



## Supporting Online Material for

### **Stability and Diversity of Ecosystems**

Anthony R. Ives\* and Stephen R. Carpenter\*

\*To whom correspondence should be addressed. E-mail: [arives@wisc.edu](mailto:arives@wisc.edu); [srcarpen@wisc.edu](mailto:srcarpen@wisc.edu)

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SOM Text

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### *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  $\alpha_{12}$  and  $\alpha_{21}$  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.

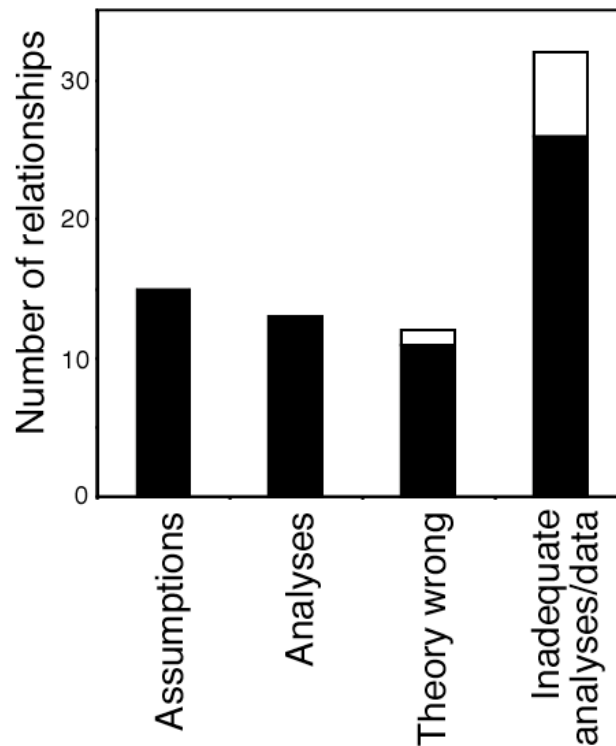
To present the mismatches, we separated studies on invasibility from the others, because as a group studies on invasibility tended to have fewer mismatches.

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.

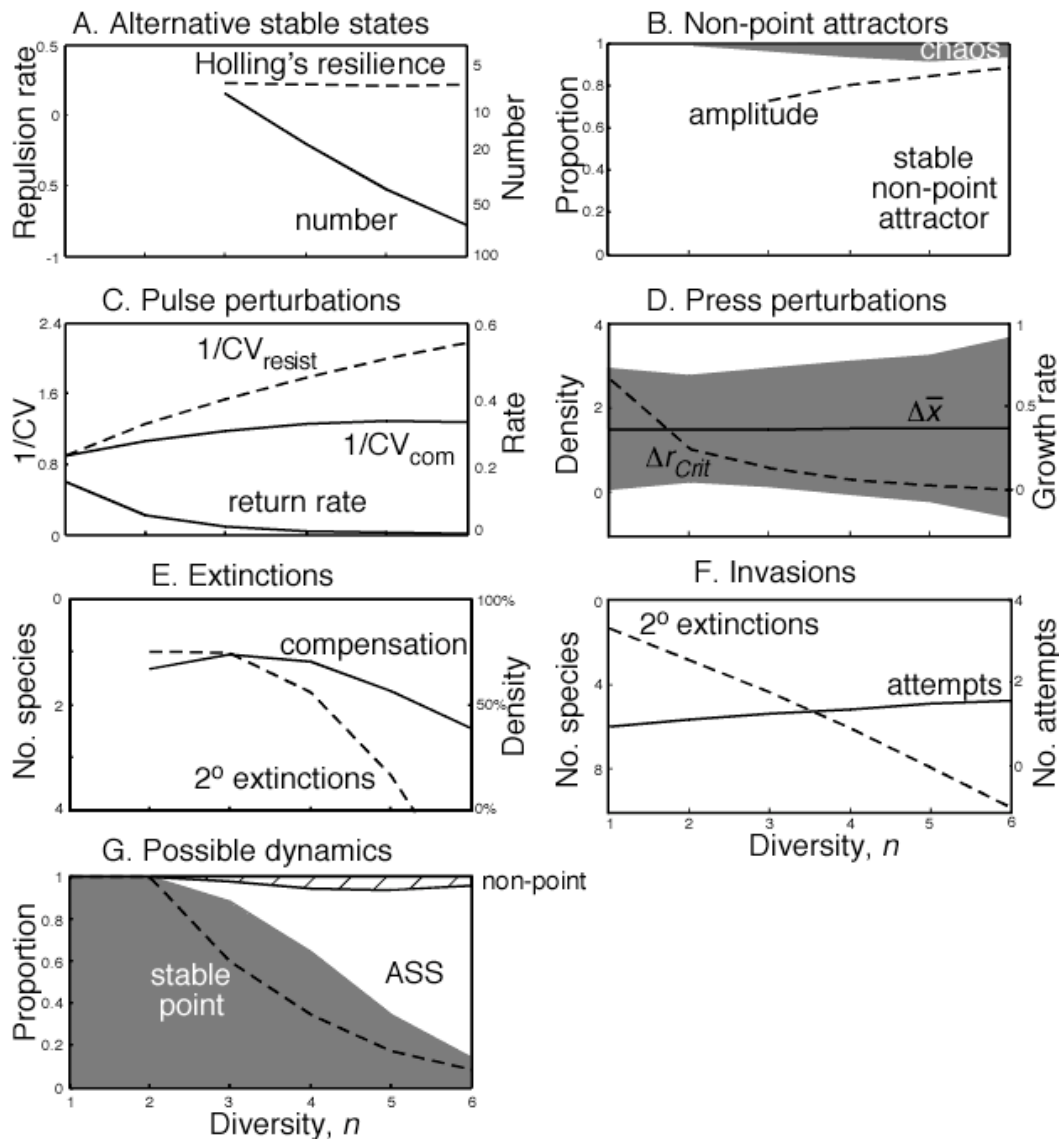
For each simulated ecosystem, we calculated 13 measures of stability and averaged these over 10,000 ecosystems to give the expected stabilities for each  $n$ . While most of these measures of stability are self-explanatory, a few need explanation. For systems with alternative stable states, we calculated 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  $\lambda^*$  is the dominant eigenvalue of the Jacobian matrix computed at the stable point. For repeated pulse perturbations (for  $\text{CV}_{\text{resist}}$  and  $\text{CV}_{\text{com}}$ ), 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 CO<sub>2</sub> 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 CO<sub>2</sub> 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
<b>Directly manipulated diversity</b>									
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 <sup>o</sup> 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 <sub>2</sub>	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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