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Diversity, productivity and temporal stability in the economies of humans and nature

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Abstract

Recent advances in ecology are of great potential relevance to economists. Here we present two ecological models of mechanisms of competition and coexistence, and use these to derive how the primary productivity of ecosystems, the amount of carbon dioxide removed from the atmosphere and stored by plants, the efficiency of resource use, and the spatial and temporal variability of productivity and resource use should depend on diversity. We then discuss the relevance of these results to (1) ecosystem services and the economic value of diversity and (2) the functioning of any competitive system, including the economy. © 2004 Elsevier Inc. All rights reserved.

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1. Introduction

Ecology, the study of nature's economy, and economics, the study of human economies, share much in common. Ecosystems are composed of many organisms interacting mainly in resource–consumer networks just as a market economy is composed of many interacting producers and consumers. Each entity, whether a species in an ecosystem or an individual or corporation in an economy, is presumed to be acting in accordance with its own self-interest [4,23]. Both natural and human economies are structured by the interactions, often competitive,

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among the various entities. Entities that find successful formulas for dealing with their environment, be they organisms in an ecosystem or firms in the marketplace, thrive, grow and replace those that do not. Selection pressures operate in both nature and the market, with surviving entities thus being relatively more efficient. Over time entities evolve, pushed by conscious search or by recombination and differential success, to more successful formulas for dealing with their environment. As a result of this evolution, the interactions among entities and the functioning of the system itself change over time.

Because ecology and economics share much in common, models and insights developed in one field may find ready application in the other. In fact, there has been a long history of such cross-fertilization between economics and biology. Charles Darwin credits Thomas Malthus for insights that lead to the theory of natural selection. More recently, economists have used ideas developed in evolutionary biology, such as the idea of evolutionarily stable strategies [16], to study the dynamic behavior of players in game theoretic models.

During the past two decades, a body of theory has developed in ecology that has been built from microeconomic views of optimal foraging and competition among individuals to macroeconomic predictions of such ecosystem processes as productivity, efficiency of resource use, and temporal stability (e.g., [6,12,13,15,19,26,28,29,31]). Consumer–resource interactions, specifically competition among many different consumer species for limited resources, form the core of these models. Here we summarize some of this work, and show how biodiversity, defined as the number of consumer species (which differ in their traits), influences ecosystem productivity, efficiency of resource use, and temporal stability.

This work is potentially relevant to economists for at least three reasons. First, improved understanding of ecology can directly improve economic modeling. There has been a long tradition of bio-economic modeling in resource economics, notably forestry and fishery models. Bio-economic models typically focus on a single species without spatial or temporal variation. Incorporating recent advances in ecology on the effects of interspecies competition and spatial and temporal variation can enrich bio-economic models (e.g., [3,5,21]). Second, natural and managed ecosystems provide many valued goods and services besides those derived from direct harvesting of resources. Examples of such ecosystem services range from generation and maintenance of production of potable water, to soil productivity to the regulation or modification of climate. Understanding “natural production functions” (i.e., ecosystem processes) is necessary for predicting possible impacts on ecosystem services from human actions and developing sound environmental policy. Third, as noted above, ecologists work on systems that in many ways resemble economic systems but often ask different questions or come at problems from a different viewpoint, and thus may generate insights that will prove useful to economists.

In this paper, we present two simple models of multispecies competition for resources that illustrate some recent advances in ecological theory, and we present a recent experimental test of these models. The first model assumes that a habitat has a single resource that limits the growth and abundance of all consumer species, and that there is also a limiting physical factor, such as temperature. An economic analogy would be a case in which a limited number of workers are hired by firms producing differentiated products facing potentially varying demand. Just as certain environmental (temperature) conditions are favorable for some species allowing them to out-compete other species and control more resource, consumer fads will be favorable for certain products allowing firms that produce those products to expand and hire more labor. The second

model assumes that all species are limited by and compete for two nutritionally essential resources. An economic analogy is a model of production that depends on capital and labor inputs. Both models have considerable empirical and experimental support in ecology [6,28,31,35], and are especially important in describing competition and coexistence among plant species. Plant species are the primary producers of ecosystems. Their production provides food, fiber and fuel both to human societies and to the animal consumer species of ecosystems. Plant productivity contributes to many valuable ecosystem services such as carbon sequestration. Both models are capable of predicting the long-term persistence or stable coexistence of a large number of competing species if the species have the appropriate tradeoffs in their requirements for limiting resources and/or other limiting factors. These models may thus give insight into characteristics of firms that lead to concentration or to a diversified economy.

Because both models are capable of explaining the coexistence of an arbitrarily large number of competing species, they can be used to determine the effects of the number of species, or biodiversity, on the functioning of ecosystems [12,31,34]. Here we will present each model and explore how biodiversity impacts the macroecological processes of primary production, the efficiency of use of limiting resources, and, for the first model, the temporal stability of production in response to periodic disturbance. We next present two analytical abstractions of these models—abstractions that capture the essence of resource competition, and use these to determine analytically the impacts of biodiversity on productivity, resource use, and stability. In doing this, we discuss the relevance of this theory to both ecological and economic questions. Finally, as a test of these theories, we present recent experimental data that show how the number of plant species in an ecosystem impacts plant primary productivity and plant storage of carbon (i.e., long-term carbon dioxide removal from the atmosphere by plant communities).

In order to explore the effects of biodiversity on ecosystem processes, it is essential to separate these from effects attributable to particular species. It is well known in ecology that individual species differ in their traits, and that such differences impact ecosystem functioning. To separate such effects from those attributable to the number of species, per se, it is necessary to have communities assembled by random draws from a common pool of potential species. By then averaging over the functioning of many such randomly constructed communities of a given level of diversity, and comparing this to other random communities with different numbers of species, it is possible to determine if species number, per se, influences ecosystem functioning.

2. Two models of multi-species competition for resources

2.1. Competition with a single resource and a physical factor

Consider an ecosystem in which plants are limited by a single resource, such as soil nitrogen, and in which there is either spatial or temporal variation in a physical factor, such as temperature. Although levels of the physical factor and the resource jointly determine the growth rates of all species, only the resource is consumed in biomass production. Because consumption influences resource levels, and these in turn influence the growth rates of all species, resource competition is the mechanism whereby species influence each other's abundances. The level of the physical factor also influences growth rates and thus also influences the dynamics and outcome of competitive

interactions. At equilibrium in a physically homogeneous habitat, a single species is predicted to competitively displace all other species [28]. Multispecies coexistence occurs in this model if there is an interspecific tradeoff such that each species is a superior competitor for a limited range of values of the physical factor, and if the physical factor is heterogeneous, i.e., variable in space and/or time [12].

We consider two measures of value generated by the ecosystem. First, productivity as measured by total plant biomass is a measure of value. Plant biomass is a good proxy for carbon sequestration, pollution filtration, or other valued ecosystem services. Plant biomass also can be harvested (e.g., timber, pulp, hay; however, our model does not formally consider harvesting behavior). Second, we consider a variant of the model in which the value of biomass differs among species. For example, some species may provide more of an ecosystem service per unit biomass, tree species differ in greater market value per unit of biomass or some grassland species may have greater nutritional value (protein) in forage or hay.

An economic analogy of the single resource model is to think of different species as different industries each with access to a different technology, and different individuals of a given species as different firms within the same industry, all having access to the same technology. As there is no analog in the ecological model to monopoly power, suppose there are enough firms within each industry to make each industry perfectly competitive. Each industry (synonymous with a technology) represents a different way of using a single input to produce a single output. In one economic interpretation, the efficiency of a technology for converting the single input into a homogeneous output depends upon stochastic environmental conditions. Technologies will be relatively efficient compared to rival technologies only for certain environmental conditions. A slightly different economic interpretation of this model is to think of each industry as using a single input to produce a single output that is differentiated from the outputs produced by other industries. Under this interpretation, the efficiency of each industry technology is fixed but demand for each differentiated product depends on stochastic consumer preferences. Under either interpretation, industries with access to profitable technologies will grow over time (acquire more resource input and produce more output) while industries with unprofitable technologies will shrink.

Formally, the model contains three types of dynamic variables: B_i , R and x , where B_i is the biomass (abundance) of species i (comparable to the capitalization of a firm), R is the concentration of the limiting resource (the amount of labor input available), and x is the value of the physical factor, which we will refer to as temperature (parameter defining the state of consumer preferences or the cost-effectiveness of a firm's method of production). The dynamics of B_i and R are then defined by the following differential equations, where there are as many equations for B_i as there are species (here there are N species, with N being species diversity):

$$\frac{dB_i}{dt} = \left(g_i(x) \frac{R}{R + K_i} - m_i \right) B_i, \quad (1)$$

$$\frac{dR}{dt} = \alpha(S - R) - \sum_{i=1}^N Q_i g_i(x) \frac{R}{R + K_i} B_i, \quad (2)$$

The function $g_i(x)$ is a Gaussian function that causes species i to have maximal growth at $x = \tau_i$: $g_i(x) = r_i \exp\left(-\frac{1}{2} \left(\frac{x-\tau_i}{w}\right)^2\right)$. K_i is the concentration of the resource at which species i grows at half of its maximal rate; m_i is the mortality rate of species i ; Q_i is the amount of resource that must be consumed to produce a unit of biomass of species i ; r_i is the maximal specific rate of biomass gain; S is the influx of the resource; and w and α are constants. Eq. (1) shows that the biomass of species i grows more rapidly at higher resource availability (R large) and when temperature (x) is closer to the optimum value for that species (τ_i). Biomass increases when the growth rate from resource intake, $g_i(x) \frac{R}{R+K_i}$, exceeds the mortality rate, m_i . Eq. (2) shows that growth of biomass, B , causes depletion of the resource stock, R . This model with its system of differential equations has a finite stable steady state because of the feedback between the equations; an increase in B decreases R , which then decreases $\frac{dB}{dt}$. Without resource consumption the environment would reach a saturating level of the resource ($R = S$). See Tilman [31] and Lehman and Tilman [12] for further explanation of this model.

For simplicity, assume that all species have identical values of r_i , K_i , Q_i , and m_i . Given this, the unique feature of each species is defined by its τ_i , which is the temperature at which it reaches its optimal competitive ability. At equilibrium, the level to which a species can reduce the concentration of the limiting resource determines the competitive ability of each species. The concentration to which species i reduces R at equilibrium in a habitat with temperature x , $R_{i,x}^*$, can be derived from Eq. (1):

$$R_{i,x}^* = \frac{mK}{g_i(x) - m}. \tag{3}$$

Note that $R_{i,x}^*$ is similar to an inverted Gaussian-curve function of x for each species (Fig. 1).

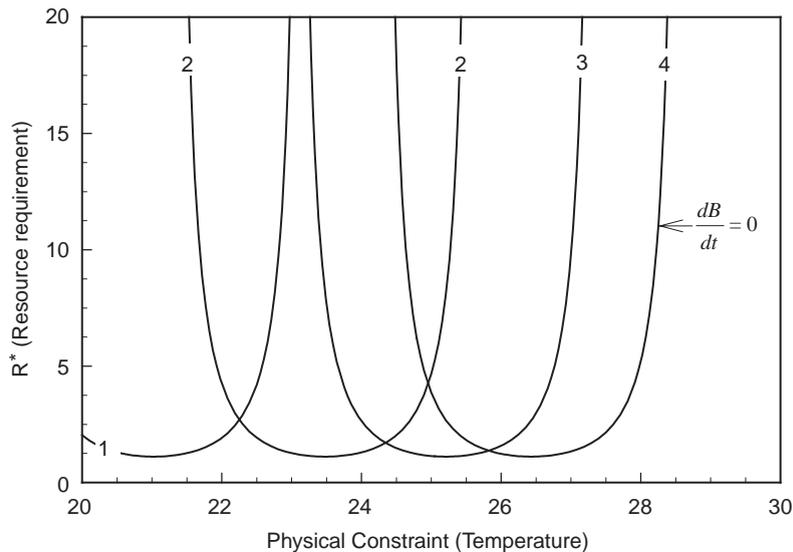


Fig. 1. Equilibril resource requirements (R^* values) for species 1–4 as a function of a physical constraint. Curves shown are isoclines on which $dB/dt = 0$ for species i . For illustration purposes, these species have wide niches ($w = 1$), whereas those used in simulations for Figs. 2 and 3 had narrower niches ($w = 1/10$).

When several species compete for a single resource in a homogeneous habitat that has a constant value of x , the best competitor, which would displace all other species at equilibrium, is the species with the lowest $R_{i,x}^*$ at that value of x [8,26,28]. Given the simplifying assumptions made above, the winning species would be the one that had its optimal temperature closest to x , i.e., the one with the smallest absolute value of $x - \tau_i$. In economic terms, under homogeneous and unchanging conditions we would predict there to be a single technology that would dominate all other technologies.

Continuing with an economic interpretation of the model, Eq. (1) represents whether a given industry contracts or expands based on profitability, which depends on availability of input and how well the industry is matched to current conditions. Eq. (2) tracks the availability of input, with greater economic activity across all industrial sectors leading to lower input availability. Eq. (3) predicts which industry would win in competition.

One could also interpret Eqs. (1) and (2) as a bioeconomic model of renewable resource harvest. Smith [24] and Sanchirico and Wilen [21] use equations similar to Eq. (1) to describe expansion or contraction of fishing effort in a fisheries model, where B_i would represent the harvesting effort of fishing boat i . Eq. (2) is similar to an equation describing the evolution of the renewable resource stock, where R represents the stock of a renewable resource. The first term on the right-hand side of Eq. (2) plays the role of the “natural growth rate”, i.e., the growth rate of the stock without harvest, while the second term plays the role of harvest. One difference between this model and a typical renewable resource model is that the “natural growth rate” component is linear in stock rather than concave, which may be more similar to a model of groundwater rather than fisheries.

Let us now consider the effects of initial biodiversity (here, simply N , the initial number of species) on the ecosystem processes of interest (biomass production) for two different cases. In the first case, the habitat is homogeneous spatially and temporally, meaning that x is constant through space and time. In the second, the habitat is heterogeneous, with spatial and/or temporal variation in x . For both cases, there will be a fixed species pool from which the initial species composition of each community will be determined by random draw. To determine the effects of diversity, we must average across the effects of particular combinations of species by having many such randomly constructed communities at each level of diversity. Because a species is specified by its τ_i value, we can use τ_i values to define the species pool. Let there be a uniform distribution of τ_i values on the interval $[t_{\min}, t_{\max}]$, with each point being a unique species. This distribution is the species pool (analogous to the set of all possible technologies). Increasing initial diversity (N) gives more random draws from the pool, allowing selection to occur from a larger set of species (wider set of technologies or differentiated products).

2.1.1. Homogeneous habitats

In a homogeneous environment of temperature x , a single species wins in unfettered competition. If, of all species originally added to a habitat, we label the species that has the lowest $R_{i,x}^*$ value as being species A , then its equilibrium biomass will be

$$B_A = \frac{\alpha(S - R_{A,x}^*)}{Qm}. \quad (4)$$

Because this species will win in competition and displace all others, its biomass is also the biomass of the entire community. When the biomass of all species is equally valuable, it is optimal (in the

sense of obtaining maximum value from the ecosystem) to let the species best adapted to environmental conditions to dominate, which results in the largest total community biomass and therefore the greatest value, since ecosystem services are, in this case, directly tied to biomass.

What is the effect of initial diversity, N , on total community biomass, at equilibrium, for this case? Let x_h be the temperature of the homogeneous habitat, where x_h falls on the interval $[t_{\min}, t_{\max}]$. Then, the mean total biomass of communities in homogeneous environments is an increasing function of N , the number of randomly chosen species with which a community was started (Fig. 2A; [12,31]). The average amount of the limiting resource that is left unconsumed is a decreasing function of average species diversity (Fig. 2C; [12,31]). The greater resource capture of the initially more diverse communities is the cause of their greater productivity. It results from the greater chance that species with any given trait, including a low R^* value, would be randomly chosen at higher diversity.

This result makes several important points. Even when only the single most competitive species (technology/product) survives at equilibrium, the average functioning of a system depends on the

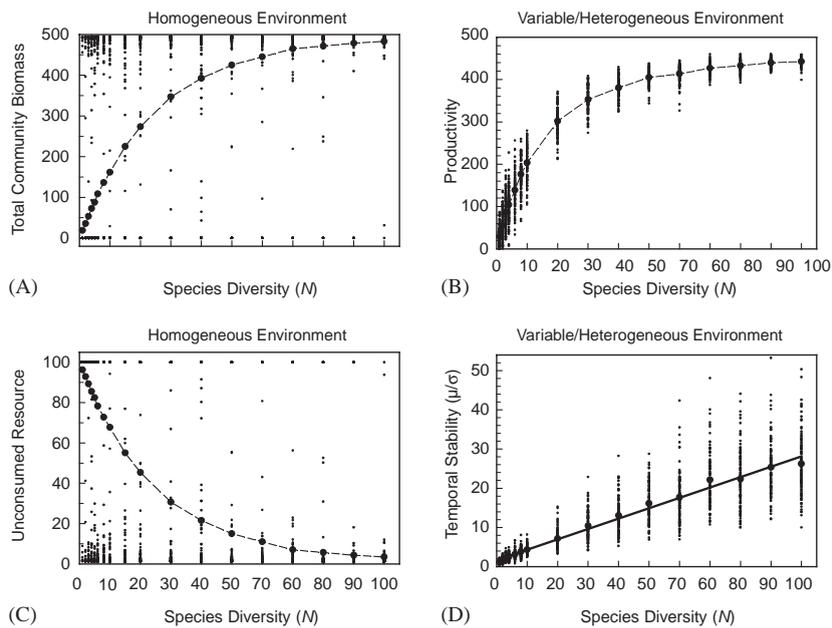


Fig. 2. Competition among species for a single resource in a spatially homogeneous and temporally constant environment (A, C) or in a temporally variable environment (B, D). Computed from Eqs. (3) and (4) with $w = 1/10$, $\alpha = 1$, $K_i = 10$, $m_i = 0.1$, $Q_i = 2$, $r_i = 1$, and $S = 100$. Temperature x and optimal growth point τ_i were randomly and uniformly selected from the range $[20, 30]$. In a constant environment (A, C), the best competitor from an initial pool of n species “wins” the competition and displaces all others. Many species persist in temporally variable environments (B, D). Small dots represent 100 randomly selected communities at a given level of diversity; large dots are their means. (A) Average biomass increases monotonically with diversity of the initial species pool for a constant, unchanging environment. (B) Average biomass behaves similarly in a variable environment, but here the upper bound of variation is, itself, an increasing function of diversity. (C) Unconsumed resource decreases monotonically with diversity for the constant environment (shown) and for the variable environment (not shown). (D) Temporal stability of total community biomass increases with diversity in the temporally varying environment.

number of species (technologies/products) that were initially present. Systems that begin with greater diversity are, on average, more productive than those started with less diversity. This effect of diversity, the sampling effect [1,10,34], illustrates that greater diversity can lead to greater productivity because greater initial diversity leads, on average, to a better fit between system constraints and the traits of competitors. On average, the more diverse a system is, the more closely the traits of some species or technologies match those that lead to maximal efficiency and productivity.

This sampling effect has three interesting signatures. First, there is high variation in productivity for communities that are started with a low number of randomly chosen species (Fig. 2A). With few species, there is some chance that the winning species will match well with the environment and some chance that it will match poorly with the environment. When communities are started with a larger number of randomly chosen species, it becomes more likely that the winning species in each community will be highly productive. The variance among productivity across communities started with the same number of species reaches its peak for communities started with low diversity, and then the variance declines toward zero (Fig. 2A; [12]). This means that, once diversity passes a threshold, greater initial diversity leads to greater predictability of system functioning. Second, mean productivity increases with initial diversity. The mean increases because there is a greater chance of having a superior competitor or technology present in a system that started with higher diversity. A third signature has to do with the upper bound. As shown in Fig. 2A, there is a flat upper bound for productivity in a homogeneous habitat. The upper bound occurs when a community contains a species for which its conditions for maximal growth exactly match the actual physical conditions (i.e., $\tau_i = x$).

The flat upper bound has important implications for managed ecosystems. Suppose that a manager has the ability to choose which species to grow from the set of species initially available. With one limiting resource and spatial and temporal homogeneity, there is a single, knowable species—the species with the lowest $R_{i,x}^*$ —that would be dominant at equilibrium in an environment with physical characteristic x . A monoculture of this species would give the greatest possible biomass yield. Thus a manager who chose this species would obtain as high a yield as would be possible with even the most diverse mixture. The assumptions of this model may apply, at least approximately, to high-intensity agriculture since nitrogen, water, and other resources are added to eliminate resource limitation and pesticides are used to eliminate competitive disease, etc. Under such intensive agricultural conditions, the only limiting resource is light, and the relevant physical factors are temperature and the length of the growing season.

So far, we have assumed that biomass production has the same economic value regardless of the species that produces it. Now consider the case in which the economic value of biomass is species specific. For each species i we randomly assigned a price per unit of biomass, p_i , from a uniform distribution on the interval $[0, 2]$. The value of biomass production for species i is then $p_i B_i$. In an unmanaged system, the species with the lowest R_i value dominates the ecosystem so that the value of biomass is equal to the value of the biomass of this winning species. If we assume the same set of parameters underlying Fig. 2A, the mean value of biomass increases with diversity because the winning species tends to be more productive (Fig. 3A; “unmanaged”). However, the winning species in terms of resource competition may or may not be the species generating the most valuable biomass.

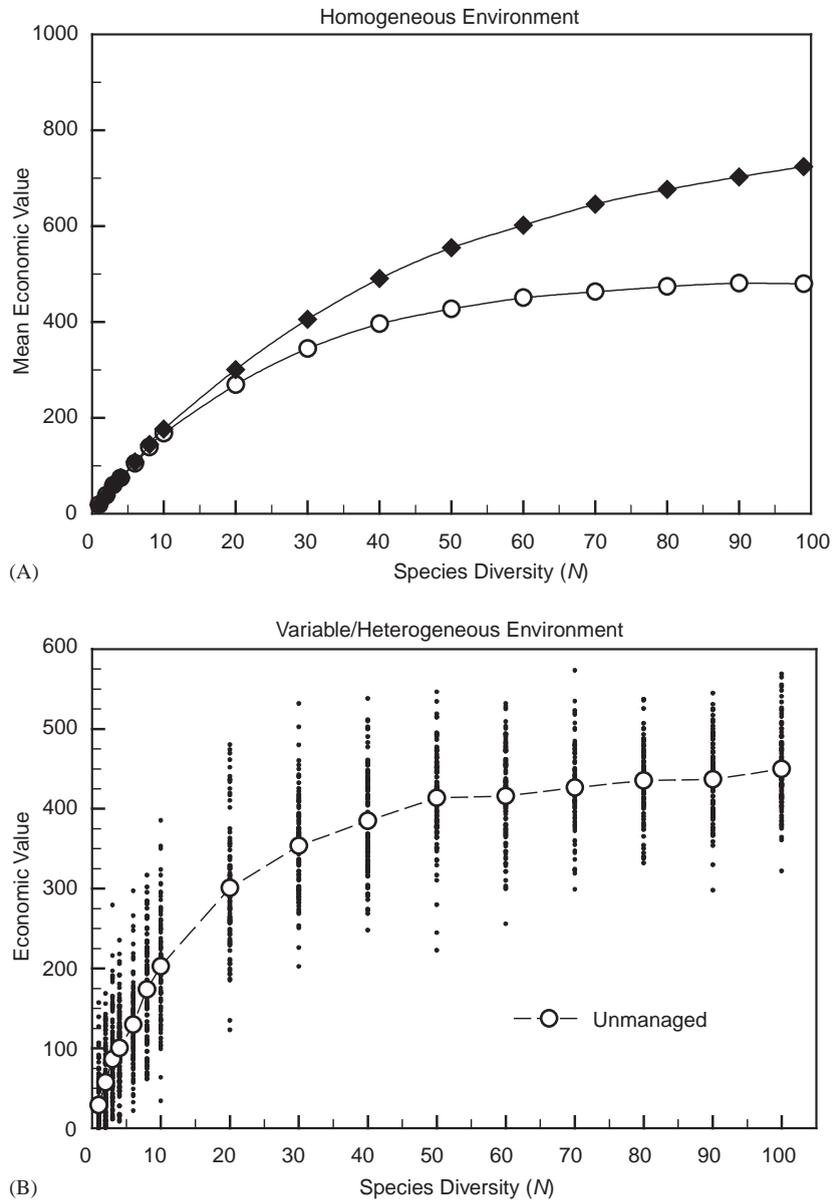


Fig. 3. (A) Mean economic value of total production for equilibrated communities generated by competition for a single resource in a spatially homogeneous and temporally constant environment. Mean value in an unmanaged system (open dots) and in an optimally managed system (solid diamonds). (B) Mean values (large open dots) and composition-dependent variation at each level of diversity (small dots) for temporally variable environments, for the case shown in Fig. 2B.

Suppose a manager can choose species composition. To maximize value, the manager should select the species with the greatest value ($p_i B_i$) and grow it as a monoculture. This species may or may not be the most productive species that would dominate at natural equilibrium. In the case

where the manager can choose species composition, we can ask how the value changes as initial diversity (N) increases. By randomly choosing many different subsets of species for each possible level of diversity, we were able to determine the maximum value that a manager could obtain. We averaged these for each level of available diversity to determine how the level of available diversity influenced the maximal value under optimal management (Fig. 3A, “optimally managed”). The gap between the mean value of managed systems (with manager selection of species composition) versus unmanaged systems (with natural selection of species composition) increases with N . When only one species is available to be selected ($N=1$), there is no choice to be made. Both managed and unmanaged systems generate the same value. As the set of available species increases, the probability that the species generating the greatest value is the same as the species generating the greatest biomass declines. Increasing initial diversity in an unmanaged system tends to increase value because of increased productivity. Increasing initial diversity in a managed system tends to increase value because of the increase of productivity times price. As shown in Fig. 3A, the increase in value from an increase in diversity (i.e., the marginal value of diversity) is larger in managed than in unmanaged systems, especially for larger values of N . Therefore, for homogeneous habitats, the conservation of diversity is of potentially greater concern for human managed systems than for unmanaged systems.

2.1.2. Heterogeneous habitats

Both spatial and temporal heterogeneity can lead to the long-term coexistence of a large number of competing species (e.g., [12,34]). Here we will consider species with parameters identical to those in the prior section, but now we have them interact in a habitat with temporal variability. Similar results are obtained if spatial heterogeneity is considered. Let us assume that the value of current temperature, x , is a random variable drawn from the uniform distribution $[t_{\min}, t_{\max}]$. Here we will be mimicking an ecosystem, such as a perennial grassland, that experiences years that differ in mean temperature, with some years being cooler (nearer t_{\min}) some warmer (nearer t_{\max}) and some moderate (nearer the middle of the range). Different species (as defined by their τ_i values) are favored in different years. Year-to-year variation in temperature thus can allow the persistence of many competing species in a region. In economic terms, this model closely corresponds to a model of consumer fads in which consumer preferences shift from year to year. In this case, no single product can establish dominance.

Let us again start a large number of communities with different numbers of randomly chosen species, and use Eqs. (1) and (2) to determine numerically the effects of the initial number of species on productivity and its temporal variability. Each community with N initial species consists of N random draws of τ_i values from the species pool. The temperature for each period was randomly drawn from $[t_{\min}, t_{\max}]$. Using numerical simulations, we recorded the average community biomass at the end of each period over 50 periods for each community. As shown in Fig. 2B, total community biomass is an increasing function of diversity [12]. However, note that both the upper bound and the lower bound of the variation in total biomass increases with diversity. Thus, for this case, in which temporal heterogeneity allows the long-term persistence of a large number of species, simulations suggest that there are no single species systems that are as productive as some systems containing two species, no two-species systems as productive as some three-species systems, etc. This identical conclusion was proven for a related case (that shown later in Fig. 6A; [33]).

In the agro-ecological literature, this pattern has been called overyielding because higher-diversity ecosystems give greater yields than is possible from lower-diversity ecosystems. A system with overyielding means that a resource manager would be unable to achieve yields with monocultures, no matter how well chosen, that were comparable to yields of some ecosystems with higher diversity. This pattern of increased productivity at higher diversity is a direct result of greater resource use by more diverse communities. In economic terms, access to a diversity of production technologies can maintain high productivity under a variety of economic and environmental conditions. Another useful analogy to this result is to product differentiation, where an increase in product diversity will generate higher welfare for the case of consumers with heterogeneous preferences.

As should be intuitively clear, at any given level of diversity, simulations suggest that the best combinations of species are those that best span the range of variability in temperature. For example, five species that have similar τ_i values are less productive than five other species that have τ_i values approximately uniformly distributed along the interval $[t_{\min}, t_{\max}]$. Thus diversity in the sense of differences in attributes of species is as important a determinant of ecosystem functioning as diversity in the sense of the number of species.

In addition to its effects on mean productivity, in these simulations diversity has a strong effect on the year-to-year variability of ecosystem productivity within individual communities. If we define the temporal stability of a system as its mean biomass divided by the standard deviation of the temporal variation in its biomass [31], these simulations show that temporal stability of total community biomass is a linearly increasing function of species number (Fig. 2D; [12]). Analytical solution of a model of competition among niche-differentiated species (the “modified broken stick” model) also predicts that temporal stability is a nearly linear increasing function of species number [12]. Temporal stability of total community biomass is an approximately linearly increasing function of species number in other models of multispecies competition [12,31]. In contrast, the temporal stability of the average species is a slightly declining function of species number. This means that the ecosystem becomes more temporally stable as diversity increases even though, on average, the individual species in it become less temporally stable, a prediction that is supported by observations in grasslands [30].

These findings accord with the notion within economics that diverse economies, i.e., those with many different industries, tend to fluctuate less over time than those dominated by a few industries. Since success of industries, like that of species, is not perfectly correlated, greater diversity should translate to lower overall system variability. What is striking in the ecological model, however, is that even while system stability increases with diversity, individual species stability decreases with diversity. This comes from the tight competitive coupling of species in ecosystems. If this were true in economies, individual corporations would have greater fluctuations within more diverse economies, which is not a result that has been demonstrated to the best of our knowledge, but might hold if data were analyzed by adjusting for correlations between corporate capitalization and diversity.

Similar to considerations of productivity alone, the mean value of production in both unmanaged (Fig. 3B) and managed systems (not shown) increases with diversity when biomass prices differ among species. The value of production in managed systems is approximated by the upper bound of the variation of Fig. 3B. Although variability in the prices of species adds variance to the results (compare Figs. 2B and 3B), the upper bound is still an increasing function of

diversity. This means both that greater diversity leads to greater mean value and that even the best low-diversity system can be beaten by a system with greater species diversity. How much improvement in value can come from management choice of particular species (rather than of just higher diversity) depends in part on how much information the manager has about future environmental conditions, and in part on how long species live relative to the length of time over which environmental conditions remain constant. Even without information about future environmental conditions, a manager could choose a mix of species with traits spanning the likely mean and variance in environmental conditions. Management would have greater value, however, with the ability to accurately predict future conditions. In general, with heterogeneity of environmental conditions, conserving and using numerous species is of value because each species generates the greatest value for a small range of environmental conditions. For long-lived organisms that experience much temporal variation during their lifetimes, such as trees, the greatest value would be generated by the most diverse systems. For short-lived organisms, such as annual crops receiving inputs of water, fertilizers, pesticides, etc., the greatest value in a given year might be generated by a single variety of a single species, but different species and/or crop varieties would perform better in different years depending on conditions. In either case, losing species will mean lower value is produced for some environmental conditions/years. With the potential for different environmental conditions in the future, even species without any economic value, given current conditions, may have option value.

2.1.3. Summary

Whether ecosystem service value is determined strictly by a biological measure, such as biomass productivity, or by a combination of biological and economic factors, such as price and productivity, increasing diversity generates increasing mean value as well as lower variance, which has an insurance value. Having more competing entities available increases the likely productivity, value, and temporal stability of a system. This is true in both ecological systems and economic systems. In a homogeneous and unchanging environment, the value of diversity arises because sampling from more species or industries allows a better fit between the winning species or industry and environmental conditions. In heterogeneous environments, diversity is of value because an array of options increases the goodness of fit between species traits and environmental conditions. Thus greater diversity allows more complete spanning of potential ecosystem or market niches. In addition, diversity tends to reduce the variance of outcomes, thus providing insurance value.

The advantages of diversification of a financial portfolio are of course well understood. A diverse portfolio of species, or financial assets, allows the same average productivity to be obtained with reduced variance. Yet another parallel between these results and results in economics is the link between diversity and option value. Even a species that currently has small biomass may play an important role in future productivity of the ecosystem should environmental conditions shift in its direction. Losing such species may result in large losses in future productivity even though there is only a small productivity effect at present. The economics literature on measures of biological diversity and “bioprospecting” for new pharmaceutical drugs has shown that more diverse sets of species have higher probabilities of conserving potentially useful genetic characteristics with consequent loss of option value with extinction (e.g., [17–18,22,25,38–40]).

2.2. Competition with two essential resources or two limiting factors

We briefly discuss two additional models. The first of these models assumes that all species are limited by and compete for two nutritionally essential resources [27,28]. For plants, these limiting resources might commonly be any two of soil nitrogen, soil water, light, or soil phosphate. Each of these is essential for growth, i.e., its lack cannot be overcome by substitution of a different resource. In economics, production is often modeled as being a function of two inputs (e.g., capital and labor). Here, production functions are assumed to be Leontief, i.e., production requires a fixed ratio of inputs yielding right angle isoquants [27]:

$$\frac{dB_i}{dt} = \text{Min}_{j=1,2}(f_{i,1}(R_1), f_{i,2}(R_2)) - m_i, \quad (5)$$

$$\frac{dR_j}{dt} = a(S_j - R_j) - \sum_{i=1}^n B_i Q_{ij} \left(\text{Min}(f_{i,1}(R_1), f_{i,2}(R_2)) \right), \quad (6)$$

where $f_{i,j}$, $j=1,2$, is the resource-dependent growth function of species i for resource j , m_i is its mortality or loss rate, S_j is the supply point for resource j , and Q_{ij} is the amount of R_j consumed to produce each new unit of biomass of species i . The second equations describe the dynamics of resource supply.

Because of differences in physiologies and morphologies, species differ in their requirements for essential resources, with the most important difference being in the ratio of the resources required for balanced (or optimal) growth. A variety of work suggests that, for a given biogeographic realm, there is an interspecific tradeoff surface that defines the best possible performance of species competing for a set of essential resources. Assuming that all species fall on such a tradeoff surface, at most no more consumer species can coexist at equilibrium in a physically homogeneous habitat than there are limiting resources [11,14,28]. However, if there is spatial or temporal heterogeneity in the supply rates of the limiting resources, a potentially unlimited number of species can stably coexist [2,9,28]. Let us first illustrate the model graphically (see Fig. 4A). Let R_1 and R_2 be the two limiting resources. Then, from Eq. (5), a right angle curve shows the environmental concentrations of R_1 and R_2 at which the biomass of this species would be constant (i.e., $dB/dt=0$). Such zero net growth isoclines define how much R_1 and R_2 each species has to have to maintain itself in a habitat (see [27,28]). If amounts were greater or lesser than this, it would increase or decrease in abundance, respectively. Note that while a zero net growth isocline looks similar to a production isoquant in economics, the isocline summarizes dynamic relationships between resources and change in biomass of a species, and shows potential equilibrium stocks of the resources, and is thus more similar to a phase diagram than to a static isoquant graph. The tradeoff curve represents the lowest amounts of R_1 and R_2 at which existence is possible for any species. If two species have such a resource tradeoff, then there would be a range of habitats in which the two species could stably coexist (see [27,28] for details). As shown in Fig. 4B, species A is the superior competitor for R_1 and species B is the superior competitor for R_2 . At the two-species equilibrium point (where the isoclines cross), species A is limited by R_2 and species B by R_1 . Assuming optimal foraging by these species, the two species would coexist for intermediate resource supply rates (formal mathematical treatments in [27,28]). This illustrates what ecologists call ‘niche differentiation’ among species, i.e., coexistence of competitors caused

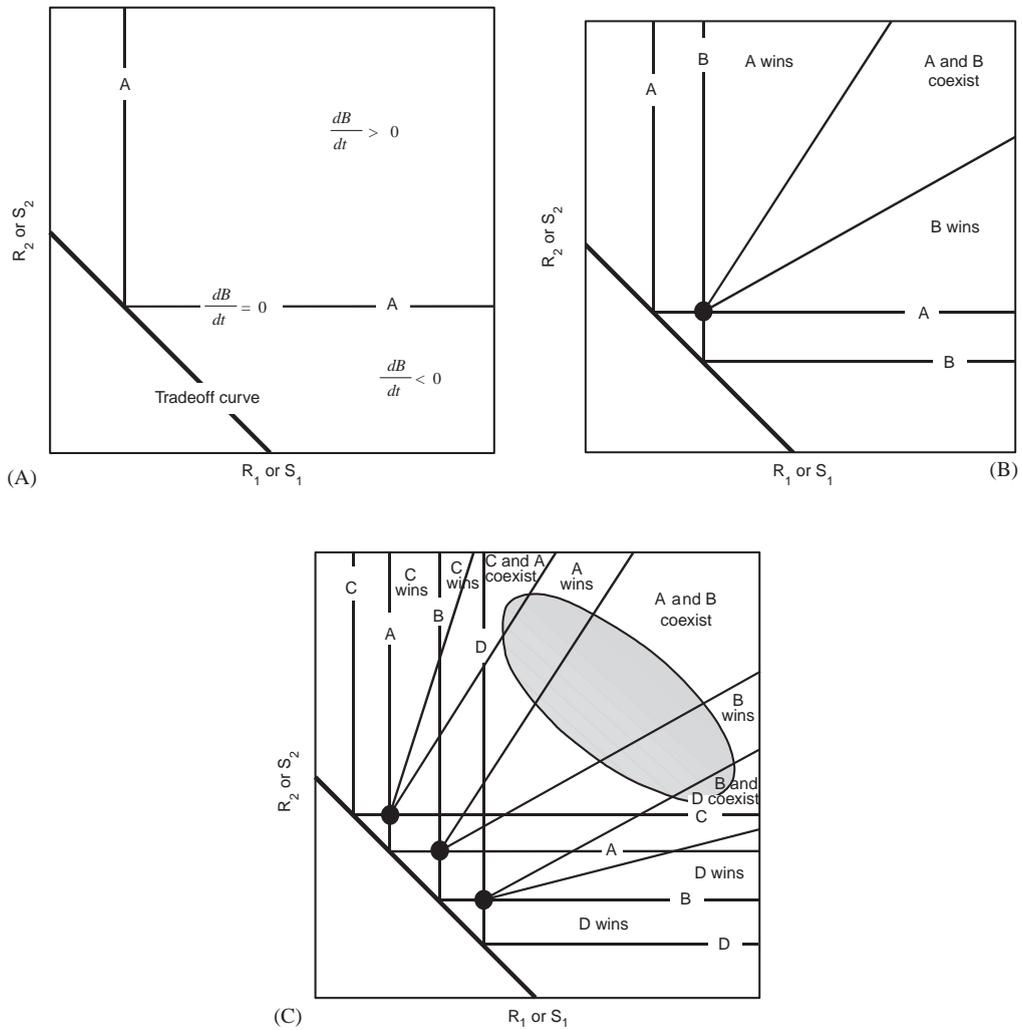


Fig. 4. (A) The resource-dependent growth isocline of species *A* shows concentrations of R_1 and R_2 for which its $dB/dt = 0$. The right angle isocline means that these resources are nutritionally essential. (B) Isoclines for two species, *A* and *B*, fall on the tradeoff curve and thus have a stable point of two-species coexistence. Habitats, defined by their values of S_1 , S_2 , can be mapped into equilibria in which species *A* wins, *A* and *B* coexist, or species *B* wins. (C) Competition among four species that have tradeoffs in R_1 and R_2 requirements. At most two species can coexist in any homogeneous habitat, but all four could coexist in a habitat with the point-to-point spatial heterogeneity in S_1 , S_2 values indicated by the shaded ellipse.

by tradeoffs in their traits. In habitats outside this region, either one or the other species would win and displace the other species. For instance, for habitats with high rates of supply of R_1 and low of R_2 , species *B* would win because it is the best competitor for R_2 .

This mechanism can easily be generalized to any number of competing species, and can lead to regions of pairwise coexistence that can, in total, allow all species to coexist in a habitat in which

there is sufficient spatial heterogeneity in the rates of supply of R_1 and R_2 . This is illustrated for four species in Fig. 4C. Note that the corner of the isocline of each species i touches an interspecific tradeoff curve at the point which is the ratio of R_1 and R_2 at which species i is equally limited by both resources. Note that the four species of Fig. 4C can all coexist in the spatially heterogeneous habitat represented by supply points, (S_1, S_2) , in the closed curve.

With Eqs. (5) and (6), one can determine analytically the abundances of all species, at equilibrium, in a homogeneous habitat or in a spatially heterogeneous habitat for which a finite probability distribution of supply points, (S_1, S_2) has been specified [27,28]. We did this numerically for a series of cases in which many random replicate communities were drawn for a range of diversity levels. Habitat resource supply heterogeneity was identical in all cases. At equilibrium, total community biomass was an increasing function of species number (Fig. 5A). Both the upper and lower bounds of composition-dependent variation in total community biomass were increasing functions of species number. In addition, the concentration of unconsumed resource was a decreasing function of diversity, with its upper and lower bounds of variation also being decreasing functions of species number (Fig. 5B). These results have the signature of niche effects, as expected for models in which tradeoffs and heterogeneity allow coexistence.

A somewhat different model with two limiting factors is described in Tilman et al. [33]. In this generalized niche model there are two continuous variables that characterize a habitat. Each species can survive for some limited range of these variables. Suppose that we can represent the conditions under which a species can survive as a circle of radius r within the range of potential conditions given by the rectangular area of width ar and height br (Fig. 6A). With increased diversity (N being the number of species), a greater proportion of the potential habitat types is covered, i.e., has species living in it because it is within the tolerance limits of some species. The proportion (P) of the habitat space covered, which is an index of habitat productivity, is

$$P = 1 - \left(1 - \frac{\pi}{ab + 2(a + b) + \pi} \right)^N. \quad (7)$$

This proportion rises asymptotically to 1 as the number of species is increased (Fig. 6B). As is true for all the niche models (e.g., Figs. 2B and 5A), the upper bound of the variation is an increasing function of diversity, illustrating that management for high diversity is crucial for maximizing value. The rate of increase depends on the range of the conditions that a species can tolerate (r) relative to the range of possible habitat conditions (ar and br). Greater diversity is necessary to achieve any given level of coverage the larger are a and b . For example, for the mechanisms considered by this model, a large number of tree species would be necessary to cover the range of conditions present on the North American continent, while in particular regions fewer species would do. Polasky et al. [17] used an almost identical model to describe the probability that a set of species would cover the space of potential genetic or morphological characteristics.

Introducing prices that differ among species introduces similar issues as in the single input model. As before, price variability across species increases the variance of value, though not the mean, in unmanaged ecosystems.

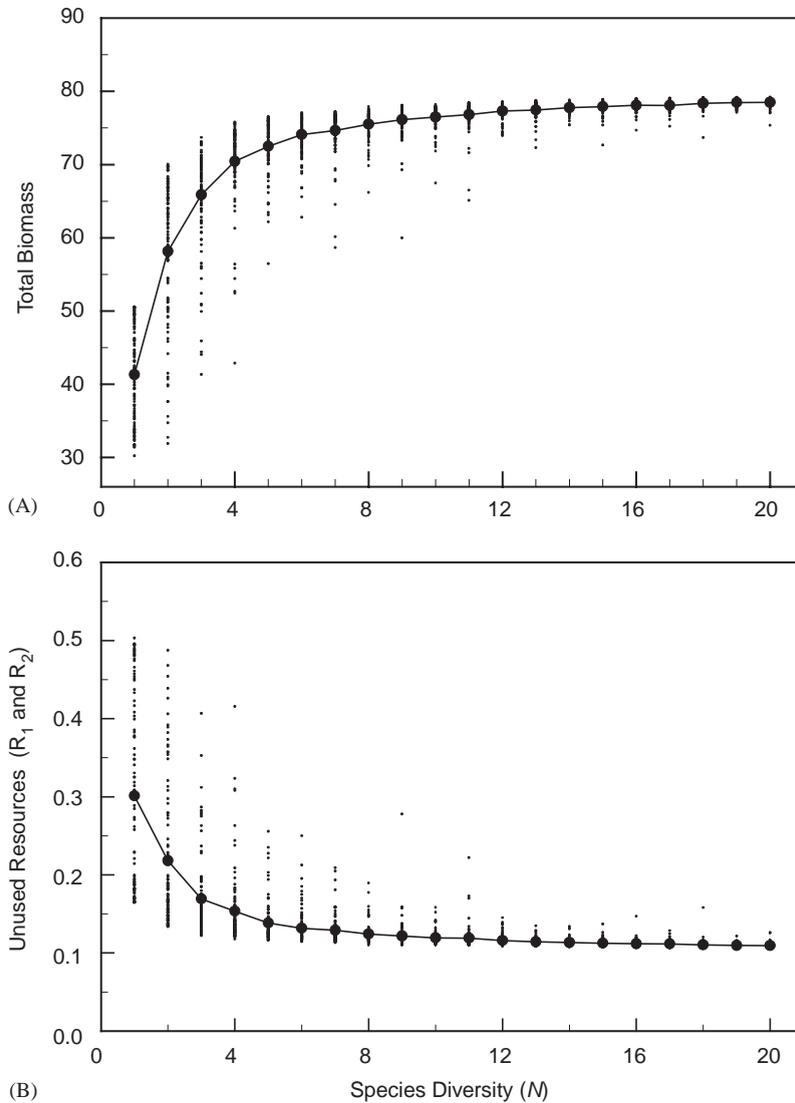


Fig. 5. Long-term results of competition for two resources (as in Fig. 4) among various numbers of species with isoclines having their corners located at points randomly selected on a tradeoff curve. (A) Dependence of total community biomass on initial species diversity (N , number of species). Note that all of the initially chosen species stably coexist and that the upper bound of variation in total biomass is an increasing function of diversity. (B) Dependence of the amount of unused R_1 and R_2 on diversity in these simulations.

3. Experimental evidence

Several recent ecological experiments have determined the effects of plant diversity (number of plant species) on plant primary productivity (comparable to the annual “yield” of plant mass), on the total amount of carbon stored in plants (i.e., carbon dioxide removed from the atmosphere

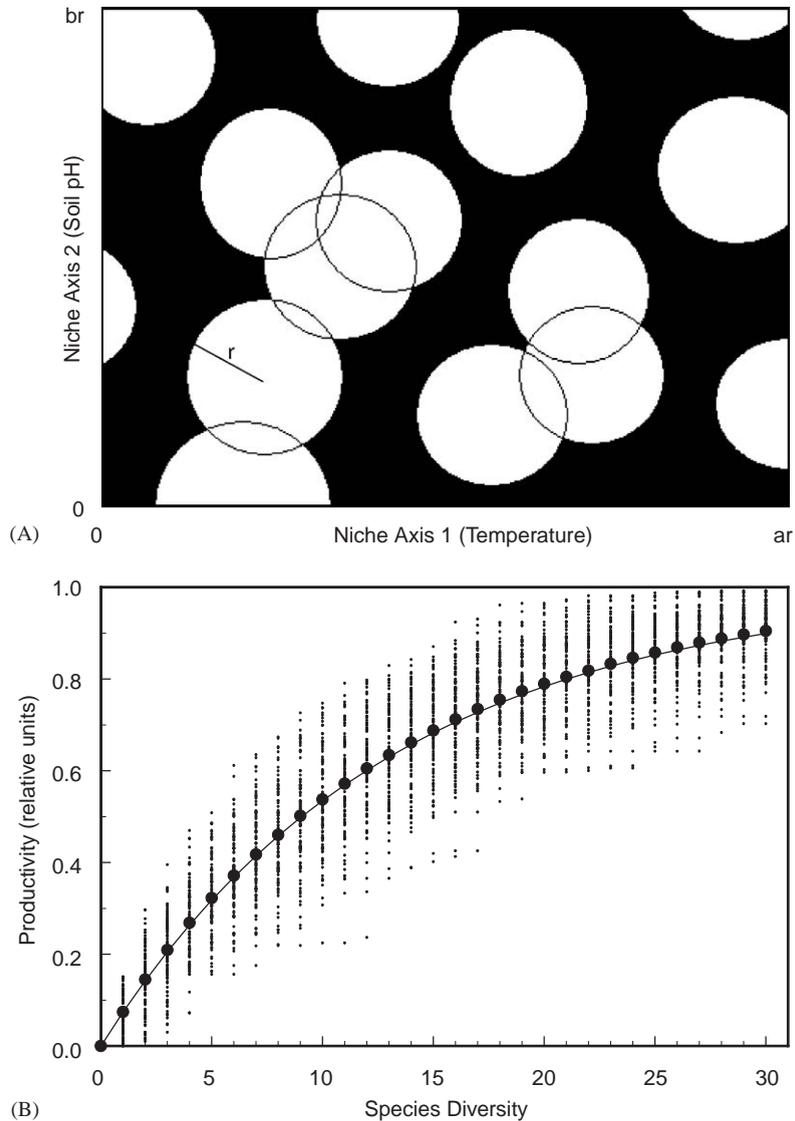


Fig. 6. A simple niche model of habitat use, the ‘snowballs on the barn’ model of Tilman, et al. [33]. (A) The full-darkened rectangle represents the spatial heterogeneity of the two niche factors in a habitat. Each circle represents the range of environmental conditions for which a species can maintain a viable population, i.e., the portion of the heterogeneous habitat in which that species survives and grows. (B) Total community productivity increases with diversity because more diverse communities are, on average, better at ‘covering’ the range of conditions that occur in a heterogeneous habitat. For the analytical treatment of this model, see Tillman et al. [33].

and stored, as C, in plants), and on the amount of nitrate that is leached through the soil and thence into groundwater (e.g., [7,20,32,35]). These studies have shown that higher plant diversity leads to greater primary productivity, greater carbon storage in plant mass, and lower levels of nitrate in ground waters.

The longest running of these studies, in which 168 plots were planted to have 1, 2, 4, 8, or 16 perennial grassland plant species [35], shows that the magnitudes of the effects of diversity on primary productivity (Fig. 7A) and on total carbon stores in plants (Fig. 7B) have increased through time. Plots planted with 16 species had significantly greater total carbon stores (for plot means from 2000, 2001 and 2002) than those planted with 8, 4, 2, or 1 species (Tukey's HSD test,

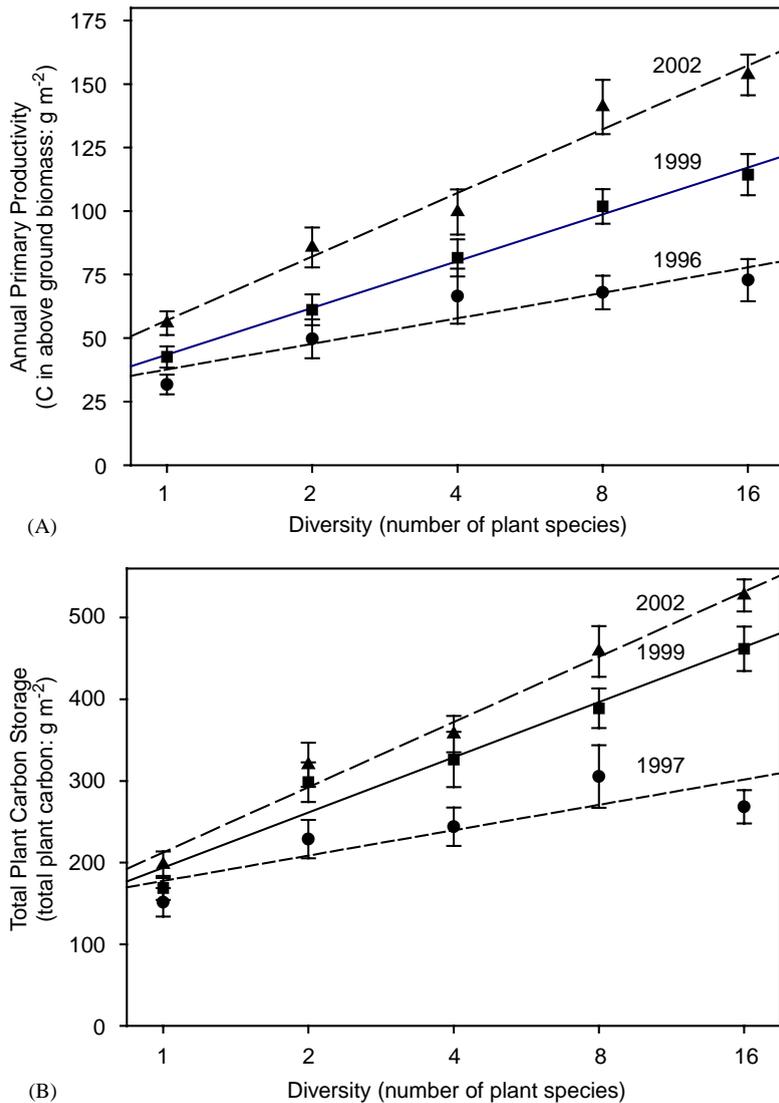


Fig. 7. The observed effects of plant species diversity on (A) annual primary productivity and (B) total carbon storage by plants for a long-term biodiversity experiment performed in prairie-grasslands of Minnesota [33,35]. Symbols show means for each level of plant diversity (1, 2, 4, 8, or 16 plant species), and bars indicate the standard error of each mean. The experiment contains 168 plots, each 9 m × 9 m in size, with an average of about 34 replicate plots for each level of diversity. Each replicate represents a separate, random draw of the appropriate number of species. The means shown thus represent the effect of diversity when averaging across the effects of many different random species compositions.

$P < 0.05$). Moreover, comparisons of the plant carbon stores of each of the 168 plots averaged across the 3 latest years of the experiment (2000, 2001, 2002) reveal that monoculture plots, on average, stored only 36% of the carbon stored by 16 species plots. Analyses of these results show that, in natural ecosystems, diversity is acting mainly through niche differentiation and complementarity rather than through sampling effects [35]. Both the mean response and the upper bound of the plot-to-plot variation in the response are strongly increasing functions of diversity. Because the mean response is best fit as being a log function of species number, the marginal increase in productivity and in carbon storage from an added species, though always positive, decreases as diversity increases.

4. Discussion

We think the models and the results presented in the previous section are of potential relevance for economists for several reasons. The results are directly relevant to the value of biodiversity to ecosystem functioning and the services provided to society by ecosystems. In particular, they show that decreased local diversity can lead to lower ecosystem productivity, lower use of limiting resources and lower temporal stability. A large number of societal practices are leading to lower local diversity in many managed and natural ecosystems. Although species extinctions clearly result in lower diversity, human impacts on local diversity are many fold greater than would be expected based on these alone. Rather, the largest human impacts on ecosystem functioning are likely to come from habitat simplification, such as results from selective harvesting, increased disturbance rates, replanting harvested ecosystems with one or a few species, and habitat fragmentation. All of these actions decrease the number of species within a habitat, and many of these lead to major changes—with diversity being an order of magnitude or more lower than in the original ecosystems of the region. The theory we have reviewed suggests that such ecosystem simplification can lead to 2–4-fold decreases in biomass productivity and to increased year-to-year variation in productivity. In addition, the decreased efficiency of resource use would often lead to increased leaching loss of nutrients from ecosystems, just as observed in a biodiversity experiment [32,35,36]. This can contribute to the nutrient eutrophication of freshwater and near-shore marine ecosystems, and also lead to a further depletion of soil fertility in the terrestrial ecosystems.

In much of this paper, we emphasized productivity in terms of biomass, or a price-weighted measure of biomass, as a proxy for the value of ecosystem services. This measure is a good proxy for some ecosystem services, such as services related to the price-weighted harvest of biomass (e.g., forage crops, timber), or to the price-weighted standing stock of biomass (e.g., forest aesthetics, or services related to nutrient uptake and retention like carbon sequestration). Biomass of different species will typically produce multiple services, typically not in fixed proportions. For example, wetlands are often highly productive systems in terms of biomass production, which may be quite valuable for nutrient retention. This biomass, however, typically has little harvest value, unlike say a cornfield that generates high harvest value but few other services. One major challenge for economists is to establish the proper set of prices for these multiple services. Is a wetland or perennial grassland system that is more diverse and more productive in terms of biomass of greater value to society than a monoculture agricultural field? The answer will depend both on

differences in various types of productivity and the prices attached to the various types of productivity.

There is an array of other ecosystem services that are not adequately represented by productivity measures, such as pollination and control of pests. Part of the joint challenge for economists and ecologists is to understand the production of ecological services and quantify these services in a way that can be valued by tools of economics.

The models also describe advances in ecological models that could be readily adapted by economists interested in bio-economic modeling. The models described here do not explicitly incorporate dynamic analysis of the harvest path that is the staple of bio-economic analysis. These models, however, do illustrate the importance of incorporating diversity and species composition effects. Often it is challenging to learn and incorporate advances in other fields. But that should not be the case here. At the heart of the models presented in this paper are competitive consumer–resource interactions among species. Certainly the study of competitive processes is something that is near and dear to the heart of most economists. As shown, interspecies competition has important effects on the species themselves as well as the overall functioning of ecosystems. To date such competition has not been integrated into bio-economic models used by resource economists with the notable exception of work by Brock and Xepapadeas [3] and Tschirhart [37]. Doing so offers great potential for improving such models.

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References

- [1] L.W. Aarssen, High productivity in grassland ecosystems: effected by species diversity or productive species?, *Oikos* 80 (1997) 183–184.
- [2] R.A. Armstrong, R. McGehee, Competitive exclusion, *Amer. Nat.* 115 (1980) 151–170.
- [3] W.A. Brock, A. Xepapadeas, Optimal management when species compete for limited resources, *J. Environ. Econ. Manage.* 44 (2) (2002) 189–220.
- [4] C. Darwin, *The Origin of Species by Means of Natural Selection*, reprinted by The Modern Library, Random House, New York, 1859.
- [5] D. Finnoff, J. Tschirhart, Protecting an endangered species while harvesting its prey in a general equilibrium ecosystem model, *Land Econ* 79 (2003) 160–180.
- [6] J.P. Grover, *Resource Competition*, Chapman & Hall, London, 1997.
- [7] A. Hector, B. Schmid, C. Beierkuhnlein, M.C. Caldeira, M. Diemer, P.G. Dimitrakopoulos, J. Finn, H. Freitas, P.S. Giller, J. Good, R. Harris, P. Högberg, K. Huss-Danell, J. Joshi, A. Jumpponen, C. Körner, P.W. Leadley, M. Loreau, A. Minns, C.P.H. Mulder, G. O'Donovan, S.J. Otway, J.S. Pereira, A. Prinz, D.J. Read, M. Scherer-Lorenzen, E.-D. Schulze, A.-S.D. Siamantziouras, E.M. Spehn, A.C. Terry, A.Y. Troumbis, F.I. Woodward, S. Yachi, J.H. Lawton, 1999, Plant diversity and productivity experiments in European grasslands, *Science* 286 (1999) 1123–1127.

- [8] S.B. Hsu, S.P. Hubbell, P. Waltman, A mathematical theory for single-nutrient competition in continuous cultures of microorganisms, *SIAM J. Appl. Math.* 32 (1977) 366–383.
- [9] J. Huisman, Population dynamics of light-limited phytoplankton: microcosm experiments, *Ecology* 80 (1999) 202–210.
- [10] M.A. Huston, Hidden treatments in ecological experiments: reevaluating the ecosystem function of biodiversity, *Oecologia* 110 (1997) 449–460.
- [11] G.E. Hutchinson, Homage to Santa Rosalia, or why are there so many kinds of animals?, *Amer. Nat.* 93 (1959) 45–159.
- [12] C.L. Lehman, D. Tilman, Biodiversity, stability, and productivity in competitive communities, *Amer. Nat.* 156 (2000) 534–552.
- [13] J.A. Leon, D.B. Tumpson, Competition between two species for two complementary or substitutable resources, *J. Theoret. Biol.* 50 (1975) 185–201.
- [14] S.A. Levin, Mechanisms for the generation and maintenance of diversity in ecological communities, in: R.W. Hiorns, D. Cooke (Eds.), *The Mathematical Theory of the Dynamics of Biological Populations II*, Academic Press, London, New York, 1981.
- [15] B. Maguire, Niche response structure and the analytical potentials of its relationships to the habitat, *Amer. Nat.* 107 (1973) 213–246.
- [16] J.M. Maynard-Smith, *Evolution and the Theory of Games*, Cambridge University Press, Cambridge, 1982.
- [17] S. Polasky, A. Solow, J. Broadus, Searching for uncertain benefits and the conservation of biological diversity, *Environ. Resource Econ.* 3 (1993) 171–181.
- [18] S. Polasky, A.R. Solow, On the value of a collection of species, *J. Environ. Econ. Manage.* 29 (2) (1995) 298–303.
- [19] D.J. Rapport, An optimization model of food selection, *Amer. Nat.* 105 (1971) 575–587.
- [20] P.B. Reich, J. Knops, D. Tilman, J. Craine, D. Ellsworth, M. Tjoelker, T. Lee, D. Wedin, S. Naeem, D. Bahauddin, G. Hendrey, S. Jose, K. Wrage, J. Goth, W. Bengston, Plant diversity enhances ecosystem responses to elevated CO₂ and nitrogen deposition, *Nature* 410 (2001) 809–810.
- [21] J. Sanchirico, J. Wilen, Bioeconomics of spatial exploitation in a patchy environment, *J. Environ. Econ. Manage.* 37 (2) (1999) 129–150.
- [22] R.D. Simpson, R.A. Sedjo, J.W. Reid, Valuing biodiversity for use in pharmaceutical research, *J. Polit. Economy* 104 (1996) 163–185.
- [23] A. Smith, *An Inquiry into the Nature and Causes of the Wealth of Nations*, Whitestone, Dublin, 1776.
- [24] V.L. Smith, Economics of production from natural resources, *Amer. Econ. Rev.* 58 (1968) 409–431.
- [25] A. Solow, S. Polasky, Measuring biological diversity, *Environ. Ecol. Statist.* 1 (2) (1994) 95–107.
- [26] D. Tilman, Ecological competition between algae: experimental confirmation of resource-based competition theory, *Science* 192 (1976) 463–465.
- [27] D. Tilman, Resources: a graphical–mechanistic approach to competition and predation, *Amer. Nat.* 116 (1980) 362–393.
- [28] D. Tilman, *Resource Competition and Community Structure*, Monographs in Population Biology, Princeton University Press, Princeton, NJ, 1982.
- [29] D. Tilman, *Plant Strategies and the Dynamics and Structure of Plant Communities*, Princeton University Press, Princeton, NJ, 1988.
- [30] D. Tilman, Biodiversity: population versus ecosystem stability, *Ecology* 77 (3) (1996) 350–363.
- [31] D. Tilman, The ecological consequences of changes in biodiversity: a search for general principles, *Ecology* 80 (1999) 1455–1474.
- [32] D. Tilman, J. Knops, D. Wedin, P. Reich, M. Ritchie, E. Siemann, The influence of functional diversity and composition on ecosystem processes, *Science* 277 (1997) 1300–1302.
- [33] D. Tilman, C.L. Lehman, K.T. Thomson, Plant diversity and ecosystem productivity: theoretical considerations, *Proc. Natl. Acad. Sci.* 94 (1997) 1857–1861.
- [34] D. Tilman, S. Pacala, The maintenance of species richness in plant communities, in: R.E. Ricklefs, D. Schluter (Eds.), *Species Diversity in Ecological Communities*, University of Chicago Press, Chicago, 1993.
- [35] D. Tilman, P.B. Reich, J. Knops, D. Wedin, T. Mielke, C. Lehman, Diversity and productivity in a long-term grassland experiment, *Science* 294 (2001) 843–845.

- [36] D. Tilman, D. Wedin, J. Knops, Productivity and sustainability influenced by biodiversity in grassland ecosystems, *Nature* 379 (1996) 718–720.
- [37] J. Tschirhart, Resource competition among plant: from maximizing individuals to community structure, *Ecol. Model.* 148 (2002) 191–212.
- [38] M.L. Weitzman, On diversity, *Quart. J. Econ.* 107 (2) (1992) 363–405.
- [39] M.L. Weitzman, What to preserve? An application of diversity theory to crane conservation, *Quart. J. Econ.* 108 (1993) 157–183.
- [40] M.L. Weitzman, The Noah's Ark problem, *Econometrica* 66 (1998) 1279–1298.