LETTER

The functional consequences of random vs. ordered species extinctions

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Abstract

Recent work suggests that the effect of extinction on ecosystem function depends on whether or not species have identical extinction risks. Here, we use a simple model of community dynamics to predict how the functional consequences of random and non-random extinction may differ. The model suggests that when resource partitioning or facilitation structures communities, the functional consequences of non-random extinction depend on the covariance between species traits and cumulative extinction risks, and the compensatory responses among survivors. Strong competition increases the difference between random and ordered extinctions, but mutualisms reduce the difference. When diversity affects function via a sampling effect, the difference between random and ordered extinction depends on the covariance between species traits and the change in the probability of being the competitive dominant caused by ordered extinction. These findings show how random assembly experiments can be combined with information about species traits to make qualitative predictions about the functional consequences of various extinction scenarios.

INTRODUCTION

The relationship between biodiversity and ecosystem functioning has emerged as a dominant research topic in ecology (Tilman 1999; Chapin *et al.* 2000; Loreau *et al.* 2001; Naeem 2002). Interest in this topic can be attributed, at least in part, to accelerating rates of global change that compel ecologists to understand how species extinction might influence important ecological processes regulated by communities within ecosystems. The vast majority of theoretical and empirical studies that have addressed how species diversity influences ecosystem functioning have manipulated diversity by randomly choosing some number of species from a species 'pool', placing these together in a closed experimental unit, and then examining how the number of randomly chosen species affects community-level processes like primary production, nutrient cycling, decomposition, rates of predation, etc. (for example, Hooper & Vitousek 1997; Symstad *et al.* 1998; Hector *et al.* 1999; Naeem *et al.* 2000; Mulder *et al.* 2001; Tilman *et al.*

2001; Cardinale *et al.* 2002, 2003; Duffy *et al.* 2003; Loreau *et al.* 2003). Using the results of these experiments to predict the ecosystem-level effects of biodiversity loss requires the assumption that species go extinct randomly – that is, all species have an equal extinction risk.

While random assembly studies have done much to articulate the hypothesis that species extinctions may influence community and ecosystem processes, the extent to which their results can be used to understand natural systems is uncertain (Schmid *et al.* 2001; Symstad & Tilman 2001; Bengtsson *et al.* 2002; Holt & Loreau 2002; Symstad *et al.* 2003; Cardinale *et al.* 2004; Covich *et al.* 2004; Giller *et al.* 2004). In part, this is because in many (if not most) natural systems, extinction risk is known to differ among species (Pimm *et al.* 1988; McKinney 1997; Ricciardi & Rasmussen 1999; Srivastava 2002), tending to be a function of population size (Tracy & George 1992), body size (McKinney 1997), trophic position (Petchey *et al.* 1999), phylogenetic history (Purvis *et al.* 2000), or sensitivity to environmental stress (Thomas *et al.* 2004). Recent

theoretical studies suggest that extinctions ordered by these factors can impact the magnitude (Solan *et al.* 2004) and stability (Ives & Cardinale 2004) of community processes quite differently than random extinctions. Despite this, there have been few attempts to establish clear, general predictions about how the functional consequences of random extinctions are likely to differ from those of ordered extinctions.

This paper provides a first step towards generating predictions about how the functional consequences of ordered vs. random extinctions differ. To do so, we use simple models that omit or simplify important biological details; yet, their simplicity permits general, precise predictions. We organize the paper by comparing the functional consequences of random vs. ordered extinctions for three widely cited mechanisms by which species richness is thought to affect community processes. The first two mechanisms – resource partitioning and facilitation – are often grouped together under the term 'species complementarity' (e.g. Loreau & Hector 2001). While models of these mechanisms can be structurally similar, they represent fundamentally different biological processes and so we consider them separately. The last mechanism – referred to as the 'sampling' or 'selection' effect of diversity (Huston 1997; Tilman *et al.* 1997) – has been the subject of considerable debate because it occurs when diversity increases the chance that a process will be dominated by a single taxon (i.e. diversity maximizes the probability of a species-specific effect).

Before proceeding, it is useful to clarify some terminology. We use the term 'random extinction' to refer to the case where all species in a community have an equal probability of going extinct. In contrast, we use 'ordered extinction' to refer to any scenario where species differ in their probabilities of going extinct, although extinctions are still stochastic. Elsewhere, 'ordered extinction' has been used to refer to a deterministic extinction order (Ives & Cardinale 2004), which can be considered the limit behaviour of what we describe here. Lastly, we use community-level biomass production as our measure of ecosystem functioning. There is nothing in our analyses that is specific to productivity as the dependent variable, and all the arguments we outline apply equally well to other processes such as nutrient cycling, decomposition, rates of predation, etc. However, we use community productivity because it has been the focal response variable for most diversity-function studies to date.

RESOURCE PARTITIONING

Few studies have convincingly demonstrated that diversity impacts productivity through resource partitioning (Schmid *et al.* 2002; Ives *et al.* 2004). A small number of studies have claimed evidence of resource partitioning, but the evidence has been indirect, typically based on observations that the impact of diversity on some resource exceeds that which can be explained by other mechanisms (Norberg 2000; Fridley 2001; Loreau & Hector 2001). Even so, resource partitioning must be viewed as fundamental to the debate over biodiversity and ecosystem functioning because most theories of long-term, stable coexistence require that species differentially utilize limited resources in time or space (Chesson 2000).

To examine the differences between ordered and random extinctions for species that partition resources, we use a Lotka-Volterra model of a monotrophic community of competitors. In this model, the dynamics of any given species are given by:

$$\frac{1}{x_i}\frac{dx_i}{dt} = r_i \left(1 - \frac{x_i + \sum\limits_{j=1, j\neq i}^{N} \alpha_{ij}x_j}{K_i} \right) \tag{1}$$

where K_i is the carrying capacity of species i, r_i is the growth rate of species i, α_{ij} determines the per capita effect of species j on the growth rate of species i, and N is the number of species in the community. While eqn 1 describes community dynamics for all time, we consider only equilibrium dynamics here, and hereafter use x_i to denote the equilibrium density of species i. To enable the analysis, we make two simplifying assumptions. First, we assume that species interactions are symmetric, and the strength of interactions are the same among all pairs of species – that is, all α_{ij} equal a common α. We later relax this assumption and investigate species that differ in competitive ability (in the section on sampling effects). Second, we assume that all species have the same carrying capacity. Specifically, if K^* denotes the total community density when all species are present (the community carrying capacity), then the carrying capacity for each individual species is

$$K_i = \frac{K^*}{N}[1 + \alpha(N-1)]. \tag{2}$$

Lastly, we connect community dynamics to community productivity by assuming that each species has a per capita productivity, c_i, and community productivity is the sum of each species population-level productivity, $\sum_{i=1}^{N} c_i x_i$.

To model the effects of extinction on community productivity, we write the expected community productivity after n species have gone extinct as

$$\sum_{i=1}^{N} c_i E[x_{i,n}]. \tag{3}$$

In eqn 3, $E[x_{i,n}]$ is the expected equilibrium abundance of species i after n species have gone extinct. This expectation

is the equilibrium abundance of species i if it has not gone extinct, multiplied by the probability that it has not gone extinct

$$E[x_{i,n}] = \frac{K_i}{1 + \alpha(N - n - 1)}(1 - P_{i,n}). \qquad (4)$$

In eqn 4, $P_{i,n}$ is the probability that species i is among the first n species to go extinct. We call this the cumulative extinction probability of species i, and emphasize that it is different from the probability that species i is the nth species to go extinct. In eqn 4, $1 - P_{i,n}$ is the probability that species i remains in the community from which n species have gone extinct, and $K_i/[1 + \alpha (N - n - 1)]$ is the equilibrium abundance of species i in such a community.

Substituting eqn 2 for K_i into eqn 4 gives

$$\begin{aligned} E[x_{i,n}] &= \frac{K^*}{N}\frac{[1 + \alpha(N - 1)]}{[1 + \alpha(N - n - 1)]}(1 - P_{i,n}) \\ &= \frac{K^*}{N}\left[1 + \frac{\alpha n}{1 + \alpha(N - n - 1)}\right](1 - P_{i,n}) \end{aligned}. \qquad (5)$$

In eqn 5, K^*/N is the equilibrium abundance of species i before any species have gone extinct, and $\alpha n/[1 + \alpha(N - n - 1)]$ is the proportional change in the abundance of species i after n extinctions (assuming species i survives). When $\alpha = 0$ (no interspecific interactions), extinction does not cause the abundance of surviving species to change and thus $\alpha n/[1 + \alpha(N - n - 1)] = 0$. However, when $\alpha > 0$ extinction releases surviving species from competition, allowing their densities to increase. Density compensation of this sort has been demonstrated in a number of theoretical and empirical studies (Frost *et al.* 1995; Fischer *et al.* 2001; Diaz *et al.* 2003; Ives & Cardinale 2004). As is thought to occur in other systems, the magnitude of density compensation here, $\alpha n/[1 + \alpha(N - n - 1)]$, increases as the strength of interspecific interactions, α, increases.

Substituting eqn 5 into eqn 3 gives a new expression for expected community productivity after n extinctions:

$$\sum_{i=1}^{N} c_i E[x_{i,n}] = \frac{K^*}{N}\left[1 + \frac{\alpha n}{1 + \alpha(N - n - 1)}\right]\sum_{i=1}^{N} c_i(1 - P_{i,n}) \qquad (6)$$

Equation 6 can be evaluated for both random and ordered extinction scenarios, allowing the two to be compared directly. For random extinction, the cumulative extinction probabilities are the same for all species, $P_{i,n} = n/N$. For ordered extinction, it is useful to leave $P_{i,n}$ unspecified. Using eqn 6, the difference between expected community productivity with random vs. ordered extinction is

$$\begin{aligned} &\frac{K^*}{N}\left[1 + \frac{\alpha n}{1 + \alpha(N - n - 1)}\right]\left[\sum_{i=1}^{N} c_i(1 - n/N) - \sum_{i=1}^{N} c_i(1 - P_{i,n})\right] \\ &= \frac{K^*}{N}\left[1 + \frac{\alpha n}{1 + \alpha(N - n - 1)}\right]\left[\sum_{i=1}^{N} c_i(P_{i,n} - n/N)\right] \\ &= K^*\left[1 + \frac{\alpha n}{1 + \alpha(N - n - 1)}\right]\text{Cov}(c_i, P_{i,n}). \end{aligned}$$
$$(7)$$

Equation 7 shows that for this model the expected difference between random and ordered extinctions is determined by the magnitude of compensatory responses by surviving species, $\alpha n/[1 + \alpha(N - n - 1)]$, and the covariance between per capita productivity c_i and cumulative extinction probability $P_{i,n}$. When eqn 7 is positive, expected community productivity after n extinctions is greater for random extinction than ordered extinction, and vice versa.

A simulation illustrates these points. This simulation considers communities beginning with $N = 10$ species, with K^* set to 1. Values of per capita productivity were drawn randomly from a uniform distribution, and then standardized to a mean of 1. We simulated four extinction scenarios – random extinction and three scenarios of ordered extinction. For the latter, each species was assigned a relative extinction risk, with a risk of 1 for the species least prone to extinction and a risk of 10 for the species most prone to extinction. For each extinction event, the probability of a species going extinct was equal to its own extinction risk divided by the sum of all remaining species extinction risks (cf. Solan *et al.* 2004). For scenario A, extinction risks were ordered by increasing productivity, so that the most productive species was the most likely to go extinct, and vice versa. For scenario B, extinction vulnerabilities were ordered by decreasing productivity, so that the most productive species was the least likely to go extinct. A third scenario was included, scenario C, where extinction risks were randomly assigned to species without regard to productivities. We include scenario C to show that differing extinction risks do not, by themselves, drive differences between random and ordered extinctions. As we will show, differences between random and ordered extinctions are driven by the covariance between differing extinction risks and species productivities.

Figure 1 illustrates the covariance between per capita productivities c_i and the cumulative extinction probabilities after 1, 5 and 9 extinctions. Figure 2 shows how the covariance between per capita productivity and extinction probability changes over the course of all nine extinctions. In scenarios A and B, the covariances between cumulative extinction probability and productivity were large. By luck of the draw, cumulative extinction probabilities in scenario C were weakly correlated with per capita productivities. Figure 2 emphasizes that, although species have constant
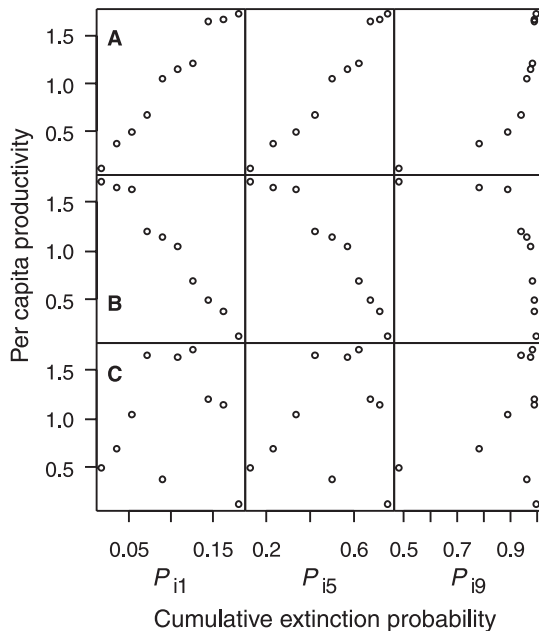
Figure 1 Per capita productivities, c_i, and cumulative extinction probabilities for 10 simulated species with differing extinction risks. Upper row of panels: extinction risk ordered by per capita productivity (scenario A); middle row: extinction risk in reverse order of per capita productivity (scenario B); bottom row: extinction risk unrelated to per capita productivity (scenario C). Left panels: probability of being the first species to go extinct. Middle panels: probability of being among the first five species to go extinct. Right panels: probability of being among the first nine species to go extinct.
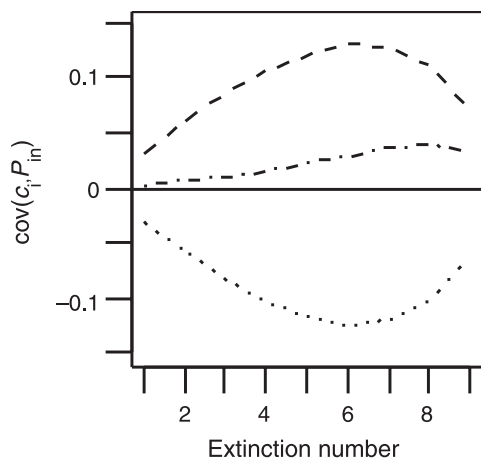

Figure 2 Covariance between per capita productivities and cumulative extinction probabilities as a function of the number of species that have gone extinct. Dashed line: extinction risk ordered by per capita productivity (scenario A). Dotted line: extinction risk in reverse order of per capita productivity (scenario B). Dot-dashed line: extinction risk unrelated to per capita productivity (scenario C).

extinction risks, cumulative extinction probabilities change as more species go extinct, and consequently the covariance between cumulative extinction probabilities and per capita productivities also changes as more species go extinct. As a result, the functional consequences of non-random extinction change as n increases (eqn 7), even when species do not interact ($\alpha = 0$). In the extinction scenario modelled here, covariance peaks when approximately half of the species have gone extinct because that is when the cumulative extinction probabilities are the most variable (i.e. $P_{i,5}$ is more variable than $P_{i,1}$ or $P_{i,9}$).

Figure 3 shows how expected community productivity changes as species go extinct for three levels of compensation: $\alpha = 0$ (no compensation), $\alpha = 0.5$ (partial compensation), and $\alpha = 1$ (full compensation). In Fig. 3, the difference between random and ordered extinction is equal to the covariance between cumulative extinction probability and productivity (Fig. 2) scaled by the increase in equilibrium density of surviving species caused by compensation. Without compensation ($\alpha = 0$), the differences between random and ordered extinctions are exactly equal to the covariances in Fig. 2. As compensation increases (greater α), increases in the abundances of surviving species caused by competitive release amplify the difference between random and ordered extinction.

FACILITATION

While studies of niche partitioning and its implications have dominated ecological thinking for decades, recent empirical work suggests that positive species interactions play a greater role in community organization than has been appreciated historically (Bertness & Callaway 1994). As a result, there has been increasing effort to incorporate interspecific interactions involving mutualisms into ecological theory (Bruno *et al.* 2003). The same Lotka-Volterra framework used in the Resource Partitioning model can be used to analyse communities of weak mutualists if $\alpha < 0$. When $\alpha < 0$, increases in the abundance of one species cause increases in the abundance of all other species through mutual facilitation. Clearly, however, facilitation cannot be too strong, or else the equilibrium becomes unstable and all species abundances will increase without limit. The mathematical manifestation of this limitation is that α must be between 0 and $-1/(N-1)$. Stronger mutualisms are still possible between subsets of species, just not between all species. With $-1/(N-1) < \alpha < 0$, the same arguments and derivations presented in the Resource Partitioning model hold true, except that now extinctions cause the equilibrium abundances of the remaining species to decrease. Consequently, the $\alpha n/[1 + \alpha(N - n - 1)]$ term in eqn 7 is negative, and approaches -1 as mutualism becomes stronger (α becomes more negative).
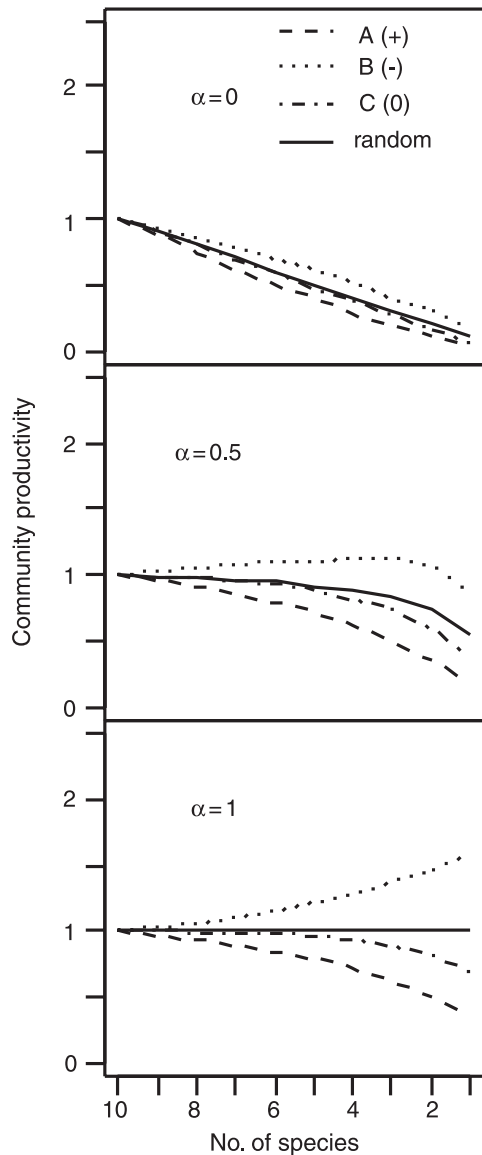
Figure 3 Expected community productivity versus number of species remaining in the community for three levels of compensation. Solid lines: random extinction (extinction risk equal among species). Dashed lines: extinction risk ordered by per capita productivity (scenario A). Dotted lines: extinction risk in reverse order of per capita productivity (scenario B). Dot-dashed lines: extinction risk differs among species but is unrelated to per capita productivity (scenario C).

Figure 4 shows the expected productivities for the same set of species considered in Figs 1–3, but now with species modelled as mutualists instead of competitors. The levels of facilitation shown are one-third and two-third of the maximum allowable values. As in Fig. 3, the expected difference between ordered and random extinction is equal to the covariance between productivity and cumulative extinction probability (Fig. 2) scaled by the changes in
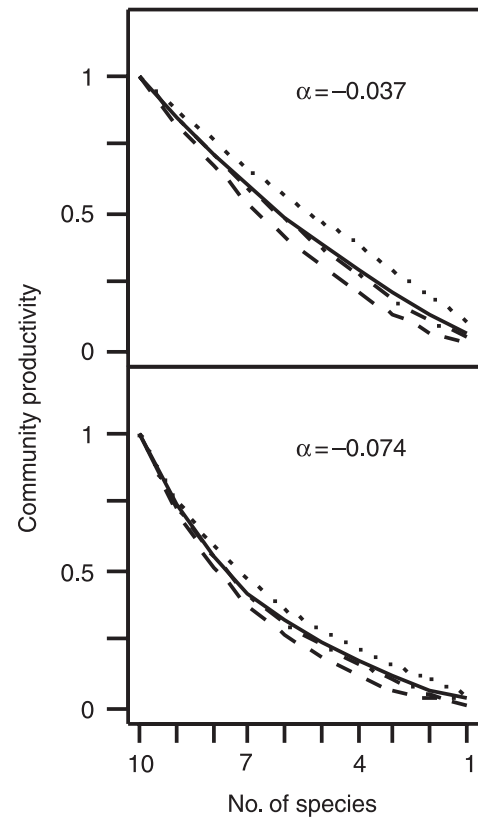

Figure 4 Expected community productivity versus number of species remaining in the community for two levels of facilitation. Solid lines: random extinction (extinction risk equal among species). Dashed lines: extinction risk ordered by per capita productivity (scenario A). Dotted lines: extinction risk in reverse order of per capita productivity (scenario B). Dot-dashed lines (nearly coincident with the solid lines): extinction risk differs among species but is unrelated to per capita productivity (scenario C).

species equilibrium abundances. With facilitation, however, species abundances decrease when other species go extinct, so the differences between random and ordered extinction also decrease as the strength of mutualism increases.

The effect of increasing the strength of facilitation might best be understood by considering the extreme case of a community where each species requires the coexistence of all other species to survive. Mathematically, this is the limiting behaviour as $\alpha \to -1/(N - 1)$. In this community, when one species goes extinct, the entire community collapses because no species can survive without the species that went extinct. As a consequence, productivity collapses to zero at the first extinction regardless of whether extinctions are random or ordered. Therefore, when facilitation is at its maximum, the difference between random and ordered extinction is zero.

SAMPLING EFFECT

Perhaps the most widely cited mechanism by which diversity influences community production is the sampling effect (alternatively called the 'selection' or 'selection-probability' effect; Huston 1997; Tilman 1999; Fridley 2001; Loreau & Hector 2001). A sampling effect occurs when species-rich communities have a greater chance of including a highly productive taxon (or combination of taxa) than species-poor communities, and competition or some other sorting process allows the highly productive taxon to differentially express its traits relative to other species (Loreau & Hector 2001; Cardinale *et al.* 2004). Our second model mimics the sampling effect by assuming that species exhibit a competitive hierarchy, and that community production is determined solely by the competitively dominant species in the community. For this scenario, we order the species index so that the most competitive species is species 1, and the least competitive species is species N.

Let b_i be the productivity of a community that is dominated by species i. After n species have gone extinct, the expected community productivity is

$$\sum_{i=1}^{N} b_i \Pr\{\text{species } i \text{ is the competitive dominant}\}. \quad (8)$$

To write eqn 8 more compactly, we use $R_{i,n}$ to denote the probability that species i is the competitive dominant in a community after n species have gone extinct. For example, with all species present in a community, species 1 is the competitive dominant, so $R_{1,0} = 1$ and $R_{i,0} = 0$ for all $i > 1$. To find $R_{i,n}$ for random extinction, we observe that there are $\binom{N}{n}$ possible combinations for the first n extinctions, and of these there are $\binom{N-i}{n-i+1}$ combinations which contain the first $i-1$ species in the competitive hierarchy but not the ith species. Under random extinction, all of these sequences are equally likely, so $R_{i,n}$ is

$$R_{i,n}^* = \begin{cases} \binom{N-i}{n-i+1} \Big/ \binom{N}{n} & i \leq n+1 \\ 0 & \text{otherwise} \end{cases} \quad (9)$$

where we have used a asterisk (*) superscript to denote random extinction (Cardinale *et al.* 2004; Ives *et al.* 2004). When extinctions are ordered, general results for $R_{i,n}$ are elusive. Nevertheless, using eqns 8 and 9, the difference in expected productivity between random and ordered extinction can be written as

$$\sum_{i=1}^{N} b_i \left(R_{i,n}^* - R_{i,n} \right) = N \mathrm{Cov}\left[b_i, \left(R_{i,n}^* - R_{i,n} \right) \right]. \quad (10)$$

Equation 10 shows that when species are arranged in a competitive hierarchy, the expected community productiv-

ities of random vs. ordered extinctions differ by an amount that is proportional to the covariance between the productivity of a community dominated by species i and the change in the probability of species i being the competitive dominant that results from ordered extinction.

Both components of the covariance in eqn 10 deserve further comment. First, the covariance in eqn 10 depends on a population-level productivity, b_i, instead of a per capita productivity, c_i (as in eqn 7), because the sampling effect model allows for the possibility that not all species attain the same density when they are the competitive dominant. However, if we were to assume that the competitively dominant species will always attain the same density K, then $b_i = c_i K$ and eqn 10 would equal $NK\mathrm{Cov}\left[c_i, \left(R_{i,n}^* - R_{i,n}\right)\right]$. Thus, the appropriate productivity term (individual or population) depends on the extent of asymmetry in the carrying capacities of different species.

Second, the difference $R_{i,n}^* - R_{i,n}$ requires some explanation. With random extinction, species differ in their probability of being the competitive dominant. At any stage of the extinction sequence, species 1 has the greatest probability of being the competitive dominant, while species N has the smallest probability. Ordered extinctions change the probability that a given species will be the competitive dominant at any point in the extinction sequence. For example, if the most productive species is the most likely to go extinct, then its probability of being the competitive dominant decreases relative to what it would be with random extinctions. The effect of ordered extinctions on expected community productivity depends on the covariance between these changes in the probability of being the competitive dominant and the productivity of a community dominated by that species. If ordered extinctions increase the chances that the most productive species will be the competitive dominant, then the covariance on the right-hand side of eqn 10 will be negative, so expected community productivity after n extinctions will be greater with ordered extinctions than with random extinctions. The reverse is also true.

A simulation illustrates the important features of eqn 10. For comparability with previous simulations, we use the same per capita productivities as before and assume that each species reaches the community-level carrying capacity, K^*, when it is the competitive dominant (i.e. $b_i = c_i K^*$). We consider two groups of simulations: one where the competitive hierarchy is arranged in order of productivity (e.g. the most productive species is the most competitive, which is the common form of the sampling effect), and a second with the competitive hierarchy in reverse order of productivity (the most productive species is the least competitive, sometimes referred to as a negative sampling effect, Polley *et al.* 2003). Extinction probabilities were determined as they were in the previous simulations. We
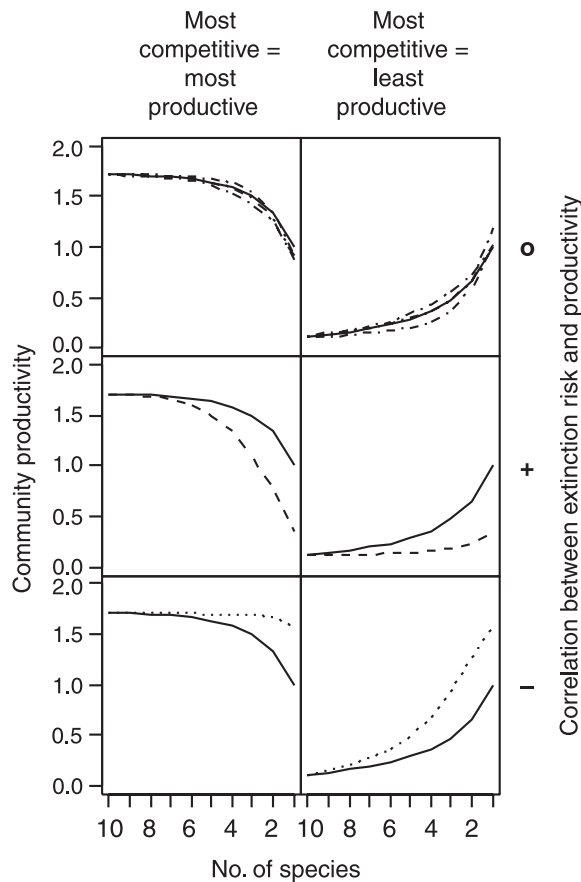
Figure 5 Expected productivity for random (solid lines) or ordered (other lines) extinction when species are arranged in competitive hierarchy. Left panels: competitive hierarchy in order of productivity. Right panels: competitive hierarchy in reverse order of productivity (negative sampling effect). Top row (dot-dashed lines): three different assignments of extinction risks, without regard to productivity or competitive ability. Middle row (dashed lines): extinction risk ordered by productivity. Bottom row (dotted lines): extinction risk in the reverse order of productivity.

simulated five assignments of extinction risks: three assignments made randomly without regard to productivity, one assignment made with extinction risk ordered by productivity, and one assignment with extinction risk in the reverse order of productivity. Expected community production for these simulations is shown in Fig. 5.

The results of this simulation confirm intuition. Consider the scenario where the best competitor is the most productive species, and also the least vulnerable to extinction (lower left panel in Fig. 5). With all species present, community productivity is determined by the most productive species. If species go extinct randomly, the chance that the competitive dominant is replaced by a less productive species increases with each extinction. Thus expected productivity declines as the number of species

declines. If extinctions are ordered and the most productive species is the least vulnerable to extinction, the probability that this species is replaced by a less productive species is less than it is when extinctions are random. Thus, expected productivity declines more slowly than it does with random extinctions. In terms of eqn 10, the probability that the most productive species is the competitive dominant is greater with ordered extinction than with random extinction, so the covariance in eqn 10 is negative, meaning that the expected productivity under ordered extinction is greater than the expected productivity with random extinction. Conversely, when the most productive species is also the most extinction-prone, then the most productive species is less likely to be the surviving competitive dominant when extinctions are ordered, and the expected productivity with ordered extinctions is less than it would be if extinctions were random (Fig. 5, middle left panel). When a negative sampling effect prevails and the most competitive species is the least productive, these patterns are reversed (Fig. 5, right panels).

DISCUSSION

We have used simple models to explore how the functional consequences of biodiversity loss differ between random and non-random (i.e., ordered) extinctions. The models not only predict the qualitative changes caused by ordered species extinctions (which in many instances are intuitive), but they also predict how the magnitude of change depends on quantifiable properties of a community. For example, when biodiversity affects community production by resource partitioning or by interspecific facilitation, the difference between ordered vs. random extinctions increases as the covariance between species cumulative extinction risks and their per capita productivity increases (eq. 7). When species per capita productivities and extinction risk are positively correlated, productivity is reduced more quickly with species loss than it is when extinctions are random, and vice versa. The difference between ordered and random extinctions also scales with the magnitude of compensatory responses (i.e. changes in density) among surviving species (eqn 7). When communities consist of competitors, stronger interactions will lead to larger differences between ordered and random extinctions because extinction results in greater compensatory gains among surviving species. However, when communities are structured by positive interactions such as facilitation, strong interactions diminish the difference between ordered and random extinctions because the loss of one species leads to larger decreases in the abundances of other species, depressing the productivity of the entire community.

In contrast to resource partitioning or facilitation, when biodiversity affects community production via the sampling

effect, the difference between ordered and random extinctions is proportional to the covariance between the productivities of communities dominated by different species, and the changes in each species' probability of being the competitive dominant (eq. 10). When ordered extinction decreases the chance that the most productive species will be the competitive dominant, then community production will decrease more quickly with successive extinctions than it would if extinctions were random, and vice versa.

These models are useful because they begin to delineate the boundaries of inference for studies that have experimentally manipulated biodiversity and examined the impacts on various community or ecosystem properties. Nearly all of these studies have randomly assembled species drawn from some species pool, which is an approach that explicitly assumes species have an equal risk of extinction (but see Naeem *et al.* 1994; Lyons & Schwartz 2001; Smith & Knapp 2003; Zavaleta & Hulvey 2004 for counter examples). Random assembly experiments are valuable because they can elucidate the basic mechanisms by which variance in biological traits (i.e. diversity *per se*) can impact ecological processes (Loreau *et al.* 2001). In addition, there are a number of instances where the assumption of equal extinction risk is useful and relevant. For example, Schmid & Hector (2004) have argued that with many different human activities threatening biodiversity, and each leading to potentially different risks of extinction among species, random extinction may be a reasonable first approximation for understanding the global consequences of species loss. Similarly, efforts to restore degraded ecosystems often mimic the assumptions of random assembly experiments because we tend to have imperfect knowledge about the order of extinction or re-colonization among species.

Even so, equal extinction risk is not the norm in ecological communities. A large body of research suggests that extinction risk in nature tends to be ordered by factors such as population size, body size, trophic position, phylogenetic history or sensitivity to an environmental stress (Pimm *et al.* 1988; Tracy & George 1992; McKinney 1997; Petchey *et al.* 1999; Ricciardi & Rasmussen 1999; Purvis *et al.* 2000; Srivastava 2002; Ives & Cardinale 2004). One important point of our models is that unequal extinction risk among species does not, by itself, lead to conclusions that differ from those produced by models of random extinction (scenario C, Figs 3 and 4). Rather, it is the strength of association between species functional traits and species extinction risks that determines by how much random and ordered extinctions differ (scenarios A and B, Figs 3 and 4). Quantifying these associations may be possible in many systems, such as those where empirical estimates of per capita productivity can be related to rank estimates of extinction risk stemming from rarity, body size, etc. By doing so, we may be able to characterize how the effects of natural extinctions differ from those predicted by random assembly experiments, and perhaps even rank systems from those most likely to least likely to be impacted by species loss, using the case of random extinction as the equivalent of a null model (sensu Gotelli & Graves 1996). In this way, studies focusing on random extinction can be complimented by studies focusing on specific scenarios of ordered extinction that are more relevant to individual study systems (Lyons & Schwartz 2001; Smith & Knapp 2003; Zavaleta & Hulvey 2004).

The models here also shed light on conclusions derived from other studies of non-random extinction. For example, Solan *et al.* (2004) used detailed simulation models to examine the effect of benthic invertebrate extinction on sediment bioturbation in marine benthic communities containing more than 130 species across multiple functional groups. One of Solan *et al.*'s conclusions was that the functional consequences of extinction depend on how species traits that influence bioturbation are correlated to extinction risk – a conclusion we obtained analytically in eqns 7 and 10. However, Solan *et al.* argue that density compensation by surviving species only stabilizes the process of bioturbation if a species risk of extinction is independent of the traits that affect bioturbation. Our models suggest that this conclusion can be refined. When extinction risks and species traits are uncorrelated, compensation can indeed buffer an ecosystem process against species loss. In addition, positive correlations between extinction probabilities and species traits do limit the potential for compensation to maintain ecosystem function, because if more productive species go extinct first, then less productive species will replace more productive ones, resulting in a net loss of function. However, if extinction risks are negatively correlated with species traits, then compensation can actually cause function to increase as species richness decreases, if more productive species replace the extinction of less productive ones (Fig. 3, scenario B). Thus, by merging species traits, extinction risk, and the factors that regulate changes in species density after extinction, the models here allow more refined predictions that, at times, lead to insights not apparent in other models.

In conclusion, this paper is a step forward in understanding how the functional consequences of random vs. ordered extinctions differ. To be sure, we have used models with many simplifications. Yet, the resulting predictions add structure to a discussion of how past studies, which have made important simplifying assumptions, can inform our understanding of more realistic ecological scenarios. In particular, the models predict that the difference between ordered and random extinctions depends on (i) the covariance between species per capita functional traits and their cumulative probability of extinction, (ii) the magnitude of compensatory responses of surviving species, and

(iii) (for communities dominated by a sampling effect) the covariance between species productivities and changes in their probability of competitive dominance. In principle, these quantities can be measured empirically, thus enabling us to predict the direction and magnitude of any difference between random and non-random extinction. Therefore, with the right information, the results of random assembly experiments may be used as a template for understanding the functional consequences of other extinction scenarios.

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