

PERSPECTIVES

THE ROBERT H. MACARTHUR AWARD LECTURE

Ecology, 80(5), 1999, pp. 1455–1474
© 1999 by the Ecological Society of America

THE ECOLOGICAL CONSEQUENCES OF CHANGES IN BIODIVERSITY: A SEARCH FOR GENERAL PRINCIPLES¹

DAVID TILMAN

Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, Minnesota 55108 USA



DAVID TILMAN, MacArthur Award Recipient, 1996

Abstract. This paper uses theory and experiments to explore the effects of diversity on stability, productivity, and susceptibility to invasion. A model of resource competition predicts that increases in diversity cause community stability to increase, but population stability to decrease. These opposite effects are, to a great extent, explained by how temporal variances in species abundances scale with mean abundance, and by the differential impact of this scaling on population vs. community stability. Community stability also depends on a negative covariance effect (competitive compensation) and on overyielding (ecosystem productivity increasing with diversity). A long-term study in Minnesota grasslands supports these predictions.

Models of competition predict, and field experiments confirm, that greater plant diversity leads to greater primary productivity. This diversity–productivity relationship results both from the greater chance that a more productive species would be present at higher diversity (the sampling effect) and from the better “coverage” of habitat heterogeneity caused by the broader range of species traits in a more diverse community (the niche differentiation effect). Both effects cause more complete utilization of limiting resources at higher diversity, which increases resource retention, further increasing productivity. Finally, lower levels of available limiting resources at higher diversity are predicted to decrease the susceptibility of an ecosystem to invasion, supporting the diversity–invasibility hypothesis. This mechanism provides rules for community assembly and invasion resistance.

In total, biodiversity should be added to species composition, disturbance, nutrient supply, and climate as a major controller of population and ecosystem dynamics and structure. By their increasingly great directional impacts on all of these controllers, humans are likely to cause major long-term changes in the functioning of ecosystems worldwide. A better understanding of these ecosystem changes is needed if ecologists are to provide society with the knowledge essential for wise management of the earth and its biological resources.

Manuscript received 11 September 1998; revised and accepted 13 January 1999.

¹ Presented 11 August 1997 in Albuquerque, New Mexico, USA.

Key words: biodiversity; community assembly; covariance effect; diversity–invasibility hypothesis; diversity–productivity hypothesis; diversity–stability hypothesis; ecosystem functioning; human-dominated ecosystems; overyielding effect; portfolio effect; productivity; stability.

INTRODUCTION

The biological diversity of the earth and its origins have long been a source of amazement and curiosity, and an area of formal inquiry ever since Wallace and Darwin. Current interest in diversity centers both on why there are so many species and on how diversity impacts population and ecosystem processes, which is the focus of this paper. In 1961, Hutchinson noted that theory predicted that the number of coexisting species should not exceed the number of limiting resources, but that most lakes contained many times more algal species than limiting nutrients. This paradox of diversity helped to attract me from physics to ecology during my undergraduate education. Ecology offered all that I had been seeking in a career: a chance to combine theory and experiments, to address the “big unknowns” of a discipline, and to have the results be of importance to the long-term welfare of society.

With the guidance of first Stephen Hubbell and then Peter Kilham, my thesis work led to a mechanistic theory of resource competition (Tilman 1977, 1980) and to the first experimental demonstration of the ability of theory to predict the outcome of interspecific interactions (Tilman 1976, 1977). The theory offered a solution to the paradox of diversity, predicting that an unlimited number of competing species could coexist at equilibrium if a habitat had spatial heterogeneity in the relative supply rates (ratios) of two or more limiting resources (Tilman 1980, 1982). Many alternative theoretical explanations for high diversity also have been discovered (e.g., Levin 1970, 1981, May 1975, 1986, Levins 1979, Armstrong and McGehee 1980, Chesson 1986, Chesson and Huntly 1997; reviewed in Tilman and Pacala 1993). These have solved the paradox of diversity, but the mystery remains. We still do not know, for example, how hundreds of plant species and thousands of insect species coexist on a hectare of rain-forest or prairie, or how millions of species coexist on earth. Because these mechanisms are poorly understood, we have but a blurry vision of the long-term impacts of habitat conversion and destruction, invasion by exotic species, nutrient enrichment, and other anthropogenic changes on species extinctions.

The ecological consequences of changes in biodiversity, the theme of this paper, are at least as poorly understood. Darwin (1872) suggested that greater plant diversity would lead to greater primary productivity, but his thoughts lay dormant for over a century (McNaughton 1993). Elton (1958) proposed that greater diversity and trophic complexity would increase population and ecosystem stability, but interest in the consequences of diversity declined after May (1973) showed that the stability of model competitive eco-

systems decreased as diversity increased. However, the accelerating effects of human activities on biodiversity and the possibility that the loss of biodiversity might impact ecosystem functioning (e.g., Ehrlich and Ehrlich 1981, Wilson 1992) renewed interest in the effects of diversity on ecosystem processes (Schulze and Mooney 1993) and on ecosystem services essential to society (Daily 1997). Moreover, the disciplines of population, community, and ecosystem ecology, which diverged markedly in the 1970s and 1980s, were undergoing a synthesis and reunification (e.g., Vitousek and Hooper 1993, Jones and Lawton 1995). A seemingly outdated idea, originally expressed in the superorganismal perspective of Clements (see Goodman 1975), again became challenging when viewed through the ongoing synthesis of evolutionary, population, and ecosystem ecology.

Recent work on the consequences of changes in biodiversity (e.g., Frank and McNaughton 1991, McNaughton 1993, Vitousek and Hooper 1993, Naeem et al. 1994, 1996, *in press*, Tilman and Downing 1994, Tilman 1996, Tilman et al. 1996, 1997a, 1998, Hooper and Vitousek 1997, Huston 1997, McGrady-Steed et al. 1997, Naeem and Li 1997, Doak et al. 1998) has led to both insights and debate, as often occurs when ideas are young and paradigms are challenged. A major debate concerns whether plant community diversity depends on productivity (e.g., Grime 1979, Huston 1979, 1997, Tilman 1982, 1988), or productivity depends on diversity (e.g., McNaughton 1993, Vitousek and Hooper 1993, Naeem et al. 1994, Tilman et al. 1996, 1997a, b), or whether causation goes in both directions (e.g., Tilman et al. 1996). Other discussions focus on the distinction between the effects of composition vs. diversity and the proper ways to design and interpret diversity experiments or field studies (e.g., Givnish 1994, Aarssen 1997, Huston 1997, Tilman 1997a, Tilman et al. 1997a, b, Wardle et al. 1997, Lawton et al. 1998, Naeem and Li 1998). The relative importance of species vs. functional diversity is also uncertain (e.g., Vitousek and Hooper 1993, Grime 1997, Hooper and Vitousek 1997, Tilman et al. 1997a).

Many variables, including disturbance, species composition, and climate, are known to influence ecosystem processes. Here, I highlight the search for general principles governing how another variable, the biodiversity of a trophic level or guild, impacts the dynamics and functioning of populations, communities, and ecosystems. Such principles are needed to increase scientific understanding of the ecological consequences of changes in biodiversity, and to guide public policy related to biodiversity, especially to the loss of biodiversity that occurs in simplified ecosystems managed for human benefit.

In exploring the theoretical consequences of biodiversity, I begin with simple, well-known processes and mechanisms, especially the mechanisms of resource competition and coexistence that were the focus of my earlier work (Tilman 1982, 1988, 1990), and extend these to multispecies communities. I use these to ask how population, community, and ecosystem processes may depend on the number of species present. In particular, I investigate the effects of diversity within a trophic level on population and ecosystem stability, on productivity and nutrient dynamics, and on invasibility. Our field studies at Cedar Creek, and those of others, are used to evaluate this theory. First, though, it is necessary to consider how the effects of species composition and species diversity can be distinguished.

COMPOSITION VS. DIVERSITY

A major finding of the past two decades has been the critical role that species composition plays in the dynamics and functioning of ecosystems (e.g., Pastor et al. 1984, Vitousek et al. 1987, Vitousek and Walker 1989, Wedin and Tilman 1990, Estes and Duggins 1995, Power 1995, Sterner 1995, Ewel and Bigelow 1996, Hobbie 1996). Composition matters because organisms drive ecological processes, and species differ in their traits. Large differences in traits, such as the presence or absence of nitrogen fixation, or of deep roots, or of flammable tissues, can have large impacts on ecosystem processes (e.g., Vitousek and Hooper 1993). Species composition is likely to be one of the major determinants of stability, primary productivity, nutrient dynamics, invasibility, and other ecosystem traits.

Diversity may also impact ecosystem processes. However, composition and diversity often are correlated in both natural and managed ecosystems, making it difficult to unambiguously attribute effects to one or the other based on observational studies. To attribute effects to diversity requires comparison of sites that differ in diversity, but do not differ, on average, in proportional species representation. This could be achieved experimentally by having the species composition of each of many plots be determined by a separate, random draw of species from a species pool, and by comparing mean responses for sets of plots that differ in diversity. On average, across many such independent draws at a given level of diversity, each species would have an equal chance of being present in a plot, thus controlling for effects solely attributable to composition. Similarly, to attribute effects to composition, it is necessary to control for differences in diversity.

I use this approach to distinguish between effects caused by diversity vs. composition. This requires that experiments, observational studies, and theory be designed as previously specified. Alternatively, statistical approaches such as multiple regression can be used to statistically control for compositional and other dif-

ferences, when testing for effects of diversity based on observational data in which there has not been appropriate manipulation of diversity. It is critical to note that all of the theory presented here applies to local scales, to sites that are populated from the same species pool and that experience similar physical conditions. It is inappropriate to attribute to diversity those patterns observed across broader gradients, such as latitudinal gradients, because composition, climate, soils, and many other factors shift simultaneously on such gradients.

THE DIVERSITY–STABILITY DEBATE

One of the more controversial issues of the past three decades has been the hypothesis that diversity influences stability. Building on work of Clements (1916), Smuts (1926), Odum (1953), and MacArthur (1955), Elton (1958) hypothesized that greater diversity causes greater stability, with high-diversity communities and their species being less oscillatory and less susceptible to invasion by exotic species. Pimentel (1961) and Margalef (1969) offered additional support. However, May (1972) found that greater diversity led to lower local stability of multispecies equilibria in a Lotka-Volterra competition model. This finding was supported by Gardner and Ashby's (1970) demonstration that systems of equations became less stable as the number of interacting entities (equations) increased. Goodman (1975) reviewed >200 papers on the issue, criticized the holistic, superorganismal perspectives then in vogue in ecosystem ecology, and concluded that the preponderance of evidence failed to support the diversity–stability hypothesis. In the “Afterthoughts” to his book, May (1973) suggested that ecosystem properties would be more stable than population properties, but this insight was overlooked. McNaughton (1977, 1985), Pimm (1979, 1984), King and Pimm (1983), and others continued to explore the impacts of diversity on stability, but for the next two decades, many ecologists considered diversity of little relevance to stability or other ecosystem processes. This attitude seems to have changed (e.g., McNaughton 1993, Givnish 1994, Tilman and Downing 1994, Tilman et al. 1994, Tilman 1996, Huston 1997, Doak et al. 1998, Tilman et al. 1998).

Stability can refer to resistance to disturbance, resilience (the rate of recovery after disturbance), and constancy (degree of temporal stability; Pimm 1984). Here, in re-exploring diversity–stability principles, I focus solely on temporal stability. Temporal variability is measured using the variance in a time series of abundances. Because average abundances may differ, variance must be scaled relative to the mean. Traditionally (e.g., May 1972, Tilman 1996), this has been done using the coefficient of variation (CV: $100 \times \text{standard deviation}/\text{mean}$, i.e., $100 \sigma/\mu$), for which smaller values represent greater stability. In this paper, temporal stability (S) will be defined as $S = \mu/\sigma$, which is the ratio

of mean abundance, μ , to its (temporal) standard deviation, σ . Larger values of S represent greater temporal stability, i.e., lower temporal variation around the mean. S measures relative stability for both non-equilibrium and near-equilibrium conditions.

Temporal stability: analytical insights

The dependence of community temporal stability on diversity (represented throughout this paper as N , the number of species present) can be derived analytically from the statistical dependence of the variance of a sum of variables on their individual variances and covariances, an approach pioneered by Doak et al. (1998). Total community biomass is the sum of the biomasses (x_i) of all species present in a community. For a community containing N species, total community biomass (i.e., $x_1 + x_2 + \dots + x_N$) will have a variance of

$$\begin{aligned} \text{Var}(x_1 + x_2 + \dots + x_N) \\ = \sum_{i=1,N} \text{Var}(x_i) + 2 \left(\sum_{i=1,N-1} \sum_{j=i+1,N} \text{Covar}(x_i, x_j) \right). \quad (1) \end{aligned}$$

Equation 1 shows that the variance in a total community trait depends on the summed variances of each of the elements of which it is composed and on the summed covariances among all possible combinations of these elements. Expressed differently, this is the sum of all terms in the full $N \times N$ covariance matrix. For the diversity–stability hypothesis to hold for a community trait, such as total community biomass, communities that are more diverse must have greater temporal stability. If total community abundance is independent of diversity, the diversity–stability hypothesis requires that the summed variances and/or summed covariances decline as diversity increases. The covariance in the abundances of two species summarizes the total effect of one species on the other in a multispecies community. For communities of competitors, many covariances would be negative, meaning that an increase in the abundance of one species was associated with a decrease in the abundance of the other.

I will explore how diversity and interspecific competition can affect these two components of community stability: summed variances and summed covariances. I first consider the effect of diversity on the summed variances by assuming that species abundances vary randomly and independently through time, and thus have covariances of zero. I next consider the impacts of overyielding or underyielding on stability, and finally the effects of interspecific covariances (i.e., interspecific interactions) on stability.

The portfolio effect

One reason why more diverse communities may be more stable is suggested by the effects of statistical averaging (Doak et al. 1998). Under many circumstances (Tilman et al. 1998), the sum of several randomly and independently varying items is less variable (has

lower variance) than the average item. Because it is a long-standing principle in economics that more diversified portfolios are less volatile (e.g., Lee 1985, Brigham and Gapenski 1988, and other textbook treatments), we call this reason for the stability of an aggregate variable, such as total community biomass, to increase as diversity increases the “portfolio effect” (Tilman et al. 1998).

For simplicity in illustrating the portfolio effect, let us assume a set of competing species that differ in traits, such that the abundance of each species varies randomly and independently in response to environmental perturbations. Given communities composed of N such species, let us assume that competitive interactions limit total community biomass to m , and that all species are equally abundant (i.e., abundances of m/N). How, then, would the temporal stability of total community biomass depend on community diversity, N ? To determine the variance in total community biomass, let the temporal variance in the abundance of species i , σ_i^2 , scale with its abundance, m_i , as a power function:

$$\sigma_i^2 = cm_i^z \quad (2)$$

where c is a constant and z is the scaling power. The assumption that abundances vary randomly and independently, which is relaxed later, means that all covariances of species i with species j are zero, causing the variance of total community biomass to be

$$\begin{aligned} \text{Var}(x_1 + x_2 + \dots + x_N) \\ = \text{Var}(x_1) + \text{Var}(x_2) + \dots + \text{Var}(x_N). \quad (3) \end{aligned}$$

These relationships make it possible to calculate how temporal stability depends on diversity. The variance scaling relationship (Eq. 2) means that the temporal variance in the abundance of a single-species community, where the single species has a mean abundance of $\mu_1 = m$, is $\sigma_1^2 = cm^z$. Thus, the temporal stability of a one-species community is $S_1 = \mu_1/\sigma_1 = c^{-1/2}m^{1-z/2}$. For a community of N species, each species has an abundance of m/N and a variance of $c(m/N)^z$. The variance in total community biomass for these N species is, from Eq. 3, the sum of N such variance terms, or $\sigma_N^2 = cm^zN^{1-z}$. Note that this variance declines as diversity increases if $z > 1$. The mean total community abundance is $\mu_N = m$. The temporal stability, S_N , of a community containing N species is $S_N = \mu_N/\sigma_N = c^{-1/2}m^{1-z/2}N^{(z-1)/2}$.

The ratio of S_N to S_1 gives the temporal stability of a community containing N species relative to that containing one species:

$$\frac{S_N}{S_1} = N^{(z-1)/2}. \quad (4)$$

This simple equation shows that the temporal stability of a multispecies community, compared to that of a single-species community, depends on diversity, N , and

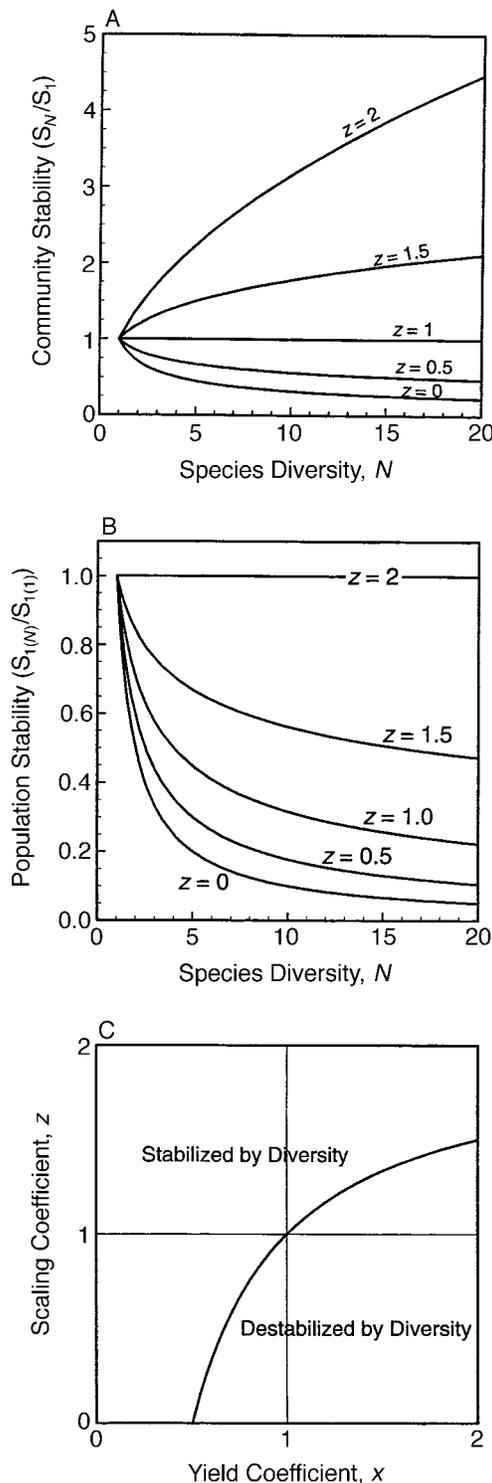


FIG. 1. (A) The portfolio effect. As shown in Eq. 4, the relative temporal stability of total community biomass for a community of N species compared to that for a monoculture depends on how variance in the abundance of each species scales with its abundance. Where z is the scaling coefficient, total community biomass is stabilized as diversity (number of species) increases if $z > 1$, and total community biomass is destabilized if $z < 1$; stability is unaffected by diversity if

on the scaling constant, z (Fig. 1A). The critical value of z is 1. If $z > 1$, the temporal stability of total community abundance increases as diversity increases, supporting the diversity–stability hypothesis. This portfolio effect occurs because community variance declines as diversity increases if $z > 1$. In contrast, if $z < 1$, more diverse communities are less stable. The factors that control how variance scales with abundance are thus a critical determinant of stability.

Overyielding

Diversity can impact total community productivity (e.g., Naeem et al. 1994, 1995, Tilman et al. 1996, 1997a, b). What might happen if total community biomass were to change as diversity changed, but all other assumptions were as before? A simple way to mimic the dependence of total biomass on diversity is to let the abundance (m_i) of each species depend on the number of species, N , as

$$m_i = \frac{m}{N^x} \tag{5}$$

where m is a constant. If $x = 1$, this gives the relationship in which the biomass of each species decreases proportionately to diversity, giving a total community biomass that is constant and independent of diversity. If $x < 1$, the abundance of each species decreases less than proportionately to diversity, causing total community biomass to increase as diversity increases (i.e., as N increases). This situation represents overyielding by all species. If $x > 1$, total community biomass decreases as diversity increases, which is underyielding by all species.

Keeping the scaling relationship of Eq. 2, it is easy to show, using Eqs. 3 and 5, that the temporal stability, S_N , of the total biomass for a community of N species divided by that for a one-species community would be

$$\frac{S_N}{S_1} = N^{1-x-(1-xz)/2}. \tag{6}$$

This shows that overyielding ($x < 1$) has a strong stabilizing effect on total community biomass (Fig. 1C). Greater overyielding increases community stability and increases the range of variance scaling relationships for which increased diversity leads to increased com-

←
 $z = 1$. (B) Population stability, as defined in Eq. 7, declines as diversity increases for $z < 2$. Although population stability increases as diversity increases for $z > 2$, there is no reason to expect z values this high, and few have been observed. (C) The effects of both overyielding and the scaling coefficient on community stability, based on Eq. 6. Community stability is independent of diversity for any points on the curve. Community stability increases as diversity increases for scaling coefficients (z) and overyielding coefficients (x) above the curve, and it decreases as diversity increases for those below the curve. Thus, a much broader range of scaling coefficients leads to stability when there is greater overyielding ($x < 1$).

munity stability. For instance, for $x = 1/2$, community stability increases with diversity for all positive values of the scaling parameter ($z > 0$), not just for $z > 1$ as occurs when there is no overyielding (Tilman et al. 1998). In field studies of plant communities, overyielding has frequently been associated with multispecies coexistence (i.e., Harper 1977). Moreover, models of coexistence of many species competing for several resources in heterogeneous environments predict that coexistence leads to overyielding (Tilman et al. 1997b). Thus, the mechanisms of coexistence are an important cause of diversity-dependent stability of primary production.

Population stability

How should diversity impact the temporal stability of individual species, i.e., population stability? The temporal stability of an individual species is its mean abundance divided by the temporal standard deviation in its abundance. Let us consider the general case in which there can be overyielding or underyielding (Eq. 5) and variance scales with the mean (Eq. 2). The ratio of the temporal stability of a single species living in a community of N species ($S_{1(N)}$) to that of a single species living by itself ($S_{1(1)}$) is

$$\frac{S_{1(N)}}{S_{1(1)}} = N^{x(z/2-1)}. \quad (7)$$

This shows that the relative temporal stability of a population depends on the diversity of the community in which it lives, and on how variances scales. The qualitative dependence of population stability on diversity comes solely from z (Eq. 7), and is independent of the degree of overyielding, x . Overyielding, though, does affect the magnitude of the impact of diversity on population stability. If $z = 2$, diversity has no impact on population stability (Fig. 1B). If $z < 2$, however, population stability decreases as community diversity increases. This occurs for all positive values of the overyielding coefficient. Population stability increases as diversity increases only if $z > 2$. If there is no overyielding, for values of z between 1 and 2, communities are stabilized by increasing diversity, but populations are destabilized. With high overyielding ($x < 1/2$), values of z from 0 to 2 cause communities to become stabilized and populations to become destabilized by increases in diversity. Both population and community stability would increase as diversity increases for $z > 2$.

Scaling relationships

Even without overyielding or negative covariance, the portfolio effect means that community stability should increase with diversity when $z > 1$. What, though, determines the value of z ? The scaling relationship that $\text{Var}(ax) = a^2\text{Var}(x)$, for which $z = 2$, holds, on average, for balls randomly drawn from an urn, and exactly applies when changing units from acres to hectares, or to any other such proportional rescaling (Til-

man et al. 1998). In nature, however, population densities change because of interspecific and intraspecific interactions rather than sampling processes. By influencing changes in population densities, such interactions determine how temporal variance depends on average abundances. For instance, an extension of May's (1972) model of logistic growth of a single species that experiences random variation in its environment shows that its variance scales linearly with mean abundance, i.e., that $z = 1$ (Tilman et al. 1998). If population densities were to change randomly, as determined by a Poisson model, z would also be equal to one.

Within the grassland plots at Cedar Creek, observed z values range from ~ 1.2 to 1.4 (Tilman et al. 1998). In studies of insect dynamics in the United Kingdom, Taylor and Woiwod (1980) found that the year-to-year variance in the abundance of individual insect species scaled according to Eq. 2. The mean for 97 aphid species was $z = 1.8$ and for 263 moth species was $z = 1.5$. Murdoch and Stewart-Oaten (1989) reviewed scaling relationships for both temporal and spatial variance and concluded, on both theoretical and empirical grounds, that $1 < z < 2$. If species in natural communities have scaling constants between 1 and 2, as the evidence suggests, then community stability should increase and population stability should decrease as diversity increases, all else being equal. In addition, if greater diversity leads to greater productivity (discussed in the following section), the overyielding effect should cause a stronger dependence of community stability on diversity.

Covariances and compensatory growth

Let us now ask what happens if species abundances covary. The variance in a total community trait depends on the summed variances and the summed covariances across all its elements (Eq. 1). If the summed covariances for a multispecies community depend on diversity, this could cause stability to depend on diversity. Pairwise competitive interactions cause negative covariance because an increase in the abundance of one species leads to a decrease in the abundance of another, and vice versa. Might interspecific competition, which is a major force in many communities (Connell 1983a, Schoener 1983), including the grasslands of Cedar Creek (e.g., Wilson and Tilman 1991, Wedin and Tilman 1993), stabilize total community biomass through such compensatory interactions?

Although covariances are unavoidably negative in a community of two competing species, indirect effects in more diverse competitive communities (Holt 1977, Lawlor 1979, Vandermeer 1980, Connell 1983b) can cause some pairs of species to have positive covariance or no covariance. Because of indirect effects in multispecies communities, it is not clear how the summed covariances might depend on diversity. To explore the effects of competition on variances, covariances, and total community biomass, a model of multispecies

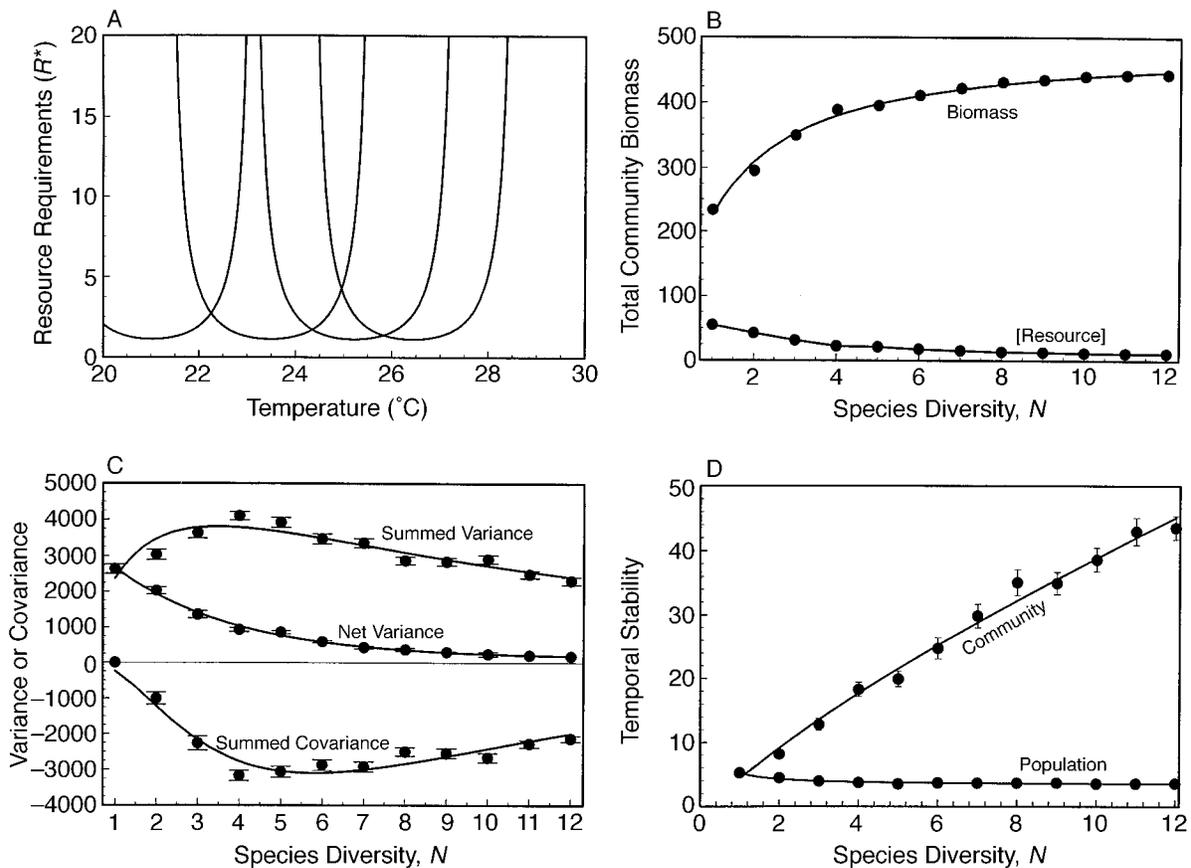


FIG. 2. (A) In the model of resource competition in a habitat in which temperature fluctuates, the resource requirements of species (R^* values) depend on temperature, with each species having its maximal competitive ability (minimal R^*) at a particular temperature. Four such species are illustrated here. (B) Based on numerous simulations of resource competition in habitats in which temperature randomly fluctuates, total community biomass is found to increase as diversity increases, and average resource levels decrease as diversity increases. Each dot shows the mean of numerous runs at each level of diversity and represents the long-term outcome of a simulation. For each simulation, the actual suite of species used was determined by a separate random draw of species from the full range of potential species traits. Note that the variance in total community biomass and the variance in resource levels both decrease as diversity increases. (C) Results of these simulations of resource competition were used to determine how the summed variances in species abundance, the summed covariances, and the net total community variance depended on diversity. Once adjusted for changes in total community biomass, net total community variance is a measure of stability. (D) The dependence of temporal stability, $S = \mu/\sigma$, for total community biomass and for the biomass of individual species (population stability), on diversity. Note that community temporal stability increased as diversity increased, whereas population temporal stability declined slightly as diversity increased.

competition was formulated. In it, species compete for a single limiting resource in a habitat in which there is temporal variability in a physical factor, temperature, that influences competitive ability (Fig. 2A). Each species has its optimal competitive ability, and thus attains its peak biomass, at a different temperature. In this model, interspecific competition favors the one species that has the lowest resource requirement at the current temperature, but fluctuations in temperature allow many species to persist. Thus, each species increases in abundance and consumes additional resources when its optimal temperature occurs. Because more diverse communities have competitive abilities that, in aggregate, span a larger portion of the full range of envi-

ronmental conditions, total community biomass increases and concentrations of unconsumed resources decrease at higher diversity (Fig. 2B).

In simulations of this model, the summed variance (variance of each species summed over all species, as in Eq. 3) increased as diversity increased from one to four species, but declined beyond this point (Fig. 2C). Summed covariance, which always was negative, became increasingly negative from one to four species, but then slowly became less negative as diversity increased beyond this point (Fig. 2C). The effect of these two changes was that net variance in total community biomass (the sum of summed variance and summed covariance) declined >20-fold as diversity increased

from one to 12 species (Fig. 2C). This, by itself, would have made community temporal stability increase strongly with diversity, but the total effect of diversity on community stability (Fig. 2D) was further strengthened by overyielding.

In this model of multispecies competition in a fluctuating environment, diversity stabilized total community biomass. These simulations also showed that the temporal stability of individual species declined by one-third as diversity increased (Fig. 2D), which is consistent with May (1972). Thus, this mechanistic model of resource competition in a non-equilibrium habitat predicted the same pattern as the variance-scaling equations (Eqs. 6 and 7). Both in this mechanistic model and in the variance-scaling equations, community stability increased and population stability decreased as diversity increased. Remarkably similar results were obtained in two additional models of multispecies competition (C. L. Lehman and D. Tilman, *unpublished manuscript*).

Tests of the diversity–stability hypothesis

McNaughton (1993) examined available studies and found that most supported the diversity–stability hypothesis. However, most of these studies were small-scale and short-term. We reported the effects of a severe drought (Tilman and Downing 1994) and of 11 years of year-to-year variation in climate (Tilman 1996) on the stability of total community biomass in 207 Minnesota grassland plots in which plant diversity had been modified by various rates of nitrogen addition. Even after statistically controlling for up to 20 potentially confounding covariates, multiple regressions revealed a highly significant stabilizing effect of plant diversity on the total community plant biomass of these plots (Tilman and Downing 1994, Tilman et al. 1994, 1998, Tilman 1996). Specifically, a comparison of total plant biomass during the drought to that just before the drought showed that plots with greater plant species diversity were significantly more resistant to drought. As would be expected, other factors, especially plant community composition, root:shoot ratios, and total community biomass, simultaneously affected drought resistance (Givnish 1994, Tilman and Downing 1994, Tilman et al. 1994, Tilman 1996). Similarly, the extent of year-to-year fluctuations in the total plant biomass in each plot, measured as coefficients of variation (the inverse of temporal stability, S) showed, both for the total data set (1984–1997) and for nondrought years (1984–1986 and 1989–1997), that more diverse plots had greater temporal stability (lower coefficients of variation) of total community biomass (Fig. 3), even with control for potentially confounding variables. Species composition and other factors simultaneously affected stability.

This experiment provides a reasonable test of the diversity–stability hypothesis. It supports it and demonstrates that several other factors, especially species

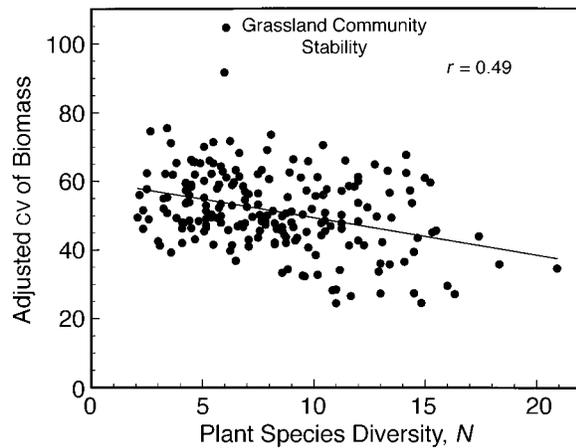


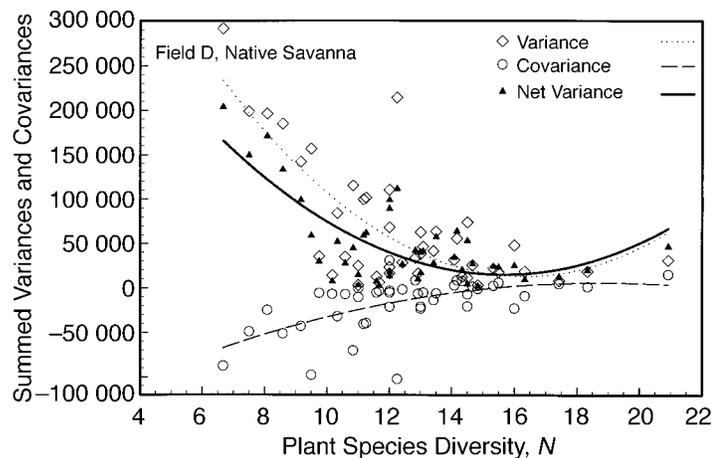
FIG. 3. The dependence of the coefficient of variation (cv) of total community biomass on plant species diversity, based on data for four Cedar Creek fields. The lower coefficients of variation of more diverse fields mean that total community biomass is stabilized by diversity. As shown in Tilman (1996), abundances of individual species are destabilized by diversity. Coefficients of variation of each field were adjusted for differences in intercepts as determined by a GLM regression. Note that temporal stability is proportional to the inverse of these coefficients of variation.

composition, are also critical determinants of stability. As pointed out in Givnish (1994) and Huston (1997), and in our original papers (Tilman and Downing 1994, Tilman 1996), any study that lacks direct experimental control of diversity will always be open to alternative interpretations, but all of the statistical analyses inspired by such concerns support the diversity–stability hypothesis.

Why did diversity lead to greater ecosystem stability? During the 1988 drought, some species were more abundant than they had ever been before the drought. These species increased in abundance, as other species declined, because of the drought (Tilman 1996). Such species combinations had negative covariance. However, it is the sum of all covariances that influences community stability. For more diverse communities to be more stable because of the covariance effect, it is necessary that the summed covariances become more negative as diversity increases. Did this occur in the Cedar Creek grasslands?

For each of our four experimental fields, the summed variances in the abundances of all species in a plot significantly ($P < 0.05$) declined with increased plant diversity. This shows that the portfolio effect was operating in all four fields, as predicted by Eq. 4, given the observed z value of ~ 1.3 . Results for one field are shown in Fig. 4. On average, across all 207 plots, the summed covariances were negative (mean of -6086) and were \sim one-fifth of the summed variances (mean of 30 352). Thus, interspecific interactions, most likely competition as reflected in the summed covariances, increased the stability of these plant communities by

FIG. 4. Summed variances, covariances, and net variance for native savanna, one of the four Cedar Creek fields. As occurred in three of the four fields, covariances, although negative, became increasingly less negative as diversity increased, indicating that negative covariances did not tend to stabilize more diverse communities. Both summed variances and net variance declined as diversity increased, indicating that the portfolio effect (scaling of variance with abundance) was likely to be the major reason why more diverse communities had lower year-to-year variability in total community biomass, i.e., had stability increase with diversity.



reducing the net variance in total community abundance. However, there was no clear dependence of the summed covariances on diversity. In one of the four fields, covariances became significantly more negative as diversity increased, whereas they became significantly less negative with diversity in the other three fields (as shown in Fig. 4). The mean summed covariance and its trend were small compared to the mean summed variance and its trend. This indicates, as suggested by Doak et al. (1998), that the portfolio effect, not negative covariance, was the stronger determinant of the dependence of community stability on diversity.

In these grassland plots, populations were destabilized by increases in diversity. Abundances of individual species had lower temporal stability (as measured by coefficients of variation) at higher diversity (Tilman 1996), which is consistent with the prediction of Eq. 7, given our observed z value of ~ 1.3 . In total, theory, experiment, and observation agree: diversity stabilizes community and ecosystem processes via portfolio, overyielding, and perhaps negative covariance effects, but simultaneously destabilizes the dynamics of individual species.

EFFECTS OF BIODIVERSITY ON OTHER ECOSYSTEM PROCESSES

As pointed out by McNaughton (1993), Darwin (1872) suggested that more diverse communities were more productive. Lawton and Brown (1993), McNaughton (1993), Vitousek and Hooper (1993), Huston (1997), and Tilman et al. (1997b) have proposed theories linking ecosystem productivity, nutrient dynamics, and predictability to diversity. The model of resource competition in a habitat with fluctuating temperature, just presented, predicts that community productivity should increase with diversity (Fig. 2B). Here, I explore the possibility that the essence of such relationships may be governed by a few simple principles.

The sampling effect

Consider a homogeneous habitat in which species differ in their competitive abilities and are limited by, and compete for, the same single resource. At equilibrium, the best competitor, of those species present, would win (e.g., Tilman 1982). The more species that are drawn from a common species pool, the better, on average, would be the competitive ability of the best competitor drawn. Because a better resource competitor is a more efficient user of the limiting resource, dominance by a better competitor would lead to greater productivity and to lower average levels of unconsumed resource. Thus, greater diversity would increase the chance that a superior competitor will be present, and interspecific interactions would cause it to become dominant. Its traits would become the major determinant of ecosystem functioning. Assuming that the traits that influence interspecific interaction also influence the ecosystem impact of a species, then increased diversity should cause a directional, but asymptotic, change in ecosystem functioning. This simple mechanism, called the sampling effect (Tilman et al. 1997b), is a fundamental effect of diversity that was simultaneously proposed by Huston (1997).

Tilman et al. (1997b) developed the sampling effect concept mathematically. Where R^* is the concentration down to which the consumable form of the limiting resource is reduced by an equilibrium monoculture of a species (e.g., Tilman and Wedin 1991), the best competitor would be the species with the lowest R^* (Tilman 1982, Wedin and Tilman 1993, Grover 1997). The R^* value of each species can be used to rank species from good to poor in competitive ability (i.e., from the lowest to the highest R^* value).

Let species be drawn, at random, from an infinite pool composed of species having all possible R^* values uniformly distributed between some minimum (R_{\min}^*) and maximum (R_{\max}^*) values. On average, the number of species drawn, which is the initial diversity, has a

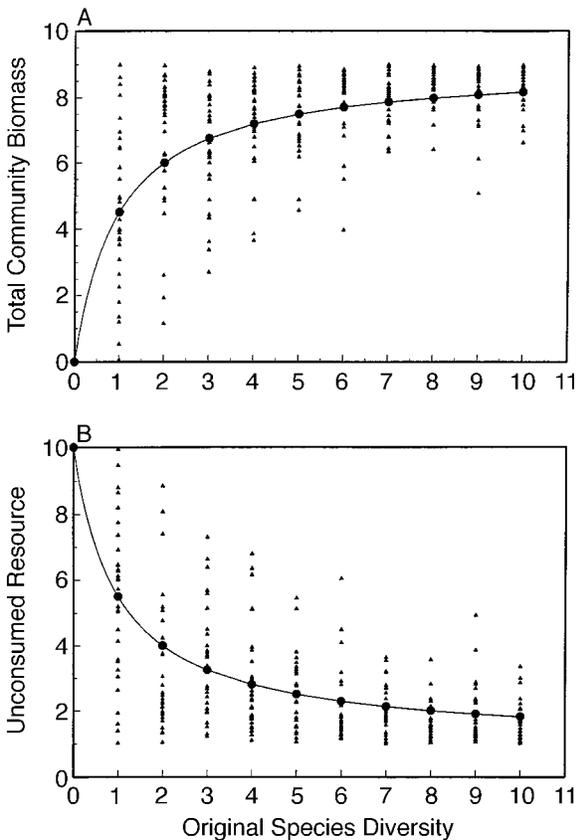


FIG. 5. Results of simulations for the sampling effect model show that (A) total community biomass increases and (B) levels of unconsumed resources decrease with diversity, just as was analytically predicted by the model. The figure is based on analyses from Tilman et al. (1997b). Original species richness refers to the number of species randomly chosen to form a community. At equilibrium, competition will have reduced diversity to the single species that has the lowest R^* value.

strong effect on ecosystem productivity and nutrient dynamics. The mechanisms inherent in the sampling effect yield a simple equation (Tilman et al. 1997b) that relates the equilibrium biomass of a plant community, $B_{(N)}$, to its original plant species diversity, N :

$$B_{(N)} = aQ \left[S - \left(R_{\min}^* + \frac{R_{\max}^* - R_{\min}^*}{N + 1} \right) \right]. \quad (8)$$

Here, a is the rate of resource mineralization, Q is the coefficient of resource conversion into biomass, and S is the rate of resource supply in the habitat. This model predicts that total community biomass asymptotically increases with plant diversity (Fig. 5A). The model assumes that all species have identical Q 's, as might be expected, i.e., equal efficiency in resource use. If better competitors had larger Q 's, community biomass would increase even more as diversity increased. The amount of unconsumed resource decreases toward R_{\min}^* as diversity increases (Fig. 5B). This equation

makes the important point that the magnitude of the effect of diversity on ecosystem functioning depends on the magnitude of interspecific differences in the species pool ($R_{\max}^* - R_{\min}^*$), providing a basis for the intuitive concept that it is greater differences among species that cause diversity to have an effect.

A species is said to overyield at higher diversity if, on average as diversity increases, its biomass declines less rapidly than its average monoculture biomass divided by N , the diversity. For the sampling effect model, half of the individual species overyield and half underyield as diversity increases.

Because communities of a given diversity can have markedly different compositions, they can differ greatly in their functioning. It is possible to analytically predict the effect of species composition and species diversity on the variance in community biomass or resource levels (Tilman et al. 1997b). The variance within each diversity level is caused differences in species composition, not by measurement error or environmental fluctuations. Rearrangement of the equations in Tilman et al. (1997b) for the mean biomass and its variance shows that the μ/σ of total community biomass increases approximately linearly with diversity, indicating that the more diverse communities are increasingly more similar in their mean biomass. The reason for this is simple: more diverse communities are more similar, on average, in the range of species traits present. This μ/σ measures the spatial stability of randomly assembled communities that differ in diversity, whereas the work on temporal stability measures variation in a time series of abundances for a given community. However, both μ/σ ratios show that increased diversity causes increased stability. Such increased stability has been reported for microbial communities (McGrady-Steed et al. 1997, Naem and Li 1997), for experimental plant communities grown in a greenhouse (Naem et al. 1994, Tilman 1997b), for the Cedar Creek biodiversity field experiments (Tilman et al. 1996, 1997a), and, based on inferences from variance-scaling relationships, for insect communities (Taylor and Woiwod 1980, Taylor et al. 1980).

Niche differentiation

The sampling effect model is a caricature of reality, because most habitats are spatially and temporally heterogeneous. Let us still consider only species on a single trophic level, but with heterogeneous habitats and species that differ in their responses to this heterogeneity. For spatial heterogeneity, let there be two factors, such as soil pH and temperature, that limit plant abundance. Each species has some combination of these factors at which it performs best, with performance decreasing as conditions deviate from this optimum. For instance, each species might have a bivariate normal distribution of competitive abilities, with the peak being its optimum. Such niche differentiation means

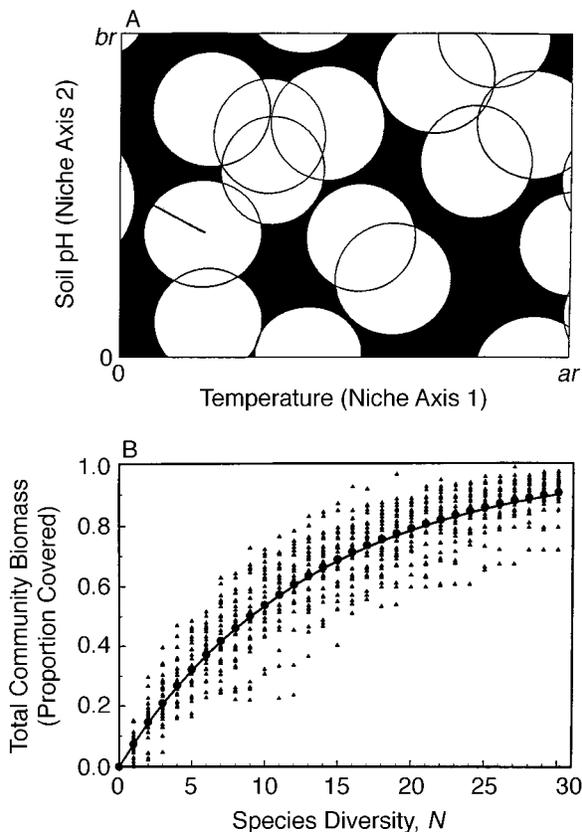


FIG. 6. (A) The niche model, in which each species has a range of environmental conditions in which it performs best (circles of radius r) and other conditions in which it cannot survive. Values range from 0 to ar for limiting factor 1, and from 0 to br for limiting factor 2. (B) This model predicts that total community biomass, as estimated by the proportion of niche space occupied by viable species, increases as diversity increases. Results of simulations closely match the analytical theory developed in Tilman et al. (1997b). The figure is based on the model and simulations presented in Tilman (1997b).

that each species covers a part of the habitat, but no species can fully exploit the entire range of conditions.

I know of no analytical solution to the general model in which species have separate, bivariate distributions, and in which competitive rules determine the outcome of interactions in zones of overlap. However, the essence of such a niche model can be approximated if it is assumed (Tilman et al. 1997b) that each species has a circular area of radius r in which it lives (Fig. 6A), that all species attain comparable abundances per unit habitat occupied, that interspecific competition proportionately reduces abundances of all overlapping species, and that the values for one limiting factor range from 0 to ar and the other from 0 to br , where a and b measure habitat heterogeneity for factors 1 and 2. The species pool consists of all species that could live in this heterogeneous habitat. As analytically derived

in Tilman et al. (1997b), this causes mean total community biomass (scaled as the proportion of environmental conditions “covered” by one or more randomly drawn species, all of which coexist) to be

$$B_{(N)} = 1 - \left[1 - \frac{\pi}{ab + 2(a + b) + \pi} \right]^N \quad (9)$$

where N is species diversity (i.e., the number of randomly drawn species) and $B_{(N)}$ is an asymptotically increasing function of species diversity (Fig. 6B). The amount of unexploited habitat is an asymptotically decreasing function of diversity, much as the concentration of unutilized resource was a decreasing function of diversity for the sampling effect model. All variance within a given level of diversity (Fig. 6B) is caused by differences in the composition of randomly assembled communities. In this model, all species overyield, i.e., the biomass of each species declines less rapidly than as its monoculture biomass divided by N . Uniform overyielding may be a signature of niche effects, distinguishing them from sampling effects.

The niche model has an additional feature. The greater the habitat heterogeneity (i.e., the greater values of a and b), the more linear is the dependence of community productivity on diversity, and the greater is the diversity required to produce a given level of productivity or coverage. Because heterogeneity increases with habitat size, this model makes the intuitively appealing prediction that greater biodiversity is required to attain a given level of productivity in larger habitats. When parameterized for a local, relatively spatially homogeneous habitat ($a = b = 1$), Eq. 9 predicts that six species are needed to attain 95% of maximal productivity. However, a spatially heterogeneous region ($a = b = 10$) requires a diversity of 135 plant species to achieve 95% of the maximum. This, interestingly, is about the number of vascular plant species in a hectare of Minnesota savanna. This effect of habitat size is of interest because of the small spatial scale of laboratory, greenhouse, and field experiments. Although these show that 10–15 plant species are adequate to cause near saturation of relationships between diversity and ecosystem functioning, these results apply only to the small spatial scales of the experiments. It is unclear how these results must be scaled up to whole communities (e.g., Grime 1997). It is certain, though, that many human-impacted ecosystems are sufficiently depauperate that further decreases in species diversity could cause significant changes in functioning. This suggests that the work presented here may be most relevant to the vast regions of the world in which ecosystems have been simplified by humans.

A major difference between the sampling effect and niche models is illustrated by comparing the composition-dependent range of variation at each level of diversity. For the sampling effect model, the upper bound of the plot-to-plot variation in total community biomass is a flat line (Fig. 5A), as is the lower bound

of the curve for levels of unconsumed resource. This flat upper or lower bound occurs because a monoculture that contains the best possible species is just as productive and creates just as low a resource level as an originally diverse plot that contains this same species. In contrast, the niche differentiation model has a lower bound, a mean, and an upper bound for total community biomass, all of which asymptotically increase with diversity (Fig. 6B). As already shown (Fig. 2B), a model of resource competition in a habitat in which a limiting physical factor fluctuates has identical features, as does an explicit model of plant competition for two essential resources in a spatially heterogeneous habitat (Tilman et al. 1997b). The niche differentiation model (Eq. 9, Fig. 6) is a simple abstraction that predicts the salient features of more realistic models of multispecies competition. For all three niche differentiation models, there is no monoculture that is as productive as some combinations of two species, no combination of two species that is as productive as some combinations of three species, etc., for all levels of diversity. This, however, is not the case for the sampling model for which there is a species that, when growing in monoculture, is as productive and uses the limiting resource as completely as the best possible multispecies mixture.

Experimental studies

Many intensively watered, fertilized, tilled, and bio-cided agroecosystems may approximately fit the assumptions of the sampling effect model, because light would be the only limiting resource. If so, the sampling effect model would predict that a monoculture of the appropriate species (and genotype) would be as productive as more diverse plantings. A review of 572 agricultural studies of annual plant intercropping showed little advantage to multispecies plantings unless one of the crops was an N-fixing species (Trenbath 1974, Swift and Anderson 1993), and, presumably, soils were nitrogen poor. However, niche theory suggests that diversity should significantly increase productivity and nutrient use in spatially and temporally heterogeneous habitats in which there are several limiting factors. Higher tree diversity is thus expected to cause natural and managed forests to be more productive and to exhibit more efficient and complete nutrient use, which should minimize leaching losses of soil nutrients, and thus cause more diverse forests to develop more fertile soils.

Several experiments have explored the effects of plant diversity on community productivity and on levels of unconsumed resources (Naeem et al. 1994, 1995, Tilman et al. 1996, 1997a). In a food web experiment, Naeem et al. 1994 (but see Lawton et al. 1998) found that greater diversity on several trophic levels led to greater productivity. A similar result occurred in a greenhouse study in which only plant diversity was manipulated (Naeem et al. 1995). In both of our field experiments, which were planted in 1994, plant diver-

sity was the independently controlled experimental variable. In the small biodiversity experiment (Tilman et al. 1996), 147 plots, each 3×3 m, were randomly assigned to have 1, 2, 4, 6, 8, 12, or 24 plant species, with the composition of each plot determined by separate random draws from a pool of 24 grassland species. The large biodiversity experiment (Tilman et al. 1997a) had 289 plots, each 13×13 m, that were planted with 1, 2, 4, 8, 16, or 32 species and/or 1, 2, 3, 4, or 5 plant functional groups. In both experiments, plant productivity was an increasing function of diversity (Tilman et al. 1996, 1997a; e.g., Fig. 7A). Soil nitrate in the rooting zone and that below the rooting zone decreased with diversity (Fig. 7B). The effect on nutrient leaching suggests that more diverse ecosystems should retain a higher proportion of the limiting nutrient, leading to increased total soil nutrient stores, and thus, eventually, to even greater productivity. Other analyses suggest that functional composition and functional diversity were major, and approximately equal, determinants of productivity and nutrient dynamics (Tilman et al. 1997a).

Several lines of evidence suggest that sampling and niche effects operated simultaneously. In the small biodiversity experiment, the first species to attain dominance was the rapidly growing forb *Rudbeckia hirta*. It was replaced by several more competitive, but slowly growing species, in particular, highly productive C_4 grass species. High-diversity plots were more likely to contain these species. Those that did generally had greater biomass than plots that lacked them. All of this supports the sampling effect model. However, most species are coexisting in all plots to which they were added, and are at relative abundances similar to those in native grassland. Such coexistence is contrary to the assumptions underlying the sampling effect model (which predicts formation of monocultures), but is consistent with the niche model. Interspecific coexistence is frequently associated with overyielding (Harper 1977). The niche model is supported by the preponderance of species that have statistically significant overyielding. In the small biodiversity experiment, for example, eight species significantly ($P < 0.05$) overyielded and only two significantly underyielded in 1997, the fourth year of the experiment. The remaining species did not have significant responses. The preponderance of overyielding supports the niche model, for which all species are predicted to overyield, but the significant underyielding by two species suggests that the sampling effect may play a role. In total, our biodiversity experiments suggest that both sampling and niche effects occur, and that, as predicted by theory, both composition and diversity simultaneously control ecosystem processes. Natural ecosystems and ecosystems impacted by human activities differ in both composition and diversity. Our results predict that changes in either will impact ecosystem processes.

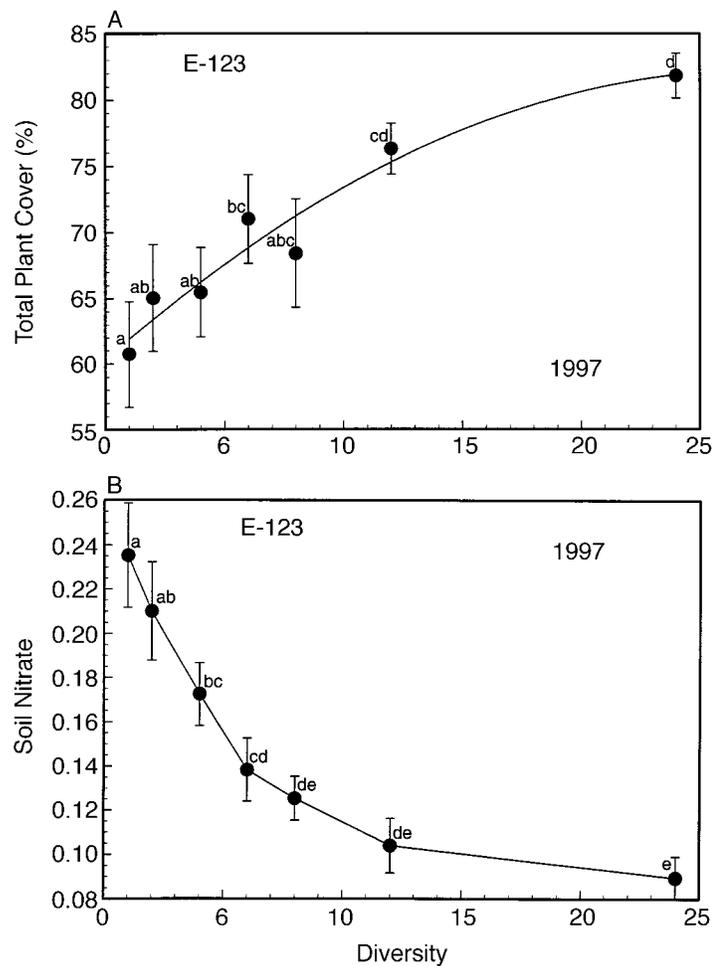


FIG. 7. (A) Total plant cover, a measure of total community plant biomass, for the small biodiversity experiment at Cedar Creek. Results are for 1997, the fourth year of the experiment. Mean responses (± 1 SE) are shown, as are results of contrasts. Means that differ significantly at the $P < 0.05$ level do not share any lowercase letter. The curve shown is fitted through all of the data. (B) The dependence of soil nitrate on diversity for this same experiment, shown similarly, for soil cores from a depth of 0–20 cm.

INVASIBILITY AND BIODIVERSITY

Elton (1958) hypothesized that more diverse ecosystems are less readily invaded by exotic species. The theory and experiments just presented suggest a mechanism that would cause invasibility to depend on diversity and on community composition: average levels of limiting resources decline as diversity increases, and depend on species composition. Because each species has a level of resource (R^*) below which it cannot survive, reproduce, and spread (Tilman 1982), greater diversity should, on average, decrease the chance that any given species would successfully invade a given habitat. The essence of this mechanism can be formalized easily. The first requirement is a curve, $g(N)$, that defines the dependence of the average resource level on community diversity. This could be empirically observed in a field experiment (Fig. 7B), or derived theoretically (Fig. 5B, from Tilman et al. 1997b). The other determinant is the R^* of the invading species. Together, these define the diversity, N^* , above which that species could not invade, on average. These relationships are readily illustrated graphically (Fig. 8A)

and have a simple mathematical basis. For species i , the critical diversity level is just $N_i^* = g^{-1}(R_i^*)$. Note that invasibility is equally dependent on species composition, disturbance, and other factors. These additional factors mean that any expectations based solely on diversity will, at best, be predicting a mean tendency around which there could be great variance. Given a set of R^* values for a community of potential invaders, it is straightforward to predict the average likely success of each invading species and the dependence of the average number of successful invaders on diversity. If, for instance, the R^* values of invaders were uniformly distributed between R_{\min}^* and R_{\max}^* , then the number of successful invaders would monotonically decline as diversity increased, with the curve having a shape like that in Fig. 8B.

Dominance by exotic species

Why have some exotic species, such as the cactus *Opuntia stricta* in Australia or the zebra mussel, *Dreissena polymorpha*, in North America, attained much greater abundances in a new habitat than in native hab-

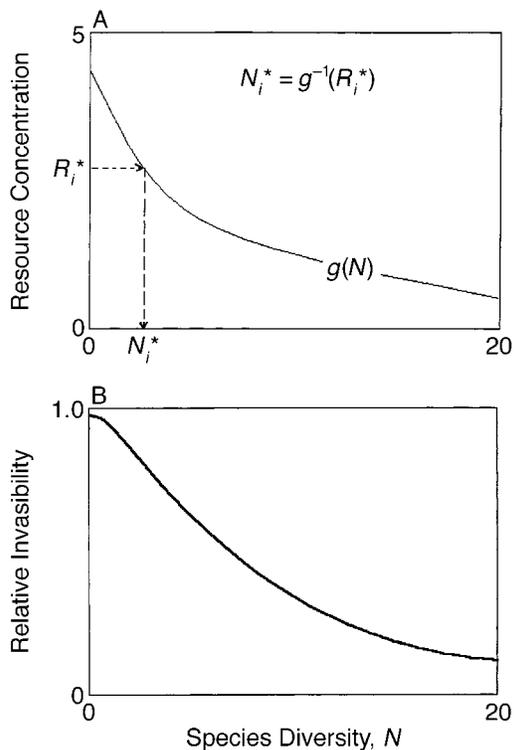


FIG. 8. (A) The resource requirement of a species (R^*) and the dependence of average community resource levels on diversity (solid curve) define the species diversity level (N^*) at and below which the species can invade a community, on average. (B) For a suite of invading species, relationships like those shown in (A) cause invasibility (the proportion that successfully invades) to decline with diversity.

itat? There are various potential explanations. One simple insight may be provided by the factors that determine R^* and, thus, competitive ability for a single limiting resource in an equilibrational habitat. R^* represents the resource level at which the resource-dependent growth of a species balances all losses. For a terrestrial plant, growth includes vegetative, sexual, and asexual components, and loss includes both death of individuals and loss of tissues and nutrients to herbivores, pathogens, senescence, etc. (Tilman 1990).

The lower its loss rate, the lower the R^* of a species will be. Indeed, if $f(R)$ is the function that defines how the growth rate of a species depends on R , and if L is the total loss rate that the species experiences, then $R^* = f^{-1}(L)$. This equation unambiguously states that the competitive ability of a species depends on its loss rate, L . For equilibrational habitats, it may be combined with the earlier result to calculate that the average diversity level, N^* , beyond which a species is unlikely to invade, increases as the loss rate declines. This comes from the relationship that

$$N^* = g^{-1}(f^{-1}(L)) \quad (10)$$

which can be illustrated graphically (Fig. 9C). Consider

a species that experiences total losses of A , which give the species a resource requirement of R_i^* . If the introduction of this species into a novel habitat causes its loss rate to be reduced to B , perhaps because a major herbivore or pathogen of this species does not occur in the new habitat, its R^* would be reduced to R_i^{**} . This lower R^* would increase its competitive and invasive abilities, causing the species to be more abundant and to spread more rapidly and into a larger range of communities than in its native habitat. This missing predator-invasion hypothesis, which is one of many potential hypotheses that might explain invasibility, is supported by cases in which such introduced species have been controlled by the introduction of pathogens, predators, etc., from their native habitat.

Rules for invasibility of biogeographic realms?

Few habitats have just one limiting resource or factor, which makes the criteria determining invasibility more complex. In general, for a group of species to coexist in a habitat, each species must have traits that fall at some point on a community-wide interspecific trade-off curve (Fig. 9A) or surface (Tilman 1988). Depending on the underlying mechanisms of interaction, each point on such a curve or surface may represent a potentially viable combination of traits, or there may be limits to similarity (e.g., Tilman 1994) such that only points spaced more than a certain distance apart represent viable species. Such trade-offs can allow the coexistence of a large, even unlimited, number of species in habitats with the appropriate spatial or temporal heterogeneity (Tilman and Pacala 1993). The position of the trade-off curve or surface reflects the traits of the species in a trophic level, the traits of their predators, parasites, pathogens, etc., and the characteristics of the physical habitat. This trade-off surface is not a static entity, but should move in response to evolutionary and interspecific forces.

The shapes and positions of such trade-off surfaces are critical determinants of invasibility. Imagine two different biogeographic realms, each with its own trade-off surface. If the trade-off surface for Realm 2 is inside that of Realm 1, then, all else being equal, species from Realm 2 could invade Realm 1 and displace species of Realm 1. Those of Realm 1 would be unable to invade or displace species of Realm 2 (Fig. 9B).

What might cause two realms to differ in their trade-off surfaces? In comparisons of most biogeographic realms, the phylogenetic origins of species are different. The desert cactus-like plants of North America, for instance, are in the Cactaceae family, whereas those of the deserts of Africa are in the Euphorbiaceae. These two groups probably had different evolutionary potential that has impacted their ability to minimize resource requirements in the face of various physical conditions and losses, causing interspecific trade-off surfaces to differ among these realms. Realms also may differ in

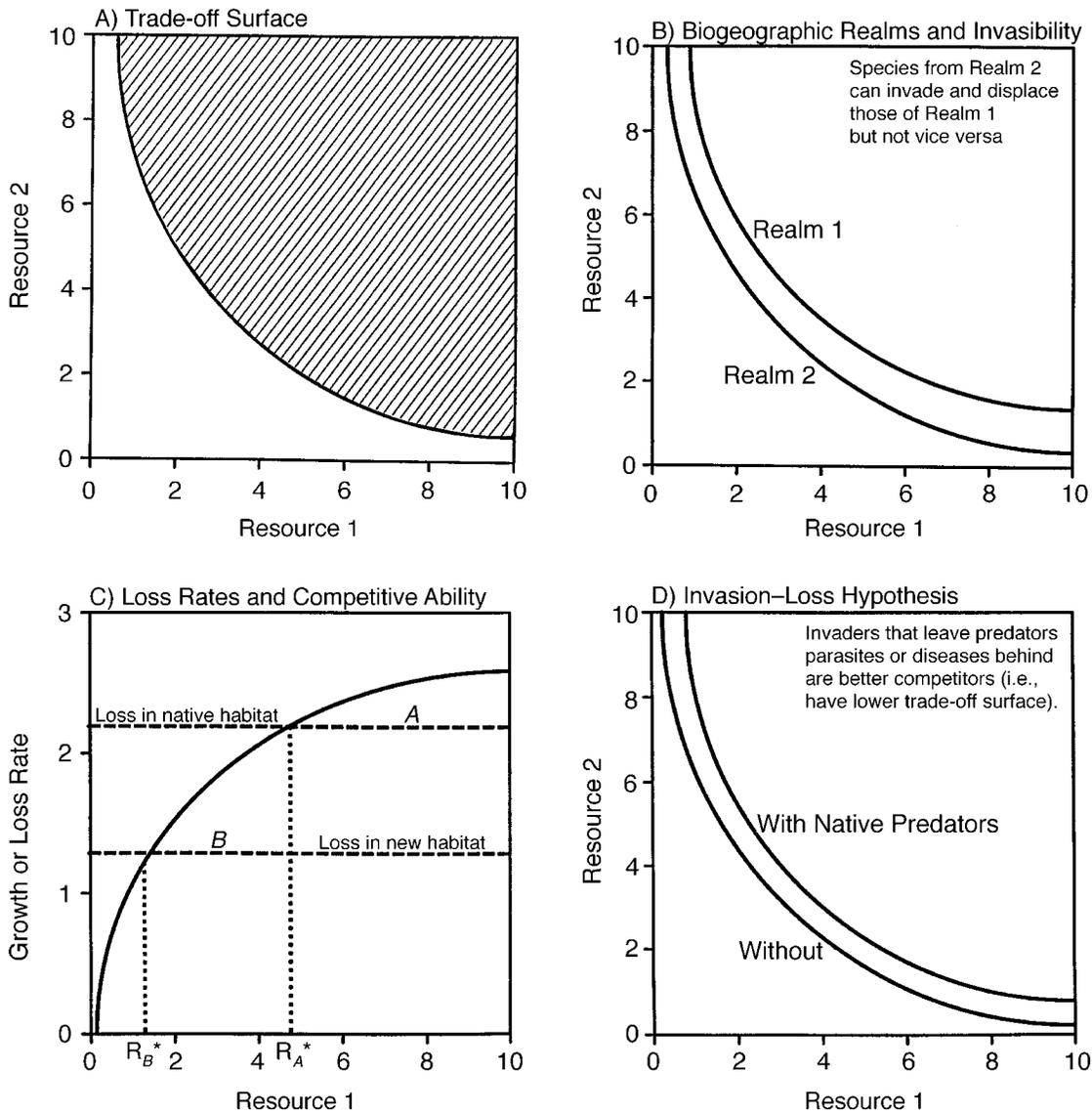


FIG. 9. (A) For a community of species competing for two essential resources, there is a trade-off curve (solid line) that shows the lowest possible combinations of resources (R^* values) at which various species can persist in a habitat. Each point on the trade-off surface represents the requirements of a particular species and thus is the “corner” of its zero net growth isocline (see Tilman 1980, 1982). A trade-off surface with this shape probably applies to plants competing for limiting nutrients. The species that compose this community can live only in habitats that have resource levels on this trade-off curve or beyond it (the shaded region). (B) The trade-off curves differ between two biogeographic realms; one realm may contain species that are, on average, superior competitors to those of the other realm. As shown, those of Realm 2 are superior to those of Realm 1. (C) The loss rate (density-independent mortality rate) experienced by a species determines its R^* for a limiting resource. (D) If, in general, invading species have lower loss rates in novel habitats than in native habitats, this would shift their trade-off curve toward the origin, making them superior competitors, in general, in novel habitats.

their geographic extent. All else being equal, regions with larger populations should have greater genetic variation, which should lead to superior trade-off surfaces. Whatever the cause, some biogeographic realms may be both inherently more resistant to invasion and inherently better at invading other realms (Fig. 9B).

It is also possible for trade-off surfaces to shift toward greater competitive ability, on average, when spe-

cies enter a new biogeographic realm. This would occur if most invading species left behind some of their predators, parasites, or pathogens (Fig. 9C). The lack of such control agents would decrease the resource requirements of species, moving their trade-off surface closer in toward the origin. If the evolutionary potential and history of different biogeographic realms were about equal, with trade-off surfaces that were similar,

then the “missing predator” effect might predominate. If so, each biogeographic realm would be susceptible to invasion by species from the same biome type of other regions. In this case of mutual invasibility, novel species would tend to have a competitive advantage because they would be free of their pests, diseases, and pathogens. This competitive advantage in a new biogeographic realm should decline through time as local pests, pathogens, or diseases evolve greater abilities to utilize a newly abundant invading species.

The opposite case, that all realms are difficult to invade and that invaders have little impact on native species, would require that trade-off surfaces shift away from the origin when species were introduced into a new biogeographic realm. Might this occur, initially, when some plant species are introduced to a new realm? Many plant species become major invaders only after being cultivated in a new habitat for a number of years. One explanation for this effect is that they have become adapted, in some way, to local conditions. They may have picked up mutualists that replaced those left behind. Or, the climate, soils, and other physical factors of each biogeographic realm may have some unique patterns of correlation to which local species are adapted and to which species from other realms must genetically adjust. However, such constraints must be minor, because many plant species have invaded and have had dramatic impacts on novel habitats (e.g., Rejmánek 1989, Vitousek 1990, D’Antonio and Vitousek 1992, Pyšek 1995). Even within a continent, species that evolved in different areas have merged together and coexisted when entering new regions following climate change (Davis 1986).

Tests of invasion theory

There have been no formal experimental tests of the resource-based mechanisms of invasibility proposed here. Several experiments at Cedar Creek provide some insights. An experiment in which seed of up to 54 plant species was added to native savanna showed that invasibility was significantly lower at higher diversity (Tilman 1997b). Similarly, the number of weedy species that invaded our small biodiversity experiment, and the total biomass of these plants, declined significantly with plant diversity. The latter effects of diversity were best explained, statistically, by the lower levels of soil NO_3 in the higher diversity plots (J. Knops, *personal communication*), which supports the resource-competition-based diversity–invasibility hypothesis.

A SUMMARY AND FUTURE DIRECTIONS

In total, simple theories, derived from well-known ecological relationships, predict that biodiversity can be one of several significant factors governing the stability, productivity, nutrient dynamics, and invasibility of ecosystems. These theories predict that greater biodiversity should, in general, (1) increase community

temporal stability; (2) decrease population temporal stability; (3) increase community standing crop and/or productivity; (4) decrease amounts of unconsumed limiting resources; (5) increase ecosystem stores of limiting nutrients by decreasing loss; and (6) decrease invasions by exotic species.

In none of these cases is diversity necessarily the only, or even the strongest, force. Species composition, productivity, disturbance regimes, climate, and edaphic factors can be as, or more, important than diversity. This does not diminish the role of diversity, but rather puts it in perspective. Diversity, itself, is both a measure of the chance of having certain species present in a system and a measure of the variation in species traits in an ecosystem. Greater diversity decreases interspecific variance in traits among sites and thereby decreases the extent of site-to-site variance in traits at a level of diversity. Diversity matters because both the chance of having certain species present and the range of traits present influence species interactions and abundances, which, in turn, influence population, community, and ecosystem processes. In total, these experiments and concepts demonstrate that diversity impacts the structure, dynamics, and functioning of ecosystems. Diversity must be added to composition, disturbance, nutrient supply dynamics, and climate as a determinant of ecosystem structure and dynamics.

Many factors in addition to those considered here merit study. Foremost among these are effects of interactions at multiple trophic levels. This paper has focused on the effects of diversity within a single trophic level. Effects of the diversity of additional trophic levels are equally worthy of pursuit, and may well yield a rich array of patterns and insights. Furthermore, even within a given guild, it would be worthwhile to determine the effects of distributions of species traits other than uniform distributions. Keystone species have traits that make them outliers, rather than part of a uniform distribution of species traits (Paine 1966, Power et al. 1996).

This paper has focused on the “pure” effects of diversity by considering effects attributable to diversity when effects attributable to species composition and other factors were appropriately controlled. This was done to clarify the roles of composition vs. diversity. Because diversity and composition can be strongly correlated in managed and natural ecosystems, care must be taken in applying these results to management issues. Ecosystem processes are just as likely to be impacted by shifts in composition, disturbance, and nutrient loading as by shifts in diversity. Attributing effects to one of these variables without controlling for others could give false answers. A myopic focus on diversity would be a poor management strategy, because diversity is only one of many factors that influence ecosystem processes.

Finally, I am drawn back to the paradox of diversity. It is the actual mechanisms of interspecific interaction

and coexistence in a community that ultimately determine the dependence of population, community, and ecosystem processes on diversity. Advances in our understanding of the causes of diversity are needed if we are to understand the consequences of biodiversity. Such knowledge is also essential if we are to maximize the number of species protected from extinction.

ECOLOGY ON A HUMAN-DOMINATED EARTH

During most of the 1900s, academic ecologists, following the traditions of early naturalists, have tended to study pristine, human-free habitats. If ecology, as a discipline, is just the study of "nature," with nature defined as species living in habitats that experience minimal human impact, it is a discipline headed toward extinction. No other species has a greater impact on the stability, dynamics, diversity, composition, structure, and functioning of earth's communities and ecosystems than humans. The massive growth of human population and per capita consumption are irrevocably changing the world and academic ecology. All of earth's ecosystems are now human-impacted (Vitousek et al. 1997b). Humans use much of the freshwaters that run off the land (Postel et al. 1996), manage, modify, and exploit much of the land surface (Vitousek et al. 1986), are a major force in the global biogeochemistry of carbon and nitrogen (Schlesinger 1997, Vitousek et al. 1997a), and own and control the entire land surface of the earth. Humans impacts merit greater attention by those who study nature.

We need to formally broaden the portion of the world open to our inquisitiveness and to the rigor of our scientific approach. Major questions for which ecology could provide answers remain unstated, unaddressed, and unanswered. Who, but ecologists, can predict the type of world that current policies and actions will create in 50, 100, or 500 years? Who, but ecologists, can provide the information needed to evaluate alternative policies and actions? Given current rates and patterns of habitat fragmentation and of introduction of exotic species, what portion of global biodiversity will be extinct in 50 or 500 years? What types of species can survive these impacts, and which species are most susceptible to extinction? What impacts would such extinctions have on the provision of various ecosystem services? How will the increasingly great human domination of the global nitrogen cycle, mainly via accelerating rates of agricultural nitrogen fertilization, impact the species composition, diversity, and functioning of the remaining fragments of terrestrial ecosystems? How will globally accelerating agricultural use of nitrogen, phosphorus, and irrigation impact freshwater, coastal, and open ocean ecosystems? Indeed, what kinds of ecosystems and what kind of a world are humans inadvertently creating? These are not the questions of classical academic ecology, but they are unavoidably the questions of its future.

We are privileged and burdened to live during the

era when humans have become a dominant force on earth. Our discipline has an obligation to fulfill: to provide society with the knowledge essential for both understanding and wisely managing the earth and its biological resources. This will require that we understand nature, and human impacts on it, well enough to predict the different types of worlds created by alternative societal actions, and that we communicate this knowledge with the public and public officials.

ACKNOWLEDGMENTS

I am immeasurably indebted to my teachers, collaborators, students, and colleagues. Don Farnum, my high school biology teacher, and John Brigham, my high school Latin teacher, shared their high standards and love of inquiry with me. Stephen Hubbell inspired me to pursue ecology and taught me the power of simple theory. Peter and Susan Kilham showed me how to be an experimentalist. The works of the great minds of our discipline, especially G. E. Hutchinson, Robert MacArthur, Robert May, and Paul Ehrlich, have inspired and challenged me. I dedicate this paper to all of these individuals. This paper has been especially influenced by Clarence Lehman, whose collaboration I cherish and gratefully acknowledge. I thank Shahid Naeem, Nick Haddad, Peter Vitousek, Bob Peet, Sam McNaughton, Bill Murdoch, Bryan Foster, Bob Sterner, and Johannes Knops for comments, Nancy Larson, and Charles Bristow for assistance, and NSF (DEB 9411972), the Andrew Mellon Foundation, and the Pew Trusts for financial support.

LITERATURE CITED

- Aarssen, L. W. 1997. High productivity in grassland ecosystems: effected by species diversity or productive species? *Oikos* **80**:183–184.
- Armstrong, R. A., and R. McGehee. 1980. Competitive exclusion. *American Naturalist* **115**:151–170.
- Brigham, E. F., and L. C. Gapenski. 1988. Financial management: theory and practice. Fifth edition. Dryden Press, Chicago, Illinois, USA.
- Chesson, P. L. 1986. Environmental variation and the coexistence of species. Pages 240–256 in J. Diamond and T. Case, editors. *Community ecology*. Harper and Row, New York, New York, USA.
- Chesson, P., and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *American Naturalist* **150**:519–553.
- Clements, F. E. 1916. *Plant succession*. Publication 242, Carnegie Institution, Washington, D.C., USA.
- Connell, J. 1983a. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* **122**:661–696.
- . 1983b. Interpreting the results of field experiments: effects of indirect interactions. *Oikos* **41**:290–291.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**: 63–87.
- Daily, G. C. 1997. *Nature's services: societal dependence on natural ecosystems*. Island Press, Washington, D.C., USA.
- Darwin, C. 1872. *The origin of species*. Sixth London edition. Thompson and Thomas, Chicago, Illinois, USA.
- Davis, M. B. 1986. Climatic instability, time lags, and community disequilibrium. Pages 269–284 in J. Diamond and T. Case, editors. *Community ecology*. Harper and Row, New York, New York, USA.
- Doak, D. F., D. Bigger, E. K. Harding, M. A. Marvier, R. E. O'Malley, and D. Thomson. 1998. The statistical inevi-

- tability of stability–diversity relationships in community ecology. *American Naturalist* **151**:264–276.
- Ehrlich, P. R., and A. H. Ehrlich. 1981. Extinction. The causes and consequences of the disappearance of species. Random House, New York, New York, USA.
- Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London, UK.
- Estes, J. A., and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecological Monographs* **65**:75–100.
- Ewel, J. J., and S. W. Bigelow. 1996. Plant life-forms and tropical ecosystem functioning. Pages 101–126 in G. H. Orians, R. Dirzo, and J. H. Cushman, editors. Biodiversity and ecosystem processes in tropical forests. Springer-Verlag, Berlin, Germany.
- Frank, D. A., and S. J. McNaughton. 1991. Stability increases with diversity in plant communities: empirical evidence from the 1988 Yellowstone drought. *Oikos* **62**:360–362.
- Gardner, M. R., and W. R. Ashby. 1970. Connectance of large dynamic (cybernetic) systems: critical values for stability. *Nature* **228**:784.
- Givnish, T. J. 1994. Does diversity beget stability? *Nature* **371**:113–114.
- Goodman, D. 1975. The theory of diversity–stability relationships in ecology. *Quarterly Review of Biology* **50**:237–266.
- Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley, Chichester, UK.
- . 1997. Biodiversity and ecosystem function: the debate deepens. *Science* **277**:1260–1261.
- Grover, J. P. 1997. Resource competition. Chapman and Hall, London, UK.
- Harper, J. L. 1977. Population biology of plants. Academic Press, London, UK.
- Hobbie, S. E. 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs* **66**:503–522.
- Holt, R. D. 1977. Predation, apparent competition and the structure of prey communities. *Theoretical Population Biology* **12**:197–229.
- Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* **277**:1302–1305.
- Huston, M. A. 1979. A general hypothesis of species diversity. *American Naturalist* **113**:81–101.
- . 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**:449–460.
- Hutchinson, G. E. 1961. The paradox of the plankton. *American Naturalist* **95**:137–147.
- Jones, C. G., and J. H. Lawton. 1995. Linking species and ecosystems. Chapman and Hall, New York, New York, USA.
- King, A. W., and S. L. Pimm. 1983. Complexity, diversity, and stability: a reconciliation of theoretical and empirical results. *American Naturalist* **122**:229–239.
- Lawlor, L. R. 1979. Direct and indirect effects of *n*-species competition. *Oecologia* **43**:355–364.
- Lawton, J. H., and V. K. Brown. 1993. Redundancy in ecosystems. Pages 255–270 in E. D. Schulze and H. A. Mooney, editors. Biodiversity and ecosystem function. Springer-Verlag, Berlin, Germany.
- Lawton, J. H., S. Naeem, L. J. Thompson, A. Hector, and M. J. Crawley. 1998. Biodiversity and ecosystem functioning: getting the Ecotron experiment in its correct context. *Functional Ecology* **12**:843–856.
- Lee, C. F. 1985. Financial analysis and planning: theory and application. Addison-Wesley, Reading, Massachusetts, USA.
- Levin, S. A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. *American Naturalist* **104**:413–423.
- . 1981. Mechanisms for the generation and maintenance of diversity in ecological communities. Pages 173–194 in R. W. Hiorns and D. Cooke, editors. The mathematical theory of the dynamics of biological populations II. Academic Press, London, UK.
- Levins, R. 1979. Coexistence in a variable environment. *American Naturalist* **114**:765–783.
- MacArthur, R. H. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* **36**:533–536.
- Margalef, R. 1969. Diversity and stability: a practical proposal and a model of interdependence. *Brookhaven Symposia in Biology* **22**:25–37.
- May, R. M. 1972. Will a large complex system be stable? *Nature* **238**:413–414.
- . 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, New Jersey, USA.
- . 1975. Patterns of species abundance and diversity. Pages 81–120 in M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, USA.
- . 1986. The search for patterns in the balance of nature: advances and retreats. *Ecology* **67**:1115–1126.
- McGrady-Steed, J., P. M. Harris, and P. J. Morin. 1997. Biodiversity regulates ecosystem predictability. *Nature* **390**:162–165.
- McNaughton, S. J. 1977. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *American Naturalist* **111**:515–525.
- . 1985. Ecology of a grazing ecosystem: The Serengeti. *Ecological Monographs* **55**:259–294.
- . 1993. Biodiversity and function of grazing ecosystems. Pages 361–383 in E.-D. Schulze and H. A. Mooney, editors. Biodiversity and ecosystem function. Springer-Verlag, Berlin, Germany.
- Murdoch, W. W., and A. Stewart-Oaten. 1989. Aggregation by parasitoids and predators: effects on equilibrium and stability. *American Naturalist* **134**:288–310.
- Naeem, S., D. Byers, S. Tjossem, C. Bristow, and S. Li. Plant neighborhood diversity and production. *Ecoscience*, in press.
- Naeem, S., K. Håkenson, J. H. Lawton, M. J. Crawley, and L. J. Thompson. 1996. Biodiversity and plant productivity in a model assemblage of plant species. *Oikos* **76**:259–264.
- Naeem, S., and S. Li. 1997. Biodiversity enhances ecosystem reliability. *Nature* **390**:507–509.
- Naeem, S., and S. Li. 1998. A more reliable design for biodiversity study? *Nature* **394**:30.
- Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* **368**:734–737.
- Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1995. Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. *Philosophical Transactions of the Royal Society of London B* **347**:249–262.
- Odum, E. P. 1953. Fundamentals of ecology. Saunders, Philadelphia, Pennsylvania, USA.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* **100**:65–75.
- Pastor, J., J. D. Aber, C. A. McClaugherty, and J. M. Melillo. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology* **65**:256–268.
- Pimentel, D. 1961. Species diversity and insect population outbreaks. *Annals of the Entomological Society of America* **54**:76–86.

- Pimm, S. L. 1979. Complexity and stability: another look at MacArthur's original hypothesis. *Oikos* **33**:351–357.
- . 1984. The complexity and stability of ecosystems. *Nature* **307**:321–326.
- Postel, S. L., G. C. Daily, and P. R. Ehrlich. 1996. Human appropriation of renewable fresh water. *Science* **271**:785–788.
- Power, M. E. 1995. Floods, food chains, and ecosystem processes in rivers. Pages 52–60 in C. G. Jones and J. H. Lawton, editors. *Linking species and ecosystems*. Chapman and Hall, New York, New York, USA.
- Power, M. E., D. Tilman, J. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. *BioScience* **46**:609–620.
- Pyšek, P. 1995. Recent trends in studies on plant invasions (1974–1993). Pages 223–236 in P. Pyšek, K. Prach, M. Rejmánek and M. Wade, editors. *Plant invasions: general aspects and special problems*. SPB Academic Publishing, Amsterdam, The Netherlands.
- Rejmánek, M. 1989. Invasibility of plant communities. Pages 369–388 in J. A. Drake, H. A. Mooney, F. DiCastrì, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. H. Williamson, editors. *Biological invasions: a global perspective*. Wiley, New York, New York, USA.
- Schlesinger, W. H. 1997. *Biogeochemistry: an analysis of global change*. Academic Press, San Diego, California, USA.
- Schoener, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* **122**:240–285.
- Schulze, E. D., and H. A. Mooney. 1993. *Biodiversity and ecosystem function*. Springer-Verlag, Berlin, Germany.
- Smuts, J. C. 1926. *Holism and evolution*. Macmillan, New York, New York, USA.
- Sterner, R. W. 1995. Elemental stoichiometry of species in ecosystems. Pages 240–252 in C. G. Jones and J. H. Lawton, editors. *Linking species and ecosystems*. Chapman and Hall, New York, New York, USA.
- Swift, M. J., and J. M. Anderson. 1993. Biodiversity and ecosystem function in agricultural systems. Pages 15–41 in E. D. Schulze and H. A. Mooney, editors. *Biodiversity and ecosystem function*. Springer-Verlag, Berlin, Germany.
- Taylor, L. R., and I. P. Woiwod. 1980. Temporal stability as a density-dependent species characteristic. *Journal of Animal Ecology* **49**:209–224.
- Taylor, L. R., I. P. Woiwod, and J. N. Perry. 1980. Variance and the large-scale spatial stability of aphids, moths and birds. *Journal of Animal Ecology* **49**:831–854.
- Tilman, D. 1976. Ecological competition between algae: experimental confirmation of resource-based competition theory. *Science* **192**:463–465.
- . 1977. Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology* **58**:338–348.
- . 1980. Resources: a graphical-mechanistic approach to competition and predation. *American Naturalist* **116**:362–393.
- . 1982. *Resource competition and community structure*. Monographs in Population Biology, Princeton University Press, Princeton, New Jersey, USA.
- . 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, New Jersey, USA.
- . 1990. Mechanisms of plant competition for nutrients: the elements of a predictive theory of competition. Pages 117–141 in J. Grace and D. Tilman, editors. *Perspectives on plant competition*. Academic Press, New York, New York, USA.
- . 1994. Competition and biodiversity in spatially structured habitats. *Ecology* **75**:2–16.
- . 1996. Biodiversity: population versus ecosystem stability. *Ecology* **77**:350–363.
- . 1997a. Distinguishing between the effects of species diversity and species composition. *Oikos* **80**:185.
- . 1997b. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* **78**:81–92.
- Tilman, D., and J. A. Downing. 1994. Biodiversity and stability in grasslands. *Nature* **367**:363–365.
- Tilman, D., J. A. Downing, and D. A. Wedin. 1994. Does diversity beget stability? *Nature* **371**:113–114.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997a. The influence of functional diversity and composition on ecosystem processes. *Science* **277**:1300–1302.
- Tilman, D., C. L. Lehman, and C. E. Bristow. 1998. Diversity–stability relationships: statistical inevitability or ecological consequence? *American Naturalist* **151**:277–282.
- Tilman, D., C. L. Lehman, and K. T. Thomson. 1997b. Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences (USA)* **94**:1857–1861.
- Tilman, D., and S. Pacala. 1993. The maintenance of species richness in plant communities. Pages 13–25 in R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Tilman, D., and D. Wedin. 1991. Dynamics of nitrogen competition between successional grasses. *Ecology* **72**:1038–1049.
- Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**:718–720.
- Trenbath, B. R. 1974. Biomass productivity of mixtures. *Advances in Agronomy* **26**:177–210.
- Vandermeer, J. H. 1980. Indirect mutualism: variations on a theme by Stephen Levine. *American Naturalist* **116**:441–448.
- Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* **57**:7–13.
- Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. Tilman. 1997a. Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* **7**:737–750.
- Vitousek, P. M., P. R. Ehrlich, A. H. Ehrlich, and P. A. Matson. 1986. Human appropriation of the products of photosynthesis. *BioScience* **36**:368–373.
- Vitousek, P. M., and D. U. Hooper. 1993. Biological diversity and terrestrial ecosystem biogeochemistry. Pages 3–14 in E.-D. Schulze and H. A. Mooney, editors. *Biodiversity and ecosystem function*. Springer-Verlag, Berlin, Germany.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997b. Human domination of earth's ecosystems. *Science* **277**:494–499.
- Vitousek, P. M., and L. R. Walker. 1989. Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs* **59**:247–265.
- Vitousek, P. M., L. R. Walker, L. D. Whiteaker, D. Mueller-Dombois, and P. A. Matson. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* **238**:802–804.
- Wardle, D. A., O. Zackrisson, G. Hörnberg, and C. Gallet. 1997. The influence of island area on ecosystem properties. *Science* **277**:1296–1299.
- Wedin, D., and D. Tilman. 1990. Species effects on nitrogen

- cycling: a test with perennial grasses. *Oecologia* **84**:433–441.
- Wedin, D., and D. Tilman. 1993. Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. *Ecological Monographs* **63**:199–229.
- Wilson, E. O. 1992. *The diversity of life*. Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA.
- Wilson, S. D., and D. Tilman. 1991. Components of plant competition along an experimental gradient of nitrogen availability. *Ecology* **72**:1050–1065.