7

Biodiversity and Ecosystem Stability: New Theoretical Insights

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7.1. Introduction

The relationship between the diversity and stability of ecological systems has been the subject of a long-standing debate in ecology (McCann 2000). The early view that permeated ecology until the 1960s was that the diversity or complexity of an ecosystem begets its stability. This view was articulated by such famous ecologists 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; that is, they are more subject to destructive population oscillations and invasions. Using a heuristic model, MacArthur (1955) proposed that the more pathways there are for energy to reach a consumer, the less severe the failure of any one pathway is for the consumer. 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", however, they became almost universally accepted.

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This “conventional wisdom” was challenged in the early 1970s by theorists such as Levins (1970), Gardner and Ashby (1970), and May (1972), who borrowed the formalism of deterministic autonomous dynamical systems from Newtonian physics and showed that the more complex and diverse a model system is, the less likely it is to be stable. In this work, stability was defined by assessing whether the system returned to equilibrium after a small perturbation – a form of stability known as local stability (see section 7.2). 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 collapse or explosion (with no distinction between these two very different outcomes). Although this theoretical work had limitations and some empirical ecologists challenged it (McNaughton 1977), the view that diversity and complexity beget instability, not stability, quickly became the new paradigm in the 1970s and 1980s because of the mathematical rigor of the theory.

The large-scale biodiversity experiments that begun in the 1990s greatly helped to articulate a more nuanced, fact-based view of the relationship between the diversity and stability of ecological systems. In these experiments, plant species richness was manipulated experimentally and the effects of confounding environmental factors were removed through a classic randomization procedure, thereby allowing detection of the direct effect of plant diversity on ecosystem functioning. These experiments showed that plant species diversity increases the stability of ecosystem-level properties, such as total plant biomass production, while at the same time decreasing the stability of population-level properties, such as biomass production of the component species, at least in grasslands (Chapter 8). These new experimental results challenged both the “conventional wisdom” and the new theoretical paradigm since they showed that the same biodiversity metric had contrasting effects on the same stability metric at different levels of organization.

Although at first sight these results seemed to resolve the old diversity–stability debate (Tilman 1996), from a theoretical angle they raised more questions than they provided answers: what then explains the contrasting effects of diversity at the ecosystem and population levels? How can the stabilizing effect of diversity on ecosystem properties be reconciled with existing theory? These questions were the starting point for the recent development of a whole body of new theory on ecosystem stability and diversity–stability relationships. In this chapter, I review these new theoretical advances and show how they provide both a resolution of the historical debate and a new perspective on ecological stability.

7.2. What is stability?

When theoretical ecologists begun to work on stability in a systematic way, they quickly came to realize that “stability” is, in fact, an ambiguous, multifaceted concept that includes a wide range of components or dimensions (Pimm 1984; Loreau *et al.* 2002; Ives and Carpenter 2007). The same system can be viewed as being more or less stable depending on the perturbation it experiences, what is being measured in the system, and what facet of its stability is being considered. For instance, a grassland subjected to a disturbance such as a fire or a drought may have greatly reduced plant biomass while keeping the same plant species composition after the disturbance; in this case, species composition will be deemed more stable than biomass. On the opposite, a grassland experiencing invasion by exotic plant species may keep roughly the same plant biomass while having a very different plant species composition after this disturbance; species composition will then be deemed less stable than biomass. Thus, it is critical to clearly identify the type of perturbation and the variable being observed to make a meaningful statement about the stability of a system.

Once the perturbation and the observed variable have been made clear, the problem is not yet resolved because the stability concept itself needs to be further defined. Ecological theory has traditionally defined stability as either local stability or asymptotic resilience because these properties are based on (relatively) simple linear algebra, and hence are mathematically tractable. *Local stability* is a qualitative property – a system is locally stable when it returns to its local equilibrium following a small disturbance, and is unstable otherwise. In contrast, *resilience* is a quantitative property, which measures the rate or speed at which the system returns to its local equilibrium following the perturbation; *asymptotic resilience* is the value of this return rate in the very long run (in principle, after an infinitely long time, hence the term asymptotic). Both local stability and asymptotic resilience make use of a single quantity, the real part of the dominant eigenvalue of the so-called “community matrix”, that is, the linear matrix whose elements describe how the population growth rate of each species (or system component) changes as the abundance of the various species (or system components) changes following a small perturbation from equilibrium. Local stability is governed by the sign of this quantity (a negative sign indicates stability, a positive sign instability), while asymptotic resilience is governed by its absolute value (more negative values indicate a higher resilience).

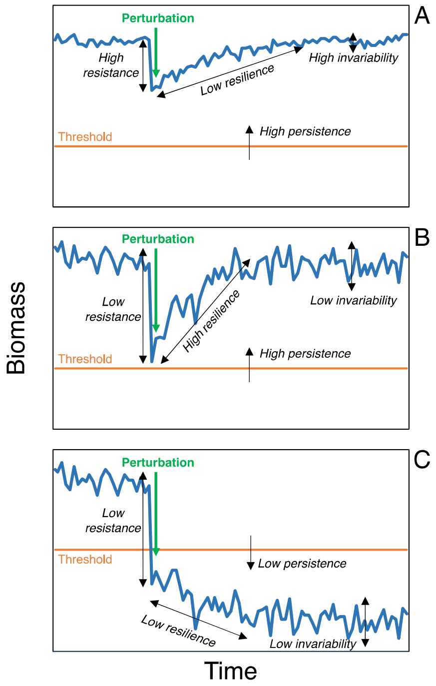

Figure 7.1. *Stability is a multifaceted concept that includes several components, the main ones of which are resistance, resilience, invariability, and persistence. The three panels show a time-series of an ecosystem property of interest – here, the biomass of some population or ecosystem component (in blue). Biomass first fluctuates around an equilibrium value, then experiences an abrupt pulse perturbation and either returns to the same equilibrium (panels A and B) or shifts to an alternative equilibrium after crossing a threshold (in orange; panel C). Panel A depicts a system with high resistance (small decrease in biomass during the perturbation), low resilience (slow return to equilibrium after the perturbation), high invariability (small fluctuations overall, in particular around the equilibrium), and high persistence (the system remains far from the threshold that defines the acceptable range). Panel B illustrates a system with low resistance (large decrease in biomass during the perturbation), high resilience (fast return to equilibrium after the perturbation), low invariability (large fluctuations overall, in particular around the equilibrium), and moderately high persistence (the system remains above the threshold). Panel C shows a system with low resistance (large decrease in biomass during the perturbation), low resilience (the system moves further away from its previous equilibrium, which can be interpreted as negative resilience), low invariability (large fluctuations overall, in particular around the equilibrium), and low persistence (the system crosses the threshold and shifts to an alternative equilibrium). For a color version of this figure, see www.iste.co.uk/loreau/biodiversity.zip*

However, this mathematically convenient solution is deceptive as it hides the true complexity of the stability concept. There are many other ways to define and measure stability (Pimm 1984; Loreau *et al.* 2002; Ives and Carpenter 2007; Donohue *et al.* 2016), including a number of definitions and metrics that are much more relevant empirically as they can readily be quantified from experimental or observational data. For instance, a continuum of non-asymptotic measures of resilience can be readily assessed experimentally by quantifying the rate at which a system returns to its equilibrium after a finite time (Arnoldi *et al.* 2016, 2018) (Figure 7.1). Shifting from asymptotic to finite-time measures of resilience has profound consequences since asymptotic resilience and finite-time resilience can have very different properties and even lead to opposite diversity–stability relationships (Arnoldi *et al.* 2018).

Resistance and persistence are other stability components that can, in principle, be readily measured and that differ strongly from resilience. *Resistance* represents the ability of a system to withstand external perturbations: if two systems are subject to the same perturbation, the more resistant system will be displaced less from its equilibrium than the less resistant one (Harrison 1979) (Figure 7.1). It is often assumed that there is a trade-off between resilience and resistance since a system that returns quickly to equilibrium should have low inertia and thus low resistance (as in Figures 7.1A and 7.1B), although the theoretical (Loreau 1994) and experimental (Chapter 8) evidence for this hypothesis remains limited. What is clear, however, is that the two stability components are very different, and hence should be largely decorrelated. A meta-analysis of the results of a large number of long-term biodiversity experiments showed that the positive effect of plant species diversity on the stability of plant biomass production in grasslands was due to a strong positive relationship between diversity and resistance, while there was no consistent relationship between diversity and resilience, suggesting that resistance, not resilience, is the stability component that mostly governs the relationship between biodiversity and ecosystem stability (Isbell *et al.* 2015).

Persistence is the ability of a system to maintain its properties within an acceptable range in spite of environmental fluctuations (Harrison 1979); *robustness* is another term that is sometimes used to capture the same idea (Donohue *et al.* 2016). The range of a variable that is deemed “acceptable” may be set purely by social norms or expectations (e.g. an acceptable level of food production), but it may also involve an ecological threshold beyond which the ecosystem shifts to an alternative stable state or dynamical regime (Scheffer *et al.* 2001) (Figure 7.1C). Some authors have used the term *ecological resilience* to denote the ability of a system to remain in the same basin of attraction and avoid shifting to an alternative dynamical regime (Holling 1973), but unfortunately this terminology has generated a great deal of confusion in the literature about the resilience concept. It seems much wiser to me to reserve the term “resilience” for its classic meaning, and use persistence or possibly other terms to capture other stability properties. Note that low persistence necessarily implies low values of resilience and resistance (which are defined as local properties in the vicinity of an equilibrium) when the system shifts to an alternative stable state (Figure 7.1C), but the converse is not true, that is, low resilience and/or low resistance do not necessarily imply low persistence (Figures 7.1A and 7.1B).

The stability component that is by far the most commonly used in empirical studies, however, is *invariability*, which describes the ability of a system to maintain a constant level of some property in spite of environmental fluctuations in either space or time. Temporal invariability is simply the inverse of temporal variability, and is generally measured either by the inverse of the temporal coefficient of variation (i.e. the ratio between the mean and the standard deviation) of a property of interest or by its square (i.e. the ratio between the squared mean and the variance) to remove effects of the mean in comparisons across systems (Haegeman *et al.* 2016; Wang *et al.* 2017; Arnoldi *et al.* 2019). Temporal invariability is so widely used in empirical studies that many authors call it simply “temporal stability”. Unless it is clearly defined, however, this terminology can be confusing since the other abovementioned stability components also fall under the umbrella of the broad “temporal stability” concept.

These various components of stability capture different aspects of the dynamical response of ecosystems to perturbations (Figure 7.1); therefore, they should logically be related to each other in some way. A few recent studies have begun to tackle the relationships between stability components by subjecting ecosystems to perturbations and examining how the various stability components are correlated, either experimentally (Donohue *et al.* 2013) or theoretically (Domínguez-García *et al.* 2019). These studies showed that stability components are correlated and thus that stability has a lower dimensionality than the number of stability metrics tested. This is a promising conclusion as it supports the view that the stability concept is not as desperately diverse as terminological profusion might suggest (Grimm and Wissel 1997). Careful theory should be able to disentangle the connections between the various stability components, and recent theoretical and mathematical developments have indeed begun to do this (Arnoldi *et al.* 2016; Haegeman *et al.* 2016).

A critical limitation of the literature on ecological stability so far is the divide between empirical and theoretical studies. As noted above, much of ecological theory has focused on either local stability or asymptotic resilience, while observational or experimental studies have mostly used temporal invariability as a stability metric. This divide appears clearly in quantitative analyses of the ecological literature (Donohue *et al.* 2016). Fortunately, new theory is now providing new approaches and predictions on empirically relevant stability components such as non-asymptotic resilience and invariability (Arnoldi *et al.* 2018, 2019). A novel insight that results from this new body of theory is that stability is inherently a multidimensional concept, not only because it contains various components, but also, more fundamentally, because each of these components is governed by different species at different timescales depending on their abundance and the type of perturbation they experience. Generally speaking, abundant species tend to govern short-term rates of return to equilibrium (and thus non-asymptotic resilience), while rare species tend to govern long-term return rates (and thus asymptotic resilience) (Arnoldi *et al.* 2018).

Temporal invariability is the outcome of a complex process that involves the type, amplitude, and direction of perturbations, the response of the system to these perturbations, and the system variable that is observed (Arnoldi *et al.* 2019). Therefore, one should not expect a single universal relationship between diversity and invariability to hold. Despite this complexity, generic relationships between community invariability and species abundances do emerge from community assembly in species-rich systems (Arnoldi *et al.* 2019). Different types of perturbations, however, yield different relationships between community invariability and species abundances, which in turn predict qualitatively different diversity–stability relationships (Figure 7.2).

These new theoretical insights have broad consequences for understanding and interpreting experimental results. In particular, they might provide a simple explanation for the contrasting diversity–stability relationships observed at the population and ecosystem levels in grassland biodiversity experiments (Chapter 8). In these experiments, ecosystem stability has usually been measured by the invariability of total plant biomass. By construction, the latter gives a predominant weight to abundant species, just as environmental-type perturbations do, and this tends to generate positive diversity–invariability relationships (Figure 7.2C). In contrast, population stability has usually been measured by the average invariability of the various component species. This average gives a predominant weight to rare, highly variable species (Haegeman *et al.* 2016), just as immigration-type perturbations do, and this tends to generate negative diversity–invariability relationships (Figure 7.2A). Thus, the new multidimensional theoretical approach to ecological stability provides both a potential resolution of the old diversity–stability debate and a new perspective on stability that helps reveal the full dynamical richness of ecological systems.

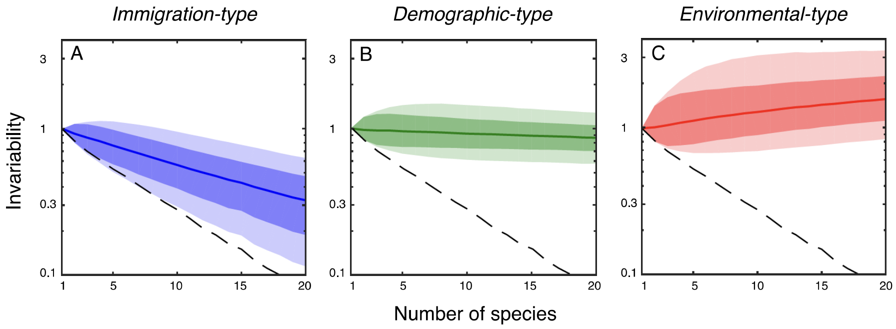

Figure 7.2. *Different types of perturbations yield contrasting diversity–stability relationships in competitive communities. Here, stability is measured by a community-wide measure of invariability that integrates all species, and biodiversity is measured by the number of species. In each panel, the solid color line shows the median invariability of randomly assembled competitive communities experiencing random perturbations (1,000 communities for each level of species richness; 1,000 perturbations for each community); the darkly shaded region shows the 5th and 95th percentiles of the distribution of invariability values; the lightly shaded region shows their minimum and maximum values; and the dashed line shows asymptotic resilience. Perturbations are of three types: immigration (i.e. they are exogenous to the system and hence independent of a species' abundance), demographic (i.e. they affect individuals independently), and environmental (i.e. they affect all the individuals of each species synchronously). After Arnoldi et al. (2019). For a color version of this figure, see www.iste.co.uk/loreau/biodiversity.zip*

7.3. Why does local biodiversity promote ecosystem stability?

While the abovementioned theory on temporal invariability and its properties provides interesting new insights into the diversity–stability relationships that can be expected under different perturbation scenarios, it does not allow a mechanistic understanding of the ecological processes that generate the positive effects of biodiversity on ecosystem stability observed in biodiversity experiments.

Two main hypotheses have been proposed to explain these effects. The first, known as the insurance hypothesis, posits that, in a variable environment, aggregate ecosystem properties (e.g. total biomass or production) will vary less in more diverse communities because declines in the performance or abundance of some species or phenotypes can be offset by increases by others due to their asynchronous responses to fluctuations in environmental conditions (Yachi and Loreau 1999). This mechanism is deeply rooted in biology since differential responses to environmental variations are ultimately based on the universal presence of trade-offs in biological systems, which constrain species to evolve towards a species-specific balance between various biological functions and thus to perform best under a species-specific set of environmental conditions. Biodiversity is viewed as providing the biological equivalent of an economic insurance because an informed decision-maker could choose to maintain a high level of biodiversity to avoid extreme lows in ecosystem functioning, even under conditions where maintaining biodiversity may entail a cost.

A second popular hypothesis, inspired by traditional competition theory, is that competition between species should generate or amplify negative covariations in their abundances because, as one species increases in abundance, it increases its negative effect on other species, thereby pushing their abundance down (Tilman 1999; Klug *et al.* 2000). Although competition often enhances the asynchrony of species abundances in models of interspecific competition, it is not necessarily the factor that generates community stability in these models. Community stability generally arises from implicit or explicit differences in the environmental preferences of the competing species (Tredennick *et al.* 2017).

Recent theory has used stochastic, discrete-time, multispecies versions of the classic Lotka–Volterra competition model (Chapter 4) to reveal and disentangle the various factors that govern local diversity–stability relationships. These models confirm that species' differential responses to environmental fluctuations, as measured by the degree of asynchrony of species' environmental responses, are the main mechanism through which biodiversity can stabilize aggregate ecosystem properties, in agreement with the insurance hypothesis (Ives *et al.* 1999; Loreau and de Mazancourt 2008, 2013; Loreau 2010). Whatever the strength of interspecific competition, when asynchrony of species' environmental responses between any two species is low, their total biomass shows the same fluctuations as does the biomass of individual species on a log scale because the fluctuations of the two species are strongly correlated positively (Figures 7.3A and 7.3C). This means that total biomass varies roughly twice as much as the biomass of each species, and since mean total biomass is also roughly twice the mean biomass of each species, the temporal invariability of total biomass, as measured by the inverse of its coefficient of variation, remains unchanged. However, when the asynchrony of species' environmental responses is high, total biomass shows strongly reduced fluctuations compared with the biomass of individual species because the fluctuations of the two species are correlated negatively and hence tend to compensate for each other (Figures 7.3B and 7.3D). In this case, the temporal invariability of total biomass is much smaller than that of the biomass of individual species because the standard deviation of total biomass decreases while its mean increases, and both these effects contribute to increasing the inverse of the coefficient of variation, which measures invariability.

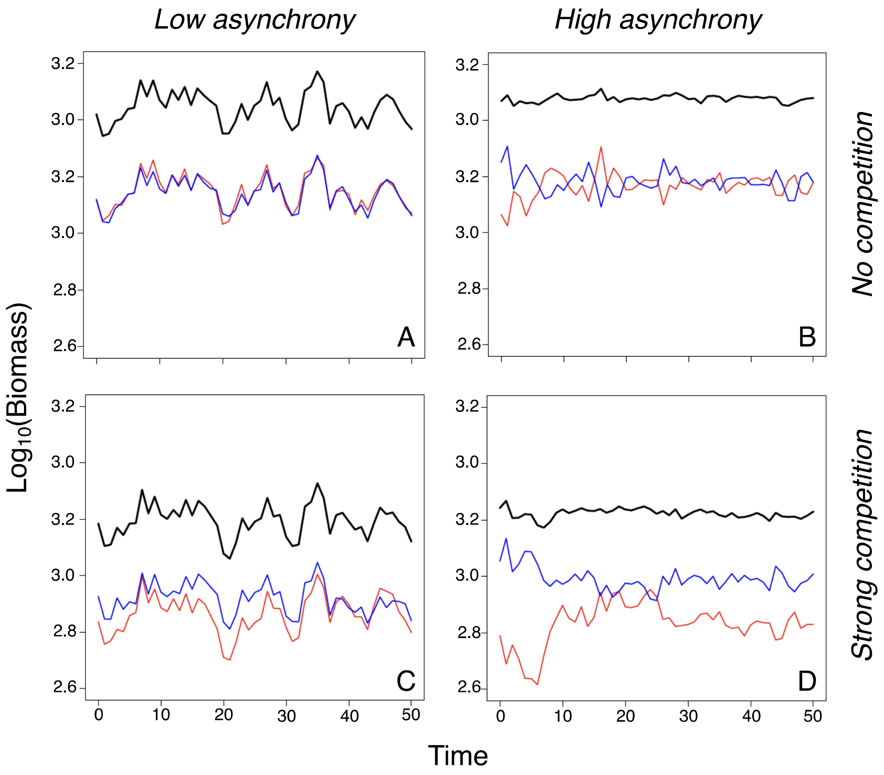

Figure 7.3. *Effects of asynchrony of species' environmental responses and interspecific competition on the temporal variability of the biomass of two species (blue and red) and their total biomass (black) in Loreau and de Mazancourt's (2013) stochastic Lotka–Volterra competition model. Left panels: minimum asynchrony between the environmental responses of the two species (maximum synchrony,* $\varphi_e = 1$*); right panels: maximum asynchrony between their environmental responses (minimum synchrony,* $\varphi_e = 0$*). Upper panels: no interspecific competition (competition coefficients* $\beta_{12} = \beta_{21} = 0$*); lower panels: strong interspecific competition (*$\beta_{12} = \beta_{21} = 0.8$*). Other parameter values: intrinsic rates of natural increase* $r_{m1} = r_{m2} = 0.5$*; carrying capacities* $K_1 = K_2 = 1500$*; demographic variances* $\sigma_{d1}^2 = \sigma_{d2}^2 = 1$*; environmental variances* $\sigma_{e1}^2 = \sigma_{e2}^2 = 0.01$*. For a color version of this figure, see www.iste.co.uk/loreau/biodiversity.zip*

By contrast, stochastic Lotka–Volterra competition models do not support the hypothesis that competition increases ecosystem stability. Interspecific competition tends to have two countervailing effects on the variability of total biomass, at least when species already differ in their environmental responses (compare Figures 7.3B and 7.3D). On the one hand, interspecific competition tends to increase the degree of asynchrony between the biomass fluctuations of individual species, which contributes to reducing the variability of total biomass. On the other hand, however, it also increases the amplitude of the biomass fluctuations of individual species, which contributes to enhancing the variability of total biomass. These two countervailing effects cancel each other in symmetric competitive systems, thereby leaving the invariability of total biomass unaffected (Ives *et al.* 1999; Loreau and de Mazancourt 2013). When competition is asymmetric (such that the competitive effect of species A on species B differs widely from the reverse effect of species B on species A), a wide range of outcomes are possible, but the most common effect of increasing the strength of interspecific competition is destabilization of aggregate ecosystem properties (Loreau and de Mazancourt 2013). Instead, a *reduction* in the strength of interspecific competition tends to stabilize ecosystem properties because it generates overyielding, that is, a higher total production and biomass (Chapter 4), which in turn reduces the destabilizing effect of demographic stochasticity on aggregate ecosystem properties (de Mazancourt *et al.* 2013; Loreau and de Mazancourt 2013).

Additional mechanisms can further contribute to ecosystem stability. One such mechanism is differences in the speed at which species respond to perturbations, which can also generate asynchronous population dynamics and thereby promote ecosystem stability (Fowler 2009). This mechanism operates under more restrictive conditions than do differences in species' responses to environmental fluctuations, but, interestingly, it appears to provide the only scenario in which strong interspecific competition can generate compensatory dynamics as envisaged by the competition hypothesis (Loreau and de Mazancourt 2013). Selection effects (Chapter 4) can also affect ecosystem stability. If species that have a higher-than-average invariability tend to dominate multispecies communities, this will generate a positive selection effect of species diversity on ecosystem stability. Conversely, if species that have a lower-than-average invariability tend to dominate multispecies communities, this will generate a negative selection effect on ecosystem stability. Such selection effects are likely to be present, and hence to interact with other factors that affect the relationship between biodiversity and ecosystem stability, under many circumstances. Lastly, observation errors, which arise from the random effects of uncontrolled factors, may significantly inflate observed ecosystem stability as they tend to decorrelate variations in abundance among species (de

Mazancourt *et al.* 2013). Thus, observation errors should be taken into account in interpretating the results of small-scale biodiversity experiments.

This brief overview of the factors known to affect diversity–stability relationships from stochastic Lotka–Volterra competition models shows that asynchrony of species' responses to environmental fluctuations provides a likely general explanation for positive effects of biodiversity on ecosystem stability, but a number of other factors can also come into play and should be considered carefully in the interpretation of experimental or observational data. It is important to realize that the range of potential factors to consider becomes even wider in complex food webs or interaction networks. In particular, one critical additional factor that may affect the stabilizing or destabilizing effect of species diversity when multiple trophic levels are considered is the combined interaction strength of animal consumers, as measured by the total per capita effect of all resources combined on their population growth rate (Ives *et al.* 2000). For species diversity to stabilize ecosystem properties, a trade-off between the niche breadth of animal consumers and their efficiency at exploiting each of their resources is required (Thébault and Loreau 2005; Loreau 2010). Such a trade-off can arise, for instance, when prey diversity forces predators to spend more time on information processing, thereby reducing their consumption efficiency (Kratina *et al.* 2007).

More generally, stochastic competition models have so far assumed that environmental fluctuations affect individuals irrespective of their density or diversity, which is a reasonable assumption as a first approximation. If, however, the effect of environmental fluctuations on per capita population growth rates were to change systematically with diversity because of changes in individual behavior as a result of species interactions, this would obviously alter model predictions. Specifically, if environmental fluctuations were to affect individuals relatively less in species-rich (species-poor) communities, this would act as an additional mechanism contributing to the stabilizing (destabilizing) effect of diversity on aggregate ecosystem properties (Loreau and de Mazancourt 2013). Although there is currently no evidence for such effects of diversity, only careful future experiments and observations will tell us whether existing theory needs to be revisited and expanded in new directions.

7.4. Scaling up diversity–stability relationships

As stability theory develops in new directions that strengthen its connection with empirical data (section 7.2), new areas of theoretical research are emerging. A particularly exciting new research area is exploring how biodiversity, ecosystem stability, and their relationship change with spatial scale (Gonzalez *et al.* 2020).

Theoretical advances in this area have been made possible by the use of temporal invariability as a stability metric. It turns out that variability or its inverse, invariability, can be scaled up in much the same way as species diversity.

Two classic approaches have been used to study species diversity across two or more scales: 1) partitioning gamma (regional) diversity into alpha (local) diversity and beta (between-community) diversity (Chapter 2); and 2) the species–area relationship (SAR), which describes how the number of species increases with study area (Rosenzweig 1999). Recent theoretical work has shown that the same approaches can be used to study ecosystem invariability across scales.

The first approach partitions gamma (regional) variability or invariability into alpha (local) and beta (between-community) components, either multiplicatively or additively, in the same way as gamma diversity is partitioned into its alpha and beta components (Wang and Loreau 2014). This partition predicts that the invariability of aggregate ecosystem properties must necessarily increase as one moves from the local to the regional scale. Interestingly, this partition can be extended to multiple nested scales or hierarchical levels, and doing so offers exciting new insights into the factors that govern ecosystem stability across scales. In particular, this hierarchical approach reveals that beta variability is equivalent to spatial asynchrony between communities, and that the factors that govern alpha invariability and spatial asynchrony are very similar to those that govern population invariability and species asynchrony, respectively, within a local community (Wang and Loreau 2014). Thus, the hierarchical partitioning of invariability provides a powerful integrative framework to understand ecological stability across scales and hierarchical levels.

Since species diversity and ecosystem stability can be studied under the same partitioning framework, the relationship between diversity and stability can also be studied under this framework. Using a dynamical model of competitive metacommunities, theorists have shown that, while alpha diversity increases local ecosystem invariability, beta diversity generally contributes to increasing spatial asynchrony among local ecosystems (Wang and Loreau 2016). Consequently, alpha diversity and beta diversity play complementary roles in stabilizing ecosystem properties at the regional scale: while local diversity provides local insurance for ecosystem functioning by enhancing species asynchrony, beta diversity provides spatial insurance for ecosystem functioning by enhancing spatial asynchrony between ecosystems. Furthermore, the model predicts that the stabilizing effect of biodiversity at the regional scale increases as the correlation between environmental conditions across space increases. This is because when environmental conditions are very heterogeneous across space, the background level of spatial asynchrony is already high and biodiversity cannot enhance it much more; in contrast, when environmental conditions are homogenous across space, the background level of spatial asynchrony is low and biodiversity can increase it dramatically. This theoretical prediction suggests that biodiversity loss may exacerbate the destabilizing effect of the homogenization of environmental conditions across space that is expected to occur under current global environmental changes (Vitousek *et al.* 1997).

The second approach to scaling up ecosystem invariability is the invariability–area relationship (IAR), which describes how ecosystem invariability increases with surface area (Wang *et al.* 2017). The IAR offers a continuous approach to the spatial scaling of ecosystem stability that is complementary to the discrete approach provided by the hierarchical partition. The shape and slope of the IAR are essentially determined by the patterns of spatial synchrony or asynchrony across scales, just as spatial asynchrony (beta variability) is the link that connects local (alpha) and regional (gamma) invariability in the hierarchical partition. In particular, when spatial synchrony decays exponentially with distance, the IAR exhibits three phases, characterized by steeper increases in invariability at both small and large scales (Figure 7.4A). Such a triphasic IAR was observed for primary productivity from plot to continental scales (Figure 7.4B). If spatial synchrony decays as a power law with distance, however, the IAR is nearly linear on a log-log plot (Figure 7.4C). This pattern was observed for the population abundance of North American birds (Figure 7.4D). The IAR provides a new quantitative tool to predict the effects of habitat loss on population and ecosystem stability and to detect possible regime shifts in spatial ecological systems, which are important goals for biodiversity conservation and ecosystem management (Wang *et al.* 2017).

Since species diversity and ecosystem stability show similar relationships with area, the link between the SAR and the IAR can also be studied. A simple theoretical model that simultaneously predicts the SAR and the IAR shows that the link between the two relationships depends strongly on whether the temporal fluctuations of the ecosystem property of interest are more synchronized within than between species (Delsol *et al.* 2018). If fluctuations are synchronized within species but not between species, the IAR is strongly constrained by the SAR. If instead the level of synchrony between individual fluctuations is governed by spatial proximity, the IAR is unrelated to the SAR. These two scenarios of synchrony between species and across space further lead to very different predictions regarding the effects of biodiversity loss and habitat destruction on ecosystem stability (Delsol *et al.* 2018). Thus, a recurrent conclusion from recent theory is that understanding the drivers and patterns of synchrony or asynchrony between species and across space is key to predicting the effects of biodiversity loss and global environmental changes on ecosystem stability.

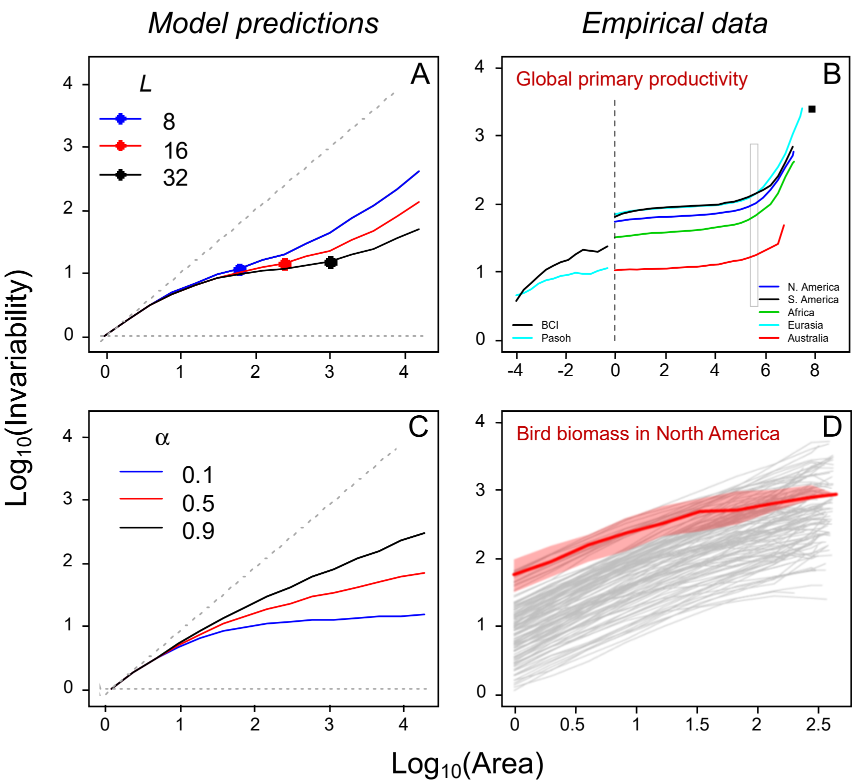

Figure 7.4. *Invariability–area relationships (IARs). Left panels: model predictions. Triphasic IARs are predicted when spatial synchrony decays exponentially with distance (panel A), while near-linear IARs on a log-log plot are predicted when spatial synchrony decays as a power law with distance (panel B). Solid lines show different IARs obtained for different values of either L, the characteristic length of the exponential decay of spatial synchrony with distance, or α, the exponent of the power law. Dotted lines show the two limiting cases where spatial synchrony is either minimum or maximum, irrespective of distance. Right panels: empirical data. Panel B: triphasic IARs observed for primary productivity from plot to continental scales on five continents, where area is measured in km^2. The black filled square on the right shows the invariability of primary productivity for the entire globe. Panel D: near-linear IARs observed for bird biomass in eastern North America, where area is measured by the number of sampling routes in the North American Breeding Bird Survey. The red line shows the median invariability of total bird biomass, and the red shade shows its 25 and 75% quantiles. The gray lines show the IARs of individual species biomass for 121 bird species. After Wang et al. (2017). For a color version of this figure, see www.iste.co.uk/loreau/biodiversity.zip*

Hierarchical partitioning of invariability has recently been extended in two alternative directions to provide consistent measures of asynchrony across hierarchical levels when there is spatial heterogeneity among communities, as is typically the case in empirical data (Wang *et al.* 2019; Hammond *et al.* 2020). The resulting mathematical frameworks have been used to quantify the relative contributions of different sources of asynchrony to large-scale ecosystem stability in several empirical datasets. Local insurance due to alpha diversity was shown to provide stronger stabilizing effects on regional ecosystem functioning than did spatial insurance in a desert grassland ecosystem (Wang *et al.* 2019) and in a kelp forest (Lamy *et al.* 2019). Other studies, however, found that spatial insurance contributed more than did local insurance to the stability of benthic marine fish communities (Thorson *et al.* 2018) and rock-pool invertebrate metacommunities (Hammond *et al.* 2020). Although clearly more work will be necessary to reach general conclusions about the respective roles of different sources of asynchrony in the stability of natural ecosystems, the fact that a complete set of conceptual and mathematical tools is now available to address this issue with empirical data is a remarkable achievement of ecological theory which still seemed out of reach a few years ago.

7.5. Conclusion

Recent studies of diversity–stability relationships have led to the development of a new body of theory that is profoundly changing our views of both ecological stability and its relationships with biodiversity.

This body of theory suggests that stability should be fully embraced as a multidimensional concept, not only because it contains different components that describe different aspects of the response of ecosystems to perturbations, but also because each of these components is governed by different species at different timescales depending on their abundance and the type of perturbation they experience. In particular, temporal invariability is an integrative measure of stability that is affected by the type, amplitude, and direction of perturbations, the response of the system to these perturbations, and the system variable that is observed. Different types of perturbations and different observed variables yield different relationships between community invariability and species abundances, which in turn yield qualitatively different diversity–stability relationships. A fully integrative theory of ecological stability that connects and integrates the various components of stability (resilience, resistance, persistence, invariability) may not yet be available, but this goal does not seem as distant today as it still seemed a few years ago based on recent advances made in that direction. The new body of theory built so far already provides both the elements to resolve the old diversity–stability debate and new perspectives on ecological stability that help reveal the full dynamical richness of ecological systems.

This body of theory has also greatly increased our mechanistic understanding of the ecological processes that generate the positive effects of biodiversity on ecosystem stability observed in small-scale biodiversity experiments. Asynchrony of species' responses to environmental fluctuations appears to provide a likely general explanation for these effects, but a number of other factors can also come into play and should be considered carefully in the interpretation of experimental or observational data.

An exciting extension of this body of theory is the recent development of new approaches to studying the relationship between biodiversity and ecosystem stability across spatial scales using temporal invariability as a stability metric. The hierarchical partitioning of invariability turns out to provide a powerful integrative framework to understand ecological stability across scales and hierarchical levels. Its continuous equivalent, the invariability–area relationship, provides a quantitative tool to predict the effects of biodiversity loss, habitat destruction, and other environmental changes on ecosystem stability – an important goal for biodiversity conservation and ecosystem management. Both approaches highlight the key role played by asynchrony between species and across space in ecosystem stability at large spatial scales. Thus, understanding the drivers and patterns of asynchrony across scales and hierarchical levels appears to be critical. The hierarchical partitioning of invariability precisely provides the necessary conceptual and mathematical tools to detect the main sources of asynchrony in empirical data.

Ecology now has a powerful set of theoretical approaches and predictions that can be connected directly to experimental and observational data across multiple organizational levels and spatial scales. This is a unique strength, which hopefully will open a new area of rigorous quantitative research into ecosystem stability and the consequences of biodiversity loss for ecosystem functioning and ecosystem services at scales relevant to management.

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7.7. References

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