

2001. Pages 213-245 in "The Functional Consequences of Biodiversity", Ann Kinzig, Stephen Pacala, and David Tilman, eds, Princeton University Press.

ENVIRONMENTAL NICHES AND ECOSYSTEM FUNCTIONING

Peter Chesson
Section of Evolution and Ecology
University of California
Davis, CA 95616

Stephen Pacala
Department of Ecology and Evolutionary Biology
Princeton University
Princeton, NJ 08544

Claudia Neuhauser
Department of Ecology, Evolution and Behavior
University of Minnesota
St. Paul, MN 55108

Original manuscript published as

Chesson, P., Pacala, S., Neuhauser, C. 2001. Environmental niches and ecosystem functioning. Pages 213-245 in "The Functional Consequences of Biodiversity", Ann Kinzig, Stephen Pacala, and David Tilman, eds, Princeton University Press.

Introduction

The physical environment is strikingly variable in time and space, providing challenges and opportunities for the organisms in any ecosystem. At first thought, such temporal and spatial variation might be expected to be disruptive to the provision of ecosystem services. However, the extent to which this is so must depend on the structure of the ecosystem. At the ecosystem level we can ask, What properties of the organisms individually and collectively maximize provision of ecosystem services in the presence of environmental variability? At the level of individual organisms, we can ask, How does natural selection acting on individuals affect the provision of ecosystem services by the communities in which the individuals belong? Provision of some ecosystem services is naturally related to fitness. High primary productivity, for example, might arise when there is a selective advantage for individual plants to have high productivity. On the other hand carbon storage, as an ecosystem service, may not be linked to fitness when it involves accumulation of dead or decayed rather than productive biomass. Moreover, other strategies for individual success, such as resistance to mortality agents, may tend to have a negative relationship with productivity.

Due to the presence of fitness tradeoffs, a species living in a variable environment is unlikely to perform well under all circumstances even if highly phenotypically plastic or consisting of a wide range of genotypes capable of specializing on particular conditions as they arise. Environmental conditions not efficiently exploited by any given set of species provide opportunities for other species, better adapted to those conditions, to make use of resources available at those times or in those places. If specialization on particular environmental conditions makes an individual species more productive, a high diversity of environmentally specialized species should make the system as a whole more productive. Thus, ecosystem service correlates of high productivity should be maximized also at high diversity. These conclusions, however, require that species be present at high enough densities, or be able to grow rapidly enough, to make full use of the available opportunities as they arise.

Underexploited environmental niches, i.e. environmental conditions for which the species present are not making maximum use of the available resources, ought to fill with time through invasion of new species or adaptive radiation. Given enough time, with a frequency of variation in environmental conditions that is sufficiently predictable, at least on a long time scale, ecosystems might be expected to fill with species specialized to a range of particular environmental conditions, provided these different species are able to coexist with one another. Such filling of environmental niches should also have the effect of minimizing temporal variation in ecosystem functioning.

As the physical environment varies temporally on many timescales, an important question is how well a system that is shaped on a particular timescale continues to deliver ecosystem services when exposed to longer-term change. The organisms in a particular

ecosystem may be adapted to year to year fluctuations in weather, and the system may be saturated with species that coexist in the presence of such year to year variation. When the physical environmental changes over the longer-term, so that average environmental conditions, or the frequency of extreme conditions, are changed, will ecosystem services, such as primary production, dramatically decline? If the species present in a system are adapted to a range of environmental conditions, then in the face of change, species adapted to the new conditions may be present, and may continue to deliver ecosystem services (Tilman and Downing 1994). Species' relative abundances are likely to shift, favoring the species better adapted to the new conditions, and there are likely to be fewer species or a less even distribution of species adapted to the new conditions. In effect, the diversity of the system is lowered. Invasion from other habitats, and longer-term evolutionary changes within species, may allow restoration of that diversity.

These various ideas are explored here in models of environmental niches. We first ask what environmental niches are, and in what manner they allow the coexistence of a diverse community of species adapted to a range of environmental conditions. We then go on to consider how ecosystem functioning within such systems varies with the diversity of the species pool, and the diversity of a community assembled from the species pool. Finally, we consider how ecosystem functioning of these systems responds to long-term environmental change.

Environmental Niches

Species adapted to different environmental conditions may be thought of as having different environmental niches. Environmental niches have both temporal and spatial aspects corresponding to the temporal and spatial aspects of environmental variation. Using an analysis of variance approach (Chesson 1985), we can think of environmental variation as divisible into a purely temporal component (the main effect of time), a purely spatial component (the main effect of space) and a purely spatio-temporal component (the space by time interaction). Environmental niches may therefore be classified in accordance with the kinds of environmental variation that they involve. Thus, niches might be temporal, spatial, spatio-temporal or some mixture of these three types, with consequences for species coexistence and also, as we shall see below, for stability of ecosystem functioning in the face of environmental change.

Temporal niches

The temporal aspect of an organism's environmental niche is defined by the organism's temporal pattern of activity, for example, when and how intensely the organism is photosynthesizing, germinating, growing, foraging, reproducing, or remaining dormant. That pattern of activity may be defined on short timescales, such as a day, or on longer timescales, such as a year, but extends to decades and centuries for long-lived organisms like trees. Patterns of activity may be cued by strict periodic phenomena such as photoperiod, less predictable but still periodic phenomena such as temperature, or may represent physiological responses to environmental conditions or

resources, such as changes in individual growth rates due to changes in temperature or variation in rainfall, or simply development time independent of the external environment as seen most strikingly in periodical cicadas. The full temporal niche also includes temporal variation in mortality rates even though mortality is not so naturally thought of as "activity." Temporal activity patterns vary from strongly deterministic, e.g. cuing by photoperiod (Rathcke and Lacey 1985), to highly stochastic, e.g. cuing of germination by specific weather conditions occurring unpredictably from year to year in arid environments (Juhren, Went et al. 1956; Loria and Noy-Meir 1979-1980; Rathcke and Lacey 1985; Bowers 1987; Baskin, Chesson et al. 1993).

In a community context, theory predicts that separation of temporal niches promotes species coexistence. It says that species with even identical resource requirements may coexist when there are appropriate differences between their temporal patterns of use of resources (Grubb 1977; Chesson and Warner 1981; Abrams 1984; Shmida and Ellner 1984; Brown 1989; Loreau 1992; Chesson 1994). A general study of species coexistence in temporally variable environments identifies two general mechanisms of coexistence associated with temporal patterns of activity. It seriously limits the possibilities of other such mechanisms. These two mechanisms go by the names *relative nonlinearity of competition*, and *the storage effect* (Chesson 1994). Relative nonlinearity of competition involves different nonlinear responses of different species to fluctuating resources. Under this mechanism, there need be no direct responses of organisms to the physical environment as distinct from the limiting resources. The storage effect involves direct responses of the organisms to the physical environment as distinct from the limiting resources, but does not require different species to have different nonlinear responses to those resources. Of the two, the storage effect appears by far the stronger and more general mechanism of coexistence (Chesson 1994) and closely corresponds to the intuitive concept of coexistence by separation of temporal niches. However, recent evidence (Huisman and Weissing 1999) suggests that relative nonlinearity of competition may be important when there are several limiting resources that are not substitutable (sensu Tilman 1982). Study of the storage effect emphasizes that it is not sufficient for species simply to have different temporal activity patterns (*species-specific responses to the environment*) for coexistence to be promoted. Indeed, the storage effect has been shown to have two other requirements termed *covariance between environment and competition*, and *buffered population growth* (Chesson 1994). These three requirements for the storage effect can be explained with reference to the common ecosystem model (Chapter ??).

To modify the common ecosystem model to include temporal niches, the per unit rate of biomass change, for a given species j , can be written

(1)

$$\frac{1}{B_j} \cdot \frac{dB_j}{dt} = r_j(t) = E_j(t)P[B., N, W] - \delta$$

where $\delta = (\gamma + \mu)$, B . is the sum of the biomasses of the n species in the system and

$$P[B., N, W] = \frac{a}{B. + K_L} \cdot \frac{N}{N + K_N} \cdot \frac{W}{W + K_W}. \quad (2)$$

Here r of the common model has been replaced by $E_j(t)a$, with $E_j(t)$ representing temporal variation in growth activity by species j , and a representing a reference value of r , for example, a species and time average of r . The $E_j(t)$ define multiplicative departures of r from a due to species and time. We refer to $E_j(t)$ as the *environmental response of species j* . The pattern of variation in the environmental response, $E_j(t)$, over time, defines the temporal niche of a species. Different species have different patterns of response to temporal variation, which separate their temporal niches and provide the first important requirement for the storage effect, *species-specific responses to the environment*. These different patterns may simply reflect different responses seasonal change, which may be represented deterministically as different periodic functions of time, or they may be stochastic, perhaps representing different responses of the species to common variation in the weather.

The function $P[B., N, W]$ summarizes the species responses to resources. If the $E_j(t)$ were all equal to 1, this system would have neutral equilibria at which all species densities remain constant and satisfy the equation $P[B., N, W] = \delta$. Under nonequilibrium conditions, the value of $P[B., N, W]$ would reflect competition between the species, among other things; but in any case, in this neutral situation, we can expect competition to tend to restore the value of $P[B., N, W]$ to δ following perturbation from equilibrium. We can therefore use the difference

$$C(t) = \delta - P[B., N, W] \quad (3)$$

as a measure of the magnitude of competition at any given time relative to the magnitude at equilibrium. The quantity (3) is sometimes referred to as the *competitive response* (Chesson and Huntly 1997), but we shall refer to it here simply as *competition*. As defined here, it is a measure of overall resource availability. Its magnitude defines the potential for growth as a function of resources, but the actual change depends also on the environment, which is expressed by rewriting the per capita growth equation (1) in terms of $E_j(t)$ and $C(t)$ as

$$r_j(t) = E_j(t)[\delta - C(t)] - \delta. \quad (4)$$

Because $C(t)$ occurs in this equation multiplied by the environmental response, $E_j(t)$, the effect that competition of a given magnitude has on population growth depends on the environment. If the environment is not favorable for species j , i.e. $E_j(t)$ is small, then the effect of $C(t)$ is small. Indeed, in the extreme case where $E_j(t) = 0$, $C(t)$ has no effect on $r_j(t)$, which then is fixed at the negative value $-\delta$. Similarly, if competition is strong, e.g. near its maximum value $C(t) = \delta$, the effect of $E_j(t)$ on population growth is reduced. This effect, where an unfavorable value of one factor (either environment or competition)

limits the impact of the other factor, especially unfavorable impacts, may be thought of as buffered population growth. For this particular model, the buffering effect results in a minimum per capita growth rate of $-\delta$ regardless of how unfavorable environmental and competitive conditions may be.

Various factors can modify the buffering effect embodied in equation (4). For example, it would be strengthened if the environmental response also modulated respiration. In the most extreme form, respiration would be proportional to $E_j(t)$, then δ would not be the sum of μ and γ , but simply μ and $r_i(t)$ would take the value $-\mu$ when $E_j(t) = 0$ although this no longer defines a minimum value for $r_j(t)$ under all conditions. In statistical terms, buffering, which is referred to also as *subadditivity* (Chesson 1994), comes from the interaction between environment and competition. The interaction determines how $r_j(t)$ changes as a result of joint changes in $E_j(t)$ and $C(t)$. The concept of covariance between environment and competition concerns how $E_j(t)$ and $C(t)$ do change jointly. These concepts are distinct, but the importance of each depends on the other. In particular, the product form of (4) that leads to the buffering effect also means that the average of $r_j(t)$ over time, \bar{r}_j , takes the following form

$$\bar{r}_j = \bar{E}_j(\delta - \bar{C}) - \delta - \text{Cov}(E_j, C) \quad (5)$$

i.e. the long-term growth of the population depends on covariance over time of the environmental response and competition (Chesson 1997).

To see that species-specific responses to the environment, buffered population growth, and covariance between environment and competition jointly act to promote species coexistence in a variable environment, we first of all consider dynamics in a constant environment. In the absence of environmental variation, i.e. if the $E_j(t)$ were constant over time, and the dynamics of resources allowed an equilibrium to occur, only one species would persist at that equilibrium and it would be the species with the largest value of E_j . That species would drive $C(t)$ to the value

$$C_j^* = \delta \left(1 - \frac{1}{E_j} \right) \quad (6)$$

at which the r_s of all other species are negative, meaning that these other species would go extinct. We can think of this results as a C^* rule for species limited in the same way by common limiting resources. It is a simple generalization of the R^* rule (Holt et al 1994, Tilman 1990) for species limited by the same resource. Note that the value of competition is a function of the environmental response of the dominant species.

When the $E_j(t)$ fluctuate over time, $C(t)$ must fluctuate over time too. In general, it should be expected that the fluctuations in $C(t)$ would be correlated with those in $E_j(t)$,

at least if species j is abundant enough to have much competitive effect. For example, if species j is the only abundant species, and $E_j(t)$ varies only slowly over time, then $C(t)$ ought to track the value given by (6), i.e. will be an increasing function of $E_j(t)$, so that the covariance, $\text{Cov}(E_j, C)$, would be positive, and therefore would decrease the value of

\bar{r}_j in the long-term growth equation (5). As discussed in detail for general models (Chesson 1994, Chesson and Huntly), species at high density tend to have positive values of $\text{Cov}(E_j, C)$, reducing their rates of increase over that predicted by the averages of E and C alone. Species at low density tend to have low values of the covariance if their environmental responses fluctuate asynchronously with those of their higher density competitors. Thus, these low density species have a growth rate advantage and tend to increase to higher densities. The presence of the covariance in formula (5) therefore tends to keep species in the system. For a single-species system, the magnitude of the covariance is approximately proportional to the variance, σ^2 , of the natural log of E_j . This means that in a two-species system, a species at low density whose environmental response is uncorrelated with the other species would be advantaged relative to the other species by an amount proportional to σ^2 . If it is negatively correlated with the other species, its advantage would be more; if positive correlated, its advantage would be less. The advantage that accrues to a species at low density tends to decrease with the number of species in the system making coexistence more difficult and decreasing rates of recovery from low density (Chesson 1994).

In summary, plant species growing and interacting through resources according to the common ecosystem model are potentially able to coexist by the storage effect when they have different temporal patterns for their environmental responses. The three ingredients of the storage effect are automatically present in this model. Coexistence is not guaranteed, however, because like most mechanisms of coexistence, the storage effect can be overcome by large average fitness differences between species (Chesson 2000a). In particular cases, formulae are available to determine the fitness differences compatible with coexistence (Chesson 1994, 2000a). Particular examples of coexistence by the storage effect are given in particular versions of the common ecosystem model below.

Spatial and spatio-temporal niches

Many different models over a long period of time have demonstrated species coexistence as a result of spatial and spatio-temporal niches (Levin 1974; Shmida and Ellner 1984; Chesson 1985; Comins and Noble 1985; Iwasa and Roughgarden 1986; Moko and Iwasa 2000). The formal development in terms of the storage effect is recent, but again reveals three key requirements: species-specific responses to the environment, covariance between environment and competition, and buffered population growth (Chesson 2000b). In the spatial domain, buffered population growth arises essentially automatically from the dispersion of populations in space, but the magnitude of the buffering is affected by the nature of dispersal and the nature of the environmental variation. In important cases, buffering in space may be shown to be equal to the

maximum attainable buffering in time (Chesson 1984, 1985, 2000b). Thus, buffering in space may often exceed buffering in time, although not necessarily by very much.

Covariance between environment and competition in space arises in many circumstances, but is not automatic; for example, pure spatio-temporal variation in mortality rates during periods when species are dormant, and not actively drawing on resources, does not lead to covariance between environment and competition and does not promote coexistence (Chesson 1985). Pure spatial variation in such mortality rates, however, does lead to covariance between environment and competition under restricted dispersal scenarios, because then population densities increase at favorable locations, producing more competition (Muko and Iwasa 2000). Species-specific responses to spatially varying environments seem widespread in nature, which means there are many situations in which spatial niches of some form are a factor in coexistence. Of most importance for the question of ecosystem functioning is the way in which spatial variation may maintain a variety of species adapted to specific environmental conditions.

Ecosystem Functioning

Although there are many results on species coexistence by means of environmental niches, as discussed above, information needed to understand ecosystem functioning is much more limited. We consider first of all simple situations that can be solved analytically for the cases of spatial and temporal niches, and then we move on to look at more a complicated model of a Mediterranean type ecosystem by means of simulation.

Ecosystem functioning with spatial niches

We suppose here that the environment varies in space, and that in equation (1) $E_j(t)$ takes the form $E_j(t) = f(x_j, E)$ where E is a quantity defining the physical environment for a given locality in space. The sole quantity distinguishing species j from other species is x_j , which defines the optimal physical environment for species j . The function f converts the distance α_j between x_j and E into $E_j(t)$, the growth activity of species j in an environment with the value E . We assume that f is non increasing has the value 1 for a perfect match of species and environment, i.e. $f(E, E) = 1$, which we may do without loss of generality.

Now consider a spatial network of a large number of local communities, each with a different value of E , and each large enough in area that inter-patch dispersal has a negligible effect on local dynamics (except during initial colonization). For simplicity, we randomly assign a value of E to each local community in the network by drawing E 's from a uniform probability density on an interval of length Δ_E . One may think of Δ_E as the regional range of environmental conditions. Similarly, we produce a regional flora of species available for colonizing the network by drawing values of x_j from a Poisson process on the E axis, with intensity λ . In other words we assume that the x 's "rain" down upon the E axis entirely at random, with an average of λ species per unit-length of

E. Although these uniformity assumptions may seem restrictive, they can be greatly relaxed without altering the qualitative outcome.

The main quantities of interest are (1) the average number of species that will coexist in a regional network, and (2) the average ecosystem function. Because $f(x_j, E)$ contains the only species specific parameter in the model, the species from the regional pool with the highest value of $f(x_j, E)$ for a particular locality will competitively exclude all others from the pool in that locality. Because of the large number of local communities, every species in the regional flora with a niche position (value of x_j) contained in Δ_E must persist because it will dominate at least one local community. On average, there will be $\lambda \Delta_E$ such species. There may be up to two additional species that persist (the species with niche positions just before and just after the interval Δ_E), but the exact expression for the expected total number of species at equilibrium (D^*) is cumbersome and so we will use the close approximation $D^* \approx \lambda \Delta_E$.

Also, rather than calculate the network-average separately for each ecosystem function, we instead calculate only f^* , the expectation of $f(x_j, E)$ at equilibrium:

$$f^* = \int_{\alpha=0}^{\infty} 2\lambda e^{-2\alpha\lambda} f(E + \alpha, E) d\alpha.$$

Average values of net primary production, carbon storage, N mineralization and evapotranspiration are all simple increasing functions of f^* under the particular circumstances assumed here. In the special case in which only one of the model's resources limits production, the average of each of the ecosystem functions increases linearly with f^* . The expression for f^* relies on the fact that the probability that no species is present in the regional flora with a value of x_j within a distance α of any particular value of E is $e^{-2\alpha\lambda}$ (the zero term from a Poisson distribution).

Suppose $f(x, E)$ is given by the exponential function: $e^{-2|x-E|/\omega}$, where ω is the niche width (f is larger than $1/e$ over a range of environmental conditions of width ω). Then, using the fact that $\lambda = D^*/\Delta_E$, we find that f^* is simply $\theta/(1+\theta)$, where $\theta = D^* \omega/\Delta_E$. Similarly, if $f(x, E)$ is approximately a step function, nearly equal to 1 over the interval $x - \omega/2 \leq E \leq x + \omega/2$, but highest at $x = E$, and equal to zero outside this interval, then approximately: $f^* = 1 - e^{-\theta}$.

These two functions for f^* , are almost identical. Each shows that ecosystem function increases with diversity, initially with slope ω/Δ_E , and asymptotes at $f^* = 1$ for $D^* \gg \Delta_E/\omega$. The critical point is that the diversity necessary to maintain ecosystem function is set by each species' capacity to buffer environmental variation (ω) and by the magnitude (Δ_E) of environmental variation present. The necessary level of diversity becomes arbitrarily large as we expand the range of environmental conditions present in the region.

Ecosystem functioning with temporal niches: lottery models

Suppose that the habitat is divided into cells, and that every occupied cell contains the same total biomass: B_{\max} . We assume discrete time and proceed from one year to the next in three steps. First, random mortality occurs, killing the biomass in each cell with probability μ . Second, analogous to the assignment of environments in the spatial model above, we choose an environmental condition E for the year from a uniform distribution on the interval Δ_E . This is done independently each year. Third, we choose the second function f from the spatial examples above for which $f(x_j, E) > 0$ only over a finite interval $(x_j - \omega/2 \leq E \leq x_j + \omega/2)$, and with its maximum at $E = x_j$. We say that a species- j 's niche contains a value of E if $f(x_j, E)$ is nonzero for that value. Species are assigned environmental niches exactly identically to the spatial problems as Poisson process on the E axis. Only species whose environmental niches contain the value of E for that year reproduce and no reproduction occurs if the environmental condition is outside every species' niche. If reproduction occurs, new recruits fill all empty space and the species identities of the new recruits are determined by lottery competition (Chesson and Warner 1981). The lottery may range from completely biased in favor of the species with the largest value of $f(x_j, E)$, so that its offspring capture all empty sites, to unbiased, so that reproducing species capture sites in proportion to their abundances.

The long-term mean and variance of total community biomass produced by this stochastic process is derived in the Appendix as:

$$\text{mean} = \frac{1-q}{q\mu} B_{\max} \ln\left(1 + \frac{q\mu}{1-q}\right)$$

$$\text{variance} = \frac{1-q}{q} \frac{B_{\max}^2}{1-(1-\mu)^2} \ln\left(\frac{1-q(1-\mu)^2}{1-q}\right) - (\text{mean})^2$$

where q is the fraction of the interval Δ_E not included within the niche of any of the coexisting species. Because a sufficient condition for the indefinite persistence of a species is that it is the only species that reproduces in some years (i.e. a portion of the species' niche is contained within Δ_E but does not overlap the niche of any other species), it is straightforward to show that $q = e^{-\omega\lambda}$.

Although we do not have a general formula for the number of species that coexist, we can produce some results for the bracketing extremes of a completely biased lottery (the species with the largest nonzero f captures all vacant sites in that year) and an unbiased lottery. The purely biased lottery is exactly like the spatial model in that all species with values of x_j contained by Δ_E will coexist, plus up to two others with niche positions just outside Δ_E . We thus can use the close approximation $D^* = \lambda\Delta_E$, for the average number of coexisting species. In the case in which q is small, so that terms of order q^2 or higher are negligible, we find that the mean total biomass reduces to $1 - e^{-\theta}$, where $\theta = D^* \omega / \Delta_E$. This is exactly the same expression obtained for the analogous spatial model. Also, the coefficient of variation squared of total biomass (variance/mean²) is simply $e^{-\theta}$, showing that the temporal stability of ecosystem function also increases with

diversity. This effect of diversity on stability is a direct consequence of the same mechanism that causes both coexistence and the effect of diversity on average functioning in systems where coexistence is caused by the partitioning of temporal heterogeneity.

Finally, in the case of a purely unbiased lottery, we can produce bounds for the amount of diversity that will be maintained in the limit of a large pool of potential species (the limit of large λ). These bounds set the level of diversity necessary to maximize both functioning (the amount of total biomass) and the stability of functioning. A necessary condition for indefinite persistence under our unbiased lottery is that each coexisting species is the only species that reproduces in some fraction of years. We thus obtain bounds on the number of coexisting species as the minimum and maximum number of line segments of length ω that can be placed along the E axis such that at least one portion of each segment both overlaps Δ_E and does not overlap any other line segment:

$$\frac{\Delta_E}{\omega} \leq D^* < 2 \frac{\Delta_E}{\omega} + 2$$

As in all of the other cases of coexistence caused by spatial or temporal heterogeneity, the diversity necessary to maximize functioning increases without bound as the capacity of each species to buffer environmental change decreases and as the amount of environmental heterogeneity increases.

Ecosystem functioning with temporal niches: a Mediterranean ecosystem

To examine ecosystem functioning in a more detailed, though less general way than has been possible with the analytical approaches above, we use simulations of equations (1) and (2) for a roughly Mediterranean-type climate (Cody and Mooney 1978; Hooper and Vitousek 1997). Thus, rainfall has a substantial peak in mid winter (Figure 1). Rather than an extreme Mediterranean pattern with very little rainfall at other times of the year, rainfall consists of stochastic variation about a sinusoidal pattern. In contrast to the analytical approach taken above, and in contrast to most studies of the storage effect, the environmental responses of the different species have been chosen to be deterministic, for example cued to photoperiod (Figure 2). Thus, the temporal niches that these species exhibit are seasonal niches. The environmental responses thus peak at different times for different species.

The amplitudes of the environmental responses vary from species to species depending on the time of year at which the environment response peaks (Figure 2), which is intended to mimic the effect of temperature on plant growth with warmer conditions promoting stronger growth for given levels of resource availability. Such amplitude differences also provide a tradeoff permitting a species that grows at a disadvantageous time with respect to rainfall to compete successfully with other species. These deterministic environmental responses are chosen to emphasize that the storage effect works both with deterministic as well as stochastic environmental responses. They provide results that complement those on stochastic environmental responses in the analytical section and in simulations published elsewhere (Lehman and Tilman 2000).

Though the niches of the species are deterministic, their growth is far from deterministic as they are affected greatly by stochastic fluctuations in resources. The presence of different species coexisting because they have different temporal niches might be expected to lead to less temporal variation in resource levels, and indeed lower average resource levels due to fluctuations in resource supply. Higher average primary productivity might also be expected. To examine these possibilities, rainfall in this system varied stochastically in several ways from year to year: total amount of rain, magnitude of seasonal fluctuation, and the phasing of the winter peak in rainfall. As rainfall affects nutrient recycling, variation in rainfall should also cause fluctuations in nitrogen availability, which might also be dampened in the presence of species coexisting with temporal niches. The nature of these temporal niches, including the fraction of respiration and tissue death that varies in proportion with growth activity, is likely to have important effects on such outcomes. Table 1 gives the parameters of this system.

For these simulations, ten species were selected that are capable of long-term coexistence in the system, as determined by their persistence together over 2000 years. These species are defined by their environmental responses as depicted in figure 2. Simulations were then done by selecting local species pools varying in size from one to nine species from this ten species global pool. For local pools of sizes one and nine there are ten possible selections, and each of which was chosen. For other local pool sizes, 20 random selections from the global pool were used. Local species pools were treated as initial local communities with species given equal biomasses summing to the equilibrium biomass for the system applicable in the absence of any temporal environmental variation. Data for the first 1000 years were discarded to remove the effect of the arbitrariness of the initial conditions. Competitive exclusions occurred during this initial period and data were collected for the final 100 years on the community surviving from the local species pool.

Three different environmental conditions were considered. A baseline of 350mm of rain per year with mean phase of zero, corresponding to the phase of the environmental response of the earliest species from the species pool. The two perturbations to this condition, which were treated separately, were (a) 400 mm per year, and (b) a shift in phase to 0.1, i.e. a delay in rainfall of one tenth of a year. As the species are distinguished by the phases and amplitudes of their environmental responses, rather than by their responses to the amount of rainfall, these perturbations correspond to (a) an environmental change orthogonal to the niche axis, and (b) a change aligned with the niche axis. Simulations were done using the Simgauss module of the Gauss Mathematical and Statistical System (Aptech Systems, Inc. Maple Valley, Washington, USA).

Simulation results: persistence and coexistence

The species always persisted in a long-term stable fashion in all single-species runs. With more than one species, competitive exclusion sometimes occurred, but the average number of coexisting species was in general only about one less than the pool

size (Figure 3). For the purposes of determining the number of coexisting species, a species was considered persistent if its average biomass in the last 100 years of the simulation was at least 1% of the total biomass in the system. In general, species regarded as coexisting by this definition persisted with stable fluctuations as depicted in Figure 4.

Comment [1]: Probably want to test this over a range of values so that you can say just how robust it actually is both for larger and smaller values than 1%

Mean ecosystem functioning

All mean ecosystem services increased with the size of the local species pool, up to a maximum achieved by approximately six species, depending just a little on the particular ecosystem service chosen (Figure 5). There is a monotonic increase in the maxima from one to three selected species in every case, after which the maxima as a function of pool size are approximately constant. The two perturbations had dramatically different effects. Increase in the amount of rainfall substantially increased all ecosystem services to a similar degree for every species pool size. A delay in rainfall also uniformly increased mean ecosystem functioning, but to a much lesser extent than the increase in rainfall. If these data are plotted against the number of coexisting species, rather than against the species pool, the picture changes a little: most features of these graphs are shifted towards the origin by one species, as one might expect from the fact that roughly one species went extinct on average.

Comment [2]: Should look into what happens when a system is a strict subset of another. Is the yield the maximum yield as determined by the sampling hypothesis, or is it something else?

Variance of ecosystem functioning

Variation over time was measured continuously, including seasonal as well as year to year components of variation. So that the mean did not get confounded with variation, relative variation in all quantities was considered. For a positive quantity, the standard deviation of the natural log of the quantity is a good measure of relative variation, and is the preferred measure here because its standard error can be calculated very easily over replicate runs. Net primary productivity, although having a positive average in persistent vegetation, has periods when it is negative, precluding the use of the standard deviation of the natural log. The coefficient of variation, which has similar properties to the standard deviation of the natural log, was used instead. When both measures were available, they were found to give nearly identical results. These measures are equivalent to the reciprocal of the stability measure of Lehman and Tilman (2000).

Variability of ecosystem functioning declined with local pool size for all ecosystem services, generally achieving an approximate minimum value with a pool size of six species (Figure 6). However, for evapotranspiration, variability continues to decrease for local pools sizes above six. Indeed, at least for 400mm of rain, it appears to decline over the entire range, 1-9, of local species pools. In these simulations, water availability was set up to be the limiting factor, and rain was a variable input. More species potentially gives more even use of water through the year reducing fluctuations in soil moisture.

The perturbations had similar effects on variability for most ecosystem services with later rain generally giving the most variability, and more rain the least variability. A notable exception is nitrogen mineralization where this pattern is reversed, presumably

explained by higher soil moisture, and higher soil moisture variability at higher rain (Figure 7) coupled with the strongly nonlinear relationship between soil moisture and nitrogen mineralization assumed in the common ecosystem model.

Discussion

The general prediction that the performance of ecosystem system services, especially primary production, should increase with the number of species was borne out. At the simplest level, this result can be understood as the filling of niche space. With niches defined temporally, this could mean simply having species present actively photosynthesizing and consuming resources for the maximum amount of time. In this way, the species present are complementary to one another, which leads to the phenomenon ofoveryielding: the combined output of the community is higher than that of the most productive species when present alone (Hector 1998; Hector, Schmid et al. 1999; Tilman 1999). This result is illustrated by our simulations, which show that the best monocultures are inferior to some mixed communities (Figure 5).

Two alternatives to niche complementarity have been discussed in the literature, positive species interactions (Hector, Schmid et al. 1999) and the sampling effect (Huston 1997; Tilman, Lehman et al. 1997; Loreau 1998; Tilman 1999; Chapter 4). Positive species interactions require one or more species to directly benefit other species, for example, by facilitating nitrogen fixation or increasing humidity, situations not accommodated in our models but that may well be important in nature (Hector et al 1999). Under the sampling hypothesis, the more species there are, the better the performance of the best species is likely to be simply because the maximum of a sample tends to increase with the sample size (Tilman 1999). Under the sampling hypothesis, the best species dominates and is responsible for the high productivity. The sampling and complementary niche hypotheses appear to be distinguished by distinct predictions. With sampling, the best multispecies community cannot be better than the best single-species community. It can only equal it by being dominated by the best species for that locality. In contrast, the complementary niche hypothesis predicts that the best multispecies system will have higher productivity than the best single-species system.

Although sampling and complementary niches do appear distinct in homogeneous environments, in heterogeneous environments that distinction is lost. For example, consider the simple model of spatial niches discussed above. In each patch, sampling prevails: the best species to arrive there dominates. However, if several patches with different environments are considered as a unit, they will likely have different species dominating them and the unit will have several species coexisting. Theoveryielding phenomenon is predicted because no one of them is superior over all environments; the productivity of the several patch system is higher than it would be under its best monoculture; and individual species have higher productivity per unit biomass because they are concentrated in localities where their performance is better.

The corresponding temporal phenomenon is illustrated above in the lottery form

of community dynamics in a temporally variable environment. In the "completely biased" version, there is a single winner in competition for any particular year. That species gains all newly available sites. However, due to the simplified assumptions of that model, there are only two possibilities for productivity: production occurs by capture of newly available sites and either all of these are taken or none of them is taken. For a given year, the model satisfies a particular version of the sampling hypothesis: either a species present is adapted to the environment of the year, and all new sites are captured by new recruits, or no species is adapted to the year, and no new sites are captured. More species increase the probability that all sites are captured, but the productivity of the year is no better than a monoculture of the best species for the environmental conditions in that year. When productivity is combined over several years with different environmental conditions, however, the best monoculture is not as good as the best mixture, because the best monoculture will likely miss capturing space in some years. The more species there are, the more years have some adapted species, and the higher the productivity is over those years. Thus, overyielding is seen for the community as a whole for productivity measured over a sequence of years.

The common ecosystem model in the form given by equations (1) and (2) also contains elements of the sampling mechanism, which are most apparent when the environment changes slowly relative to population growth rates. The most productive species for a particular environmental state would tend to be dominant, driving other species to low density. Thus, the system would be dominated most of the time by the most productive species for the environment of the time, assuming of course that the conditions for species coexistence are satisfied and all species do remain in the system. In the short-term, the predictions of the sampling hypothesis prevail, but again, when averaged over time, the predictions of complementary niches prevail.

When the rate of population growth is more comparable to the rate of environmental change, a mixture of species will be present at any one time, which will most likely mean that productivity at any given time is lower than in cases where the best species for that time comes to dominate. For example, in the simulated Mediterranean system, turnover of biomass was low because tissue death was only 0.1 per unit biomass per year, while species' activity functions go through their full cycle within a year. Thus, species do not greatly change their biomass within a year, even though their productivity undergoes dramatic changes. One might ask how close to the full effect of sampling this could be. Although, we cannot fully answer this question, it is clear that for temporal niches to achieve the same effect as sampling at any given time, species would have to be completely inactive, and hence not drawing on water and nitrogen when they are not the best. During this time also, they should not suffer respiratory losses or tissue death and should not block the light of other species (light limitation is minimal or species are deciduous). Deviations from any of these conditions will reduce productivity. Thus, the strongest performance of ecosystems where species coexist by temporal niches is predicted to occur when species go dormant at times when they are not dominant, and are able to build up quickly in size and number when they are dominant. Annual species and perennials that die back or are deciduous at their disfavored times add some of these

elements to a community, but a system consisting of species that are dormant whenever not dominant exists only as theoretical fantasy.

Spatial and spatio-temporal niches share the property with temporal niches that mean ecosystem functioning is lower than would obtain if for any place and time, the best species for that time and place were present alone at its equilibrium density. In general, a given time and place will have species in addition to the best species for the environmental conditions there. However, a close match to the maximum set by the sampling process is possible with pure spatial variation as the best species at a site will tend to dominate there if dispersal is low (Chesson 2000b). Indeed, one might think of environmental niches as an elaboration of the sampling hypothesis, adding to it the mechanism of maintenance of regional diversity on which it depends, and which is omitted from general descriptions of the hypothesis. Where the sampling hypothesis has been examined empirically (Hector et al 1999), there is no expectation that the best species on a plot would fully displace other species, and so in practice productivity would never equal that of the best monoculture. Thus, in practice, the sampling hypothesis does not achieve the theoretical sampling maximum. The truth is that the sampling and niche complementarity hypotheses are not distinct. If it is accepted that differential performance in different environments defines niche differences, as in our definition of environmental niches, niche complementarity and sampling in a variable environment simply cannot be thought of as different phenomena. Indeed, complementary environmental niches allow the sampling mechanism to occur locally in time and space, but its original predictions will not be borne out when the sampling unit includes ecologically distinct environments, either spatially or temporally. Instead, the predictions of niche complementarity will prevail.

The purported properties of the sampling process also depend on the postulate that the best competitor is the most productive (Loreau 1998), an assumption that is sometimes violated in nature (Hooper and Vitousek 1997). This requirement follows from the assumptions made here that species differ only in their environmental responses as defined in equation (1). If species differ in water use efficiency or in the ratio of respiration to tissue death, this assumption can be violated. In principle, it would be possible for net primary productivity to decline with the size of the species pool if water use efficiency declined sharply with competitive ability or respiratory losses increased.

Reduction in variance with number of species has also been found in several different theoretical studies (Doak, Bigger et al. 1998; Tilman, Lehman et al. 1998; Ives, Gross et al. 1999; Tilman 1999; Yachi and Loreau 1999) and in empirical studies of experimentally constructed communities (Tilman 1999). Ives et al (1999) make the point that must the species in a community must be diversified in their responses to environmental conditions for such results to occur, but they provide no mechanism leading to this outcome. Temporal niches provide this mechanism. The requirement of species-specific responses to the environment means that coexisting species are necessarily diversified in their environmental responses. The species coexist because of their complementary use of resources over time. Species can genuinely be seen as taking

advantage of temporally arising opportunities. A diverse species pool improves the probability of a good match between species and the available environmental conditions, and leads to reduction in variance with diversity over the full range of ecosystem services.

A system diversified with respect to responses to environmental conditions would also be expected to show maintenance of ecosystem function in the face of environmental change. The simulations here considered two different sorts of environmental change of comparable magnitude, but of very different nature. Delaying the peak rainfall by a tenth of a year increased mean delivery of ecosystem services but by less than 5% in general. As the system is diversified along the seasonal axis, the smallness of this effect is not surprising. For a given set of coexisting species, relative abundances shift reflecting the change in conditions, emphasizing species more suited to the new conditions (Figure 8) and therefore maintaining ecosystem function. More surprisingly, this delay in rainfall was accompanied by higher variance in the delivery of ecosystem services, perhaps reflecting the greater probability that rainfall would occur when species were not so available to make use of it.

Increasing rainfall by 50mm per year had a much greater effect than a change in timing. As water was the limiting resource, this is hardly surprising. Being orthogonal to the niche axis, it is one that would be expected to affect all species equally. Consistent with this prediction is the absence of appreciable change in the mean phase of the environmental response for communities experiencing this perturbation (Figure 8). The decreased temporal variation with increased rainfall is to be expected as the ratio of winter to summer rain decreased with the increase in annual rainfall, likely decreasing seasonal differences in productivity.

With changes along an axis of differentiation, such as timing of rainfall, presence in the species pool of species adapted to the new conditions is critical. Such species may exist in low abundance, maintained perhaps by the tails of the distribution of environmental events for the unperturbed situation. Those rare species may be the mainstay of a system after perturbation. The same may be true for space. Parts of the habitat that are seen as extreme, may become the norm, and species dominating there, but rare because their habitat is rare, may become the mainstay following an environmental change. Indeed, such rare species may provide much of the resistance to perturbation of a system's ecosystem services. These considerations lead to the prediction that the maintenance of ecosystem services in the presence of long-term change should decline with declining diversity. There is little evidence of this phenomenon in the results of the simulation studies, perhaps because of the modest nature of the perturbation of the environment compared with the niche breadths of the species. This result is to be contrasted with the major effect of diversity on variance in ecosystem functioning in the presence of seasonal and year to year environmental variation, and the important effects of diversity on mean ecosystem functioning found here in association with environmental niches.

Acknowledgements

We are especially grateful to Ann Kinzig for guidance in parameterizing the simulation model, and to Clarence Lehman for helpful discussion of the topic. This work was supported by NSF grant 9981926.

Appendix

To obtain the mean and variance expressions for the lottery model, we begin by setting total biomass density ($B(t)$) at B_{\max} . If T is the first time the environmental condition (E) hits a value contained by a species' niche, then $B(T)=B_{\max}$ and $B(k)=B_{\max}(1-\mu)^{k-1}$, for $k=1,2, \dots, T-1$. At time T , we reset time to zero and repeat the process. The distribution of T is geometric with $\text{Prob}(T=k)=q^{k-1}(1-q)$, where q is the fraction of ΔE not contained by any species' niche. We define $B([0,m-1])$ as:

$$B([0, m - 1]) = \frac{1}{m} \sum_{i=0}^{m-1} B(i)$$

Then, the long-term average biomass is the expectation of $B([0,T-1])$, which is calculated as the sum over all possible values of k of $\text{Prob}(T=k)$ times $B([0,k-1])$:

$$\sum_{k=1}^{\infty} q^{k-1} (1 - q) \frac{1}{k} \sum_{i=0}^{k-1} (1 - \mu)^i B_{\max}$$

which reduces after some algebra to the mean biomass given in the text. Similarly, the expectation of $B([0,T-1])^2$ is given by:

$$\sum_{k=1}^{\infty} q^{k-1} (1 - q) \frac{1}{k} \sum_{i=0}^{k-1} \left[(1 - \mu)^i B_{\max} \right]^2$$

After subtracting the square of the mean biomass, this reduces to the expression for the variance of biomass which is given in the text.

Table 1: Parameters of the Simulation Model

Parameter description	Parameter symbol	Value
Reference value of r	a	1077
respiration loss	γ	0.1
tissue death	μ	0.1
light half saturation	K_L	50
nitrogen half saturation	K_N	0.005
water half saturation	K_W	200
water use efficiency	U	0.001
litter fraction to fast carbon pool	f	0.5
water loss from root zone	$s + \epsilon$	0.55
Nitrogen leaching	ζ	0.2667
Nitrogen deposition	D	0.004
Effect of water availability on decomposition	ϕ	0.00002
Fast C pool decomposition	λ_f	1
Nitrogen to carbon ratio of slow carbon pool	v_s	0.00444
Nitrogen to carbon ratio of fast carbon pool	v_f	0.06666
<p><i>Rainfall:</i> The rainfall pattern was generated by the formula</p> $R_{t+u} = a_{t+u} + b_{t+u} \{1 + \cos[2\pi(u - \theta_{t+u})]\},$ <p>where R_{t+u} is the rain intensity at time u ($0 < u < 1$), in year t, in units of mm per annum; for integer t, a_t and b_t are lognormal random variables with means 100 (150 for higher rain) and 250 respectively with standard deviations of their natural logs equal to 0.25; θ_t is normal with mean zero (0.1 for later rain) and standard deviation 0.2; and $a_{t+u} = (1-u)a_t + ua_{t+1}$, with corresponding definitions for b_{t+u} and θ_{t+u}.</p>		

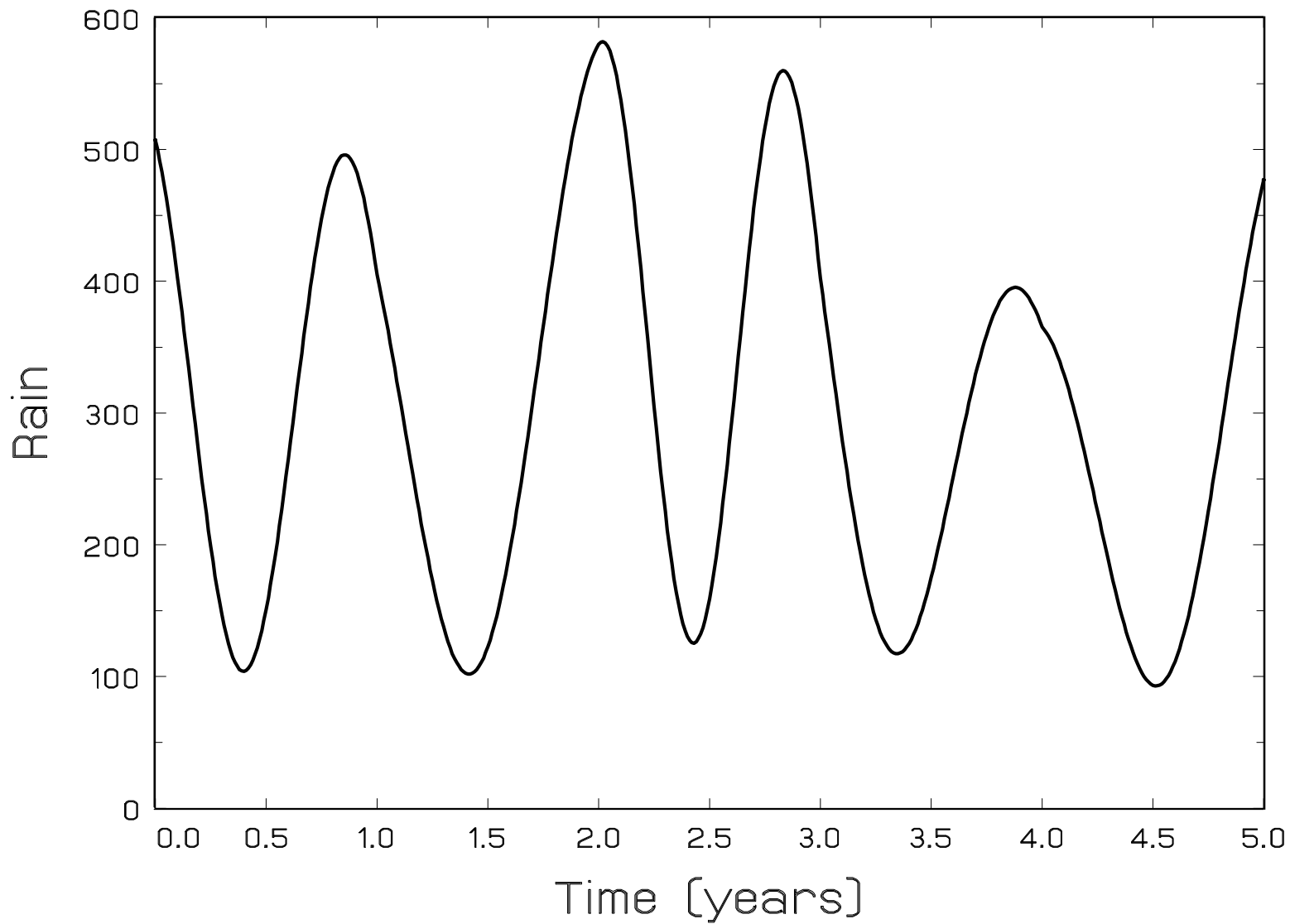
Figure Legends

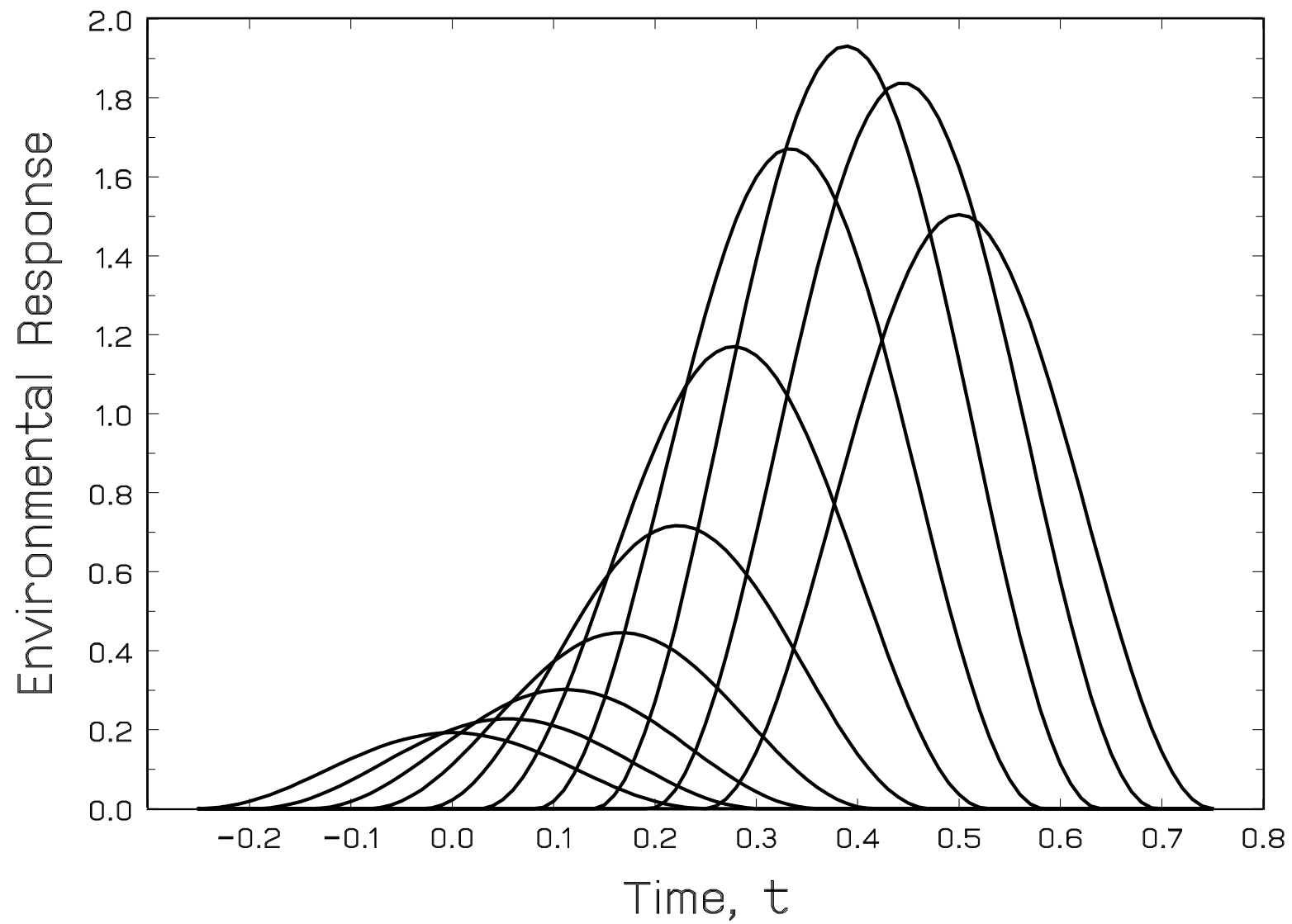
1. A sample of the pattern of rainfall over five years in the simulations for the base parameter set. Integer values of time coincide with mean peak rainfall and mean minimum rainfall is midway between integer values. Units are mm per year. Table 1 explains the generation of this pattern.
2. Environmental responses, $E_j(t)$, of the ten species in the global species pool. Each response is a complete cycle of a sin wave over a six month period, and is zero outside this period. The change in peak height of $E_j(t)$ with the location of the peak (phase) defines a tradeoff promoting coexistence of these species. Time t is time in fractions of a year, and 0 defines the mean time of peak rainfall for the unperturbed system.
3. Persisting species for each local pool size, ○: unperturbed, +: higher rain, ×: later rain. Means are given respectively by solid, dotted and dashed lines.
4. Sample of a simulation run giving biomasses of a three species community. The bottom, middle and top curves are respectively the first, fifth and tenth species of the global species pool labeled in order of phase their environmental responses (see Figure 2).
5. Means of ecosystem services for communities arising from randomly chosen local species pools of different sizes. Each point is the mean of five replicates for a particular local species pool and environmental regime, ○: unperturbed, +: higher rain, ×: later rain. Means are given respectively by solid, dotted and dashed lines. Units are kg/m²/year (net primary production), mm/year (evapotranspiration), g/m²/year (N mineralization), and kg/ m²/year (carbon storage).
6. Variability of ecosystem services defined as coefficient of variation over time for net primary production, and standard deviation of the log over time for the other ecosystem services which always take positive values. Symbols as for Figure 5.
7. Soil water content (mm) and temporal standard deviation of water content for the simulations. Symbols as for Figure 5.
8. Mean phase of the environmental response in each simulated community for each environmental regime. (Mean phase is calculated as the average of the phases of the constituent species weighted by their mean biomasses.)

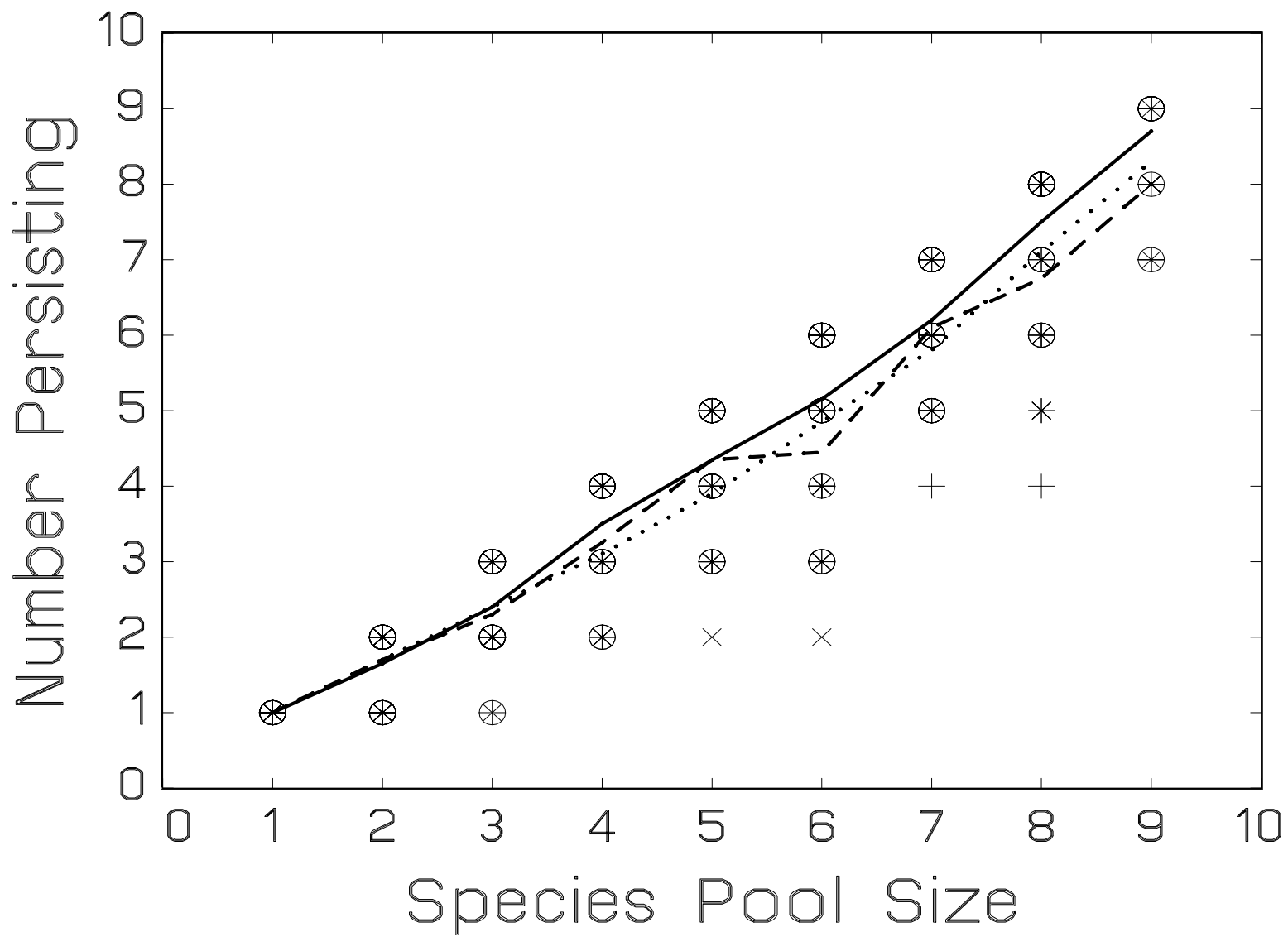
Literature Cited

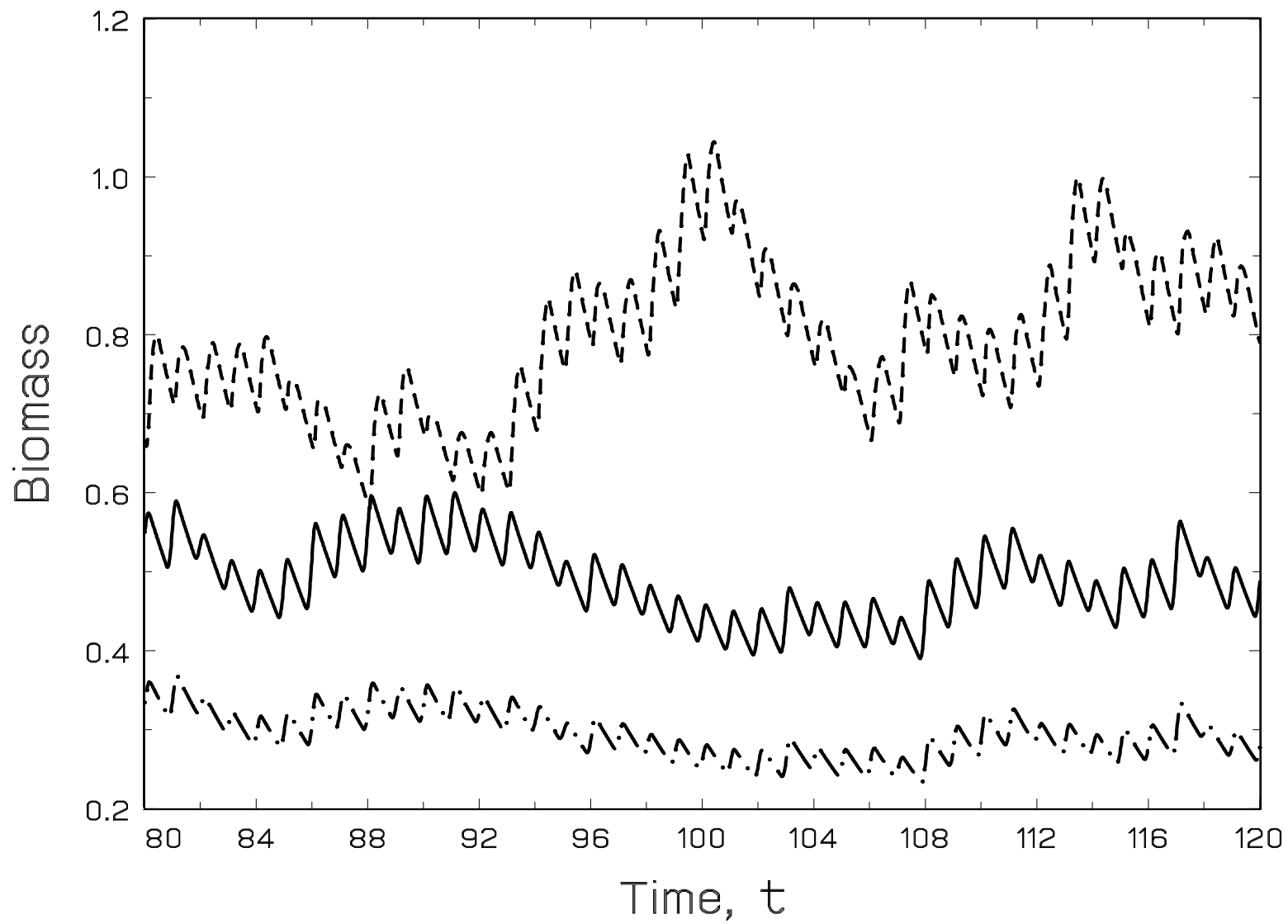
- Abrams, P. (1984). "Variability in resource consumption rates and the coexistence of competing species." Theoretical Population Biology **25**: 106-124.
- Baskin, C. C., P. Chesson, et al. (1993). "Annual seed dormancy cycles in two desert winter annuals." Journal of Ecology **81**: 551-556.
- Bowers, M. A. (1987). "Precipitation and the relative abundance of desert winter annuals: a 6-year study in the northern Mohave Desert." Journal of Arid Environments **12**: 141-149.
- Brown, J. S. (1989). "Coexistence on a seasonal resource." The American Naturalist **133**: 168-182.
- Chesson, P. (1994). "Multispecies competition in variable environments." Theoretical Population Biology **45**: 227-276.
- Chesson, P. (2000a). "General theory of competitive coexistence in spatially-varying environments." Theoretical Population Biology **58**: in press.
- Chesson, P. (2000b). "Mechanisms of maintenance of species diversity." Annual Review of Ecology and Systematics **31**: 343-366.
- Chesson, P. and N. Huntly (1997). "The roles of harsh and fluctuating conditions in the dynamics of ecological communities." The American Naturalist **150**(5): 519-553.
- Chesson, P. L. (1984). "The storage effect in stochastic population models." Lecture notes in Biomathematics **54**: 76-89.
- Chesson, P. L. (1985). "Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability." Theoretical Population Biology **28**: 263-287.
- Chesson, P. L. and R. R. Warner (1981). "Environmental variability promotes coexistence in lottery competitive systems." The American Naturalist **117**(6): 923-943.
- Cody, M. L. and H. A. Mooney (1978). "Convergence versus nonconvergence in mediterranean-climate ecosystems." Annual Review of Ecology and Systematics **9**: 265-321.
- Comins, H. N. and I. R. Noble (1985). "Dispersal, variability, and transient niches: species coexistence in a uniformly variable environment." American Naturalist **126**: 706-723.
- Doak, D. F., D. Bigger, et al. (1998). "The statistical inevitability of stability-diversity relationships in community ecology." The American Naturalist **151**(3): 264-276.
- Grubb, P. (1977). "The maintenance of species-richness in plant communities: the importance of the regeneration niche." Biological Review **52**: 107-145.
- Hector, A. (1998). "The effect of diversity on productivity: detecting the role of species complementarity." Oikos **82**(3): 597-599.
- Hector, A., B. Schmid, et al. (1999). "Plant diversity and productivity experiments in European grasslands." Science **286**(5442): 1123-1127.
- Hooper, D. U. and P. M. Vitousek (1997). "The effects of plant composition and diversity on ecosystem processes." Science **277**: 1302-1305.
- Huisman, J. and F. J. Weissing (1999). "Biodiversity of plankton by species oscillations and chaos." Nature **402**: 407-410.

- Huston, M. A. (1997). "Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity." Oecologia **110**: 449-460.
- Ives, A. R., K. Gross, et al. (1999). "Stability and variability in competitive communities." Science **286**(5439): 542-544.
- Iwasa, Y. and J. Roughgarden (1986). "Interspecific competition among metapopulations with space-limited subpopulations." Theoretical Population Biology **30**: 194-214.
- Juhren, M., F. W. Went, et al. (1956). "Ecology of desert plants. IV. Combined field and laboratory work on germination in the Joshua Tree National Monument, California." Ecology **37**: 318-330.
- Lehman, C.L. and D. Tilman (2000). "Biodiversity, stability and productivity in competitive communities." The American Naturalist, in press.
- Levin, S. A. (1974). "Dispersion and population interactions." The American Naturalist **108**: 207-228.
- Loreau, M. (1992). "Time scale of resource dynamics, and coexistence through time partitioning." Theoretical Population Biology **41**: 401-412.
- Loreau, M. (1998). "Ecosystem development explained by competition within and between material cycles." Proceedings of the Royal Society of London series B **265**: 33-38.
- Loreau, M. (1998). "Separating sampling and other effects in biodiversity experiments." Oikos **82**: 600-602.
- Loria, M. and I. Noy-Meir (1979-1980). "Dynamics of some annual populations in a desert loess plain." Israel Journal of Botany **28**: 211-225.
- Muko, S. and Y. Iwasa (2000). "Species coexistence by permanent spatial heterogeneity in a lottery model." Theoretical Population Biology **57**: 273-284.
- Rathcke, B. and E. P. Lacey (1985). "Phenological patterns of terrestrial plants." ARES **16**: 179-214.
- Shmida, A. and S. Ellner (1984). "Coexistence of plant species with similar niches." Vegetatio **58**: 29-55.
- Tilman, D. (1982). Resource Competition and Community Structure. Princeton, New Jersey, Princeton University Press.
- Tilman, D. (1999). "The ecological consequences of changes in biodiversity : a search for general principles." Ecology **80**(5): 1455-1474.
- Tilman, D. and J. A. Downing (1994). "Biodiversity and stability in grasslands." Nature **367**: 363-365.
- Tilman, D., C. Lehman, et al. (1998). "Diversity-stability relationships: statistical inevitability or ecological consequence?" The American Naturalist **151**(3): 277-282.
- Tilman, D., C. L. Lehman, et al. (1997). "Plant diversity and ecosystem productivity: theoretical considerations." Proceedings of the National Academy of Science USA **94**: 1857-1861.
- Yachi, S. and M. Loreau (1999). "Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis." Proc. Nat. Acad. Scie **96**: 1463-1468.

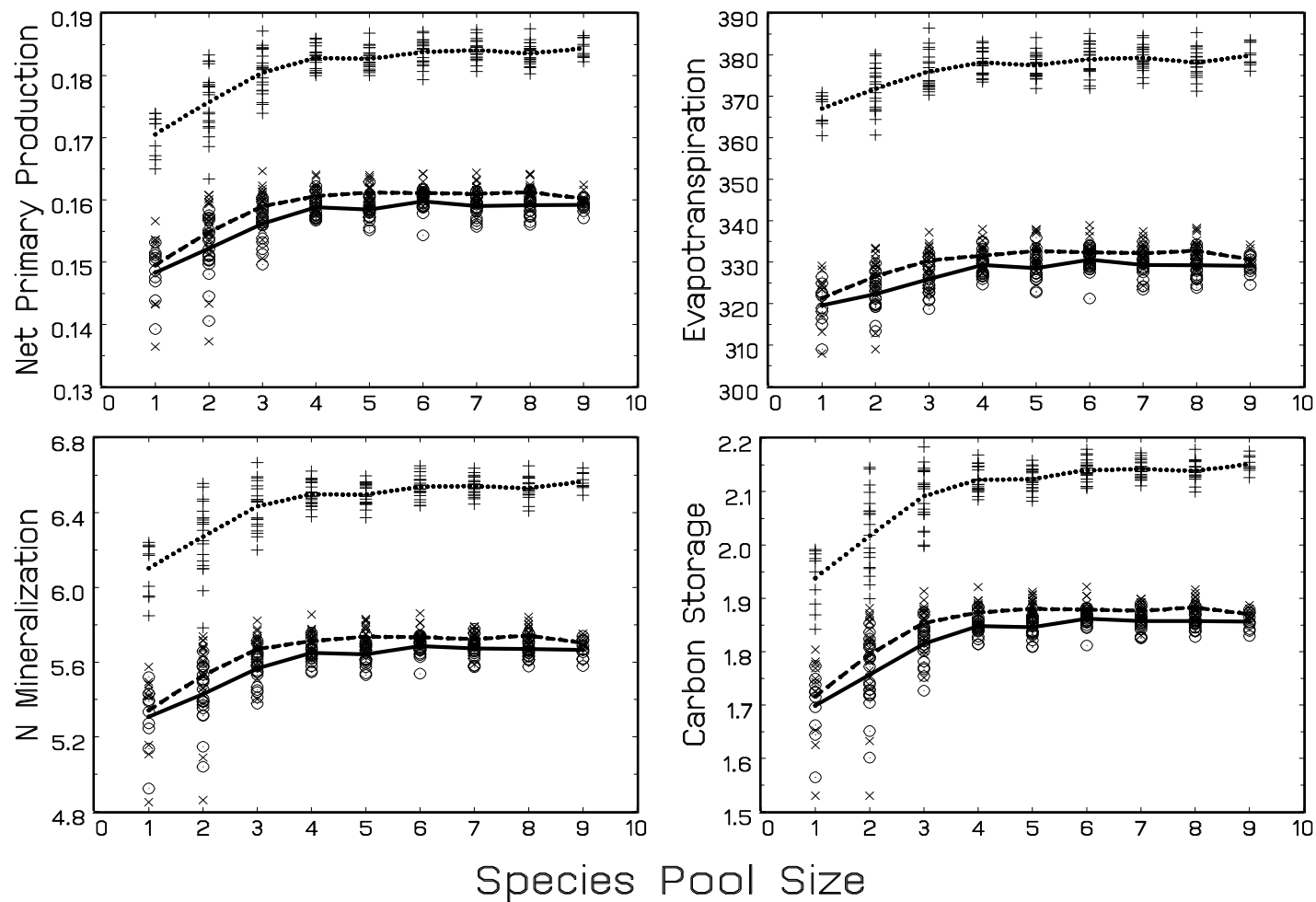








Mean Ecosystem Functioning



Variability of Ecosystem Functioning

