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Science **317**, 58 (2007);
DOI: 10.1126/science.1133258

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Stability and Diversity of Ecosystems

Anthony R. Ives¹ and Stephen R. Carpenter²

Understanding the relationship between diversity and stability requires a knowledge of how species interact with each other and how each is affected by the environment. The relationship is also complex, because the concept of stability is multifaceted; different types of stability describing different properties of ecosystems lead to multiple diversity-stability relationships. A growing number of empirical studies demonstrate positive diversity-stability relationships. These studies, however, have emphasized only a few types of stability, and they rarely uncover the mechanisms responsible for stability. Because anthropogenic changes often affect stability and diversity simultaneously, diversity-stability relationships cannot be understood outside the context of the environmental drivers affecting both. This shifts attention away from diversity-stability relationships toward the multiple factors, including diversity, that dictate the stability of ecosystems.

Stability has a rich history in ecology. Theoretical research has explored how numerous features of ecosystems affect stability, including diversity (number of species), the strength of interactions among species, the topology of food webs, and the sensitivities of species to different types of environmental perturbations. Empirical studies have generally focused more specifically on diversity, particularly in the past 15 years. This is because diversity is easier to measure and manipulate than other features of natural ecosystems, and because such research is relevant to the debate about the worldwide loss of biodiversity (1, 2).

Historically, the relationship between diversity and stability has been contentious. Different theoretical results contradicted each other, empirical results were inconsistent, and theoreticians and empiricists often disagreed. Although the storm has begun to subside, we fear that ecologists risk becoming complacent about the diversity-stability debate. Are we asking the right questions about diversity and stability? Are we asking them in the right way? Our goal here is not so much to answer these questions as to show that they still need to be asked.

Concepts of Stability

A fundamental problem in this context is that stability can have many different definitions (3–5), and each definition gives a different diversity-stability relationship. Different theoretical concepts of stability apply, depending on the type of inherent dynamics exhibited by a system and the type of perturbation the system experiences. Here, we give an overview of some types of stability (6). We focus on concepts of stability that involve some integrated measure of the entire ecosystem, such as the summed density of

all species, rather than species-level measures; these are not generally independent, but neither are they completely inseparable (7).

Systems may have alternative stable states (Fig. 1A), in which the final densities of species, or even the persistence of species, depend on their initial densities (8–10). For example, Scheffer *et al.* (11) showed that shallow Dutch lakes can occur in either a clear-water state dominated by green algae or a turbid-water state dominated by blue-green algae; once blue-green algae get established, they shade and thereby repel green algae, creating a self-perpetuating stable state. For systems with alternative stable states, one concept of stability depends on the number of alternative stable states: More stable systems are those with fewer stable states. Another concept of stability, Holling's resilience (9), describes the ease with which systems can switch between alternative stable states, with more stable systems having higher barriers to switching.

Owing to interactions among species, systems might fluctuate even in the absence of environmental perturbations (Fig. 1B). The resulting population dynamics are governed by "attractors" that can themselves be stable and hence regular (periodic), or can be unstable (chaotic) (12, 13). The most familiar nonpoint attractor is a predator-prey stable limit cycle, in which the strong interactions between prey and predator generate perpetually oscillating densities (14). One measure of the stability of systems with nonpoint attractors is whether the attractor is chaotic. Another concept of stability that applies to either chaotic or nonchaotic systems depends on the amplitude of fluctuations, with more stable systems having lower-amplitude fluctuations of some aggregate measure of the system.

If the system has a single, stable equilibrium point, species densities will not fluctuate in the absence of environmental perturbations. Nonetheless, environmental perturbations may occur in the form of pulses or shocks that change species densities (Fig. 1C). If these pulse

perturbations occur rarely, stability can be measured by the rate at which the system returns to equilibrium (15). If shocks occur frequently and stochastically, the impact of these shocks depends on community resistance (5), which can be measured by the variability in the change in combined densities, from one time point to the next, caused by repeated shocks. These two concepts of stability—the rate of return to equilibrium, and the change in combined densities in response to repeated shocks—together determine a third measure of stability: the overall system variability. For example, a more resistant system is knocked less by environmental shocks, and rapid return rates pull the system more quickly toward its equilibrium, both of which lead to lower overall community variability (16).

In addition to shocks, environmental perturbations may also cause permanent, "press" changes in demographic characteristics of species (17), such as decreasing intrinsic rates of increase. For example, Frost *et al.* (18) divided a lake with an impermeable membrane and then acidified one half, showing how the direct effect of acidification on planktonic species, and the interactions among them, changed the structure of the community. Press perturbations may change not only the equilibrium (19) but also, when severe enough, the dynamics around equilibrium (20) (Fig. 1D). A more stable system might be one whose combined species densities at equilibrium change more slowly when subjected to a press perturbation, or one that can sustain greater press perturbations before the dynamics undergo a qualitative change (e.g., one species goes extinct, or a point equilibrium bifurcates into a cyclic attractor).

Perturbations might also include the extinction of species (Fig. 1E) or the invasion of new species (Fig. 1F). When an extinction occurs, stability could be measured by the number of other species that go secondarily extinct, or by the compensatory change in combined densities of all species (21–23). When invasions occur, stability could be measured as the chance that an invader is successful, or the number of secondary extinctions it causes if it is successful (24).

This collection of stability concepts sets an empirical challenge. Before designing an empirical study, it is necessary to know enough about the dynamics of an ecosystem and the environmental perturbations that impinge upon it to select appropriate definitions of stability; there will often be several appropriate definitions. These concepts also identify key features—we will refer to them as mechanisms—that together dictate stability. These mechanisms involve the strength of interactions among species, the mode in which species interact (whether they are competitors, predators, mutualists, etc.) that gives the food-web topology, and the ways in which species experience different types of environmental perturbations. Because both species interactions and environmental perturbations can

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drive fluctuations in species densities, these must be sorted out and quantified to understand their mechanistic roles in diversity-stability relationships.

Review of Empirical Studies

We performed a survey of 52 studies giving 64 diversity-stability relationships (table S1); 48 of the 52 were published since 1990, reflecting the burgeoning interest in empirical tests of such relationships. Of the 52 studies, 37 directly manipulated diversity; the remaining 15 either used indirect manipulations of diversity or intentionally selected systems that differed in diversity. The most common definitions of stability were invasibility, variability, resistance, and return rates, making up 59 of 64 relationships; of these 59, the authors reported positive relationships in 41 cases (69%) and negative relationships in only 8 cases (14%), with no or ambiguous relationships for the remainder (table S2). Positive relationships were most commonly reported for studies on the success of invasive species (85%). Of the 18 studies measuring community variability, 72% showed positive relationships, consistent with the “consensus” view that greater diversity leads to less variable communities (25). Nonetheless, empirical studies have focused on only a subset of possible definitions of stability; more than half of the commonly used theoretical definitions have not been investigated experimentally to determine the role of diversity (table S2).

A striking feature of the studies is how heterogeneous they are. Thirty-three studies investigated grassland or herbaceous plant communities, 9 investigated microbial communities, and 10 investigated other types of ecosystems. Forty-one studies included measurements on only a single trophic level; the remainder measured multiple trophic levels or included measurements that integrated over three or more trophic levels, such as microbial studies measuring CO₂ production. With this heterogeneous mix, it would be incautious to perform a meta-analysis to try to derive broad conclusions about diversity-stability relationships.

Another striking feature of the studies is how few rigorously investigate the mechanisms—species-species interactions, food-web topology, and the sensitivities of species to environmental perturbations—underlying reported diversity-

stability relationships. Exceptions are some studies on invasibility. For example, Stachowicz *et al.* (26) showed that more-diverse intertidal communities leave less rocky surface exposed, thereby inhibiting invasive species, and Duker (27) obtained a similar result for grassland communities; these studies thus show the role of species interactions in determining invasibility. Understanding the mechanisms underlying other types of stability is more difficult, especially those involving population dynamics (e.g., return rates and community variability). However, if the

mechanisms underlying diversity-stability relationships are not identified, it is unclear whether an observed diversity-stability relationship can be generalized to any other system.

Our understanding of such mechanisms can be aided by statistically tying data to theoretical models. Although all empirical studies qualitatively compare their results to theory, too often mismatches between experiment and theory made it impossible for us to assess the experiments in the context of theoretical predictions (fig. S1). If we wish to assess empirical results in

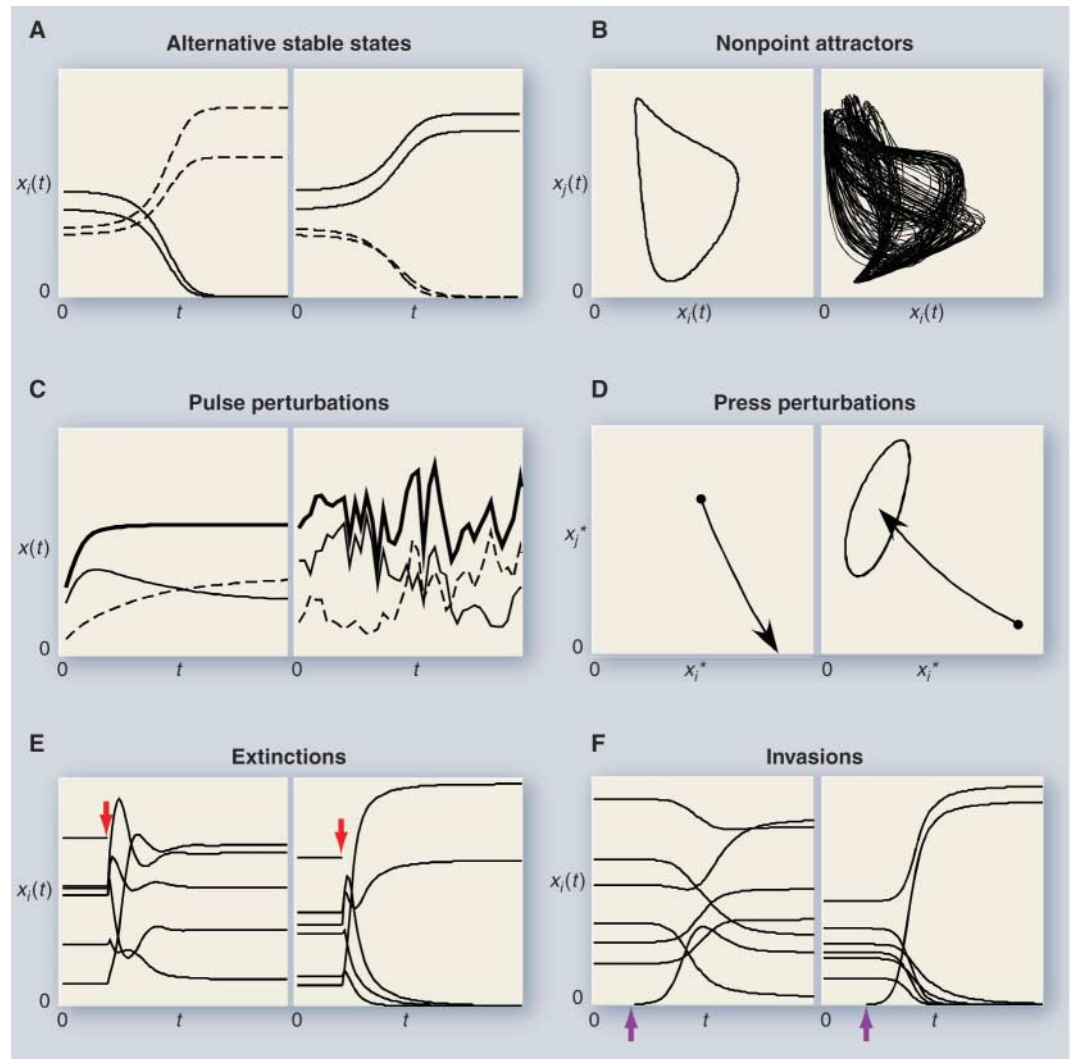


Fig. 1. Different types of stability, depending on the inherent dynamics of a system and the type of perturbation it experiences. **(A)** Alternative stable states, in which the initial densities of four species determine which species persist; pairs of alternatively persisting or nonpersisting species are shown with solid and dashed lines, respectively. **(B)** Nonpoint equilibria, illustrated by a stable and a chaotic attractor. **(C)** Pulse perturbations to systems with a stable equilibrium. The left panel shows the dynamics of a two-species system after a single pulse perturbation, with species densities shown by light and dashed lines, and combined densities shown by the heavy line. The right panel gives the same system with repeated (stochastic) pulse perturbations. **(D)** Press perturbations to systems with a stable equilibrium. The arrows trace the equilibrium densities of species *i* and *j* in a six-species ecosystem as the environment degrades (intrinsic rates of increase decline for all species). In the left panel, the equilibrium point collides with the unstable point at which species *j* goes extinct; in the right panel, the equilibrium point bifurcates into a stable nonpoint attractor. **(E)** Response of ecosystems to extinctions of the most common species (extinction marked by arrow). In the left panel, no other species went extinct; in the right panel, three additional species went extinct. **(F)** Response of ecosystems to invasion (invasion marked by arrow). In the left panel, the invading species persisted with the original six species; in the right panel, five of the original species went extinct. See fig. S2 for details.

the light of theory, it is not sufficient for theory to predict correctly whether the diversity-stability relationship is positive or negative; models could give the right prediction for the wrong reasons. Instead, theoretical models must be judged by their ability to capture the entire dynamics of the empirical system. For example, for a study focusing on stability measured by community variability, the test of the model is its ability to fit the dynamics of all species in the community in a statistically rigorous way. The process of model fitting requires the explicit identification and quantification of species interactions, as well as the response of individual species to environmental perturbations (16, 20).

We know of no study on diversity and stability that explicitly fits a mechanistic model to data. But if we drop the requirement that the study focus on diversity, there are numerous studies on stability that fit models to data. For example, Wootton (28) tested the ability of a Markov chain model to predict the consequences of species extinctions on the densities of species remaining in intertidal communities; the success of this model relied on its ability to quantify the key interactions among species. As another example, Klug *et al.* (29) measured the responses of freshwater plankton to pulsed and press decreases in pH, determining both the sensitivity of species to the perturbation and how species-species interactions propagated the perturbation through the food web. Although these studies do not reveal the role of diversity, they suggest how the systems might change if different species were lost.

Review of Theory

There is a vast theoretical literature that is relevant to the relationship between diversity and stability (6). To order this literature, we used a single, simple model (Fig. 2). The use of a single model emphasizes that the same system may exhibit numerous diversity-stability relationships arising from different definitions of stability. It also shows that the same mechanisms can lead to different diversity-stability relationships. Our model considers only competitive interactions (one trophic level), although a version with two trophic levels (fig. S2) gives many similar relationships. Although this exercise is exactly the type of theory that is not useful for understanding real data from real systems, it is nonetheless valuable to hone our intuition and catalog numerous possible diversity-stability relationships.

Of 13 diversity-stability relationships that we computed for 13 definitions of stability, four were positive, six negative, and three nearly zero (Fig. 2, A to F). Furthermore, species-rich systems were more likely to show a greater range of diversity-stability relationships; the prevalence of systems with alternative stable states and nonpoint attractors increased with diversity (Fig. 2G). The patterns exhibited by the simple model are generally consistent with the broader theoretical literature (6), although some diversity-

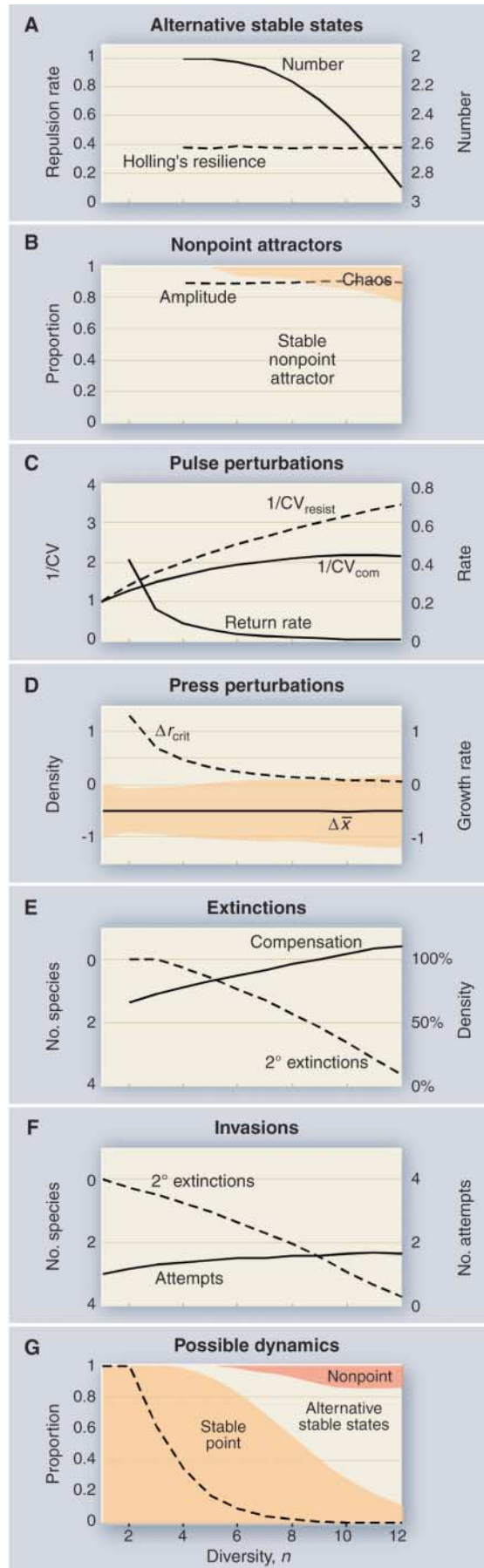


Fig. 2. Stability of randomly constructed competitive communities versus diversity n , portrayed so that positive diversity-stability relationships have positive slopes. (A) For systems with alternative stable states, the average number of stable states and Holling’s resilience, measured by the rate at which population densities are repelled from the unstable stationary point between stable states. (B) For systems with nonpoint attractors, the prevalence of cyclic (white region) versus chaotic (orange region) attractors, and the amplitude of fluctuations in combined species densities, measured by the minimum density divided by the maximum density (dashed line). (C) For systems with stable equilibria, the characteristic return rate, $1/CV_{resist}$ and $1/CV_{com}$, where CV_{resist} is the coefficient of variation in the change in abundance between samples, and CV_{com} is the coefficient of variation of the community density through time. (D) The change in mean combined densities, $\Delta\bar{x}$ (with 95% inclusion bounds given by the orange region), when all species experience a press perturbation that decreases intrinsic rates of increase. Δr_{crit} measures the magnitude of the press perturbation before the stable equilibrium bifurcates, creating either a cyclic nonpoint attractor or an attractor with one species extinct. (E) For systems with a stable equilibrium, the numbers of secondary (2°) extinctions caused by removing the most common species, and compensation (calculated as the increase in combined abundances of surviving species immediately after extinction relative to the abundance of the species that went extinct). (F) For systems with a stable equilibrium, the number of attempts before an introduced species successfully invaded, and the numbers of secondary extinctions caused by the invader. (G) For randomly constructed communities, prevalence of stable points, alternative stable states, and nonstationary attractors. The dashed line gives the proportion of randomly constructed communities that were feasible (i.e., had an equilibrium point with positive densities of all species), which is a requirement for the three types of dynamics. For each level of diversity n , 10,000 random communities were constructed. See fig. S2 for details.

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stability relationships have not received sufficient attention to make general theoretical predictions with any confidence (table S2). Also, we caution that these patterns represent the averages of 10,000 randomly constructed communities; for any given model community, the diversity-stability pattern might differ (e.g., Fig. 2D).

Despite this picture of complexity, there are some generalities. For definitions of stability involving dynamics, species-species interactions (competition) tend to create negative diversity-stability relationships. Specifically, species-species interactions underlie the existence of alternative stable states (Fig. 2A) and nonpoint attractors (Fig. 2B). Similarly, species-species interactions cause the decrease in return rates with increasing diversity (Fig. 2C). Conversely, species-environment interactions underlie the positive diversity-stability relationship for resistance, $1/CV_{\text{resist}}$, when species respond differently to environmental variation, the variation in their combined, ecosystem-level response decreases with increasing diversity n , because the decreases in abundance of some species are counterbalanced by increases in others. In the parameterization of the model used for Fig. 2, the effect of species-environment interactions to increase community resistance dominates that of species-species interactions to decrease return rates, causing a positive diversity-stability relationship when stability is measured in terms of variability, $1/CV_{\text{com}}$. Nonetheless, the destabilizing effect of species-species interactions is seen in the decrease in $1/CV_{\text{com}}$ relative to $1/CV_{\text{resist}}$; in the absence of competition, these two measures would be the same.

Rather than generalities, the model more successfully reveals complications. For example, two measures of stability in response to the same perturbation can show opposite diversity-stability relationships. This is seen for perturbations caused by extinctions: After extinctions, species-rich communities are more likely to suffer secondary extinctions (negative diversity-stability relationship) yet also show greater compensation (positive relationship). In the model, compensation is so strong that despite secondary extinctions, combined species abundances on average increase when the most common species goes extinct from ecosystems with 12 species. Similarly, species-rich communities are more likely to repel invaders (positive diversity-stability relationship), yet if the invader is successful it is likely to cause more secondary extinctions (negative relationship).

As another complication, the same mechanism can have different effects. For example, competition generally destabilizes dynamics, increasing the likelihood of alternative stable states and nonpoint attractors, and decreasing return rates to a stable equilibrium point. Nonetheless, for definitions of stability not involving dynamics, competition is not destabilizing. For press perturbations (Fig. 2D), the average decrease in abundance is 0.5, the same as would occur if

there were no competition. For compensation after extinctions, competition is stabilizing, because in the absence of competition, no compensation would occur. In these examples, competition is destabilizing, neutral, and stabilizing, respectively. These complications underscore the need to understand the mechanisms underlying diversity-stability relationships.

Finally, we return to the empirical studies and compare them with the broad theoretical patterns. Of the four types of stability most heavily represented (59 of 64 relationships), two (invasibility and resistance) generally give theoretical diversity-stability relationships that are positive, and a third (variability) will give a positive relationship when the effect of diversity on resistance is large; together, these make up 50 of 64 relationships. This suggests that the preponderance of empirical studies showing positive relationships (43 of 64, table S2) do so because they use definitions of stability that are likely to show positive relationships. Nonetheless, theory generally predicts negative diversity-stability relationships for stability measured as return rates, yet eight of the nine empirical studies that used this measure reported a positive or no relationship (table S2). Given the frequent mismatches between empirical studies and theory, we think it is difficult to draw any strong conclusions from the empirical studies. This reemphasizes the need to statistically fit models to data.

Which Diversity-Stability Relationships?

With the many definitions of stability, we must ask which definitions are most relevant for applied problems surrounding the loss of biodiversity. The pressing questions of applied ecology involve human drivers, including climate change, nutrient input, toxins, invasive species, overexploitation of biological resources, and land use change (30). These drivers may interact; for example, climate change and species interactions have altered fire regimes in Alaskan boreal forest, thereby altering the dynamics of the spatial mosaic of land cover (31). Furthermore, many changes are occurring at broad spatial scales across a landscape that is increasingly divided into small, relatively homogeneous fragments greatly different from the former, contiguous whole (30).

All of the definitions of stability we have described are relevant to at least several applied problems (table S3). Nonetheless, stability in the face of press perturbations is often central, because many human drivers change hydrology, biogeochemical inputs, or habitat characteristics that alter population growth rates, biotic interactions, biomass production, and numerous other processes that affect how an ecosystem functions. Some of these press perturbations will lead to ecological surprises as a result of unexpectedly extensive or irreversible changes in some processes or in ecosystem structure (32). The Millennium Ecosystem Assessment (30) concluded that “there is established but incomplete evidence

that changes being made in ecosystems are increasing the likelihood of nonlinear changes (including accelerating, abrupt, and potentially irreversible changes) with important consequences for human well-being” (p. 11).

Increasing the relevance of empirical studies for applied problems argues for increasing the range of definitions of stability. It also highlights the interactions among multiple factors affecting stability. In much of the literature on diversity and stability, diversity is treated as an independent variable, with experiments designed to test for the effects of diversity “per se” by selecting species randomly from a species pool. However, diversity is unlikely to change in isolation from other drivers affecting ecosystem stability, and in fact these other drivers will likely be the main causes of loss of diversity. For example, land use change has a direct effect on ecosystem production, respiration, and carbon storage but also changes the diversity of plants and consumers, leading to further changes in carbon budgets (33). Thus, diversity is not a primary driver, but it might be a secondary driver. A key consideration is that if anthropogenic change decreases diversity, it will likely do so in a nonrandom way, as specific species are encouraged or eliminated by human action. In this case, the effects of loss of diversity cannot be disentangled from the effects of changing species composition (34), making the secondary effect of diversity on production understandable only in the context of the primary driver changing the ecosystem.

Recommendations

The relationship between diversity and stability has interested ecologists since the inception of the discipline (35), and the absence of a resolution reflects the complexity of the problem. Much of the complexity derives from the multiplicity of diversity-stability relationships, depending on the definitions of diversity and stability and on the context in which an ecosystem is perturbed. We cannot expect a general conclusion about the diversity-stability relationship, and simply increasing the number of studies on different ecosystems will not generate one.

Rather than search for generalities in patterns of diversity-stability relationships, we recommend investigating mechanisms. A given diversity-stability relationship may be driven by multiple mechanisms, and the same mechanisms may evoke different diversity-stability relationships depending on the definitions of diversity and stability. We need more studies revealing exactly what these mechanisms are. This requires models joined to empirical studies that can reproduce, in a statistically robust way, not only a diversity-stability relationship but also the dynamics exhibited by a system.

Several definitions of stability—in particular, stability against press perturbations—have received relatively little attention. Nonetheless, these definitions of stability are key to understanding emerging global challenges. Diversity is

rarely a primary driver of stability but is instead a secondary driver, itself subject to the same anthropogenic drivers affecting stability (36, 37). Although this does not diminish the importance of understanding the effect of diversity loss, it means that the consequences of diversity loss for stability can only be understood in the context of other environmental change. Thus, rather than studying diversity-stability relationships, it will be more profitable to study stability comprehensively, including diversity as only one of the possible factors that affect ecosystem responses to environmental change.

Finally, a finding common to many empirical studies is that the presence of one or a handful of species, rather than the overall diversity of an ecosystem, is often the determinant of stability against different perturbations. We suspect that, depending on the types of stability and perturbation, different species may play key roles. Predicting which species, however, is unlikely to be aided by general theory or surveys of empirical studies; each ecosystem might have to be studied on a case-by-case basis. In the face of this uncertainty and our ignorance of what the future might bring, the safest policy is to preserve as much diversity as possible.

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SOM Text

Figs. S1 and S2

Tables S1 to S3

10.1126/science.1133258