

Plant diversity and ecosystem productivity: Theoretical considerations

(biodiversity/resource competition/soil fertility/nutrient use/retention)

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ABSTRACT Ecosystem processes are thought to depend on both the number and identity of the species present in an ecosystem, but mathematical theory predicting this has been lacking. Here we present three simple models of interspecific competitive interactions in communities containing various numbers of randomly chosen species. All three models predict that, on average, productivity increases asymptotically with the original biodiversity of a community. The two models that address plant nutrient competition also predict that ecosystem nutrient retention increases with biodiversity and that the effects of biodiversity on productivity and nutrient retention increase with interspecific differences in resource requirements. All three models show that both species identity and biodiversity simultaneously influence ecosystem functioning, but their relative importance varies greatly among the models. This theory reinforces recent experimental results and shows that effects of biodiversity on ecosystem functioning are predicted by well-known ecological processes.

Recent studies have shown that several community and ecosystem processes are correlated with species diversity (1–12), but why this should occur remains mathematically largely unexplained. Here we report that three different ecological models predict that ecosystem productivity, standing crop, and resource use depend on species diversity, much as has been experimentally observed (3, 4, 6). Our models provide simple mechanisms that explain how such dependencies can arise and help resolve the controversy over the importance for ecosystem functioning of species identity versus species diversity.

The functioning of ecosystems has long been known to depend on the identities of the species the ecosystems contain (13–19), and hypothesized to depend on the number of species. However, recent work, plus early observations by Darwin (20), have left open two major questions: Are effects of biodiversity on ecosystems the logical outcome of fundamental ecological processes, such as interspecific competition for resources, or must deeper explanations be sought? And, what are the potential impacts of the rapid increases in global extinctions (e.g., ref. 21) and of the extreme simplifications of human-dominated ecosystems (e.g., ref. 22) on ecosystem functioning?

Because the functioning of an ecosystem may depend both on the identities and the numbers of its species, it is necessary to distinguish between these two dependencies in both experimental and theoretical studies. This requires, first, that the group of all potential species, called the “species pool,” be defined. Then, to attribute effects to species diversity, effects must occur in comparisons of the average responses of two or

more levels of diversity. At each level of diversity, there must be numerous replicate ecosystems, each with a random and independent combination of species chosen from the species pool. By having many random species combinations drawn from a large species pool, the mean response among replicate ecosystems at a given level of diversity becomes independent of particular species combinations. The differences among mean responses for different levels of diversity then measure the effect of diversity. The variance among the various species combinations at a given diversity level measures the effects of alternative species compositions.

We apply this approach to two models of interspecific plant competition for nutrients to determine the predicted effects of plant species diversity on primary productivity and nutrient use. The first is a model of competition for a single resource, the second a model of competition for two resources (7). For both models we derive the predicted effects of plant diversity on equilibrium total plant community standing crop (a measure of primary productivity), which we henceforth call “total plant biomass,” and on ecosystem nutrient consumption. A third model explores cases in which species are differentiated along orthogonal niche axes. We do not consider keystone species, functional groups, multitrophic-level interactions, and other complexities, all of which merit additional theoretical exploration. Rather, we consider simpler cases in hopes of abstracting some fundamental effects of diversity.

The Three Models

Competition for One Resource. As the simplest possible case consider homogeneous habitats in which all species compete for and are limited only by a single resource, and in which all individuals experience identical resource concentrations at any given moment. According to resource competition theory (23, 24), of all the species initially present in a habitat, the one species with the lowest requirement for the resource would dominate at equilibrium, displacing all other species. The resource requirement of each species is measured by its R^* , which is the concentration to which the resource is reduced by an equilibrium monoculture of that species. Although all habitats become monocultures at equilibrium, it is instructive to ask how initial species diversity influences their equilibrium total plant biomass and nutrient use. The answer, derived in mathematical detail below, is that, on average, total plant biomass increases with diversity because better competitors produce more biomass and because the chance of having better competitors present increases with diversity.

Let the species pool be a collection of plant species that are identical in all other ways but differ in their R^* values. In any community selected from this species pool, the one species with the lowest R^* would reduce the resource concentration to its R^* , competitively dominate the community, and ultimately determine total plant biomass and resource use.

In this model, better competitors produce more biomass because they obtain more of the limiting nutrient. If the supply

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rate of the resource is S and species i is the best competitor present (smallest R^*), living plant biomass is approximated by

$$B = aQ(S - R_i^*), \quad [1]$$

where a is the rate of resource mineralization and Q the coefficient of resource conversion into biomass (23, 24). If no species is present, the equilibrium resource concentration (i.e., the effective R^*) is S , giving $B = 0$.

The effect of diversity on total plant biomass depends on how diversity influences, on average, the R^* value of the best competitor present in a community. To determine this, let the species composition of a community be a random draw from a species pool. In this case, the pool consists of all possible R^* values along the interval $[R_{min}^*, R_{max}^*]$, and thus the species pool is infinitely large. Results similar to those below also occur for finite species pools. The number of species drawn, N , is the habitat's original species diversity. Given this, it is shown below that the average (expected) value of the smallest R^* for a random subset of N species, when R^* values are uniformly distributed on $[R_{min}^*, R_{max}^*]$, is

$$E[\text{Min}\{R^*\}] = R_{min}^* + ((R_{max}^* - R_{min}^*)/(N + 1)). \quad [2]$$

This average value of the smallest R^* monotonically decreases toward R_{min}^* as diversity (N) increases, which causes total plant biomass to increase with diversity.

To see the derivation of Eq. 2, first let the R^* values of species be uniformly distributed on the interval $[0, 1]$; then select N points randomly and uniformly from this interval. Each selected point is the R^* of a species. The probability that the lowest R^* value is in the subinterval $(x - \Delta x, x)$ approaches $N(1 - x)^{N-1} \Delta x = P(x)\Delta x$ as Δx approaches 0. The expected value of the lowest R^* drawn is therefore

$$\begin{aligned} E[\text{Min}\{R^*\}]_{(N)} &= \int_0^1 xP(x)dx \\ &= \int_0^1 xN(1 - x)^{N-1}dx = 1/(N + 1). \end{aligned}$$

Thus, for randomly drawn sets of N species, the average value of the smallest R^* is $E[\text{Min}\{R^*\}] = 1/(N + 1)$. This average value of the smallest R^* is simply $1/2, 1/3, 1/4, \dots$ for species richness of 1, 2, 3, etc. It becomes the expected value given in Eq. 2 when the interval is generalized to $[R_{min}^*, R_{max}^*]$.

The environmental concentration of the limiting resource given in Eq. 2 is the value that occurs on average over many random species combinations at each level of species diversity. This value decreases as species diversity increases because higher diversity leads to a higher probability that a species with a lower R^* is present in the initial species mixture. That species will be competitively dominant and drive the level of unconsumed resource to its R^* . Substituting this result into Eq. 1 gives the average (expected) total plant biomass, $B_{(N)}$, for a community that originally contained N randomly drawn species:

$$B_{(N)} = aQ\left(S - \left(R_{min}^* + \frac{R_{max}^* - R_{min}^*}{N + 1}\right)\right). \quad [3]$$

For $S > R_{max}^*$, total plant biomass, $B_{(N)}$, asymptotically increases with species richness (Fig. 1A).

This predicted dependence of expected total plant biomass on diversity occurs simply because the chance of better competitors being present increases with original diversity and because better competitors, when present, become dominant, reduce the concentration of the limiting nutrient, and increase productivity.

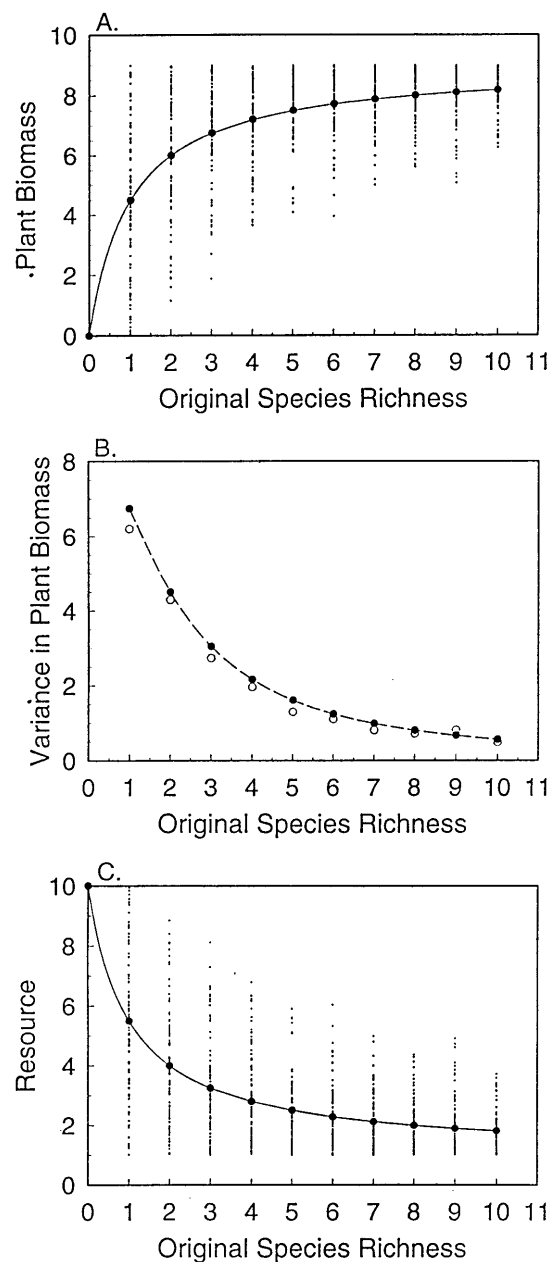


FIG. 1. Multispecies competition for a single resource. (A) Biomass increases with original species richness in simulations in which R^* values for each of N species were drawn randomly from a uniform distribution on the interval $[1, 10]$, and the best competitor among them (the lowest R^*) identified. \bullet , the biomass of that best competitor, computed with $a = 1, Q = 1$, and $S = 10$, for each of 100 cases at each level of N . The solid curve and \bullet were analytically calculated using Eq. 3. (B) Variance in biomass calculated from simulations (\circ) and analytically with Eq. 4 (\bullet , curve) using parameters above. (C) Ambient level of resource remaining unused in the habitat versus original species richness. \bullet , resource levels for individual simulations and \bullet and curve are predicted by Model 1.

Assuming that all else is equal, the average effect of diversity increases with the magnitude of interspecific differences, i.e., $R_{max}^* - R_{min}^*$, as stated in Eq. 3. If species were identical, diversity would have no effect. In more realistic models, species also would differ in Q , which is comparable to nutrient use efficiency. Nutrient use efficiency generally is higher in species that are better nutrient competitors (25). This effect would cause plant biomass to increase even more rapidly with diversity than indicated in Eq. 3. The potential effects of diversity then would depend on the magnitudes of interspecific variation in both R^* and Q .

Interspecific differences cause various species combinations to behave differently, leading to variance in equilibrium plant biomass among replicate ecosystems within the same level of species richness. The magnitude of this variance (Fig. 1A and B) is a measure of the effects of species identity (composition) on ecosystem productivity. The variance depends on N and can be analytically derived from the above distribution $P(x)$ and the mean $E[\text{Min}\{R^*\}]$. For species drawn randomly from the unit interval, $[0, 1]$, the variance in plant biomass among replicates at a given level of diversity becomes

$$\sigma^2 = \int_0^1 (1/(N + 1) - x)^2 P(x) dx = N/((N + 1)^2(N + 2)).$$

Hence the variance for N species drawn randomly and uniformly from the interval $[R_{min}^*, R_{max}^*]$ is

$$\sigma_{(N)}^2 = ((aQ)(R_{max}^* - R_{min}^*))^2 \left(\frac{N}{(N + 1)^2(N + 2)} \right). \quad [4]$$

This variance applies to an unlimited species pool. This variance is not caused by measurement or environmental stochasticity but by interspecific differences, i.e., $R_{max}^* - R_{min}^*$, and by random sampling of species. Variance declines with species richness (Fig. 1B), and would decline more rapidly with increased diversity for cases with a finite species pool.

Total plant biomass depends both on the original species richness of a community and on its species composition (Fig. 1A and Eqs. 3 and 4). One measure of the relative importance of these two factors is provided by an analysis of variance. The analytically predicted dependence of the average total plant biomass on species richness (Eq. 3) explains 37.2% of the variance in total plant biomass of Fig. 1A. The remainder of the variance, 68.2%, is caused by the effects of interspecific differences on the total plant biomass of communities that differ in their original species composition. Thus, for this case, diversity explains about one-third of the variance in total plant biomass, whereas species identity explains about two-thirds.

The decreased average R^* values that occur at higher diversity (Eq. 2; Fig. 1C) may have a long-term effect on soil fertility. These R^* values are concentrations of unconsumed soil nutrients. For soil nitrogen, these would be the sum of NO_3 and NH_4 dissolved in soil pore water. Because NO_3 is readily leached, lower NO_3 concentrations would decrease nitrogen leaching losses, causing ecosystems originally started with high diversity to have, on average, a greater level of total soil nitrogen, further increasing productivity. On average, ecosystems started with sufficiently low diversity could experience net losses of nutrients, i.e., declines in soil fertility. Similarly, if superior nutrient competitors have greater nitrogen use efficiency (25), the lower carbon:nitrogen ratio of their litter could lead to increased nitrogen immobilization, decreased leaching, and increased soil nitrogen stores in high-diversity ecosystems. Such effects, though, would saturate at high diversity.

In total, this simple model illustrates a potentially important effect of diversity—the sampling effect. All else being equal, greater original diversity increases the chance that species that have a given impact on a community or ecosystem process are present. If interspecific interactions cause such species to become dominant, then, on average, the rate or intensity of this community or ecosystem process will depend on diversity. This model also demonstrates that the effects of diversity are unavoidably the effects of species differences, and that it is possible to distinguish between the effects of the number of species versus their identity. Finally, for this case, the effects of various species combinations explain more of the observed variance in ecosystem performance than does diversity, rein-

forcing the long-held view of the importance of species composition for ecosystem functioning.

Competition for Two Resources. Biodiversity could have additional effects on ecosystem processes if species differed in their abilities to acquire two or more resources in a heterogeneous habitat, or had other “niche” differences. For instance, when consuming essential nutrients, such as soil nitrogen and phosphorus, each plant species has its optimal competitive ability at a particular ratio of nitrogen to phosphorus (22, 23). In a habitat in which supply rates of these nutrients are spatially heterogeneous, no species would be competitively superior throughout the entire habitat. Rather, each species would leave sufficient unconsumed resources in regions away from its optimum ratio that some other species could invade and persist there. Such invasion would decrease resource concentrations and increase standing crop. This can be easily illustrated graphically (Fig. 2A and B). Amounts of unconsumed but potentially consumable resources (shaded regions) decrease as diversity increases (Fig. 2A and B). Only an infinite number of species could totally consume all consumable resources (i.e., all points above the interspecific tradeoff curve).

We numerically evaluated this model of competition for two essential resources (the analytical model of ref. 23) for a heterogeneous habitat to determine the quantitative relationship between species richness and equilibrium standing crop for species drawn from a pool consisting of all possible plant species (i.e., all points of isocline tangency to the tradeoff curve). For numerous random draws of 1–19 species, we numerically determined mean equilibrium standing crop in the

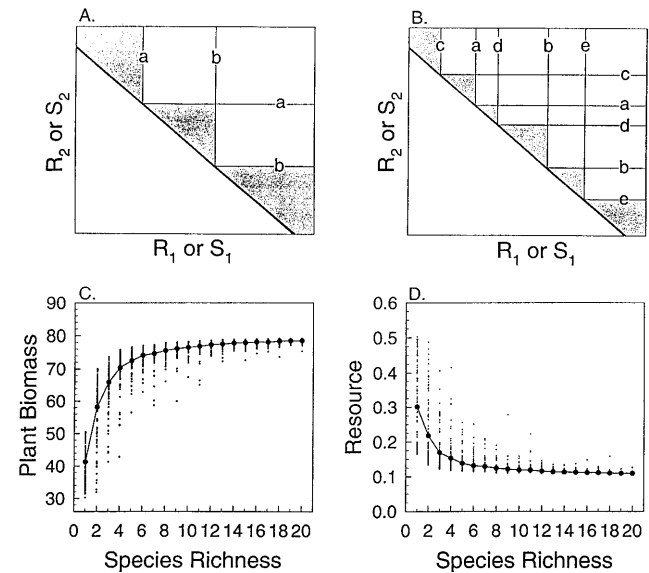


FIG. 2. Competition for two resources. (A) Competition among two species (a and b) for two limiting essential resources (as in ref. 23). Curves labeled a and b are resource-dependent zero net-growth isoclines for species a and b. The thick diagonal line is the interspecific tradeoff curve, i.e., the lowest concentrations of the two resources for which any plant species can survive. Resources outside the tradeoff curve are potentially consumable, but unconsumed. Shaded regions show unconsumed, but potentially consumable, resources. (B) A similar case, but with five species (labeled a–e). Note the greater resource use as indicated by the lower area (shaded) of unconsumed, but consumable, resources. (C) Results of simulations of the underlying analytical model (23) for a heterogeneous environment with 1000 different resource supply points and with N species drawn randomly from an unlimited pool of species with zero net-growth isoclines touching the tradeoff curve $R_2^* = 1/5$ m R_1^* . •, individual samples of N species; ●, means of those samples. Each mean summarizes 100 samples; each sample averages across a heterogeneous habitat containing 1000 supply points in an elliptical cloud. (D) Levels of resource 2 occurring in simulations for C.

spatially heterogeneous habitat. Standing crop increased, variance in standing crop decreased, and concentrations of unconsumed resources decreased with increasing diversity (Fig. 2 C and D). Similar patterns occurred for two other cases with finite species pools.

A Generalized Niche Model. Now consider a habitat in which two factors limit species abundances, i.e., there are two orthogonal axes of niche differentiation, such as temperature and soil pH. Presumably because of interspecific physiological and morphological tradeoffs and past interspecific interactions, each species would have some combination of these two factors at which it performed best, and its performance would decrease away from this point, much as for a bivariate normal distribution for which this point is its peak. Each species thus “covers” a portion of the habitat, but no single species can fully exploit the entire range of environmental conditions.

As a simple analytical approximation that captures the essence of this case, let each species have a range of conditions in which it can survive, as represented by the circles in Fig. 3A. Assume that the species pool consists of all possible circles of radius r that intersect the region shown. The effect of diversity (N) on the proportion [$P_{(N)}$] of environmental conditions “covered” by at least one species (which is assumed to approximate total community biomass) depends on the size of the niche of each species (i.e., the radius, r) relative to the range of environmental conditions. Consider any point in a rectangular habitat space of size ar by br . Let q be the probability that a randomly placed circle of radius r will not cover the point. Then $1 - q^N$ is the probability that at least one of N randomly placed circles will cover the point. Proportion q is simply one minus the ratio of the area of any circle (πr^2) to the area of the region where the centers fall, which in turn is the area of the habitat space (abr^2) plus the area of a border of uniform width r around the habitat space ($2ar^2 + 2br^2 + \pi r^2$). Combining and simplifying gives

$$P_{(N)} = 1 - \left(1 - \frac{\pi}{ab + 2(a + b) + \pi} \right)^N \quad [5]$$

This result assumes that species are chosen at random, with the second term being the probability that a site is not covered by a set of N species. It predicts that total community biomass asymptotically increases with diversity (Fig. 3B), with the rate of approach to the asymptote depending on the amount of spatial heterogeneity in the two niche axes (i.e., on a and b) relative to niche size (r), and on niche shape. Variance in coverage increases at low diversity and then asymptotically approaches zero as diversity approaches infinity (Fig. 3C). Analysis of variance showed that the analytically predicted dependence of $P_{(N)}$ on species richness (Eq. 5) explained 88.6% of the variance in total community biomass, with the remainder being caused by differences among various species combinations.

Preliminary work on a different model, one of multispecies competition in spatial habitats (26), gave results qualitatively like those reported here, except there were special cases in which total community site occupancy decreased with diversity. The effects of diversity on ecosystem functioning also should be explored, both experimentally and theoretically, for other cases, including more trophically complex ones.

Discussion

Each of our models was built on a fundamental mechanism of interspecific interaction. Each demonstrates how biodiversity interacts with that mechanism to influence productivity and resource use. Our models show that the effects of diversity come from variation among species. Greater original species diversity incorporates, on average, greater variation in species traits. This variation is magnified by interspecific interactions,

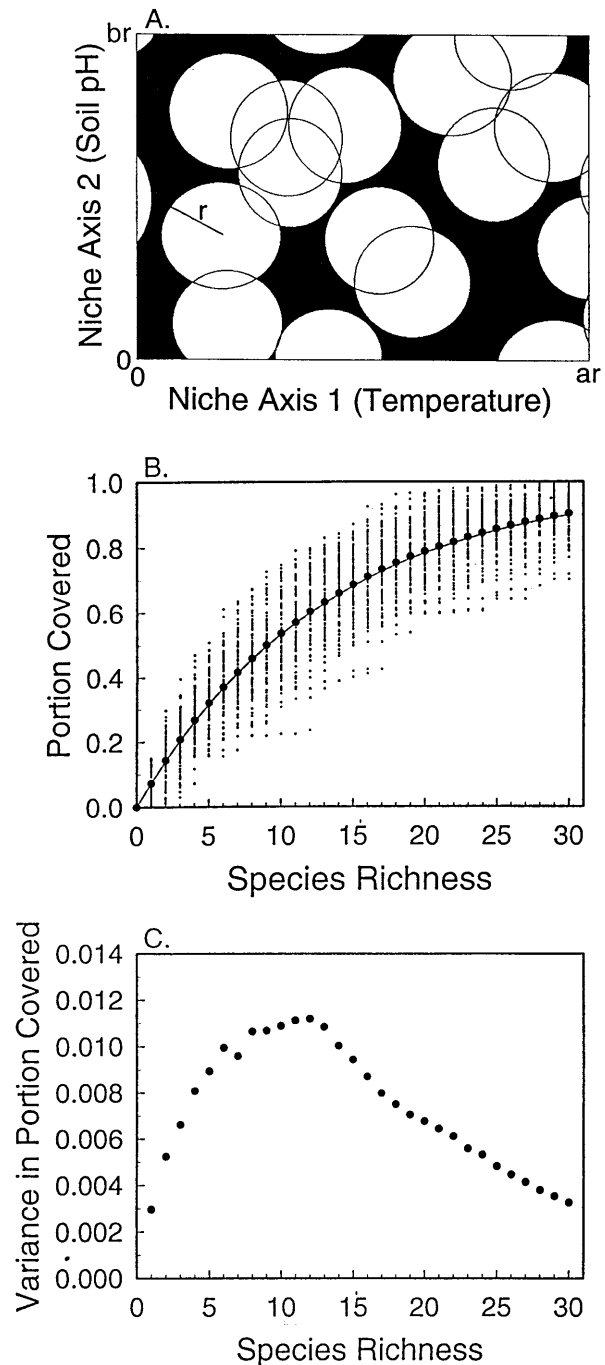


FIG. 3. Orthogonal niche axes. (A) Circular niches of radius r randomly intersecting a habitat space with orthogonal axes of lengths ar and br . (B) Expected portion of habitat space covered by species increases asymptotically with number of species in the community. One-thousand trials were made for each value, N , of species richness. In each trial, a set of N circular niches of radius 0.218 were randomly placed on a habitat space in which axes ranged from 0 to 1, and the portion of the habitat space covered by this set of N species determined. At least some part of the niche (circle, A) of a species had to intersect the habitat space. ●, means of 1000 trials; ○, 100 random trials for each value of N . The solid curve is the theoretical value from Eq. 5. (C) Variance in coverage declines to zero from a peak at intermediate values of species richness.

which cause the average ecosystem response to differ from the response to the average species. For the cases of multispecies resource competition considered here, greater diversity led to greater resource use and thus greater total community biomass. The magnitude of the response to diversity depended on

the extent of interspecific differences. In all cases, the greater resource use associated with higher plant diversity would reduce ecosystem nutrient losses, leading to long-term increases in ecosystem carbon and nutrient stores, which would increase productivity. In total, these models show that well-known, fundamental mechanisms of interspecific interaction, when extended to multispecies communities, cause ecosystem processes to depend on plant diversity in ways qualitatively similar to those experimentally observed (3, 4, 6).

The variance that occurs among replicate ecosystems that have the same number of species comes from the effects of different species combinations. This variance can be large, but there also can be a large difference between the average responses of ecosystems with low versus high diversity. Numerical solutions of the first two models show about a doubling of average total plant biomass when comparing monocultures with high-diversity ecosystems, and the third model shows about a 10-fold effect for this same comparison (Figs. 1–3).

The predicted variance among replicate ecosystems may explain the seemingly “idiosyncratic” dependence of ecosystem functioning on diversity (27). This variance would make it difficult to detect the effects of diversity either if there were only a few replicate plots at each level of diversity or if there had been a biased draw of species. This highlights the need to compare the average responses of many random species combinations at each level of diversity, as proposed here. Only this approach can separate the effects of diversity, per se, from the effects of particular species combinations.

Although our models are vast simplifications of natural ecosystems, they suggest that biodiversity may have both a direct value to natural resource managers in modifying average ecosystem productivity and nutrient retention and an “insurance value” associated with lower variance in these, i.e., lower risk. These effects are expected to occur in managed agroecosystems in which habitats are made to be homogeneous (often with a single limiting resource, light), for which the sampling effect may predominate. They should also occur in more natural ecosystems that have several limiting factors and spatial heterogeneity in these factors. For instance, high tree diversity may maximize productivity, minimize soil nutrient loss, and reduce risk when managing forested ecosystems for fiber production or for global carbon storage.

In our first model, the lower bound of the variation about the mean standing crop (Fig. 1A) increased with diversity because of competitive elimination of unproductive species, but, interestingly, the upper bound was fixed by the productivity of the species with the lowest R^* , i.e., by R_{min}^* . This means that an “all-knowing” manager trying to maximize plant biomass in an equilibrium habitat in which there was a single limiting nutrient and no multitrophic level effects (e.g., no pathogens, herbivores, etc.) could achieve just as great total biomass growing the appropriate monoculture as could be obtained from a diverse mixture drawn from the pool of desired species. However, if the best performer were unknown or unknowable because of unpredictable temporal variation, a diverse initial planting still would maximize productivity. In contrast, for the second and third models, the upper bound of the variation in total biomass (Figs. 2C and 3B) increased with species richness, indicating that no single species could have total biomass as great as some combinations of two species, no combination of two species could do as well as some combinations of three species, and so on. Thus, for cases with heterogeneous habitats

and two or more limiting factors, not even the best manager could find a community of N species that was as productive and nutrient conserving as some communities of $N + 1$ species. Thus, the theoretical predictions presented here, and their correspondence with recent experiments, suggest that the current rapid rates of species extinctions and of species loss from managed ecosystems may have significant effects on their productivity and sustainability.

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