

The Causes and Consequences of Compensatory Dynamics in Ecological Communities

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Key Words

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Abstract

Ecological communities are constantly responding to environmental change. Theory and evidence suggest that the loss or decline of stress-intolerant species can be compensated for by the growth of other species. Compensatory dynamics are a long-term feature of community dynamics across a broad range of models, and they can have strong stabilizing effects at the community level. Coexistence theory indicates that distinct environmental responses are required for compensatory dynamics and deemphasizes competition. Compensatory dynamics have been detected under experimental conditions, but are not dominant in a metaanalysis of field surveys. Recent progress has been made in quantitative methods that detect compensatory dynamics at different temporal scales. Appropriate null models are required to sharpen our understanding of compensatory dynamics in nature. An integrated theory of compensation and compensatory dynamics will improve our ability to understand when communities maintain sufficient response diversity to buffer the effects of environmental change and anthropogenic stress.

1. INTRODUCTION

Ongoing environmental change is causing widespread reorganization of ecological communities. Sustained environmental stress in the form of pollutants, habitat transformation, and climate warming can cause local extinctions or shifts in distribution and abundance of species, which in turn can have profound effects upon community structure and functioning (Karieva et al. 1993, Suttle et al. 2007). Theory and evidence suggest that the loss or decline of stress-intolerant species can be compensated for by the growth of other species (Ives & Cardinale 2004). Longer-term compensatory dynamics are the basis of community stability and ecosystem resilience (Holling 1973), but they are difficult to detect because population dynamics are governed by the direct effects of environmental change on demography and species interactions. A deeper understanding of the causes and consequences of compensation and compensatory dynamics is a major challenge for the emerging synthesis between community and ecosystem ecology (Loreau 2010).

Earlier work on density compensation by MacArthur et al. (1972) set the stage for current thinking. Density compensation is said to occur when the total density or biomass of an island community maintains the same level as that found on the mainland despite species loss following isolation. The conditions for “ecological release” (Crowell 1962) whereby depauperate communities can maintain constant total biomass have been worked out using competition theory for guilds of similar species (Case et al. 1979). These results, largely formulated within an equilibrium framework, form the conceptual basis of current thinking on compensation and the relation between biodiversity loss and ecosystem functioning under extinction (e.g., Adler & Bradford 2002, Bunker et al. 2005, Jiang 2007, Solan et al. 2004). Compensation need not necessarily involve local extinction, but it does imply a significant reorganization of community dominance in response to environmental change.

Ecosystem ecologists have long evoked compensatory dynamics as a fundamental mechanism for ecosystem stability (McNaughton 1977, Patten 1975). As Patten (1975, p. 531) stated, “Speciation, local introductions and extinctions, and species replacement provide buffering mechanisms by which ecosystem-level dynamic characteristics are maintained invariant. Component behaviors may be quite irregular, as in population fluctuations, but whole system attributes such as production, metabolism, and biomass remain relatively fixed.” Thus, although the original concept of density compensation was concerned with explaining changes in the level of total aggregate biomass, compensatory dynamics in this context pertain to the stability of aggregate ecosystem variables.

Aggregate community processes, such as total biomass production, will be stabilized by differences in the magnitude and timing of species responses to environmental change. Compensatory fluctuations at the population level result in a stabilizing effect at the community level (Ives et al. 1999, 2001; Micheli et al. 1999; Yachi & Loreau 1999). Furthermore, increasing species diversity can stabilize aggregate measures by increasing the range of species responses to environmental fluctuations (Chesson et al. 2001, Elmquist et al. 2003, Hughes & Roughgarden 1998, Ives & Carpenter 2007, Ives & Hughes 2002, Ives et al. 1999, Loreau & de Mazancourt 2008, Loreau et al. 2003, McNaughton 1977, Norberg et al. 2001, Yachi & Loreau 1999). Compensatory dynamics involve countervailing modes of growth and decline between species in response to environmental change occurring at one or more temporal scales (Keitt 2008, Vasseur & Gaedke 2007). However, they may not be easy to detect or accurately measure by simple correlations or covariances (Loreau & de Mazancourt 2008, Ranta et al. 2008).

Recent advances in fluctuation-based coexistence theory (Chesson 2000) suggest that compensatory fluctuations can be a long-term feature of species dynamics. For example, theories

of species coexistence suggest an important role for environmental variability (Chesson 2000, Ebenhöh 1988, Levins 1979, Loreau 1989), whereby species can partition their use of the variable environment by adaptation to distinct intervals of environmental conditions (e.g., dry versus wet seasons). One corollary of temporal niche differences is that species of similar ecology (e.g., resource competitors) will be expected to show variable and asynchronous dynamics in response to environmental change; as the environment changes, declines in abundance of dominant species will be compensated by increases in other species adapted to the new conditions. Compensatory species dynamics are thus expected to be an important signature of balancing selection in a variable environment that may occur at multiple timescales within the same community (Gonzalez & De Feo 2007, Keitt & Fischer 2006, Vasseur & Gaedke 2007).

Recent research on the prevalence and detection of compensatory dynamics suggests there is a great deal still to be learned (Houlahan et al. 2007, Keitt 2008, Keitt & Fischer 2006, Loreau & de Mazancourt 2008, Vasseur & Gaedke 2007). We lack knowledge regarding the mechanisms that affect the tempo and scale of compensatory dynamics in species-rich systems and how best to detect them in nature (Keitt 2008, Vasseur & Gaedke 2007). Here we review current theoretical and empirical knowledge of the causes and consequences of compensation and compensatory dynamics in communities. Section 2 provides general definitions. Section 3 reviews existing theoretical explanations for the causes of compensation. Section 4 covers compensatory dynamics and identifies intrinsic and extrinsic causes from theory. Section 5 reviews the time series methods used to detect compensatory dynamics and discusses the role of neutral models. Section 6 reviews the evidence for compensatory dynamics. We close with some suggested avenues for future research.

2. DEFINING AND LINKING COMPENSATION AND COMPENSATORY DYNAMICS

Ecological communities are perturbed by environmental fluctuations over a great range of scales. Species interactions and differential species responses to the environment ensure that the assemblage is always dynamic. Compensation and compensatory dynamics refer to particular modes of change in response to the environment that have distinct literatures. They are highly interrelated concepts that address different aspects of species' responses to environmental change, and we feel they should be integrated within a common framework.

Both concepts can be defined as the presence of countervailing responses to environmental change (abiotic or biotic) between at least two species within a community. The difference between these concepts can be clarified using the analogy of pulse and press perturbations (Bender et al. 1984; see also Frost et al. 1995, Ives 1995). Compensation can be viewed as the adjustment in densities of an entire community in response to a sustained press perturbation, whereby the press perturbation represents a sustained environmental shift for natural (biotic or abiotic) or anthropogenic reasons. Compensatory dynamics involve repeated phases of population growth and decline among species in response to continuous environmental pulses, where pulses represent high-frequency environmental fluctuations.

Compensatory dynamics can occur in the presence or absence of a long-term trend in the environment, whereas compensation can occur in the presence or absence of compensatory dynamics (**Figure 1**). However, with the notion of scale in mind, environmental change should be seen as composed of trends and abrupt fluctuations at all scales (Halley 1996). Compensation and compensatory dynamics are therefore distinct manifestations of the same response process expressed at different temporal scales; a process of compensation over a short scale can be viewed as part of a compensatory dynamic of fluctuating species abundance over longer timescales. This can be seen even within the short time series represented in **Figure 1**.

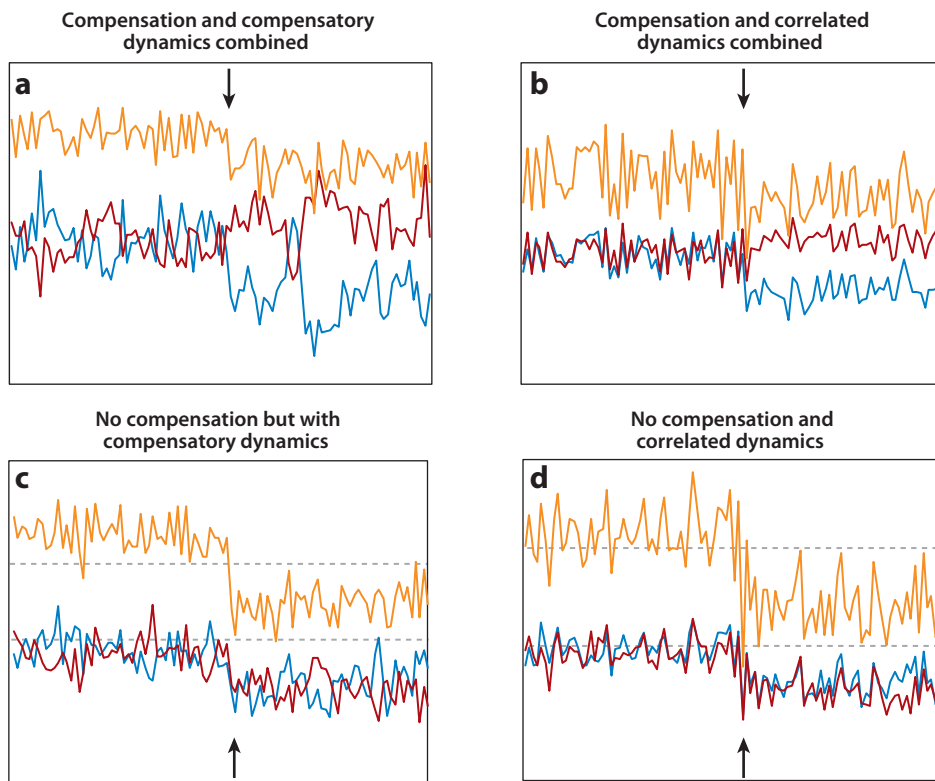


Figure 1

The four possible scenarios whereby compensation and compensatory dynamics can co-occur within the same two-species community of competitors (red and blue lines). Total population abundance is represented by the orange line. The point at which a press perturbation is applied is shown by the arrow. In the presence of compensation (a and b) the level of total biomass remains relatively unchanged, because the decline of one species is countered by the increase in the other. In a and c compensatory dynamics are indicated by the opposed increases and decreases in the species fluctuations through time. In the absence of compensation (c and d) total biomass declines, but the variability of total biomass is greater in the presence of correlated species dynamics (d), indicated by the two dotted lines.

Compensation and compensatory dynamics have been the focus of attention over the past 30 years because of the effects they have on aggregate community and ecosystem processes (e.g., MacArthur et al. 1972, McNaughton 1977, Patten 1975). Ecologists are struck by the fact that although environmental change can create significant community reorganization, it often results in relatively small net change in community structure and ecosystem functioning. The effect of compensation can thus be measured as the extent to which the level of aggregate biomass—or some other aggregate variable or function—is maintained in the face of sustained declines, or loss of species, by countervailing population growth or colonization (Ernest & Brown 2001b). Compensatory dynamics involve repeated phases of growth and decline (cyclic or aperiodic) due to diverse species responses to environmental fluctuations. Their effect is to dampen the temporal stability of aggregate ecosystem variables. Both effects are linked through the response diversity of the community (Elmqvist et al. 2003, Ives et al. 1999), but their theoretical foundations are distinct.

3. DENSITY AND FUNCTIONAL COMPENSATION

Under density compensation the loss or decline of stress-intolerant species can be rapidly compensated by the growth of other species. Thus, an important consequence of density compensation is the maintenance of total community density or biomass, even in the face of species extinctions. The first cases of this were observed for species-poor island faunas (Crowell 1962, 1973; MacArthur et al. 1972). A large number of papers have examined this phenomenon (summarized by Faeth 1984, Wright 1980), and have sought to explain why in some cases aggregate densities were lower (density undercompensation) or higher (density overcompensation) on islands when compared with equivalent mainland assemblages.

Density undercompensation is predicted from niche theory and the habitat appropriateness hypothesis. Niche theory predicts that if exploitation competition is predominant, then the realized niche of each species will be restricted to the part of the resource spectrum for which it is the most efficient consumer. Total resource exploitation by more species-rich mainland communities should be greater than island communities, resulting in a greater total density of biomass. The subsets of species occurring on islands are expected to expand their realized niches and increase their population sizes. However, niche expansion comes at the cost of reduced resource-use efficiency, which should translate into lower aggregate consumer and resource densities. The habitat appropriateness hypothesis asserts that the ability of species-poorer communities to compensate for the biomass of extinct species depends upon the quality of the island habitat and population fitness in that habitat (MacArthur et al. 1972). The extent of density undercompensation will thus depend upon how fitness is adjusted as species find themselves in higher- or lower-quality habitat.

Density overcompensation is possible if interference competition by inefficient species is predominant on the mainland. Loss of these species on islands will then allow species-poorer communities to consume resources more efficiently and support higher total densities than the mainland (Case et al. 1979). Overcompensation is also expected if resource overexploitation is occurring. Preferential loss of these consumers will lead to higher overall resource abundance in species-depauperate communities. Finally, islands are expected to maintain disproportionately fewer predatory species. If predators regulate prey abundances, then the total biomass of a guild of prey species should be greater in more predator-depauperate communities.

Many of these historical explanations for compensation are evident in the current literature on biodiversity and ecosystem functioning. The concepts of niche complementarity and selection effects and how they relate to overyielding or underyielding in long-term biodiversity experiments are grounded in these ideas (Loreau & Hector 2001). Density compensation predicts little effect of species loss on ecosystem functioning, because of expected community-wide increases in mean population abundance. Thus, density compensation is inversely related to complementarity (Loreau 2004). As the current field of biodiversity and ecosystem functioning shifts to studying the impacts of nonrandom extinction over many generations, early thinking on density compensation will find renewed relevance (Adler & Bradford 2002, Bunker et al. 2005, Jiang 2007, Solan et al. 2004).

Lawton & Brown (1993) identified functional compensation as a specific form of compensation in which an ecosystem function (e.g., primary production or decomposition) is maintained constant in the face of species loss or environmental change because of functional degeneracy among species. The term *degeneracy*, the ability of elements that are structurally different to perform the same function, is more appropriate than *redundancy*, which derives from engineering. Functional compensation may not involve an obvious change in density, but may be related to compensation at the individual level due to changes in physiology or behavior (Ruesink & Srivastava 2001). Thus, compensation is also associated with a number of allied terms such as *functional redundancy*

(Naeem 1998, Rosenfeld 2002, Walker 1995) and *complementarity* (Frost et al. 1995, Ives 1995, Loreau 2004, Petchey 2003). Like density compensation, functional compensation is expected to occur most likely in diverse assemblages of functionally similar species that have complementary responses to the environment.

3.1. Theoretical Expectations

Ives et al. have proposed a theoretical framework for density compensation in arbitrarily complicated communities that explicitly incorporates environmental stress (e.g., Frost et al. 1995, Ives 1995, Ives & Cardinale 2004, Ives et al. 2001). Model communities with different interaction structures can be defined with discrete-time Lotka-Volterra equations:

$$x_i(t+1) = x_i(t) \exp \left[r_i + a_i s(t) + \sum_j b_{i,j} x_j(t) + \varepsilon_i \right], \quad 1.$$

where $x_i(t)$ is the abundance of species i at time t , r_i is its intrinsic rate of increase, $b_{i,j}$ is the per capita interaction strength representing the effect of species j on i , $s(t)$ is the magnitude of an environmental stressor, a_i governs the direct effect of the stressor on the population growth rate of species i , and ε_i is a random variable representing variability in population growth rates not represented by s . If all a_i values are assumed <0 , then an increase in an environmental stressor, $s(t)$, will cause a decrease in the per capita growth rate of all species i . This equation makes the simplifying assumption that all effects are additive, which facilitates application of the framework.

An analysis of this model at equilibrium (e.g., Frost et al. 1995, Ives 1995) shows that the propensity for compensation increases as the degree of functional similarity increases between species. Here functional similarity is defined as the density-dependent effect of species on the population growth rates of all species in the community. The potential for compensation is greatest when the effect of the environmental stressor is very different from the effects of the species interactions. If the direct effect of the environmental stressor on population growth is similar to the effects of species interactions, then compensation will only occur between functionally similar species.

Using this framework, Ives & Cardinale (2004) report a theoretical study that examined the impact of extinctions on resistance to environmental change. They explored two contrasting scenarios of species extinction—random versus ordered—and how they affected compensation. Nonrandom extinctions proceed in order of the sensitivity of a species to increasing environmental stress over time. In general, ordered extinctions tended to result in residual communities with greater average tolerance. In the presence of interspecific interactions, compensation resulting from extinction transiently increased average tolerance, but continued extinction ultimately eroded the potential for communities to compensate in the presence of environmental change. Food web interactions decreased the predictability of extinction, because extinctions dynamically reshuffled species tolerances. Although initial extinctions can increase average community tolerance, ultimately extinctions decreased the potential for a community to exhibit density compensation.

3.2. Evidence for Compensation

Density compensation is both a community- and population-level phenomenon. Empirical studies often report small changes in the level of community density despite species loss or significant environmental degradation. The evidence for density compensation comes from a range of ecosystems and taxa. Early evidence, although consistent with the theory (Faeth 1984), was observational

and lacked clear experimental manipulations required to test the underlying processes (Wright 1980). Since then, field and laboratory manipulations have yielded more compelling examples of density compensation.

In the laboratory McGrady-Steed & Morin (2000) manipulated species richness in microbial food webs. They found that densities of nearly half of the species declined as species richness increased, suggesting community-wide density compensation across multiple trophic groups. Jiang (2007) also found support for density compensation as total biomass was unaffected by experimentally reduced species diversity. In an environmental warming experiment, Petchey et al. (1999) found that diverse communities retained more species than species-poor communities, suggesting that perhaps species-rich systems contained more tolerant species. In contrast, Fox & Morin (2001) found no evidence of compensation in simple two-species communities subjected to environmental warming.

A 30-year study of rodent dynamics by Brown and colleagues provided striking evidence of delayed colonization and compensation some 20 years after the experimental removal of three dominant kangaroo rat species. Ernest & Brown (2001a) reported that none of the resident species had been able to compensate for the removal of this keystone group. However, since 1995 the colonization of the plots by a pocket mouse species, *Chaetodipus baileyi*, has compensated for 66% of the annual energy used by the excluded kangaroo rats. These results suggest an important role for spatial dynamics in the strength and likelihood of compensation following species loss (Ernest et al. 2009).

The study of the impacts of environmental disturbance on stream invertebrate communities has revealed clear evidence of compensation. Hawkins et al. (2000) found that although disturbed sites differed from reference sites in the abundance of the taxa and composition of the communities, on average, little difference existed in total densities or in assemblage dominance diversity relationships. Overall, taxa that were rare (rank > 150) at reference sites tended to compensate for the declines in abundance taxa at disturbed sites. This result is significant because of the remarkable constancy in community properties across more than 200 taxonomic groups and 200 study sites.

Clear examples of compensation also arise from human-harvested assemblages, where declines in the abundance of target species can be (partially) offset by increases in the residual community (e.g., hunted primate assemblages; Peres & Dolman 2000). Dulvy et al. (2002) studied the changes in species composition of two apparently stable skate fisheries in the northeast Atlantic. Despite the extinction of two species, and significant declines in three large-bodied species, the increase in abundance and biomass of the smaller skate species resulted in temporal stability in aggregated catch data. The significant dietary overlap among species suggests the increase in abundance of the smaller species may be due to competitive release as the larger species declined.

4. GENERATING AND MAINTAINING COMPENSATORY DYNAMICS

4.1. Theoretical Models

According to theory, compensatory fluctuations may be induced endogenously by species interactions, externally by environmental forcing, or a by combination of both. The generation and maintenance of compensatory dynamics has been explained using neutral models of competition (Loreau & de Mazancourt 2008), Lotka-Volterra models with nonneutral symmetry (Ives et al. 1999, 2001; Loreau & de Mazancourt 2008), lottery models in variable environments (Chesson et al. 2001), and consumer-resource models (Armstrong & McGehee 1976, Chesson et al. 2001, Gonzalez & De Feo 2007, Lehman & Tilman 2000, McCann et al. 1998, Vandermeer 2006, Vasseur & Fox 2007). Many of these studies have simultaneously analyzed the effect of increasing diversity, and how it enhances community stability, by increasing the range of compensatory

responses to the environment within an assemblage (Chesson et al. 2001; Ives et al. 1999, 2001; Norberg et al. 2001)—an effect dubbed the insurance hypothesis (Yachi & Loreau 1999).

It is useful to classify theories addressing compensatory dynamics according to whether they belong to fluctuation-independent or fluctuation-dependent models of coexistence (*sensu* Chesson 2000), as opposed to neutral models where coexistence is unstable.

4.1.1. Fluctuation-independent models. Ives et al. (1999, 2001) and Loreau & de Mazancourt (2008) have applied the Lotka-Volterra framework to show that it is the range of species responses to environmental variation that is critical to maintaining compensatory dynamics and stabilizing community biomass. In these models (structurally similar to Equation 1) species coexistence is independent of the environmental fluctuations that are imposed upon the species dynamics. Coexistence occurs because of implicit species differences that ensure that intraspecific competition dominates over interspecific competition. The environment is not explicitly modeled, but differences between species in their response to the environment are introduced as additive random terms of small variance with a specific variance-covariance structure (the ε in Equation 1 are species specific). Perhaps the most important conclusion from these models is that “competition and species number have little influence on community-level variances; the variance in total community biomass depends only on how species respond to environmental fluctuations” (Ives et al. 1999). This result counters arguments that interspecific competition causes decreases in community-level variability by driving negative covariances between species abundances. These models show that negative covariances are counteracted by increased species-level variances created by interspecific competition. Competition only effects community stability through its effect on mean population abundance. Loreau & de Mazancourt (2008) emphasize that the long-term fluctuations in realized population dynamics may in fact be correlated and may mask the stabilizing compensatory responses of the various species to the environment.

4.1.2. Neutral models. Neutral models assuming strict equivalence of individuals within a stochastic community are forcing a reappraisal of a number of fundamental patterns and processes in community ecology. Loreau & de Mazancourt (2008) studied a neutral model of competition, based on stochastic population dynamics theory (Lande et al. 2003), to generate a neutral expectation for compensatory dynamics. Their model generalizes Hubbell’s (2001) because, whereas it maintains the zero-sum constraint on the changes in relative species abundance, it allows for fluctuations in total community size due to density dependency and exogenous environmental fluctuations. This feature is crucial to their counterintuitive findings. Most significantly, Loreau & de Mazancourt (2008) find that fluctuations in community size tend to correlate the fluctuations in absolute abundance, even though changes in relative species abundance are negatively correlated because of the zero-sum assumption; Hubbell’s model predicts negative covariances in both absolute and relative species abundance. Thus, if total community size is allowed to vary, the neutral expectation is positive covariation between species abundances, not statistical independence. One cannot, therefore, use positive correlations in species abundance as the sole means of rejecting compensatory dynamics in natural communities (Houlahan et al. 2007). Loreau & de Mazancourt (2008) further suggest analyzing covariation in per capita population growth rates as a means of evaluating the presence of compensatory dynamics, because it is more predictable than covariation in species abundance.

4.1.3. Fluctuation-dependent models. Compensatory dynamics are also common in models where population fluctuations are required for species coexistence. Population fluctuations may be

generated by species interactions with shared resources (endogeneous) or by external fluctuations in the environment (exogenous) that alter competitive dominance.

4.1.3.1. Endogenous compensatory cycles. Compensatory cycles, where species populations oscillate periodically, may arise endogenously by mechanisms of relative nonlinearity of competition for shared live resources (e.g., Abrams & Holt 2002, Armstrong & McGehee 1976). Coexistence of the two consumer species can occur when the species with a saturating growth response generates population cycles of the resource and has a lower resource requirement for zero population growth. Compensatory cycles can be generated in several ways (Abrams 2006): (a) by differences in growth parameters in the resources, (b) by differences in the birth and death rates of the consumers of specialist consumers, and (c) by competition between two resources, which can produce asynchrony in their consumers (McCann et al. 1998, Vandermeer 2006). Recent work (e.g., Abrams 2007, Abrams & Holt 2002, Vandermeer 2006) shows that persistent cycles can be achieved over a wide range of relative efficiencies of the interacting consumers, especially when adaptive prey switching behavior is included.

Endogenous cycles are also created in the presence of abiotic resources. Huisman & Weissing (1999, 2001) extended the mechanism of relative nonlinearity to show that plant competition for multiple limiting abiotic resources can generate coexistence with oscillating and complex compensating cycles. The key advance here is the multidimensionality of the resource environment. Although the theory is grounded in trait-based resource competition (Litchman & Klausmeier 2008), and has been frequently tested for two species competing for a single limiting resource (e.g., Descamps-Julien & Gonzalez 2005), remarkably little experimental work has been aimed at validating this mechanism for creating compensatory dynamics.

If endogenous compensatory cycles are widespread in nature, then they must be robust to the synchronizing effects of environmental stochasticity. Recently, Vasseur & Fox (2007) showed that stochastic environmental variability can disrupt phase-lagged consumer-resource oscillations. Stochastic variation created synchronous declines in resource density that reduced the amplitude of the top predator's cycles. It is important to note that this stabilizing effect was not due to a change in the phase of the resource cycles, but rather it was due to the disrupting effect of the environmental noise on their procession.

4.1.3.2. Exogenously driven compensatory fluctuations. The storage effect (Chesson 1994, 2000) explicitly evokes differential species' responses to environmental variation. The covariance between the effects of the environment and competition on the per capita growth rate of a population is stabilizing and creates strong compensatory population fluctuations between species through time. Chesson et al. (2001) show that compensatory fluctuations arising from the storage effect are strongly stabilizing at the ecosystem level. A mechanism that buffers population numbers when the environment is unfavorable for a species is essential to long-term persistence of the compensatory dynamics. This buffering effect may be achieved by dormancy (e.g., resting stages and seed banks) or immigration from source populations. Norberg et al. (2001) also show that environmental fluctuations can maintain diversity and that the long-term productivity of a diverse assemblage may be higher than the best single species system because compensatory dynamics allow it to better track environmental change.

Differences in the mode and tempo of compensatory cycles maintained by the storage effect depend upon the type of environmental fluctuations. Gonzalez & De Feo (2007) studied compensatory dynamics in a resource competition model in which the state of the environment determined the rate at which resources were consumed. The environment was modeled as a $1/f$ process (Halley 1996; see also Vasseur 2007). That is, the autocorrelation of the environmental

fluctuations was adjusted from none to highly autocorrelated over long timescales. Species had distinct environmental optima but competed for a single limiting resource. In temporally uncorrelated environments, compensatory dynamics were of small amplitude, and populations maintained a steady state far from zero. Increasing the dominance of low-frequency fluctuations increased the autocorrelation of the environment and led to outbreak compensatory dynamics (**Figure 2**). This result may help explain why the time series of compensatory species fluctuations cover a range of types from steady-state population dynamics of relatively small amplitude to outbreak dynamics typical of zooplankton (e.g., Little Rock Lake dynamics described by Frost et al. 1995, Keitt & Fischer 2006), small mammals (e.g., Fryxell et al. 1998), and annual plants (Adler & HilleRisLambers 2008).

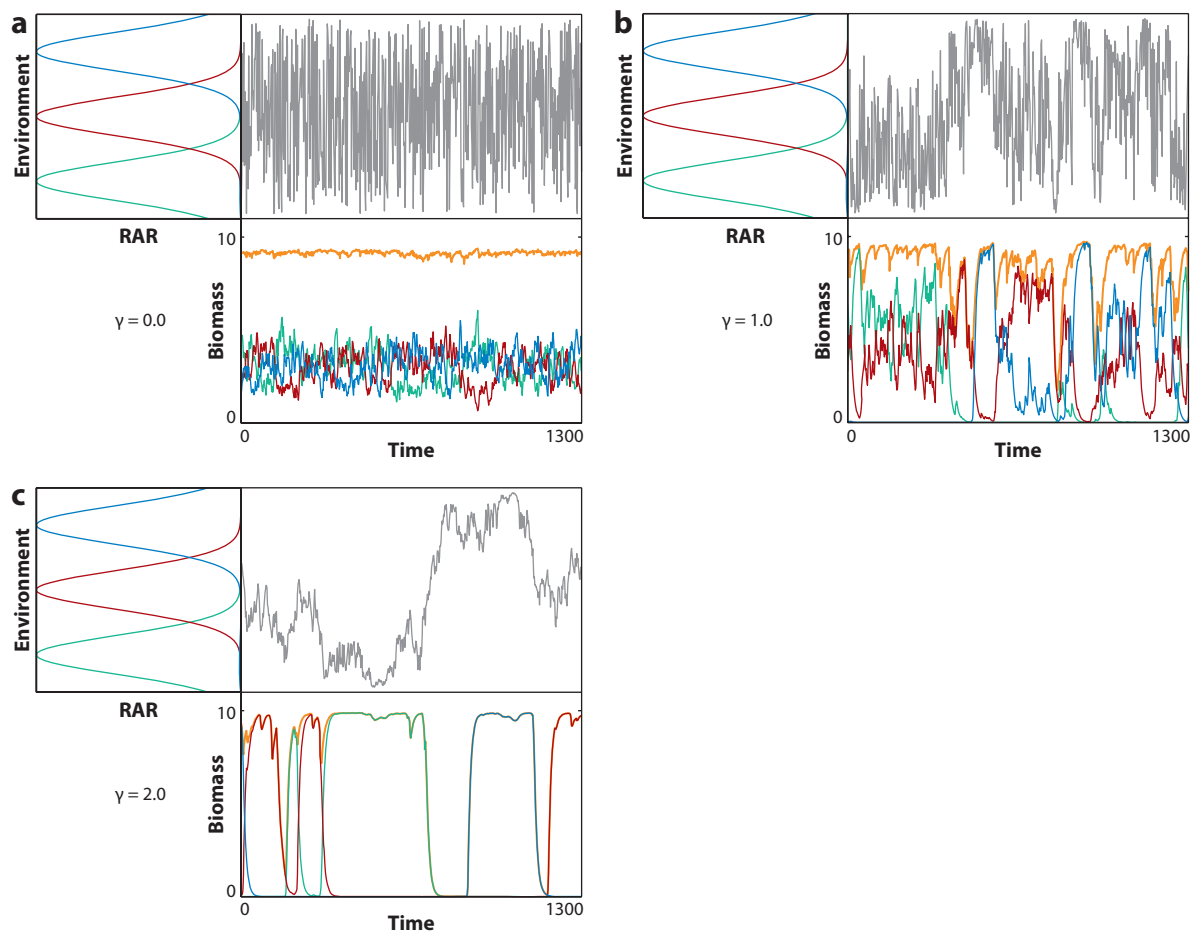


Figure 2

The effects of environmental autocorrelation on the form of compensatory dynamics. Environmental fluctuations are shown in gray (the variance was equal in each case over the duration of the simulation). To the left is shown the Gaussian-shaped environmental niche for the resource assimilation rate (RAR) of each species. Below, the colored lines show the fluctuations in species biomass; the orange line indicates the fluctuations in total community biomass. The three cases correspond to (a) no autocorrelation, (b) intermediate levels, and (c) high levels of autocorrelation in the environment. Note the change in the frequency and amplitude of the compensatory fluctuations with increasing autocorrelation (after Gonzalez & De Feo 2007).

4.2. Dispersal Maintains Compensatory Dynamics in Metacommunities

During environmental change, compensating species must increase from rare. Any factor that causes the local extinction of rare species will compromise ecosystem resistance to future environmental change. Dispersal and regional diversity may thus be important factors maintaining compensatory dynamics and ecosystem resistance at large spatial scales. Loreau et al. (2003) introduced the spatial insurance hypothesis to formalize the notion that dispersal contributes to ecosystem stability by maintaining compensatory dynamics. Using a source-sink metacommunity model, based upon resource competition within communities, they showed a unimodal relationship between dispersal rate and aggregate biomass stability. Intermediate levels of dispersal are required to minimize variation in aggregate biomass at local and regional scales; too little dispersal did not allow communities to maintain compensatory responses to environmental variation, whereas too much dispersal led to a well-mixed, species-poor system that contained the species best adapted to the average conditions and oscillated synchronously across the landscape through time. This model predicts that changing habitat connectivity may fundamentally alter the compensatory dynamics of communities at local and metacommunity scales (see also Leibold & Norberg 2004).

5. DETECTING COMPENSATORY DYNAMICS

5.1. A Broader View of Synchrony

Detecting compensatory dynamics in community time series is essential if we are to understand the resilience of ecological communities to environmental change. The current literature equates compensatory dynamics with summed negative covariances, and they are even used as a proxy for competition and community stability (e.g., Houlahan et al. 2007). Environmental variation (biotic and abiotic) is multidimensional and represents a mixed set of forces that will rarely directly translate the negative covariation in species responses to the environment into the realized multispecies dynamics. Environmental responses maintaining species out of phase may be countered by fluctuations in another dimension (e.g., drought caused by low rainfall or dynamics of a dominant competitor) that tend to bring species fluctuations into phase, that is, are synchronizing. If the latter dominates over the former, then compensatory dynamics will not be represented by negative covariances because of the correlated response of the entire assemblage, or functional group, to the stronger driving variable (Ripa & Ives 2007). Fortunately, even small differences in the phase of species fluctuations will have a stabilizing effect at the community level, with stability increasing with phase lag. Detecting the scales at which this occurs is an important challenge. Negative covariances in abundance (not just phase) likely occur at some temporal scale within a community time series, and perhaps only between a subset of the species, but they are only a part of a broader understanding of how compensatory dynamics are realized in multispecies data (Ranta et al. 2008). Recent developments in phase analysis (e.g., Cazelles & Stone 2003) and null models are enhancing our ability to detect the signature of out-of-phase species fluctuations; they also reduce our reliance on simple correlation statistics.

5.2. Quantitative Methods

Various quantitative approaches have been taken to reveal compensatory dynamics and to quantify their scale and importance as a stabilizing mechanism. These approaches can be broadly split into a statistical approach based on a variance-covariance decomposition of community dynamics (Frost et al. 1995, Fischer et al. 2001, Schluter 1984) and a frequency-analytic approach that uses Fourier

analysis (Vasseur et al. 2005, Vasseur & Gaedke 2007) or wavelet analysis (Keitt 2008, Keitt & Fischer 2006) to isolate scale-specific compensatory dynamics.

5.2.1. The variance ratio. This metric of compensatory dynamics is based on the ratio of the relationship between the variance of the aggregate variable [typically the sum of the component populations (C)] and the variances of the individual species populations (P_i),

$$VR = \frac{\text{var}(C)}{\sum_{i=1}^n \text{var}(P_i)}$$

where

$$C = \sum_{i=1}^n P_i$$

$$\text{var}(C) = \left[\sum_{i=1}^n \text{var}(P_i) \right] + \left[2 \sum_{i=1}^n \sum_{j=1}^{i-1} \text{cov}(P_i P_j) \right].$$

A variance ratio (VR) that is less than 1 indicates that the sum of covariances among species is negative. A VR greater than 1 occurs when the sum of covariances among species is positive, and indicates correlated dynamics among species. A VR equal to 1 is the null hypothesis and indicates that the sum of covariances is zero. This will hold when species fluctuations are statistically independent or, because the VR is a combined measure, when positive and negative covariances between subgroups of species cancel each other out.

The null hypothesis has been tested against the two alternatives—significant compensation or significant correlation—using randomization (e.g., Fischer et al. 2001, Vinebrooke et al. 2003). The statistical significance of the VR for a given multivariate time series is evaluated by creating a reference distribution by randomly shuffling the times series values for each species independently and recalculating the VR value. However, in addition to breaking any dependency between species fluctuations, this procedure also breaks the autocorrelation (serial dependency) structure of each population in the community time series. This creates a biased null model that can lead to spurious detection of compensatory dynamics, especially if the populations display moderate to strong autocorrelation (Inchausti & Halley 2002, Pimm & Redfearn 1988). Alternative time series bootstrapping methods are available (phase scrambling; e.g., Braun & Kulperger 1997), which make no assumption about the form of autocorrelation. Solow & Duplisea (2007) applied this test to multispecies fisheries data and showed that not accounting for temporal autocorrelation would have led to the incorrect conclusion of significant compensatory dynamics.

5.2.2. Frequency-based analyses. Simple statistics may fail to detect compensatory dynamics if they are timescale specific. For example, high-frequency compensatory dynamics (subannual) may be superimposed on correlated, perhaps sinusoidal, fluctuations operating at lower frequencies (annual or greater). This confounding effect can be addressed using frequency-based analyses in the form of Fourier and wavelet analysis.

5.2.2.1 Fourier analysis. Vasseur & Gaedke (2007) applied Fourier analysis to the Lake Constance data set to reveal compensatory dynamics among phytoplankton and crustacean communities at subannual scales, despite the presence of correlated dynamics at other temporal scales. This approach involves the comparison of the mean frequency spectrum of the component populations with the spectrum of the aggregate community. Compensatory dynamics at a given frequency are revealed by the loss of a peak in the community spectrum that is observable in the mean

population spectrum; negative correlation between two populations at a given frequency will mask the contribution of that frequency in the community spectrum.

To identify the temporal scales at which compensatory dynamics occur, they developed a metric analogous to the VR, the explained variance ratio (EVR),

$$EVR = \hat{S}_C(f) / \hat{S}_P(f),$$

which estimates the relative change in explained variance (S) at a given frequency (f) from the mean population spectrum to the community spectrum. EVR has a maximum value of 1 when population dynamics are perfectly correlated and a minimum value of 0 when population dynamics are perfectly compensatory. The framework developed by Vasseur & Gaedke (2007) has the great advantage of being able to deal with the timescale-specific structure of compensatory fluctuations.

5.2.2.2 Wavelet analysis. Wavelet analysis of community time series data has revealed additional aspects of compensatory dynamics (Keitt 2008, Keitt & Fischer 2006). Wavelet analysis is appropriate when time series are nonstationary and when the temporal structure of the time series displays distinct and abrupt discontinuities and sharp peaks through time. These properties are common in ecology, because communities often show nonlinear responses to experimental perturbations (e.g., acidification), and many temperate systems are characterized by outbreak population dynamics. The wavelet transform replaces the Fourier transform's sinusoidal waves by a set of translations and dilations of a window called a wavelet. Wavelet analysis thus creates a scale-time decomposition of the variance and covariance in a time series (Cazelles et al. 2008).

Keitt & Fischer (2006) and Keitt (2008) estimated the strength of compensatory dynamics in the Little Rock Lake zooplankton data set using the modulus ratio. The numerator of the modulus ratio quantifies aggregate biomass variation at a given time and scale, whereas the denominator captures individual species variation; the major difference from the EVR is that the modulus ratio is scale-time specific. Compensatory dynamics are revealed when the modulus ratio tends to 0, because aggregate variation is small relative to species variation, whereas with coherent species fluctuations, aggregate variation approaches the sum of species variation and the modulus ratio tends to 1. We discuss further results of these analyses below.

5.2.3. Other methods. Loreau & de Mazancourt (2008) introduce a new statistic of community-wide synchrony,

$$\varphi_P = \frac{\text{var}(C)}{\left(\sum_{i=1}^n \sqrt{\text{var}(P_i)}\right)^2},$$

where $\text{var}(C)$ is the variance of community size and $\text{var}(P_i)$ is the variance of individual species populations as above. The denominator is the maximum value of the variance of community size when all populations are perfectly correlated, so that this statistic is standardized between 0 (perfect asynchrony) and 1 (perfect synchrony). This versatile statistic can also be applied to measure the synchrony of species environmental responses, which is the key mechanism underlying the stabilization of aggregate community properties through compensatory dynamics (Loreau & de Mazancourt 2008).

Other time series analyses are available that offer alternative approaches to the VR and frequency-based analyses described above (Cazelles & Stone 2003). The VR does little to analyze the detailed trends of species in response to environmental change, whereas frequency-based analyses require long-term data sets and significant mastery of advanced methods. Two multivariate time series that might profitably be used to evaluate the presence of compensatory dynamics

in short, nonstationary time series are minimum/maximum autocorrelation factor analysis and dynamic factor analysis. These methods can extract and identify multiple common trends from time series to evaluate interactions between response variables and to determine the effects of environmental explanatory variables (Solow 1994; Zuur et al. 2003a,b).

5.2.4. Neutral models revisited. Ecological null models have only recently been applied to compensatory dynamics. (Keitt 2008, Loreau & de Mazancourt 2008, Vasseur & Gaedke 2007). It is generally assumed that the appropriate null model for the pattern of correlation in species fluctuation is statistical independence. Intuitively, this would seem appropriate because statistically independent fluctuations can have a stabilizing affect at the community level (Doak et al. 1998, Vlad et al. 2007), and we would like to know the additional stabilizing effect due to negative correlations between species. However, we know that such portfolio effects do not always result in greater community stability (Doak et al. 1998, Lhomme & Winkel 2002, Tilman et al. 1998, Vlad et al. 2007) and that the outcome depends upon important assumptions about how population variance scales with the mean, the heterogeneity in species productivity, and the correlation in species responses to the environment. More fundamentally, statistically independent fluctuations may already involve compensatory dynamics when community size varies under the joint effects of density dependency and environmental forcing. Therefore, Loreau & de Mazancourt (2008) argue that a properly parameterized neutral model provides the appropriate reference for establishing the significance of nonneutral (i.e., niche) causes of compensatory dynamics. To our knowledge, no neutral model has been parameterized with the aim of quantifying the importance of environmentally driven compensatory dynamics in natural or experimental communities.

6. EVIDENCE FOR COMPENSATORY DYNAMICS

Strong tests of compensatory dynamics require experimental press or pulse manipulation of a community (e.g., species richness) and/or environmental variables, appropriate reference systems and controls, and the measurement of multispecies dynamics. Analyses should also demonstrate aggregate variable stability, owing to countervailing growth responses to the environment.

6.1. Laboratory Studies

Aquatic microcosms are an ideal venue for experimental tests of compensatory dynamics, because of the rapid generation time of plankton species and the ease with which environmental conditions can be controlled.

Descamps-Julien & Gonzalez (2005) generated compensatory dynamics in an experimental test of the storage effect. Here, two diatom species competed for silica in the presence of oscillating temperature. Temperature variation at the right frequency created covariance between temperature and competition that allowed both species to increase when rare and their densities to track temperature change. The phase-lagged oscillations in this experiment are a clear example of compensatory dynamics.

McGrady-Steed & Morin (2000) showed a decline in the variability of total abundance within trophic groups (e.g., herbivores and predators), but they did not report an analysis of the species dynamics through time, so we cannot infer that compensatory dynamics increased with species richness. The absence of an environmental treatment indicates that this stabilizing effect was associated with the endogenous dynamics of the communities. Steiner et al. (2005) conducted a similar experiment and found that the stabilizing effect of increasing species richness was robust to increasing nutrient supply.

A few microcosm studies have combined a manipulation of the physical environment with manipulations of species richness and measured species covariances (Gonzalez & Descamps 2004, Petchey et al. 2002, Zhang & Zhang 2006). Petchey et al. (2002) found that increasing diversity destabilized total community biomass, and although environmental variability tended to decrease summed species covariances, overall the coefficient of variation (CV) of community biomass increased because of the destabilizing effects of increased population variability and strong heterogeneity in biomass across species. Gonzalez & Descamps (2004) found that autocorrelated stochastic temperature variability drove compensatory responses to temperature that significantly lowered summed species covariances when compared to constant temperature conditions. Zhang & Zhang (2006) manipulated nutrient availability and imposed a pulsed temperature drop. They observed compensatory growth among species due to the temperature drop only in the nutrient-poor treatment, whereas in the nutrient-rich environment community biomass was reduced because of the absence of compensatory dynamics. None of these microcosm studies adopted the more advanced methods of detecting compensatory dynamics discussed above, even though in some cases the data are amenable to these tests.

6.2. Field Studies

Field evidence arises from two classes of study: field-based mesocosm experiments and long-term field surveys in the presence or absence of large-scale manipulations of a stressor (e.g., pH).

6.2.1. Mesocosm studies. Klug et al. (2000) manipulated pH in an in-lake microcosm experiment, which imposed both a short-term pulse and pH perturbation. The plankton assemblages responded to pH treatment (e.g., reduced biomass), and compensatory dynamics were observed among phytoplankton functional groups and within the large herbivore functional group. Autoregressive models fitted to the time series data suggested that the strongest compensatory dynamics (lowest VRs) occurred when two taxa interacted and at least one of the taxa was directly affected by the pH perturbation. Furthermore, compensatory dynamics among phytoplankton groups (diatoms and chlorophytes) led to increased primary production in the acidified treatments relative to the control. In contrast, compensatory dynamics within large herbivores resulted in only partial compensation of large herbivore biomass.

Downing et al. (2008) report the results from an experiment with seminatural pond communities that clearly reveal compensatory dynamics in the multispecies time series. A nutrient (N and P) pulse perturbation was applied at different periodicities. They used the VR in combination with a wavelet decomposition of the time series to reveal that compensatory dynamics ($VR < 1$) occurred within the zooplankton community at the 60-day period in the pulsed-nutrient communities (all three groups combined), whereas constant nutrient communities exhibited $VR \approx 2$. Compensatory oscillations at this scale do not correspond to the intrinsic periodicity (20 days) typical of zooplankton-phytoplankton interactions, but were perhaps due to the dynamical outcome of more complex trophic interactions. Pulsed-nutrient communities were correlated ($VR > 1$) at shorter timescales, corresponding to the periodicity of the nutrient pulses (10–20 days).

6.2.2. Lake manipulations. Whole-lake manipulation experiments have been used to study the resistance of lake ecosystems to environmental stress (Schindler 1990). A series of studies of the Little Rock Lake zooplankton time series have revealed a mixture of correlated and compensatory responses to acidification over the past 20 years (Fischer et al. 2001, Frost et al. 1995, Keitt 2008, Keitt & Fischer 2006). In particular, these papers have applied increasingly sophisticated

techniques to detect compensatory dynamics, from the VR to multivariate autoregressive models, and most recently wavelet analyses. Frost et al. (1995) and Fischer et al. (2001) employed the VR to reveal that within zooplankton functional groups (copepods and cladocerans) some species pairs show correlated dynamics in the reference basin, and yet show negative correlations in response to a drop in pH. Interestingly, neither compensatory nor correlated dynamics are found at the scale of the entire zooplankton community, suggesting that aggregations of functionally disparate groups can mask compensation and correlation occurring at lower levels of aggregation (e.g., functional groups).

Keitt & Fischer (2006) applied wavelet analysis to reveal that herbivorous cladocerans shifted to strong negative correlations at the 4- to 7-year scale. By studying the timescales of covariance between different specific species pairs, they were able to detect the scale at which shifts to compensatory dynamics in response to acidification occurred. Keitt (2008) used the modulus ratio to detect compensatory dynamics in multiple species. Although compensatory dynamics occurred in the reference basin at the scale of 2 years, the near loss of acid-sensitive, winter-dominant copepod species in the acid-treated basin created inflated seasonal variability and the appearance of correlated dynamics at the annual timescale. These results reveal that changes in species covariation occur at multiple timescales and are unpredictable from reference basin data, and that species loss due to long-term environmental change can diminish the response diversity required to buffer strong seasonal variation in temperate lakes.

Vinebrooke et al. (2003) studied acidification in a boreal lake (302S), but also included the responses of phytoplankton and fish assemblages in their analyses. They also used the VR to detect compensatory dynamics. Their study suggests that functional group diversity is critical for maintaining buffered responses to acidification. In particular, species-rich groups such as phytoplankton and rotifers exhibited compensatory dynamics (VR ratios < 1) in response to acidification and correlated dynamics (VR values > 1) in a neighboring reference lake. Relatively species-poor cladoceran, copepod, and fish assemblages all lost species, showed VR values ≈ 1 , and exhibited declines in total biomass. The researchers conclude that compensatory species dynamics are apparent in species-rich groups of fast-growing and widely dispersing organisms (e.g., phytoplankton), but that higher trophic ranks are unable to compensate for long-term environmental stress because they maintain lower levels of species diversity.

6.2.3. Grassland studies. The hypothesis that community stability arises from compensatory fluctuations between species received strong support from studies of plant productivity in the face of nutrient additions and herbivory (Hurd et al. 1971, McNaughton 1977). More recent research has confirmed that population fluctuations in grasslands tend to be compensatory and stabilizing (Bai et al. 2004, Tilman et al. 2006).

Tilman (1996) reported that compensatory dynamics in response to drought were more likely in species-rich plots. Whereas a number of confounding factors were identified (Huston 1997), these results were consistent with theory indicating that diversity should enhance ecosystem resistance. Tilman et al. (2006) provide clearer evidence that negative correlations in species fluctuations contribute to community stability across 207 Minnesota grassland plots in which diversity was manipulated experimentally.

Bai et al. (2004) report evidence that species compensatory fluctuations in response to climate fluctuations can lead to greater aggregate stability at both the level of functional groups and total community biomass. Their analysis of 24-year time series data from grassland in Inner Mongolia revealed that that January–July precipitation is the primary climatic factor causing compensatory fluctuations in the biomass production of perennial rhizomes, perennial bunchgrasses, and perennial forbs.

6.3. Analysis of Field Surveys

Houlahan et al. (2007) conducted the most extensive review of compensatory dynamics to date. Their motivation was to test the zero-sum assumption of Hubbell's neutral model, which predicts negative covariances between species on average. The authors report an analysis of 41 different plant and animal data sets using the VR to identify the prevalence of compensatory dynamics. Thirty-one of the data sets had VR values greater than zero; unfortunately, no null hypothesis was used to assert whether any of the observed VR values were larger or smaller than is expected by chance. On the basis of this evidence, Houlahan et al. (2007) concluded that positive covariances are far more common than negative covariances and that this suggests that the evidence for compensatory dynamics and competition playing a major role in the dynamics of communities is very weak compared with other driving factors (perhaps abiotic) that entrain correlated responses in most species.

The evidence covered in this review suggests that these conclusions may be premature. For example, the Portal data sets used in their study did not include small mammals, yet this is one of the very best examples of competition structuring compensatory dynamics (Ernest & Brown 2001a,b; Ernest et al. 2009). Other studies of lake time series data (Vasseur et al. 2005) have revealed that compensatory dynamics exist at various scales and that only scale-resolving methods can detect them. It would also be useful to introduce a fuller range of temporal and spatial scales by including large lake plankton data sets (e.g., Rusak et al. 2002) and paleo data sets. More critically, recent advances in neutral models of competition, which incorporate fluctuations in community size, reveal that positive covariances in abundance can be entirely consistent with compensatory dynamics (Loreau & de Mazancourt 2008). Alternative statistical analyses are required to successfully infer interaction sign and strength from time series data (Ripa & Ives 2003, 2007). As reviewed above, a battery of sophisticated analytical and statistical techniques can be used to reexamine the patterns of covariance in these data sets. Detecting compensatory dynamics is a challenge that we are now equipped to deal with.

SUMMARY POINTS

1. Theory suggests that compensation and compensatory dynamics are an important component of community stability. It is the diversity of responses to environmental change that enhances the capacity of a community to buffer environmental change.
2. Although compensation is relatively easy to detect, the prevalence of compensatory dynamics in nature is uncertain and contingent upon how we measure them.
3. Traditional approaches to compensatory dynamics are based on an equilibrium view of the world that assumes environmental constancy and zero-sum constraints. Although some aspects of communities and ecosystems can be approximated by such a view, a nonequilibrium hierarchical view of ecological variability is required to fully comprehend how compensatory dynamics reduce the variability of community properties compared with that of component species.
4. Advances in quantitative analysis suggest an integrated theoretical-empirical framework for compensation and compensatory dynamics is within reach. This is an urgent requirement, as ongoing environmental change and population extinction may be compromising the compensatory capacity of many natural communities.

FUTURE ISSUES

1. A closer integration of experimental and quantitative methods would refine our ability to detect compensation and compensatory dynamics.
2. Theory and experiments are needed to address whether communities can compensate in the face of multiple stressors (Vinebrooke et al. 2004).
3. Spatio-temporal compensatory dynamics are relatively unstudied, and progress can be made within a metacommunity framework.
4. We know little about the role of contemporary evolution in compensatory dynamics. This could be addressed with eco-evolutionary models of community dynamics.

DISCLOSURE STATEMENT

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Errata

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