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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 CO_2 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

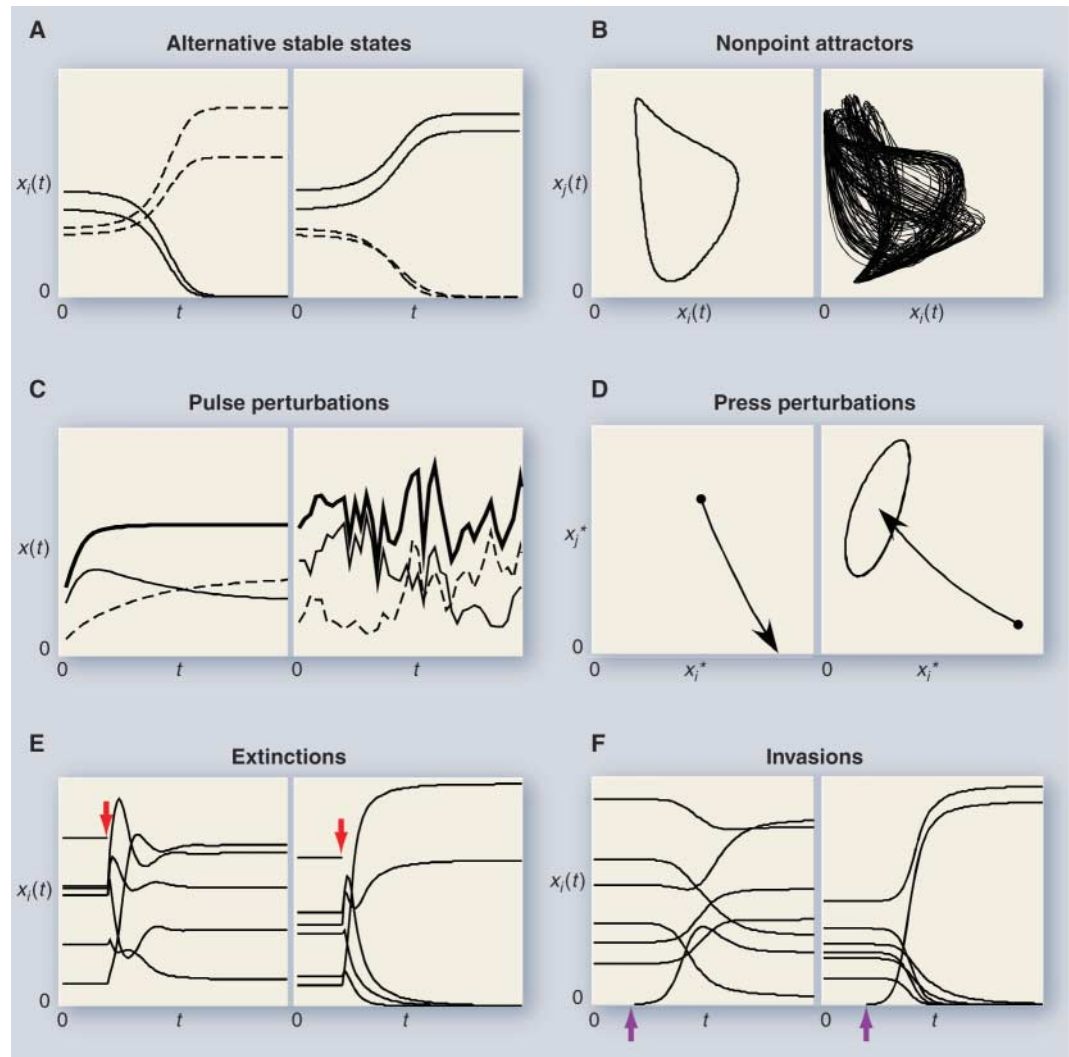


Fig. 1. Different types of stability, depending on the inherent dynamics of a system and the type of perturbation it experiences. **(A)** Alternative stable states, in which the initial densities of four species determine which species persist; pairs of alternatively persisting or nonpersisting species 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-

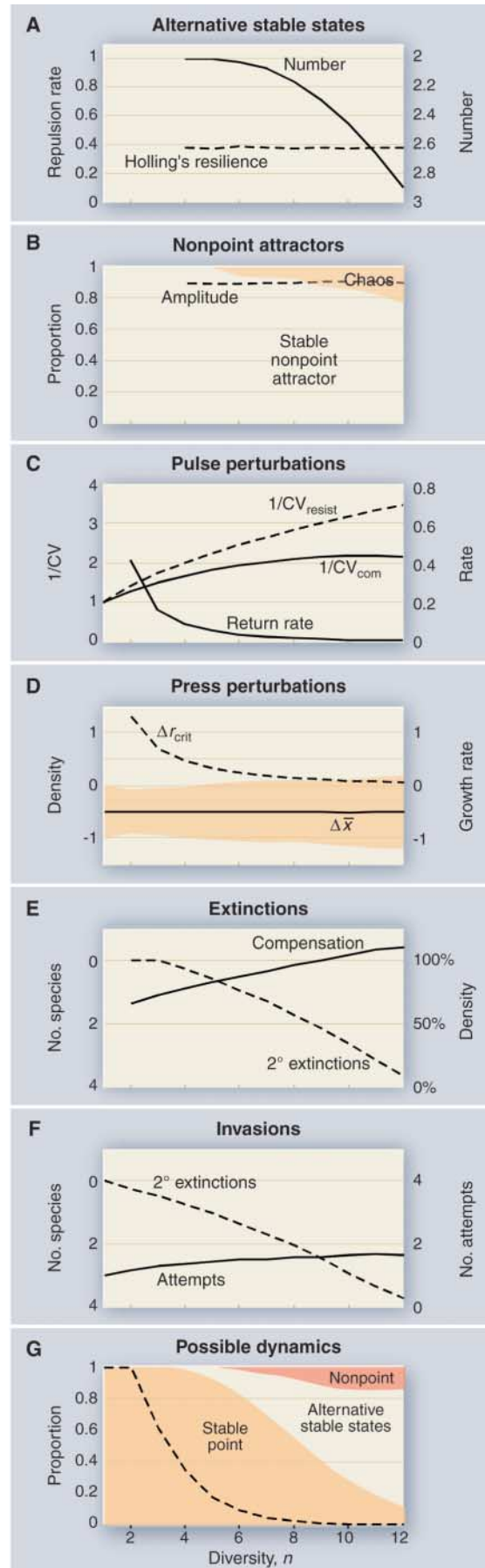


Fig. 2. Stability of randomly constructed competitive communities versus diversity n , portrayed so that positive diversity-stability relationships have positive slopes. (A) For systems with alternative stable states, the average number of stable states and Holling's resilience, measured by the rate 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.

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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Figs. S1 and S2

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References

Review of theoretical literature on stability

We give a brief review of the theoretical literature relevant to different types of stability, followed by a brief review of studies integrating theory and data. We organize this review around the six different categories illustrated in Fig. 1. Although the specific diversity-stability relationships we present in Fig. 2 were generated by a single, simple model, this appendix shows that similar relationships arise from a wide variety of models and approaches.

(A) Alternative stable states

Theoretical literature – Alternative stable states occur when there are multiple stationary points that are locally but not globally stable (*S1-3*). These stationary points can include zeros, in which case alternative stable states are alternative species compositions in an ecosystem. Perhaps the oldest and most familiar case of alternative stable states in the ecological literature comes from the Lotka-Volterra competition equation for two species when the competition coefficients α_{12} and α_{21} are both greater than one (*S4*). In this case, both the point at which species 1 is at carrying capacity and species 2 is absent, $(K_1, 0)$, and the point at which the converse is true, $(0, K_2)$, are locally stable, with the winner of competition depending on initial species densities. Alternative stable states may also occur with positive densities for all species; different alternative stable states contain different species densities. These require per capita population growth rates to depend on population densities in nonlinear ways. When alternative stable states occur, stability can be measured by the difficulty of ecosystems switching between domains of attraction to the different stable states; this has been called resilience by Holling (*S2*).

Alternative stable states generate hysteresis. If structural changes occur in the equations governing the dynamics of a system that allow a shift from one domain of attraction to another, then a reversal of these structural changes will not necessarily lead to a return of the ecosystem to its original state (*S5, S6*). Similarly, stochastic events can cause jumps between domains of attraction, leading to long-term changes in system behavior (*S1*).

Van Nes and Scheffer (*S7*) studied the prevalence and characteristics of alternative stable states in simulated communities, and derived results similar to those illustrated in Fig. 2. Alternative stable states can also be produced in metapopulation dynamics (*S8*), and it is possible to have alternative stable states where the states themselves are non-point attractors (*S9*).

Theoretical/empirical literature – There is a growing number of empirical examples of alternative stable states (*S5, S10*), and researchers have become more aware of the management implications of alternative stable states (*S6, S11, S12*). A central issue in this literature is the importance of scale, and how alternative stable states at the local scale can lead to spatial patterns at a landscape scale (*S13-15*).

(B) Non-point attractors

Theoretical literature – Non-point attractors can be either stable or chaotic (*S16, S17*). A stable limit cycle is an example of a stable non-point attractor, since trajectories initiated nearby the limit cycle move towards it through time. In discrete-time models, the non-point attractor equivalent to a stable limit cycle is an invariant closed curve. The common diagnostic for a chaotic attractor is a Lyapunov exponent that is greater than zero, indicating that nearby trajectories diverge from each other (*S18, S19*).

There is a huge theoretical literature on predator-prey cycles, much of it aiming to explain the seemingly low prevalence of cycles in nature (*S20-23*). Chaos has similarly generated much theoretical study, because it gives a possible explanation for highly variable, seemingly unpredictable dynamics of populations and diseases (*S17, S24*).

We know of no formal theory leading to a relationship between the dimensions of a system and the likelihood of non-point attractors. Nonetheless, in continuous-time models 2 dimensions are needed for stable non-point attractors, whereas chaos requires 3 dimensions (*S18, S25*). For discrete-time models, chaos can arise in models with a single dimension (*S16*). For purely competitive models such as the one we analyzed with relatively low values of the intrinsic rate of increase, r (see Eq. S1, caption for Fig. S2), cyclic attractors require 3 dimensions (species) engaged in a rock-paper-scissors type of non-transitive hierarchy (*S26*), while chaos requires more dimensions and interactions between two or more rock-paper-scissor hierarchies. For competitive models incorporating dynamical resources (i.e., explicitly including 2 trophic levels), chaos can occur with 3 resources (*S27*).

Theoretical/empirical literature – A large number of studies demonstrates cyclic dynamics in natural systems (*S21, S28-35*). These are generally assumed to be caused by exploiter-victim interactions (predator-prey, disease-host, and consumer-resource interactions) whenever cycle length is greater than the generation times of the species and there is no obvious cyclic environmental driver.

Compelling empirical examples of dynamics more complex than simple cycles have been generated for *Tribolium* beetles in laboratory microcosms (*S9, S36, S37*). Using a remarkably tight coupling between experimental system and model, Costantino and colleagues (*S37, S38*) performed an empirical bifurcation experiment in which *Tribolium* demography was manipulated to give complex dynamics predicted by theory. This provides the best example to date of complex dynamics and chaos exhibited by a real, albeit laboratory system.

Several authors have searched for evidence of chaos in data sets from natural systems (*S39-41*). Real systems will have environmental variability, and although chaos is well-defined for stochastic systems, chaos nonetheless loses much of its qualitative distinctness from non-chaotic dynamics (*S42*). This means that the specific question of whether a given natural system is chaotic or not is less compelling, with the real interest being the role of species interactions in driving population dynamics.

(C) Pulse perturbations to systems with stable stationary points

Theoretical literature – Many of the theoretical studies on diversity and stability have focused on systems with stable points (S43-S51). If the system is deterministic, then dynamics near the stable point are described by the characteristic return rate – how rapidly densities return towards the stable point if perturbed away (S52). If the system experiences environmental stochasticity, then it will be continuously perturbed from the stable point. Nonetheless, densities will always be drawn towards the stable point, creating a stationary probability distribution (S53).

In deterministic systems, ecological stability is generally associated with rapid characteristic return rates, measured by the eigenvalues of the Jacobian matrix computed at the stationary point (S52). The maximum (dominant) eigenvalue gives the rate of return by the slowest component of the system; by component, we mean a linear combination of densities. For competition models such as ours (Fig. 2), the sum of densities of all species generally returns relatively rapidly towards the stationary point. In contrast, the densities of species may fluctuate, as the densities of symmetrically balanced competitors change slowly with respect to each other (see Fig. 1C). Thus, for competitive systems the combined densities of species generally returns towards the stationary point more rapidly than the densities of individual species (S46). This is the basis for May's conclusion (S54) that competition may increase the variability of populations (decrease population stability) while having no effect on the variability of the entire community. Tilman (S55) has emphasized the important distinction between population and community stability in understanding real systems.

In stochastic systems, ecological stability can be measured by the variance (possibly scaled by the mean to give the coefficient of variation, CV) of the stationary distribution. The variance of the stationary distribution depends on both species-species and species-environment interactions (S56, S57). Species-environment interactions are summarized by the variances and covariances in population growth rates among species (in our model, $\varepsilon_i(t)$; see Eq. S1), with greater environmental variance generating greater variance in per capita population growth rates. The net variance of the stationary distribution depends on how this environmental variance is propagated by species-species interactions. This creates a close tie between population variance and characteristic return rates, because rapid return towards equilibrium in deterministic systems lowers the variance of the corresponding stochastic system, as environmental perturbations are more rapidly damped (S56, S58).

A common misconception is that compensation due to competitive interactions acts to decrease community variability and thereby stabilize systems. This misconception is due to the fact that competition may cause negative covariances among the fluctuations in species densities. Nonetheless, at the same time as decreasing covariances, competition will also increase the variances in species fluctuations. In models in which the magnitude of interspecific competition is the same for all species (i.e., competition is symmetric), to a linear approximation the effect of competition to decrease covariances is perfectly offset by the increase in variances, and competition has no net effect on the variability in combined species densities (S44, S46, S54).

Theoretical/empirical literature – Whenever a model is fit to time-series data, information is obtained about the stability of the system. For many, if not most multispecies data sets, sufficient information and data are not available to construct realistic, nonlinear models. A pragmatic solution is to fit simplified, linear or near-linear models and perform standard

statistical diagnostics to identify large aberrations (S57). Even when applied to nonlinear systems, linear stochastic models may give reasonable descriptions of the data (S59). Nonetheless, model mis-specification may badly inflate the perceived magnitude of environmental variability, creating poor estimates of intrinsic stability.

Lehman and Tilman (S47, S60) proposed a set of tests to understand the processes underlying the diversity-stability relationship when stability is measured by community variability. These consist of estimating (i) the relationship between the mean and variance in species abundances, (ii) the covariance in abundances among species, and (iii) changes in mean species abundances with increasing diversity n . However, these tests do not separate the role of species-species interactions from the effect of environmental variability on individual species. For example, the relationship between the mean and variance in species abundances depends on the strength of competition with other species (S46) and therefore is not a measure of “statistical averaging” caused by the differing responses of species to environmental fluctuations. Similarly, the covariances in species abundances depend on both competitive interactions and the possible similar responses of species to environmental fluctuations (S58); therefore, covariances do not measure the effect of competition on stability. Because species-species interactions and species-environment interactions combine in complicated ways to generate system variability, we do not think there is a robust method for understanding the processes underlying ecosystem stability short of fitting a model to data.

(D) Press perturbations to systems with stable stationary points

Theoretical literature – Press perturbations (S61) can be defined as changes to the parameters of a model, rather than pulse perturbations to species densities. Thus, they represent “slow,” structural changes to the system, as might be caused by global climate change, nutrient mobilization, or land-use change (S12). Press perturbations might occur not only by direct effects of environmental change on species, but also by changing how species interact with each other. For example, habitat homogenization might increase competition among plant species by reducing species-specific niches.

Press perturbations can affect the location of the stable point, that is, the stable values of species densities or other ecosystem variables. For linear models or linear approximations to nonlinear models, structural changes to the location of stable points are relatively easy to compute (S62), and general conclusions about the roles of species-species interactions can be derived (S63). These results, for example, underlie conclusions about the consequences of bottom-up effects of nutrient additions to food chains (S64). For complex nonlinear systems, simple generalities are not possible.

Structural changes may also affect the dynamics around the attractor (S18, S19). A stable point may become a stable non-point attractor (e.g., a Hopf bifurcation, right-hand side of Fig. 1D; or a period-doubling bifurcation); a stable point may collide with an unstable attractor (e.g., a transcritical bifurcation, left-hand side of Fig. 1D); or a stable point may split into two stable points (e.g., a supercritical pitch-fork bifurcation), among other possibilities. A classical ecological example is the paradox of enrichment in which fertilization causes a resource-consumer system to change from a stable point to a limit cycle (S65). In stochastic systems, structural changes to the “deterministic skeleton” of the system can lead to increased variances, signaling a change in the dynamical character of the attractor (S66, S67).

We do not know of any systematic studies of the effect of diversity *per se* on structural stability.

Theoretical/empirical literature – Many if not most of the concerns about environmental effects on ecosystems involve press perturbations (*S1, S6, S11, S12*); see Table S3. Whole-ecosystem experiments altering inputs to many kinds of ecosystems, such as forest watersheds, streams, lakes and patches of ocean, involve press perturbations (*S68*). For example, experimenters have manipulated nutrient inputs, pH, or food webs of lakes (*S69-72*). In these experiments, and in management problems in general, information about individual species is often unknown and possibly not critical; structural changes occur for entire functional groups and trophic levels. This leads to two related questions: how species diversity within functional groups affects the response of the functional group to press perturbations (*S45, S73, S74*), and how diversity of functional groups or trophic topology affects the response of the ecosystem to structural change (*S75, S76*).

(E) Extinction of species

Theoretical literature – Extinction can be viewed as a type of perturbation that reduces the dimension of the dynamical system. Following extinctions, the community might lose additional species through secondary extinctions, or the total abundance of species in the community might change.

Several models have investigated the role of community structure on secondary extinctions (*S77-83*). With a model similar to ours, Eklof and Ebenman (*S84*) studied the consequences of complexity in systems with three trophic levels, where complexity was measured as the connectance (proportion of possible interactions that were realized) between trophic levels. They found that increasing connectance decreased the number of secondary extinctions, so greater complexity led to greater stability. This is reminiscent of MacArthur's famous postulate that greater numbers of species provide redundant energy pathways from base to top of food webs (*S85*). However, it contrasts our model in which secondary extinctions increase with the number of species (Fig. 2E). This contrast presumably arises because we addressed the number of species in competitive communities rather than the connectance between trophic levels.

The effect of species extinctions on total species abundance is closely related to the effect of diversity on ecosystem biomass. Species extinctions lead to less-diverse ecosystems, and there is a large, relevant literature on the relationship between diversity and biomass (*S86-88*).

Theoretical/empirical literature – Much of our knowledge about the consequences of extinctions on ecosystems comes from studies on keystone species, when loss of one or a few species has large impacts on ecosystems (*S89, S90*). Since anthropogenic extinctions are often biased towards species at top trophic levels (*S91*), this has focused research on cascading impacts of species loss (*S77, S80, S92*).

For the most part, the theoretical literature has been linked only qualitatively to data. For example, several studies have searched for patterns of food-web structure in natural ecosystems, with theory used to provide possible qualitative explanations of patterns (*S83, S93*). Nonetheless, detailed quantitative studies involving the removal of key species from

communities (S94-96) can reveal the role of species interactions and diversity on the stability and abundance of species (S97).

(F) Invasions

Theoretical literature – Invasions, like extinctions, can be viewed as perturbations to ecosystems, with more stable ecosystems being more likely to resist invasions and less likely to have secondary extinctions if an invader is successful (S98, S99).

Questions about invasibility are closely related to questions about species coexistence, because for a species to coexist with other species in a community, it must be able to increase from low density. Thus, the huge theoretical literature on species coexistence is relevant. Theoretical studies addressing specifically how diversity affects invasibility have shown that, as communities are assembled by the successive addition of species, invasibility becomes successively more difficult (S50, S99-101). We found the same result in our model (Fig. 2F). These community assembly models only scratch the surface of possible relationships between diversity and invasibility.

Theoretical/empirical literature – There have been numerous impressive empirical studies of community invasibility (S51, S102, S103). Few of these studies have been tightly tied to theoretical models, with models fit statistically to data. Nonetheless, measuring invasibility in experiments, and performing analyses and ancillary experiments to reveal the processes underlying invasibility, appear to be simpler than for other types of stability; of the experimental studies we reviewed on the relationship between diversity and invasibility, almost all showed clear results, often with convincing evidence for why more-diversity ecosystems were more difficult to invade (Table S2).

Figure S1: Mismatches between empirical results and theory

We evaluated each of the 52 studies for mismatches between empirical results and existing theory, where mismatches make it difficult or impossible to determine whether the experiments and analyses either support or reject theoretical expectations as described by the authors. We stress that a very good and informative empirical study nonetheless might not match any existing theory. We do not judge the value of an empirical study based on its ability to “test theory.” We do, however, want to point out the difficulty of assessing theory, and also assessing and generalizing empirical results, due to common mismatches between theory and experiment (S86, S104). All of the 52 articles used existing theoretical ideas to motivate their empirical studies, and many studies claimed to support or reject theory.

For the 64 diversity-stability relationships, we scored four types of mismatches:

1. Assumptions – The basic assumptions under which the tested theory was derived were not met by the empirical system under study. For example, some studies investigated patterns of ecosystem variability using measures that incorporated species from multiple trophic levels. Nonetheless, the theory that was supposedly tested was derived only for communities with a single trophic level. Another common mismatch arose in studies of ecosystem variability where the system under study showed strong trends through time and therefore were not at stationarity (i.e., the dynamics were dominated by transients).
2. Incorrect analyses – The analyses were inappropriate to quantify the type of stability under study. In some cases, this mismatch coincided with and was caused by a mismatch in assumptions (#1). In other cases, analyses were performed that could not lead to the conclusion about the diversity-stability relationship claimed by the authors.
3. Incorrect statement of theory – Some authors described the expectations of theory incorrectly, making it impossible to relate the data and analyses to the actual theoretical expectations.
4. Incomplete analyses or inadequate data – The analyses did not extract sufficient information from the data to evaluate the theory being tested in terms of the mechanisms driving the theoretical results. For example, the relationship between diversity and variability depends upon the combined effects of species-species interactions and species-environment interactions. Without analyses to separate these components of variability, it is difficult to assess the underlying mechanisms producing the empirical results. In some studies there were not enough data to assess the theory.

To present the mismatches, we separated studies on invasibility from the others, because as a group studies on invasibility tended to have fewer mismatches.

In assigning mismatches, we acknowledge that a certain amount of subjectivity is unavoidable; no study is perfect, and different researchers might have different thresholds before declaring a mismatch. Nonetheless, we applied two criteria to decide if there was a mismatch. First, are the data and analyses sufficiently clear to convince us of the authors’ conclusions about the direction (positive, negative, or zero) of the diversity-stability relationship they claim to test. Second, do the analyses give enough information to evaluate the presence of the mechanisms assumed by the theory to generate the predicted diversity-stability relationship. Generally, the

second criterion was not met due to mismatches involving incomplete analyses or inadequate data (#4). Over all studies, only 25/64 diversity-stability relationships satisfied both criteria. Of the 21 relationships with stability defined as invasibility, 15 satisfied these criteria. Excluding studies of invasibility, only 10/43 studies satisfied the criteria.

Figure S1: Enumeration of mismatches between 64 empirical diversity-stability relationships and corresponding theoretical predictions. The same relationship can be counted multiple times if it contains multiple mismatches. Numbers for relationships involving invasibility are given by the open bar, while black bars give the remaining diversity-stability relationships.

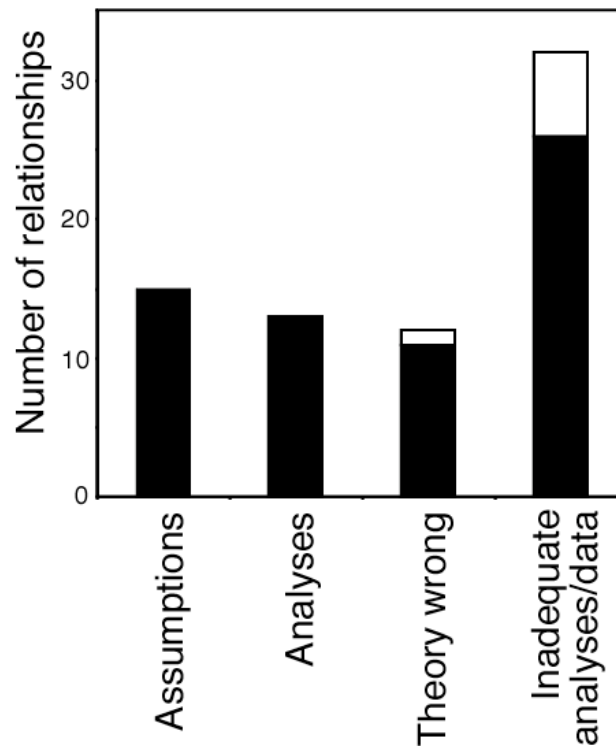


Figure S2: Models illustrating diversity-stability relationships

Here, we describe the competition model we used to organize the theoretical literature review and produce Figs. 1 and 2. We selected a competition model, because many empirical studies focus on systems with single trophic levels. Nonetheless, systems with multiple trophic levels often show similar results, and to illustrate this, we also present a model with two trophic levels (Fig. S2) which shows many of the same patterns as the competition model.

Figs. 1 and 2 were produced using the Lotka-Volterra-like model

$$x_i(t+1) = x_i(t) \exp \left(r - \sum_{j=1}^n b_{ij} x_j(t) + \varepsilon_i(t) \right), \quad (\text{S1})$$

where r gives the intrinsic rate of increase, $b_{ij} > 0$ gives the competitive effects of species j on species i , and $\varepsilon_i(t)$ represents environmental, “unexplained” variation. To simulate ecosystems of n species, we constructed species by randomly selecting strengths of competition with other species. To incorporate environmental variation, we included random variables $\varepsilon_i(t)$ that give stochastic changes in per capita population growth rates of species i through time t . For $n = 1$ to 12 species, we constructed 10,000 ecosystems that contained a positive stationary (equilibrium) point; these ecosystems were “feasible,” because a positive stationary point is a necessary (but not sufficient) condition for all n species to persist indefinitely. We considered additional procedures for assembling communities, including adding species sequentially and allowing larger communities to “relax” through extinctions to the target n . These different procedures all gave similar patterns as those illustrated in Fig. 2.

For each simulated ecosystem, we calculated 13 measures of stability and averaged these over 10,000 ecosystems to give the expected stabilities for each n . While most of these measures of stability are self-explanatory, a few need explanation. For systems with alternative stable states, we calculated Holling’s resilience as the magnitude of the dominant eigenvalue at the unstable stationary point; this gives a rough measure of the rate at which populations are repelled from the ridge between domains of attraction. To determine whether a non-point attractor was chaotic, we computed Lyapunov exponents. For systems with a stable equilibrium, we computed the characteristic return rate as $-\log \lambda^*$, where λ^* is the dominant eigenvalue of the Jacobian matrix computed at the stable point. For repeated pulse perturbations (for $\text{CV}_{\text{resist}}$ and CV_{com}), we assumed $\varepsilon_i(t)$ had variance 1 (with no autocorrelation or covariance among species), while for all other measures of stability we set the variance to zero. For press perturbations, we assumed $\bar{\varepsilon}_i(E)$, the mean effect of the environment on the per capita population growth rate of each species i , decreases as an environmental driver E increases. The rate of decrease in $\bar{\varepsilon}_i(E)$, $\partial \bar{\varepsilon}_i(E) / \partial E$, was selected for each species at random from a uniform distribution from -1 to 0 .

In addition to the competition model, we produced a model with two trophic levels having the same structure as Eq. S1. Pairs of prey (sp 1) and predator (sp 2) were constructed with $b_{11} = 1$, $b_{12} = 0.75$, $b_{21} = -0.75$, and $b_{22} = 0$. To create diverse communities, from 1 to 6 predator-prey pairs (from 2 to 12 total species) were assembled, with the interactions between species in different pairs equal to $q_{kl}b_{11}$, $q_{kl}b_{12}$, $q_{kl}b_{21}$, and 0 , where q_{kl} was selected at random from a uniform distribution between 0 and 1 for each combination of predator-prey pairs k and l . Therefore, the model contained direct competition among all prey species, predation between all prey and all predators, but no direct interactions between predator species (although indirect

interactions occurred through changes in shared prey densities). This model can be envisioned as creating communities with n primary predator-prey modules (with interaction strengths b_{11} , b_{12} , b_{21} , and b_{22}) connected together with random interaction strengths. Measures of stability were based on the summed densities of only the prey species, extinction perturbations were performed by removing the most common prey, and all invaders were prey species. All other calculations were performed as in the competition model.

There are two notable differences between the diversity-stability relationships produced by the competition model (Fig. 2) and those from the predator-prey model (Fig. S2). First, the number of alternative stable states in the predator-prey model was much greater than the number in the competition model. Second, extinctions did not necessarily lead to compensation in the predator-prey model.

Figure S2: Diversity-stability relationships for a model with two trophic levels, where n gives the number of predator-prey pairs. See legend for Fig. 2 in the text. In (A) note \log_{10} scale.

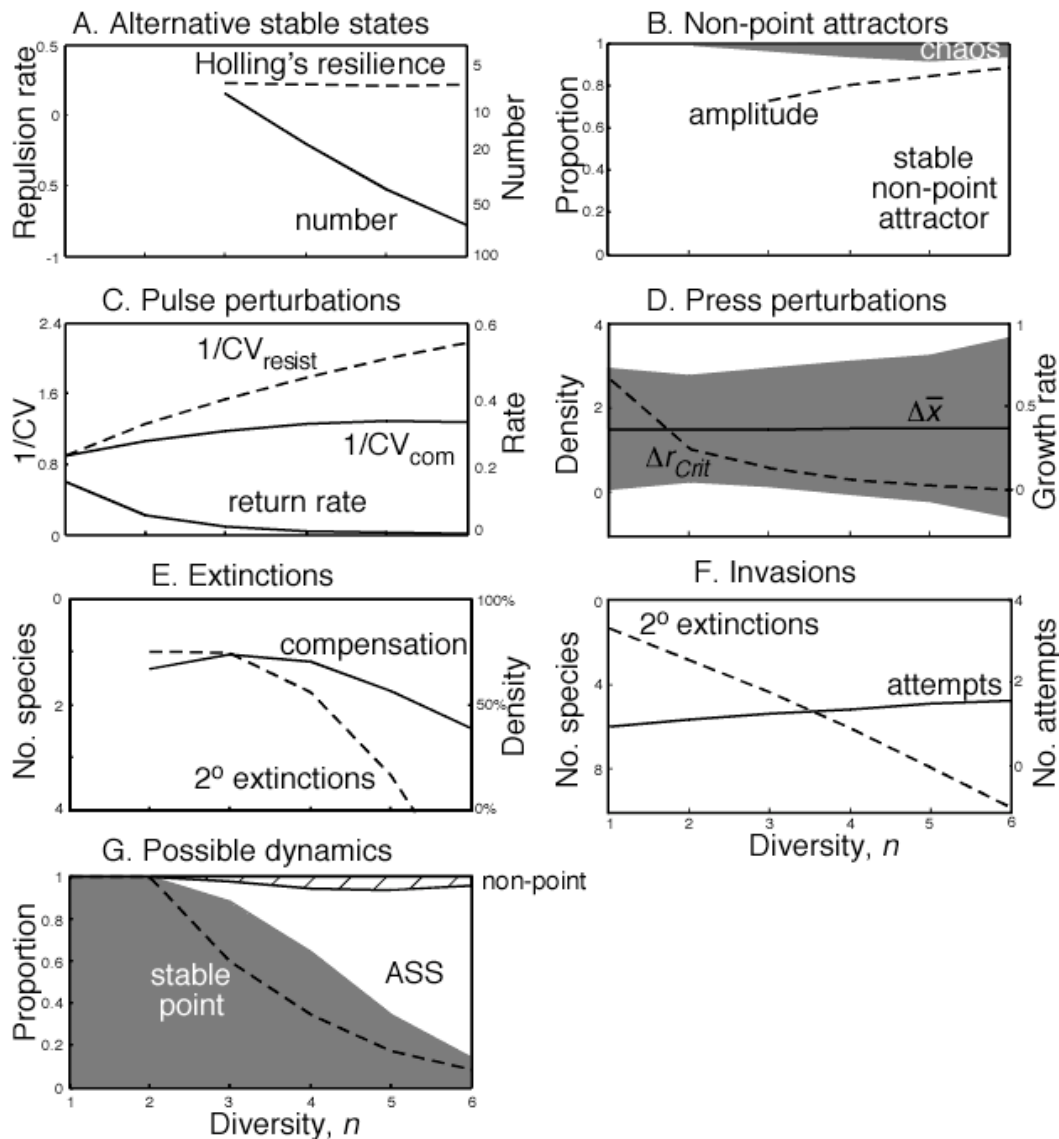


Table S1: Sixty-four diversity-stability relationships

We performed a survey of 52 articles presenting empirical studies on the relationship between diversity and stability. Several studies were intentionally excluded because their measures of either diversity or stability were difficult to categorize (*S105-109*), and we did not include studies that investigated persistence, that is, the probability that species would remain in an assembled community (*S110, S111*).

Of the 52 studies, 37 directly manipulated diversity, while the remaining 15 either selected sites that differed systematically in diversity or imposed treatments (e.g., fertilization) that altered diversity. 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, 6 considered two or more trophic levels, and 5 included measurements that integrated over three or more trophic levels, such as microbial studies measuring CO₂ production.

From the 52 studies we identified 64 diversity-stability relationships. We included only community-level measures of stability, rather than the population-level measures of stability reported in some studies. Twelve studies contained two diversity-stability relationships, because either two perturbations were investigated, or two measures of stability were used. For example, Griffiths et al. (*S112*) subjected microbial communities to both a pulsed heat shock and a press perturbation by applying toxic copper. Similarly, Dukes (*S113*) measured stability both by the ability of a plant community to repel an invader and the impact of the invader on the growth of the resident community if the invader was successful. Also, some studies focused on species diversity (number of species), others used a diversity index that incorporated information about relative abundances, while still others focused on functional diversity (number of functional groups). Because in these studies increasing diversity measured by a diversity index or functional diversity was coincident with increasing species numbers, we do not distinguish among the different measures of diversity. Finally, in contrast to Wardle (*S114*) we treat “sampling effects” as bona fide effects of diversity.

Table S1 gives the sign of diversity-stability relationships as reported by the authors: positive (+), negative (–), or neither (0). In some cases, this forced a simplification of the reported results. For example, in their study using microbial microcosms, McGrady-Steed and Morin (*S115*) give the relationship between species richness and the variability of four functional groups (producers, bacteriovores, herbivores, and predators). For three of these functional groups, the diversity-stability relationship was positive, while for the fourth (producers) it was hump-shaped; nonetheless, we scored this study as giving a positive diversity-stability relationship. In a few cases we used the relationship exhibited in the analyses rather than that emphasized by the authors. The category “0” between positive and negative includes relationships that the authors state are either non-existent or ambiguous. Two of the four relationships listed under “press” stability came from microbial studies by Griffith et al. (*S112, S116*) in which microbial ecosystems were subjected to a copper toxin, and stability measured by the change in CO₂ production; the remaining two are from Petchy et al (*S117*) who compared the biomass of communities under constant or increasing temperatures. Overall, 67% (43/64) of the relationships as stated by the authors were positive, and 88% (56/64) were non-negative.

Table S1. Sixty-four diversity-stability relationships as stated by the authors of 52 studies.

| First author | Year | Citation | System | Trophic levels | Diversity | Type of stability | Perturbation | Response | Claimed relationship |
|---------------------------------------|------|----------|----------------|----------------|---------------|--------------------|--------------|-------------------|----------------------|
| Directly manipulated diversity | | | | | | | | | |
| Allison | 2004 | (S118) | marine algae | 1 | spp | resistance | temperature | cover/biomass | 0 |
| Arenas | 2006 | (S119) | marine algae | 1 | fnct | invasibility | invasion | invader biomass | 0 |
| Beisner | 2006 | (S120) | rock pools | 1 | spp | invasibility | invasion | success | + |
| Britton-Simmons | 2006 | (S121) | seaweed | 1 | fnct | invasibility | invasion | success | + |
| Brown | 1987 | (S122) | forest/crops | 1 | spp | variability | herbivory | leaf area | + |
| Caldiera | 2005 | (S123) | grassland | 1 | spp | variability | drought | biomass | + |
| | | | | | | return time | drought | biomass | 0 |
| Craine | 2003 | (S124) | grassland | 1 | spp | variability | weather | biomass | + |
| Crawley | 1999 | (S125) | grassland | 1 | spp | invasibility | invasion | success | + |
| Dimitrakopoulos | 2005 | (S126) | grassland | 1 | spp | invasibility | invasion | success | + |
| Dukes | 2001 | (S113) | grassland | 1 | spp/fnct | invasibility | invasion | biomass | + |
| | | | | | | impact of invasion | invasion | biomass | + |
| Fargione | 2005 | (S127) | grassland | 1 | spp | invasibility | invasion | biomass/ number | + |
| France | 2006 | (S128) | seagrass | 2 | herbivore spp | variability | weather | biomass | – |
| Giffiths | 2001 | (S116) | microbes | ? | spp | return time | temperature | CO2 production | 0 |
| | | | | | | press | toxin | CO2 production | 0 |
| Gonzalez | 2004 | (S129) | microbes | 2 | spp | variability | temperature | biomass | – |
| Hector | 2001 | (S130) | grassland | 1 | spp | invasibility | invasion | success | + |
| Kennedy | 2002 | (S131) | grassland | 1 | spp | invasibility | invasion | success/size | + |
| Knops | 1999 | (S132) | grassland | 1 | spp | invasibility | invasion | success | + |
| Levine | 2000 | (S133) | tussock plants | 1 | spp | invasibility | invasion | success | + |
| McGrath-Steed | 2000 | (S115) | microbes | 3 | spp | variability | none | abundance | + |
| Morin | 2004 | (S134) | microbes | 4 | spp | variability | none | CO2 production | + |
| Mulder | 2001 | (S135) | mosses | 1 | spp | resistance | drought | biomass | + |
| Petchey | 1999 | (S117) | microbes | 3 | spp/fnct | press | temperature | productivity | 0 |
| | | | | | | press | temperature | number of species | 0 |
| Petchey | 2002 | (S136) | microbes | 1 | spp | variability | temperature | biomass | 0 |
| Pfisterer | 2002 | (S137) | grassland | 1 | spp | resistance | drought | biomass | – |
| | | | | | | return time | drought | biomass | – |
| Prieur-Richard | 2000 | (S138) | grassland | 1 | spp/fnct | invasibility | invasion | biomass/fecundity | + |

| | | | | | | | | | |
|-------------|------|--------|------------|----|----------|--------------|-------------|-------------------|---|
| Romanuk | 2006 | (S139) | rock pools | 1? | spp | variability | none | abundance | 0 |
| Stachowicz | 1999 | (S98) | intertidal | 1 | spp | invasibility | invasion | success | + |
| Steiner | 2005 | (S140) | microbes | 4 | spp | variability | none | biomass | + |
| Steiner | 2006 | (S141) | microbes | 4 | spp | return time | dilution | biomass | + |
| Symstad | 2000 | (S142) | grassland | 1 | fnct | invasibility | invasion | success | + |
| Tilman | 2006 | (S143) | grassland | 1 | spp | variability | weather | biomass | + |
| van Ruijven | 2003 | (S144) | grassland | 1 | spp | invasibility | invasion | # spp/density | + |
| von Holle | 2005 | (S145) | herbs | 1 | spp | invasibility | invasion | success | 0 |
| Wardle | 2000 | (S146) | plants | 2 | spp/fnct | resistance | drought | numerous | 0 |
| Zalaleta | 2004 | (S147) | grassland | 1 | spp | invasibility | invasion | biomass/fecundity | + |
| Zhang | 2006 | (S148) | algae | 1 | spp | resistance | temperature | biomass | — |
| Zhang | 2006 | (S149) | algae | 1 | spp | variability | none | biomass | + |
| | | | | | | resistance | temperature | biomass | 0 |

Indirectly manipulated diversity

| | | | | | | | | | |
|------------|------|--------|---------------|---|-----------|------------------------|--------------|----------------|---|
| Bai | 2004 | (S150) | grassland | 1 | spp | variability | climate | biomass | + |
| Dodd | 1994 | (S151) | grassland | 1 | spp | variability | weather | biomass | + |
| Frank | 1991 | (S152) | grassland | 1 | index | resistance | drought | biomass | + |
| Giffiths | 2000 | (S112) | microbes | ? | spp/fnct? | return time | temperature | CO2 production | + |
| | | | | | | press | toxin | CO2 production | + |
| Hurd | 1971 | (S153) | old field | 3 | spp | resistance | fertilizer | plant biomass | + |
| | | | | | | | | insect numbers | — |
| Kahmen | 2005 | (S154) | grassland | 1 | spp | resistance | drought | productivity | + |
| Leps | 2004 | (S155) | meadow | 1 | spp/index | variability | extinction | biomass | 0 |
| | | | | | | variability | nutrient | biomass | + |
| MacDougall | 2005 | (S156) | grassland | 1 | spp | invasibility | fire | success | + |
| | | | | | | return time | fire | light | + |
| McNaughton | 1977 | (S157) | grassland | 1 | index | return time | drought | biomass | + |
| | | | | | | return time | grazing | biomass | + |
| Mellinger | 1975 | (S158) | grassland | 1 | index | resistance | nutrients | biomass | + |
| Robinson | 1995 | (S159) | grassland | 1 | spp | invasibility | invasion | success | — |
| Rodriquez | 1994 | (S160) | grassland | 1 | index | resistance | drought | biomass | — |
| Tilman | 1996 | (S55) | grassland | 1 | spp | variability/resistance | none/drought | biomass | + |
| | | | | | | return time | drought | biomass | + |
| Tilman | 1997 | (S161) | grassland | 1 | spp/fnct | invasibility | invasion | success | + |
| Valone | 2003 | (S162) | desert plants | 1 | spp | variability | none | number | + |

Table S2: Summary of diversity-stability patterns for empirical studies and theoretical predictions

To summarize both empirical and theoretical diversity-stability relationships, we constructed Table S2 to include information from Table S1 and the review of the theoretical literature given in the Supporting online text. To summarize empirical studies, we counted the number that addressed each of the 13 types of stability we describe in the main text, and report the percentages of studies showing a positive or a non-negative diversity-stability relationship. For theoretical studies, we assigned positive, negative, or in some cases both positive and negative relationships as dictated by the preponderance of existing theory. We also designate relationships that are either uncertain or poorly studied with a question mark.

Table S2. Summary of diversity-stability patterns for empirical and theoretical studies. The number of empirical studies addressing each type of stability are given, along with the percentages of those studies that show positive or non-negative diversity-stability relationships. Theoretical relationships are assigned positive (+), negative (–) or zero (0) based upon the broad literature, and ? denotes relationships that are uncertain and understudied.

| Context | Definition of stability | Empirical relationships | | Theory |
|-------------------------------|--|-------------------------|---------------------------|--------|
| | | Number | % Positive (non-negative) | |
| (A) Alternative stable states | number of ASSs | 0 | | –? |
| | Holling's resilience | 0 | | 0? |
| (B) Non-point attractors | chaos | 0 | | – |
| | amplitude | 0 | | –? |
| (C) Pulse perturbations | resistance | 12 | 42% (67%) | +,0 |
| | return rate | 9 | 67% (89%) | –,0 |
| | variability | 18 | 72% (89%) | +, – |
| (D) Press perturbations | rate of change in equilibrium | 4 | 25% (100%) | 0? |
| | sensitivity of dynamics around equilibrium | 0 | | – |
| (E) Extinctions | number of 2 ^o extinctions | 0 | | – |
| | density compensation | 0 | | +,–? |
| (F) Invasions | invasibility | 20 | 85% (95%) | + |
| | Impact of invasion | 1 | 100% (100%) | +,–? |

Table S3: Types of Stability Relevant to Applied Problems of Ecology

Applied ecology frequently addresses ecosystem change, for example, changes from an ancestral condition to a degraded condition of ecosystems, or restoration of ecosystems to a preferred condition. We considered 13 problems of applied ecology (Table S3). For each problem, we identified relevant types of stability that were addressed explicitly in the literature or could be inferred from published data. Structural stability to press perturbations was the most commonly relevant type of stability (13 of 13 cases), followed by alternate stable states (7 of 13), stability to invasion (5 of 13), stability to extinction (4 of 13), variability and resistance around stochastic attractors (3 of 13), and non-point attractors (3 of 13). Any such compilation will be somewhat subjective, depending on the list of applied problems and the available studies. Nonetheless, Table S3 demonstrates that multiple definitions of stability are relevant to problems of applied ecology, and some types of stability that are often relevant for applied ecology are not often considered by experimental studies.

Table S3. Types of stability encountered in problems of applied ecology. For each problem we present the types of ecosystem considered, the proximate drivers (biological, chemical, and physical drivers), ecological response variables, relevant types of stability, and references.

| Problem | Ecosystem type | Drivers | Response Variables | Type of stability | Ref. |
|---|--|---|---|---|--------------|
| Acidification | lakes, rivers | atmospheric deposition, bedrock geology, biogenic alkalinity generation, soils | biogeochemical cycles, productivity, species composition, trophic structure | structural stability to press perturbations, variability, response to extinction | (S163, S164) |
| Climate impact on biota | all | warming, drying (terrestrial ecosystems), altered disturbance regime | population densities, species composition, trophic structure | structural stability to press perturbations, variability, response to extinction | (S165) |
| Coral reef decline | coastal tropical ocean | excessive fish harvest, food web change, nutrient runoff, ocean acidification | coral cover, species composition | structural stability to press perturbations, alternative states | (S166) |
| Desertification | drylands | climate change, erosion, excessive grazing, invasion of weeds, salinization | hydrology, productivity, species composition, soil characteristics, vegetation cover | structural stability to press perturbations, alternative states, response to invasion | (S167) |
| Drought exacerbated by land-use change | drylands | excessive clearing of vegetation, overgrazing | climate, hydrology, vegetation cover | alternative states, structural stability to press perturbations | (S14) |
| Eutrophication | coastal oceans, freshwater lakes and rivers | excessive nutrient input, food web change, land-use change | biogeochemical cycles, productivity, species composition, water quality | alternative states, structural stability to press perturbations, non-point attractors | (S6) |
| Extirpation of rare or endangered species | various | various, especially land use, climate, nutrient deposition, migration, atmospheric CO ₂ | species composition | structural stability to press perturbations, alternative states, response to extinction | (S168) |
| Fishery collapse | oceans, freshwater lakes and rivers | climate, harvest trends, food web dynamics | loss of harvested species, species composition | structural stability to press perturbations | (S169, 170) |
| Insect outbreaks | forests | climate, interaction with fire regime, predators, spatial pattern of vegetation | fire risk, loss of harvested timber, species composition | structural stability to press perturbations, non-point attractors | (S171) |
| Land-use change | terrestrial, freshwater and coastal ecosystems | expansion of food or biofuel production, urbanization | species richness, landscape heterogeneity, production of food and forests, water quantity and quality, aquatic biota, regulation of climate and air quality, mitigation of infectious disease | all | (S172) |
| Restoration of plant communities | various | fire, grazing, herbicides, hydrologic modification, nutrient manipulation mowing and cutting, physical changes of habitat, planting | species composition | structural stability to press perturbations, alternative states, response to invasion or extinction | (S173) |
| Spread of invasive species | various | various, especially migration, nutrient deposition, land use, climate | species composition | structural stability to press perturbations, response to invasion | (S168) |
| Woody invasion of rangeland | grassland | livestock prices, overgrazing, climate, fire regime | loss of forage for livestock, species composition | structural stability to press perturbations, response to invasion | (S174) |

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