The diversity–stability debate

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There exists little doubt that the Earth's biodiversity is declining. The Nature Conservancy, for example, has documented that one-third of the plant and animal species in the United States are now at risk of extinction. The problem is a monumental one, and forces us to consider in depth how we expect ecosystems, which ultimately are our life-support systems, to respond to reductions in diversity. This issue — commonly referred to as the diversity–stability debate — is the subject of this review, which synthesizes historical ideas with recent advances. Both theory and empirical evidence agree that we should expect declines in diversity to accelerate the simplification of ecological communities.

We now realize that the world's flora and fauna are disappearing at rates greater than the mass extinction events whose collapses punctuate the fossil record[1–3]. It is also true that species invasions have been elevated to unprecedented rates accompanying the increased globalization of our world[4,5]. These high rates of extinction and invasion put ecosystems under enormous stress, making it critical that we understand how the loss, or addition, of a species influences the stability and function of the ecosystems we rely on. We are, in a very real sense, deconstructing the Earth under the implicit assumption that ecosystems have evolved the ability to withstand such assault without collapse.

Several advances in the diversity–stability debate form a conceptual thread that suggests that diversity can be expected, on average, to give rise to ecosystem stability. This does not infer that diversity is the driver of this relationship. Instead, diversity can be regarded as the passive recipient of important ecological mechanisms that are inherent in ecosystems. One promising mechanism that has been proposed recently is that weakly interacting species stabilize community dynamics by dampening strong, potentially destabilizing consumer–resource interactions[6]. Empirical descriptions of the distribution of interaction strengths in real communities are consistent with this theory. If this is true then, all else being equal, decreasing biodiversity will be accompanied by increases in average interaction strengths within ecosystems, and a concomitant decrease in ecosystem stability.

Historical perspectives of the diversity–stability debate

The relationship between diversity and stability has fascinated ecologists. Before the 1970s, ecologists believed that more diverse communities enhanced ecosystem stability[7–9]. A strong proponent of this view was Charles Elton[8], who argued that "simple communities were more easily upset than that of richer ones; that is, more subject to destructive oscillations in populations, and more vulnerable to invasions". In fact, both Odum[7] and Elton[8] arrived at similar conclusions based on the repeated observation that greatly simplified terrestrial communities are characterized by more violent fluctuations in population density than diverse terrestrial communities. For example, invasions most frequently occur on cultivated land where human influence had produced greatly simplified ecological communities, and outbreaks of phytophagous insects occur readily in boreal forests but are unheard of in diverse tropical forests. These observations led Elton[8] to believe that

complex communities, constructed from many predators and parasites, prevented populations from undergoing explosive growth. His ideas were closely akin to MacArthur[9], who reasoned that multiplicity in the number of prey and predator species associated with a population freed that population from dramatic changes in abundance when one of the prey or predator species declined in density.

These early intuitive ideas were challenged by the work of Robert May[10] in 1973. May turned to mathematics to rigorously explore the diversity–stability relationship. By using linear stability analysis on models constructed from a statistical universe (that is, randomly constructed communities with randomly assigned interaction strengths), May found that diversity tends to destabilize community dynamics. Other ecologists, using similar approaches, found results that were consistent with this hypothesis[11,12]. The results were puzzling, as real ecosystems were undoubtedly complex and diverse. The results also seemed to counter the ideas of Elton[7], Odum[8] and MacArthur[9]. Yodzis[13] heightened this paradox by showing that models structured from compiled food-web relationships, with plausible interaction strengths, were generally more stable than randomly constructed food webs. Although the early food-web data that Yodzis structured his models around were incomplete, these data reflected real feeding relationships. Yodzis' result indicated that interaction strength was probably crucial to stability; but the exact reason for this remained elusive. If diversity and stability were positively correlated, as early empirical evidence had indicated, then more had to be happening than simply increasing the number of species and the number of pathways. Something fundamental was missing from the early arguments.

In the remainder of this paper I review recent investigations of the diversity–stability debate. I first discuss a change in perspective that is beginning to allow us to unravel this long-standing problem and then review two different lines of investigation. One approach has searched for a general diversity–stability relationship, and a second, more mechanistic approach has sought a relationship between food-web structure and stability.

Changing perspectives

Much of ecological theory is based on the underlying assumption of equilibrium population dynamics. Although this assumption is aesthetically pleasing, in that it suggests the balance of nature is infinitely precise, an alternative and viable ecological perspective exists. As real populations are variable, it is possible that the persistence of complex communities depends to some degree on population fluxes (that is, the

Figure 1 The Ecotron experiment creates model multitrophic community assemblages containing plants, herbivores, parasitoids and decomposers in 16 different chambers. The Ecotron is an ambitious attempt to bridge the scale between field communities and laboratory experiments. (Photographs show the inside of an Ecotron chamber and a technical service corridor between two banks of chambers; courtesy of the Centre for Population Biology, Imperial College at Silwood Park.)

fairly regular waxing and waning of a population's density). Such background population variability, whether driven by biotic or abiotic processes, can provide species with the opportunity to respond differentially to their environment. In turn, these differential species responses weaken the destructive potential of competitive exclusion.

Because such variability can significantly change our understanding of ecological interactions[6,14–19], ecologists have begun to relax equilibrium-based measures of stability. A recent theoretical analysis[17] has shown that population fluctuations, driven by competition, can actually promote the persistence of large numbers of competing phytoplankton communities on a minimal number of limiting resources (but greater than two resources). Coexistence was found to rely on the fluctuation in population densities, while community-level densities (the summation of the competing plankton densities) varied little. We will see that a similar relationship appears in diversity–stability experiments. Here, too, the evidence points to variable population densities that sum to produce a relatively constant biomass at the community level.

Definitions of stability

Definitions of stability in ecology can be classified generally into two categories (Table 1) — stability definitions that are based on a system's dynamic stability, and stability definitions that are based on a system's ability to defy change (resilience and resistance in Table 1). Despite the breadth of definitions, ecological theory has tended traditionally to rely on the assumption that a system is stable if, and only if, it is governed by stable equilibrium dynamics (that is, equilibrium stability and equilibrium resilience). As discussed in the previous section, these are strong assumptions with no *a priori* justification. In fact, the variable nature of population dynamics found both in field and in laboratory experiments has led experimentalists to use measures of variability as indices of a system's stability. This discontinuity between stability experiments and equilibrium-based theory has made it difficult to unite theory and experiment in the diversity–stability debate.

More general definitions of stability exist. In Table 1, general stability is defined such that stability increases as population

densities move further away from extremely low or high densities. This is a broad definition, including equilibrium and non-equilibrium dynamics as well as subsuming the definition of permanence[18] (a population is considered permanent if the lower limit to its density is greater than zero). Because the definition of general stability implies decreased variability (owing to greater limits on density), it is closely related to field measurements of stability, which tend to rely on variability in population or community densities as a measure of stability. One can also extend equilibrium resilience to a less biologically restrictive form by defining resilience as the return time after a perturbation to an equilibrium or a non-equilibrium attractor (Table 1). In a nonlinear system there is no reason to believe that an equilibrium that attracts weakly in a local setting (near the equilibrium) also attracts weakly far away from the equilibrium, where the issue of a species' permanence is resolved[18]. For the remainder of the paper, unless stated otherwise, the definitions of general stability and variability will be used to consider empirical and theoretical results on the relationship between diversity and stability under a common framework.

The search for a general diversity–stability relationship

In 1982, David Tilman began a long-term study to delineate experimentally the relationship between diversity and stability in plant communities. The undertaking involved four grassland fields at Cedar Creek Natural History Area, Minnesota, divided into over 200 experimental plots, and gathered information on species richness, community biomass and population biomass through time. The results of this and other extensive studies converge on the finding that diversity within an ecosystem tends to be correlated positively with plant community stability (that is, decreased coefficient of variability in community biomass)[20–23]. At the same time, diversity seems to show little influence on population variability[22]. The basic arguments for a positive relationship between diversity and stability for primary producers at the community level have been classified into two, not mutually exclusive, hypotheses called the averaging effect[24] and the negative covariance effect[25] (see Table 2 for the underlying logic behind these ideas). In essence, these hypotheses argue that diversity

(species richness) increases stability at the community level because diverse plant communities respond differentially to variable background processes. The differential responses of populations sum, through time, to give stable community dynamics.

If diversity and stability are positively correlated, then both the averaging and negative covariance effect predict that population variance has to scale as a function of mean population densities in a precise way (see Table 2). Tilman[20] has used these predictions to show that his field experiments are consistent with the interpretation that increasing diversity increases community stability. Although this is a clever combination of theory and experiment, it cannot be used to infer that diversity is responsible directly for stability[26,27]. As a counter example, no correlation was found between diversity and stability at the cross-ecosystem scale[26]. Other experiments have found that the positive diversity–stability correlation is not a pure species effect (that is, a diversity effect), and have indicated that ecosystem function and stability are more directly related to functional diversity (for example, graminoids or grasses, nitrogen-fixing legumes and other herbs)[27–30].

In a similar manner, plant community stability and productivity in European grasslands were shown to be tightly coupled to the functional diversity of mutualistic arbuscular mycorrhizal fungi (AMF)[31]. In this system, large fluctuations in plant biomass were associated with low diversities of AMF, whereas more constant biomass and greater productivity accompanied high AMF diversities. This study highlights that higher-level interactions, which are inherent in food webs (for example, microbial interactions, herbivory and predation), are of great importance in understanding the relationship between the diversity and stability of whole ecological communities. The complexity of whole ecological communities — the basis from which Odum, Elton and MacArthur formed their diversity–stability hypotheses — cannot manifest itself in experiments that focus on single trophic levels.

Field tests at the scale of the food web are few in number. But one thorough examination[32] tested seven different stability–diversity criteria in the grazing ecosystem of the Serengeti under naturally variable conditions (that is, strong seasonal changes). Of these seven stability measures, five were positively related to diversity whereas two were unrelated to diversity. The study found that greater diversity reduced the relative magnitudes of fluctuations in productivity induced by seasonal change. Although a relationship between stability and diversity exists within the Serengeti, the evidence again points to the importance of functional species in understanding this relationship. For example, the grazing-tolerant plant species have a disproportionately large role in the Serengeti community dynamics by preventing herbivores from dramatically reducing plant biomass.

The paucity of field tests at the scale of the food web reflects the fact that such experiments require an enormous undertaking. As an alternative, ecologists have approached this problem by investigating how diversity influences stability and function within a multitrophic setting in controlled microcosm experiments (often referred to as bottle experiments as they are attempts to create realistic ecological communities within a controlled setting). The main advantage of microcosms is that the experiments can easily be manipulated and replicated[33]. Nonetheless, the issue of how scale influences outcome looms over microcosm experiments — can we extrapolate results to the whole ecosystem? Ambitious experimental set ups such as that currently underway in the Ecotron (Fig. 1) are attempting to bridge the gap between the complexity of real field communities and the simplicity of laboratory or greenhouse experiments.

The evidence that has emerged from microcosm experiments, regardless of scale and system type (that is, terrestrial or aquatic), has tended to agree that diversity is positively related to ecosystem stability[34–39]. In addition, and consistent with field experiments on plant communities, experiments using aquatic microcosms have shown that population-level variation is relatively uninfluenced by diversity, whereas community-level variance tends to decrease with increased diversity[35]. Two ideas have been advanced in explanation of these findings. One explanation is that increasing diversity increases the odds that at least some species will respond differentially to variable conditions and perturbations[37–39]. The second is that greater diversity increases the odds that an ecosystem has functional redundancy by containing species that are capable of functionally replacing important species[37–39]. Taken together, these two notions have been called the insurance hypothesis (Table 2). This idea has been extended to suggest that the greater the variance in species' responses contained in a community then the lower the species richness required to insure the ecosystem[40]. As with the averaging and negative covariance effect,

Table 1 Definitions of stability

Term	Definition
Definitions of dynamic stability	
Equilibrium stability	A discrete measure that considers a system stable if it returns to its equilibrium after a small perturbation away from the equilibrium. A stable system, therefore, has no variability in the absence of perturbations.
General stability	A measure which assumes that stability increases as the lower limit of population density moves further away from zero. Under non-equilibrium dynamics, such limits to population dynamics generally imply a decrease in population variance (see variability definition below).
Variability	The variance in population densities over time, usually measured as the coefficient in variation. Common in experimental tests of stability.
Definitions of resilience and resistance stability	
Equilibrium resilience	A measure of stability that assumes system stability increases as time required to return to equilibrium decreases after a perturbation. A rapid response means that a system recoils rapidly back to its equilibrium state.
General resilience	A measure of stability that assumes system stability increases as return time to the equilibrium/non-equilibrium solution decreases after a perturbation. A rapid response means that a system recoils rapidly back to its equilibrium/non-equilibrium state.
Resistance	A measure of the degree to which a variable changes after a perturbation. Frequently used as a discrete measure that assesses a community's ability to resist invasion (that is, if an invader fails, the community resists invasion).

Table 2 General diversity–stability theory

| Theory	Underlying logic
Averaging effect[24,25]	Assume covariances between species are zero and variance (s_i^2) in abundance of individual species i in a plant community is equal to cm_i^z, where c and z are constants and m_i is the mean density of species i. Given that all k species of a community are equal in abundance and sum to m (that is, $m_i = m/k$), then the coefficient of variation (CV) of community abundance can be determined as: $$CV = 100s/m = 100(c/k)^{1/z}$$ For the case $z > 1$, increasing k (species number) decreases the variation in biomass for the plant community.
Negative-covariance effect[25]	If covariances between species (say, species a and b) are negative (that is, cov(a,b) < 0), then the variance in the abundance of two species $$s_{(a+b)}^2 = s_a^2 + s_b^2 + 2cov(a,b)$$ will be less then the sum of the individual variances (that is, $s_a^2 + s_b^2$), and so will decrease overall biomass variance in the plant community.
Insurance effect[37–40]	An ecosystem's ability to buffer perturbations, loss in species and species invasions is dependent on the redundancy of the species having important stabilizing roles, as well as on the ability of the species in the community to respond differentially to perturbations. Increasing diversity increases the odds that such species exist in an ecosystem. This idea has been extended[40] to suggest that the greater the variance of species' responses in a community then the lower the species richness required to buffer an ecosystem.
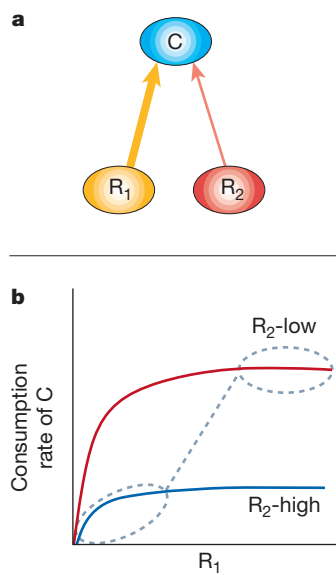
Figure 2 Consumer–resource interactions. **a**, A simple food-web diagram depicting a strong consumer–resource interaction (C–R$_1$) coupled to a weak consumer–resource interaction (C–R$_2$). **b**, Consumption rates by consumer C of R$_1$ for two different densities of R$_2$. Because the resources negatively covary, the actual consumption response is qualitatively similar to a combination of these two curves (dashed circles and line). In the presence of R$_2$, resource R$_1$ is less influenced by consumption when at low densities.

which are intimately related, the insurance hypothesis does not infer that diversity actively promotes stability.

In summary, the results indicate that within an ecosystem, diversity tends to be correlated positively with ecosystem stability. This correlation does not necessarily extend to population-level stability. Much work is still required to determine the driver of the positive diversity–stability relationship; however, it seems that community-level stability is dependent on the differential response of species or functional groups to variable conditions, as well as the functional redundancy of species that have important stabilizing roles. I now turn to a separate approach that has not focused on diversity, but has concentrated instead on understanding the implications of common food-web structures on stability.

Food-web structure and stability

In an important theoretical contribution, Chesson and Huntley[41] showed that diversity cannot be maintained by variation alone. Rather, maintenance of diversity requires the two following components: the existence of flux or variability in ecosystems; and populations capable of differentially exploiting this flux or variability. Regardless of the source of the variability (for example, whether spatially or temporally generated), their results indicate that coexistence requires that populations must be released, either directly or indirectly, from the limiting influences of species interactions such as predation and competition. Species interactions, therefore, must be important in maintaining and promoting persistence in diverse communities in spite of, and perhaps because of, the variability that underlies ecosystems. Several more specific models can be included under this general framework, and all reveal that flux interacting with specific biotic, nonlinear responses can promote persistence[6,14,17]. We now turn to a set of food-web models that have shown how persistent, complex ecosystems can be an outcome of this combination of flux and density-dependent food-web interactions (that is, competitive and predatory influences that vary with density).

The weak-interaction effect

Over the past decade, ecologists have begun to replace the conceptu-

alization of the ecosystem as a linear food chain with the view that food webs are highly interconnected assemblages[42–45] characterized by recurrent food-web structures (for example, omnivory and apparent competition). Because combinations of competition and predation can represent these common food-web structures, the use of simple food-web modules has been advocated[46] to explore the repercussions of these ubiquitous species interactions.

Several model investigations have grown out of this approach to show that natural food-web structures can, indeed, enhance ecosystem stability[6,47–49]. These food-web models are extensions of a bioenergetic consumer–resource model[50] that constrains parameters to empirically determined relationships of body size. The approach is akin to the dynamic modelling of a population's energy budgets through time, and has the important consequence of placing food-web models within a biological universe with reasonable constraints operating on energy flow between any consumer–resource interaction — a feature that is considerably different from a statistical universe. The result is that increasing diversity can increase food-web stability under one condition: the distribution of consumer–resource interaction strengths must be skewed towards weak interaction strengths. I will refer to this as the weak-interaction effect (Table 3), and to connect this to general diversity–stability theory I briefly discuss the stabilizing mechanisms behind this effect.

Two general stabilizing mechanisms underlie the weak-interaction effect. First, the weak-interaction effect generates negative covariances and promotes community-level stability. Second, these negative covariances ensure that the weak interactors dampen the destabilizing potential of strong consumer–resource interactions. These mechanisms can be best understood with a simple example.

Figure 2a depicts a simple food-web interaction in which a strong consumer–resource interaction (C–R$_1$) is coupled to a weak consumer–resource interaction (C–R$_2$). Being a weakly interacting species, R$_2$ is an inferior competitor whose ability to persist is mediated by the top predator. This food-web relationship ensures that the resources negatively covary. For example, R$_2$ is released from competitive limitation to flourish whenever R$_1$ is suppressed by high densities of consumer C. This occurs because R$_2$ is weakly coupled to C and so is not strongly influenced by high densities of C. In this manner, the weak interaction drives the differential responses of species.

We can use the knowledge of this negative covariance to determine qualitatively the consumption rate of C on its preferred resource, R$_1$. Figure 2b depicts C's consumption rate on R$_1$ under two different densities of R$_2$, assuming an optimally foraging, type II multispecies functional response (for full details, see refs 49, 51). High densities of R$_2$ reduce the overall consumption rates on R$_1$. Because the resources negatively covary, then for low densities of R$_1$ we expect C's consumption rates to fall on the R$_2$-high curve in Fig. 2 (the lower dashed circle). Similarly, for high densities of R$_1$ we expect consumption rates to be on the R$_2$-low curve in Fig. 2 (the upper dashed circle). Piecing these functions together we see that the asynchrony in resource densities drives a sigmoid-shaped response that is qualitatively similar to what ecologists refer to as a type III functional response. This has the non-equilibrium effect of releasing the prey (R$_1$) from strong consumptive pressures when it is at low densities, and thereby the weak interaction dampens the oscillatory potential of the strong C–R$_1$ interaction. Consistent with the above discussion is the fact that investigators have found that donor control (in which a consumer responds numerically to a resource but has no influence on resource dynamics) also promotes community stability[45,48]. Donor control can generate differential responses of species by allowing species using these resources to disconnect themselves from fluxes that are inherent to the community.

I have discussed the weak-interaction effect within the context of relatively simple food-web modules. Does the effect operate for real, complex communities with enormous numbers of direct and indirect interactions? It is still too early to tell, but Kokkoris et al.[52] followed the distribution of interaction strengths as competitive

model communities were assembled. They found that as the assembly process progressed, larger permanent communities (that is, with a lower limit above zero) attained lower mean interaction strengths. They also found that communities with lower mean interaction strength were more resistant to invasion. These results are encouraging and indicate that the weak-interaction effect might scale to the whole ecosystem. If the weak-interaction mechanism is operating in real communities then the distributions of interaction strengths will be skewed towards weak interactions in order that a few potentially excitable consumer–resource interactions are muted. I now turn to empirical investigations of food-web structure and stability, first reviewing experiments concerned with the distribution of interaction strengths in natural communities before examining experiments that have investigated directly the influence of food-web structure on stability.

Interaction strength and species invasions

Although quantitative field estimates of interaction strength are still in the process of development, work by a few ecologists has enabled a preliminary glimpse into the nature of the distributions of interaction strength within real food webs[53–57]. The early data indicate unequivocally that distributions of interaction strength are strongly skewed towards weak interactions[53–57]. Nonetheless, these experiments also highlight that the removal or addition of a single key species can have pronounced impacts on the dynamics and persistence of the species in the enclosure or exclosure. For example, experimental removal of the predatory starfish, *Pisaster ochraceus*, resulted in greatly simplified lower-intertidal communities because the mussel, *Mytilus californianus*, competitively dominates all other sessile benthic organisms when freed from predation[58].

A recent experiment[59] has confirmed the abundance of weak interactions in ecosystems, but showed that weak average interaction strength in a rocky intertidal community tends to be correlated with high variability in interaction strength. In this study, variation in the magnitude of the weak interactions seemed to excite spatial variation in community structure. The variation in interaction strength may be important in generating landscape-scale variation that promotes the maintenance of diversity, an area that demands further investigation.

It is important to know if these phenomena can be extended beyond the scale of the enclosure/exclosure experiment. Species invasions may be seen as the uncontrolled version of species addition experiments. Similar to the experiments described above, the current evidence indicates that, although most species invasions have a weak impact on ecosystems[60], the occasional invasive species alters an ecosystem profoundly[61–63]. For example, a recent study[61] used stable isotopes to document energy flow through food webs. Lakes that were uninvaded by bass were compared with lakes that had just been invaded, and the recently invaded lakes showed marked differences in energy flow patterns (implying a severely altered food-web structure) as well as rapid declines in forage fish diversity[61]. These results indicate that the addition of a single species can precipitate a form of ecosystem collapse that sends a wave of extinction through the ecosystem. Another noteworthy case concerns the introduction of the large predatory fish, the Nile perch (*Lates niloticus*), in Lake Victoria in the 1950s. The addition of the Nile perch was followed by a sequence of amazing ecological and genetic changes that culminated in a cascade of cichlid extinctions[63]. Overall, however, the invasion literature is harmonious with enclosure/exclosure experiments[60] — most invasions have a weak impact with infrequent occurrences of an invasive species capable of precipitating monumental changes to an ecosystem.

Food-web structure and stability experiments

Some direct experimental tests of stability and food-web structure exist. In a clever experimental manipulation, Fagan[64] tested community response to a perturbation (aphicide application) as a function of the degree of omnivory. Fagan accomplished this by controlling

Table 3 Food-web structure and stability theory

Theory	Underlying logic
Weak-interaction effect[6,46–48]	Weak interactions serve to limit energy flow in a potentially strong consumer–resource interaction and, therefore, to inhibit runaway consumption that destabilizes the dynamics of food webs. In addition, the weak interactions serve to generate negative covariances between resources that enable a stabilizing effect at the population and community level. The negative covariances ensure that consumers have weak consumptive influences on a resource when the resource is at low densities. See text and Fig. 2 for further clarification.
	Berlow[57] suggested an additional influence of weak interactions. Weak interactions in intertidal communities seem to be extremely variable in strength, and as a result may drive spatial variability in community structure. This community variability in space can provide a canvas for species to respond differentially, and so may further promote the maintenance of diversity.

the relative proportion of nonomnivorous damselbugs versus omnivorous wolf spiders in arthropod assemblages of the Mount Saint Helen 'blowdown zone'. The results showed that increasing the degree of community omnivory (that is, increasing the proportion of wolf spiders) decreased variation in the population responses after an aphicide application.

In an earlier investigation, de Ruiter *et al.*[65] investigated model communities constructed from empirical estimates based on some well-studied food webs from native and agricultural soils. Their results are consistent with the experiments on interaction strength and the weak-interaction effect discussed above, as most interactions had only a negligible impact on community dynamics. Although their results indicate that energetics are important in constraining interaction strength, they found no positive correlation between feeding rates and community impact. This, too, is consistent with the weak-interaction effect. Similarly, experiments on both terrestrial and aquatic microcosms have tended to find that increasing the number of prey items enhances stability[66–68], although one microcosm experiment[69] found that the addition of an alternate prey destabilized community dynamics. This last case can be reconciled with other experiments as the alternate prey introduced was efficient fare for the predator. In essence, the alternative prey energetically fuelled the predator, and so the experiment may be viewed as evidence that a strong consumer–resource interaction is potentially destabilizing.

Conclusion

Taken together, recent advances indicate that diversity can be expected, on average, to give rise to ecosystem stability. The evidence also indicates that diversity is not the driver of this relationship; rather, ecosystem stability depends on the ability for communities to contain species, or functional groups, that are capable of differential response . All of these views are consistent with the ideas put forth by the influential figures of Odum[7], Elton[8], MacArthur[9] and May[10]. May's result reflects the fact that random distributions (that is, a null universe where dynamics are influenced by diversity alone), on average, do not create the necessary tension between community members that forces differential response and community stability. In a randomly constructed community, for example, strong interactions are not necessarily coupled to weak interactions that mute their destabilizing potential. In fact, one can expect that random communities will generally not create such couplings, and so tend to produce diverse communities with complex, wildly oscillatory dynamics. Furthermore, Odum, Elton and MacArthur recognized that real food webs contain a complex array of energetic pathways that can act as buffers against dramatic population explosions. Specifically, MacArthur's hypothesis — that greater connectance drives community and ecosystem stability — seems a strong possibility provided most pathways are constructed from weak interactions that mute the potentially destabilizing roles of a few strong consumer–resource interactions.

The current empirical evidence indicates that communities may be dominated by such weak trophic interactions. If this is true, then it is also true that the removal, or addition, of any species (weak or strong) can lead to pronounced changes in community composition and structure. It follows that decreasing biodiversity will tend to increase the overall mean interaction strength, on average, and thus increase the probability that ecosystems undergo destabilizing dynamics and collapses. Just how much ecosystem deterioration is sufficient to precipitate a collapse is difficult to assess, but current experiments and theory agree that drastic community changes can accompany the removal or addition of even a single species. Furthermore, if Elton's observation is correct — that simplified communities are more vulnerable to invasion — than we should also expect an increase in frequency of successful invaders as well as an increase in their impact as our ecosystems become simplified. The lessons for conservation are obvious: (1) if we wish to preserve an ecosystem and its component species then we are best to proceed as if each species is sacred; and (2) species removals (that is, extinction) or species additions (that is, invasions) can, and eventually will, invoke major shifts in community structure and dynamics.

It is important to point out that the mechanistic ideas outlined here omit higher-scale ecosystem influences that are likely to be linked intricately to ecosystem stability and function[70–73]. Some promising work is now beginning to show us how we can link models of nutrient and energy flow[70–72] as well as uncover the potential influence of diversity and stability on large-scale biogeochemical processes[73]. Investigations of this sort will be necessary to bridge important stabilizing processes that act across ecological scales. □

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