diets and economies of many coastal communities in the world's poorer countries. Collating data from the world's fisheries, Worm *et al.* (2006) found that the proportion of collapsed fisheries in a region was negatively related to its fish taxonomic diversity. Furthermore, they discovered that the likelihood of recovery from fisheries collapse was positively associated with species richness across large marine ecosystems. Causality is difficult to infer from this correlative approach, but the results support the supposition that diversity increases both resistance to – and recovery from – over-exploitation. Those harvesting the fish benefit from greater diversity, as the reliability and abundance of total catches increases with diversity. Humans act as switching, wide-ranging predators, releasing stocks from predation as they become scarce (McCann 2000) and changing to a more abundant species, thus deriving a stable supply from numerous fluctuating resources (Worm *et al.* 2006). This mechanism may partly explain why diverse fisheries are less likely to collapse – it is more profitable to switch targets if more abundant species are available. The well-known collapse of the Newfoundland cod fishery could be attributed to a single target species, compared to the diverse portfolio of taxa exploited in tropical subsistence fisheries, for example. Further efforts to explore the role of species diversity in mediating various aspects of the stability of ecosystem service delivery will both inform the management of such services, and also contribute to our general understanding of diversity–stability relationships in real-world systems. Such studies will also help to integrate our understanding of the drivers of species diversity and its ecological effects.

6.4 Conclusions

Recent studies have yielded great progress in understanding diversity's effects on the stability of ecosystem functioning in increasingly complex systems. Clearly, however, there is still much work to be done to reconcile theory, experimental results, and observations from natural or human-altered systems. A key step towards this goal must be elucidating the mechanistic basis of diversity effects on aspects of stability in a range of systems; a challenge that requires greater integration of theoretical and empirical work (Box 6.2). Insights from a growing body of food web analyses and simulations may help to explain the findings of BEF stability studies in multi-trophic systems.

To increase the applicability of diversity–stability research the effects of realistic diversity changes on valuable ecosystem services must be investigated. Studies across gradients of anthropogenic impacts have great potential to address this need, as these gradients incorporate both local (habitat) and landscape factors responsible for shifts in diversity (Chapter 14). Long-term measures of diversity and related ecosystem services across these land-use gradients, combined with modelling and mesocosm studies based on the communities occurring across these gradients, would help to elucidate the effect of biodiversity on the stability of key ecosystem services and potentially shed light on the underlying mechanisms. Recent work in the field of ecological economics shows that stability adds additional economic value to ecosystem services in the form of insurance (Chapter 17), further underlining the importance of a thorough understanding of the effect of biodiversity on ecosystem functioning and associated services.