

Effects of species diversity on the primary productivity of ecosystems: extending our spatial and temporal scales of inference

Bradley J. Cardinale, Anthony R. Ives and Pablo Inchausti

Cardinale, B. J., Ives, A. R. and Inchausti, P. 2004. Effects of species diversity on the primary productivity of ecosystems: extending our spatial and temporal scales of inference. – *Oikos* 104: 437–450.

The number of studies examining how species diversity influences the productivity of ecosystems has increased dramatically in the past decade as concern about global loss of biodiversity has intensified. Research to date has greatly improved our understanding of how, when, and why species loss alters primary production in ecosystems. However, because experiments have been performed at rather small spatial and short temporal scales, it is unclear whether conclusions can be readily extrapolated to the broader scales at which natural communities are most likely to influence ecosystem functioning. Here we develop a simple patch-dynamics model to examine some of the scale-dependent and independent qualities of the diversity-productivity relationship. We first simulate a typical diversity-productivity experiment and show that the influence of species richness on productivity is temporally dynamic, growing stronger through successional time. This holds true irrespective of whether resource partitioning or a sampling effect is the underlying mechanism. We then increase the spatial scale of the simulation from individual patches to a region consisting of many patch types. Results suggest that the diversity-productivity relationship is not influenced by spatial scale per se, but that the mechanism producing the relationship can change from sampling effects within individual patches to resource partitioning across patch types composing the region. This change occurs even though model dynamics are the same at both scales, suggesting that sampling effects and resource partitioning can represent different descriptions of the same biological processes operating concurrently at differing scales of observation. Lastly, we incorporate regional processes of dispersal and disturbance into the model and show that these processes can amplify the effect of species richness on productivity, resulting in patterns not easily anticipated from experiments. We conclude that the relative control of community structure by local versus regional processes may be a primary determinant of the diversity-productivity relationship in natural ecosystems. Therefore, past experiments having focused only on local processes might not reflect patterns and processes underlying diversity-productivity relationships in communities where disturbance and dispersal regulate species biomasses.

B. J. Cardinale and A. R. Ives, Dept of Zoology, The Univ. of Wisconsin, Madison, WI 53706, USA (bjcardinale@wisc.edu). – P. Inchausti, UMR CNRS 6553 Université de Rennes 1, campus de Beaulieu, bât 14, FR-35042 Rennes, France.

Human activities are triggering some of the most rapid losses of biodiversity in the history of life on Earth (Pimm et al. 1995, Vitousek et al. 1997, Rosenzweig 1999, Sala et al. 2000). Among the many potential consequences of biodiversity loss, it is thought that

species extinction could alter how efficiently solar energy is captured, and how rapidly matter is cycled in ecosystems (Chapin et al. 2000, Cardinale et al. 2002). Because transformations of energy and matter ultimately govern the productivity of ecosystems, understanding

Received 16 September 2003

Copyright © OIKOS 2004
ISSN 0030-1299

the link between species diversity and primary productivity continues to be a fundamental challenge for ecological research (Loreau et al. 2001, Naeem 2002).

Most of our understanding of how species diversity influences productivity has come from experiments performed with assemblages of terrestrial plants (reviewed by Johnson et al. 1996, Waide et al. 1999, Schwartz et al. 2000, Schmid et al. 2001). Several of these experiments have shown that reducing species richness can lead to less efficient capture of resources and, in turn, lower production of biomass in a system (Naeem et al. 1994, Tilman et al. 1996, Hector et al. 1999). While these experiments have articulated the hypothesis that species loss can affect important aspects of ecosystem functioning, the generality of their results is uncertain. Not only have studies begun to outline a variety of ecological scenarios where the effect of diversity on production is highly variable (Dukes 2001, Mulder et al. 2001, Cardinale and Palmer 2002, Fridley 2002), the relevance of past experimental conditions to natural systems is debatable. Experiments have typically been performed at small spatial and short temporal scales in homogeneous environments to maximize experimental control (Cardinale et al. 2000, Bengtsson et al. 2002, Giller et al. 2004). In natural environments, however, spatial and temporal heterogeneity of resources are ubiquitous features that regulate both richness and the distribution of biomass among taxa (Paine and Levin 1981, Petraitis et al. 1989, Tilman and Kareiva 1997). Studies to date have also created gradients in diversity by randomly drawing N species from some colonist pool, and then placing those species together in a habitat isolated from regional processes of dispersal and disturbance (Loreau et al. 2001, Schmid et al. 2001). Yet, naturally occurring communities are often non-random associations of species (Diamond 1975, Case and Diamond 1986, Drake 1990, Belyea and Lancaster 1999) where the exchange of propagules among patches in differing stages of succession determines the persistence, diversity, and productivity of taxa (Hanski 1989, Caswell and Cohen 1991, Hastings 1991, Palmer et al. 1996). It is, therefore, unclear whether conclusions from past experimental studies can be readily extrapolated to other systems, or to the scales at which natural communities and ecosystems persist.

The limitations outlined above highlight the need to extend our spatial and temporal boundaries of inference about the diversity-productivity relationship. We need to know whether patterns and processes observed in experiments persist at larger spatial scales and longer time scales where species extinctions are likely to have their greatest ecological consequences (Bengtsson et al. 2002, Symstad et al. 2003). We also need to know how the 'openness' of systems – that is, the exchange of propagules among the habitat patches that comprise natural ecosystems – might influence the diversity-

productivity relationship (Symstad and Tilman 2001, Holt and Loreau 2002, Giller et al. 2004). Extending these boundaries empirically will require novel experimental designs (Giller et al. 2004). In the meantime, theory can serve to focus questions and generate specific predictions about the role of species diversity at the large spatial and temporal scales neglected thus far.

Here we develop a patch-dynamics, metacommunity model to examine how a broader spatial and temporal perspective might alter conclusions about the ecosystem-level consequences of biodiversity loss. We begin by using a model to simulate an 'experiment' that is comparable to the design of many previous experiments addressing how changes in biodiversity influence ecosystem functioning. We examine the model at several temporal scales of resolution to ask (1) how does the effect of diversity on productivity change through time? We then increase the spatial scale of the simulated experiment to a 'region' composed of many different patch types and ask (2) do conclusions about the effects of diversity on productivity depend on the spatial scale of observation? Lastly, we use the model to couple local ecological processes (growth and interspecific interactions) with regional processes (dispersal and disturbance) to ask (3) do the effects of diversity on productivity change when local and regional processes operate simultaneously? Our findings lead to a series of qualitative predictions about how spatial and temporal scale influence the effects of species diversity on ecosystem productivity, and we use these predictions to suggest further avenues of research needed to understand the scale-dependent and independent consequences of species loss.

Model development and results

A simulated diversity-productivity experiment

We begin by outlining a model that mimics the approach followed by field experiments that have manipulated species richness. In these experiments, species are typically sampled randomly from some initial species pool and distributed among spatially homogeneous patches (e.g. experimental plots). The production of biomass in a patch is then measured through time as a proxy for primary production (Hector et al. 1999, Tilman et al. 2001). The model is intended to give a simple portrayal of ecological systems and is not designed to provide a quantitatively correct depiction of any particular ecosystem. Rather, we capitalize on its simplicity to illustrate general patterns that might be shared by many natural systems.

The initial model assumes there are 2000 identical, spatially homogeneous patches to be used as experimental units. There are a maximum of $N = 20$ species in the species pool. To simulate an experiment, we varied

the number of species in the initial colonist pool of a patch, N_{col} , from 1 to the maximum of 20 species. For each level of species richness, we used 100 randomly selected species or species combinations in different patches. There were, therefore, 20 levels of initial richness \times 100 randomly chosen species combinations.

Initial colonization of the patches was standardized so that the total initial biomass of colonists, $B(0)$, was held constant over all levels of initial species richness, N_{col} ; thus, the biomass of colonists for any given species i was $b_i(0) = B(0)/N_{\text{col}}$. This is equivalent to starting the experiment with the same number of propagules (for example, seedlings) regardless of the number of species used to colonize patches, which is the widely used 'replacement series' experimental design (Harper 1977). For each patch, discrete-time Lotka–Volterra equations were used to describe the biomass of each species i as:

$$b_i(t+1) = b_i(t) \exp \left[r_i \left(1 - \frac{b_i(t) + \alpha \sum_{j \neq i}^N b_j(t)}{K_i} \right) \right] \quad (1)$$

where K_i is the carrying capacity of species i , defined as the equilibrium biomass achieved in the absence of any other species, r_i is the intrinsic rate of increase in the biomass of species i , and α is the interspecific interaction coefficient. We assumed that species varied in growth rate with values of r_i assigned so that the geometric mean for all 20 species was 0.2 with values evenly spaced between $\log 0.2 - 0.1$ and $\log 0.2 + 0.1$.

We modeled two distinct cases involving differences in K_i 's and α 's to represent the range of behavior of the model. For case I, we assumed that all α 's = 1 with values of K_i normally distributed among the N taxa (Fig. 1a). Setting intraspecific and interspecific competition equal ($\alpha = 1$) implies that species have identical resource requirements and, therefore, there is no partitioning of resources among species within a patch. When coupled with interspecific differences in K_i , these conditions simulate a competitive hierarchy that allows only one species to exist in a patch at equilibrium. For case II, we assumed that all α 's = 0.2 with values of K_i the same for all species (Fig. 1e). Setting intraspecific competition greater than interspecific competition implies that species use resources differently and, therefore, they exhibit resource partitioning within a patch. When coupled with values of K_i that are equal for all species, these conditions allow the local coexistence of species with no competitive hierarchy.

To perform the experiment, we ran simulations of the model for 200 time steps to track changes in the biomass of species in each patch after the start of the experiment ($t = 0$). The units of time in the simulation are relative – they could represent hours or days for algae in aquatic systems, weeks or months for terrestrial assemblages of herbaceous vegetation, or years for tree species in a

forest. The important point is that the time period was sufficient for biomass to increase from approximately zero at $t = 0$, to an equilibrium at $t = 200$. This is shown in Fig. 1, which illustrates the temporal dynamics of the model for a simplified case of $N_{\text{col}} = 3$ randomly chosen species in three replicate patches (b–d for case I, f–h for case II). During this successional period, we did not allow any new species to colonize a patch; thus, all changes in biomass resulted from local processes of growth and species interactions. This is comparable to how empirical work has been performed in the past, where experimental plots of vegetation have typically been weeded to maintain an initial community composition. In contrast to many of those experiments, however, we began with small numbers of individuals in the patches to allow for a period of exponential growth where competitive interactions between species were minimal.

The temporal scale of observation

We begin our analyses by asking “how does the effect of species diversity on productivity change through time?” To address this question, we examined the relationship between the number of species in the initial colonist pool, N_{col} , and the total biomass in a patch at early ($t = 20$ time steps), mid ($t = 50$), and late stages of community succession ($t = 200$). Comparison of these time points showed that the diversity-productivity relationship was indeed temporally dynamic. For case I, we found that N_{col} had no influence on the mean biomass produced in a patch in early stages of succession (Fig. 2a). Differences in the intrinsic rate of increase, r_i , among species led to considerable variation in biomass among patches having different species or species combinations. However, the magnitude of this variation decreased as N_{col} increased.

As the duration of the experiment was extended, there was an increasingly positive effect of N_{col} on patch productivity, one that became highly curvilinear in late stages of community succession (Fig. 2b–c). The diversity-productivity relationship appeared to change through time because competitive interactions became stronger, leading to dominance by individual taxa. By intermediate stages of succession, local competitive interactions had resulted in the extinction of nearly 50% of the species initially established in a patch (Fig. 2d; note the slope for $t = 50$ is ≈ 0.5). By late succession only 25% of the species persisted ($t = 200$, Fig. 2d). The coefficient of variation in biomass among species in a patch increased through time (Fig. 2e), indicating greater dominance by individual species. Dominance also increased with N_{col} in late succession ($t = 200$, Fig. 2e) because there was an increased probability that the species having the highest K_i would be included in the

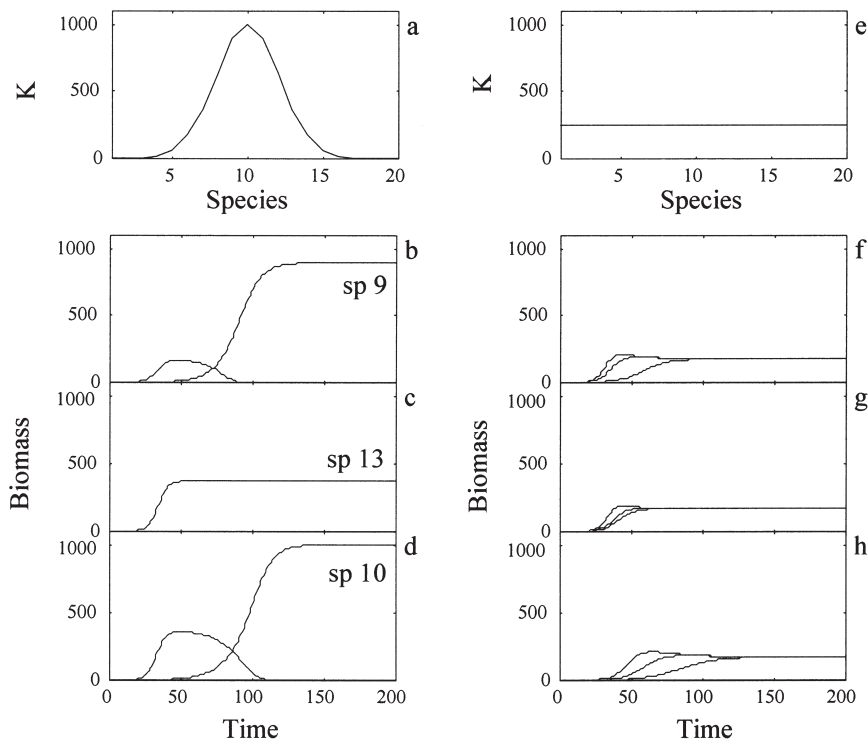


Fig. 1. The distribution of carrying capacities, K , for (a) case I where K varies among species with $\alpha = 1$, and (e) case II where K is the same for all species and $\alpha = 0.2$. The dynamics of the model (Eq. 1) are shown for the simplified scenario of initial species richness, $N_{\text{col}} = 3$ randomly chosen species in three replicate patches for case I (b–d) and case II (f–h). The identity of the species dominating the patch at equilibrium is shown for case I.

community. This is what has been referred to as the sampling effect of diversity, where initial species richness determines the probability that biomass will be dominated by a single, highly productive taxon (Aarssen 1997, Huston 1997, Wardle 1999). Thus, case I (Fig. 2a–c) illustrates how the diversity-productivity relationship might be expected to change through time when a sampling effect determines patch biomass.

Case II produced patterns similar to those of case I, with no effect of N_{col} on patch biomass in early stages of succession (Fig. 2f), but an increasingly positive effect of N_{col} on patch biomass in mid- and late succession (Fig. 2g–h). In case II there was no competitive displacement of species; all of the initial species in each patch coexisted throughout the duration of the experiment (Fig. 2i; note the 1:1 relationship between N_{col} and richness in a patch for all time periods). Although variation among species in intrinsic rates of increase, r_i , gave rise to dominance of biomass by individual species in early succession, dominance decreased in mid and late successional communities (Fig. 2j). As a result, there was little variation among different species or species combinations in late succession (contrast the lack of variation around the mean line in Fig. 2h to that around the mean in 2c). The diversity-productivity patterns for case II resulted because all α 's were less than one, implying that species used resources differently within patches. Thus, case II (Fig. 2f–h) illustrates how

the diversity-productivity relationship might be expected to change through time when species exhibit resource partitioning within a spatially homogeneous patch.

Analytical expressions

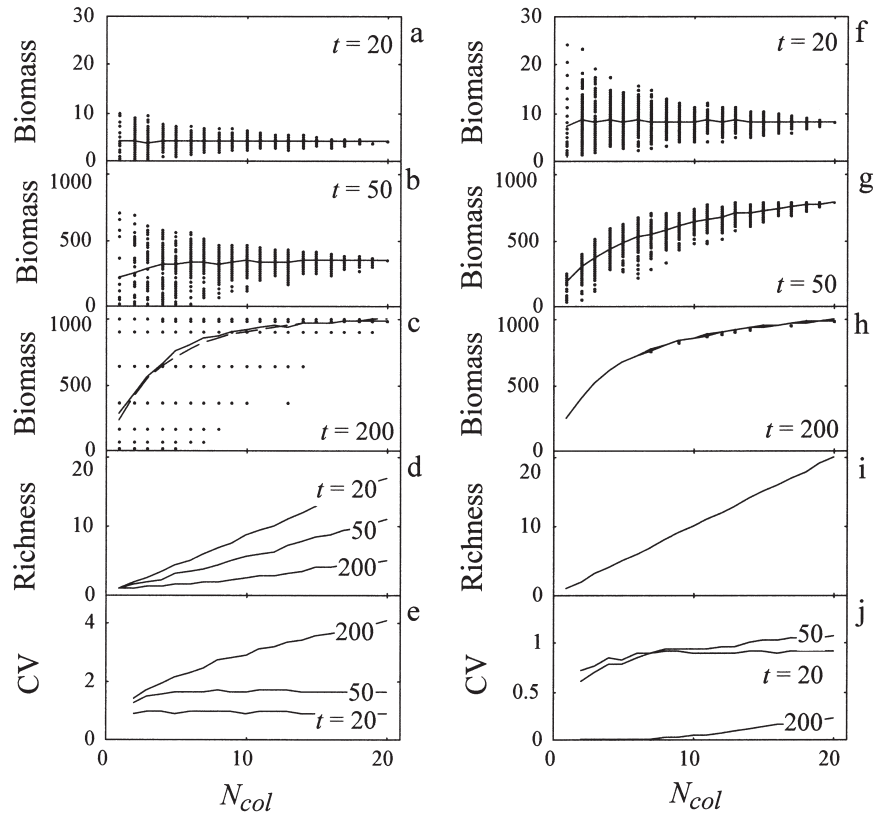
The sampling effect (case I, Fig. 2a–e) and resource partitioning (case II, Fig. 2f–j) are the most widely cited mechanisms by which species diversity influences the productivity of experimentally assembled communities (Loreau et al. 2001). Despite the operation of these different mechanisms, it is interesting to note that case I and case II produced similar mean patterns. The comparable influence of the sampling effect and resource partitioning on the diversity-productivity relationship can be seen more clearly by considering two extreme cases: when patches are sampled very early and population growth is still exponential, and when patches are sampled very late after species have reached their equilibrium biomasses.

In early stages of succession when species have exponential growth, if species i occurs in a patch, then its biomass at time t will be:

$$b_i(t) = \exp(r_i t) b_i(0) \quad (2)$$

where $b_i(0)$ is the initial biomass of species i in the patch. The contribution of species i to the total biomass in a

Fig. 2. The effect of initial species richness, N_{col} , on the production of patch biomass for communities in early ($t = 20$), mid ($t = 50$), and late stages of community succession ($t = 200$). Panels (a–c) show temporal trends from case I where species varied in carrying capacities, K , and $\alpha = 1$. Panels (f–h) are for case II where all species had the same K with $\alpha = 0.2$. Data were produced by simulations of Eq. 1 run for 100 randomly chosen species combinations; dots give the patch biomass for individual species combinations, solid lines give the mean. In panels (c) and (h) the dashed line shows values predicted by Eq. 5 and 7 – the latter is coincident with the solid line in panel (h). The mean number of species in a patch, and the coefficient of variation in biomass among species (a measure of dominance) are also shown for the three time periods for case I (d–e) and case II (i–j).



patch at time t is the probability that species i is in the patch, N_{col}/N , multiplied by $b_i(t)$. Thus, the expected total biomass in a patch at time t is

$$B(t) = \sum_{i=1}^N \frac{N_{col}}{N} b_i(t) = \frac{N_{col}}{N} \sum_{i=1}^N b_i(t) \quad (3)$$

Note that $B(t)$ is simply the mean biomass per species, $(1/N)\sum_{i=1}^N b_i(t)$, multiplied by the number of species in the initial colonist pool, N_{col} .

In our simulated experiment, each patch was initiated with the same biomass of colonists regardless of initial species richness (as with a replacement series design, Harper 1977). Thus, the initial biomass of a species in a patch, $b_i(0)$, was $B(0)/N_{col}$ where $B(0)$ was held constant across all levels of richness, N_{col} . Therefore,

$$B(t) = \frac{N_{col}}{N} \sum_{i=1}^N b_i(t) = B(0) \frac{1}{N} \sum_{i=1}^N \exp(r_i t) \quad (4)$$

From Eq. 4, it is evident that the biomass of an assemblage in early stages of succession is independent of the initial number of species in the patch, N_{col} . This is why neither case I nor case II produced a positive diversity-productivity relationship (Fig. 2a, f). Note, however, that this conclusion is not applicable to

other experimental designs. Suppose we had set up our experiment with initial biomass in a patch increasing as a function of the number of species in the colonist pool (as an ‘additive-series’ design). Then the value of $b_i(0)$ would not depend directly on the biomass of other species, and the contribution of species i to the total biomass in a patch at time t would be the probability that species i is in the patch multiplied by $b_i(t)$. The expected total biomass in a patch would then increase linearly with N_{col} as in Eq. 3. The short-term effects of diversity on productivity will, therefore, very much depend on how species biomass is initially standardized in an experiment. It follows that the effect of diversity on the productivity of natural communities in early stages of succession will depend on how the total density of colonists relates to species richness of the colonist pool.

A second feature worth noting in Eq. 4 is that, even when species are randomly sampled from a species pool having interspecific differences in growth rates, r_i , a positive diversity-productivity relationship does not necessarily occur. This contrasts with the interpretation of some experiments. Studies performed in terrestrial grasslands, for example, have found that during the first several years of an experiment, primary production is a

positive, curvilinear function of initial diversity with an upper bound in productivity equal to that of the best species monoculture (Hector et al. 1999, Tilman et al. 2002). A common explanation for this pattern is that increasing the number of species in the initial colonist pool increases the probability that the species with the highest growth rate will be included in an assemblage (Aarssen 1997, Grime 1997, Huston 1997). In our model, increasing N_{col} did increase the probability that the species with the highest r_i would be included in an assemblage. Differences in growth rates among species also led to dominance of biomass by individual taxa at the early successional stage (Fig. 2j, $t = 50$). Yet, differences in species intrinsic rates of increase did not, by themselves, generate a positive diversity-productivity relationship (Fig. 2a, f, Eq. 4). This suggests that a sampling effect only occurs when the sampled species differ in traits that influence their interactions with other species.

To illustrate why species interactions were a prerequisite for the sampling effect, consider case I (with $\alpha = 1$) at late succession when species have reached their equilibrium biomasses determined by their carrying capacities, K_i . To calculate the diversity-productivity relationship at equilibrium, let $K_{(m)}$ be the highest carrying capacity of any species in a patch (i.e. the highest value of K in Fig. 1a), $K_{(m-1)}$ be the next highest, and so on. Because competition between species is strong ($\alpha = 1$), only one species will be present in the patch at equilibrium. If this species is the one having the highest carrying capacity, then the patch biomass will be $K_{(m)}$; if it has the second highest, then the patch biomass will be $K_{(m-1)}$; etc. From this, the expected biomass in a patch is:

$$B(\infty) = \frac{N_{\text{col}}}{N} K_{(m)} + \left(1 - \frac{N_{\text{col}}}{N}\right) \left(\frac{N_{\text{col}}}{N-1}\right) K_{(m-1)} + \left(1 - \frac{N_{\text{col}}}{N}\right) \left(1 - \frac{N_{\text{col}}}{N-1}\right) \left(\frac{N_{\text{col}}}{N-2}\right) K_{(m-2)} + \dots \quad (5)$$

Eq. 5 describes the sampling effect of initial species richness. The probability that the species having $K_{(m)}$ occurs in the patch is N_{col}/N , giving the first term in Eq. 5. The probability that this species does not occur in the patch is $(1 - (N_{\text{col}}/N))$, while probability that the species with carrying capacity $K_{(m-1)}$ occurs is $(N_{\text{col}}/(N-1))$. Combining these terms, the probability that the species dominating the patch has carrying capacity $K_{(m-1)}$ is $(1 - (N_{\text{col}}/N))(N_{\text{col}}/(N-1))$, giving the second term in Eq. 5. Other terms are derived similarly for $K_{(m-2)}$, etc. Note that whenever $K_{(m-1)}$, $K_{(m-2)}$, etc. are greater than zero but are not equal (as in Fig. 1a), Eq. 5 predicts productivity will be a positive, curvilinear function of diversity (see dashed line in Fig. 2c).

Interestingly, resource partitioning within patches produces the same positive, curvilinear relationship between diversity and productivity at equilibrium as does the sampling effect. To illustrate this result, consider the case of resource partitioning within patches (case II) where all taxa had equal carrying capacities (Fig. 1e) and $\alpha < 1$. At equilibrium all species had the same biomass, $b(\infty)$, and for any patch:

$$b(\infty) + \alpha(N_{\text{col}} - 1)b(\infty) = K \quad (6)$$

From this, the total biomass in any patch was:

$$B(\infty) = \frac{N_{\text{col}}K}{1 + \alpha(N_{\text{col}} - 1)} \quad (7)$$

Eq. 7 shows that the production of biomass in a patch is a positive, curvilinear function of N_{col} whenever $0 < \alpha < 1$ (the solution for Eq. 7 is entirely coincident with the solid line in Fig. 2h for $\alpha = 0.2$). Thus, the pattern predicted by Eq. 7 is very similar to that predicted by Eq. 5, illustrating why the sampling effect and resource partitioning within patches produced similar diversity-productivity relationships at equilibrium (Fig. 2c, h). This conclusion corroborates patterns evident in similar models developed by Tilman et al. (1997) and Loreau (1998).

The spatial scale of observation

Our analyses so far have focused on the relationship between initial species richness and the production of biomass within a single type of patch. This relationship, which we call the local relationship, is the spatial scale of observation used in most diversity-productivity experiments. Natural ecosystems, however, are composed of many different patch types (Giller et al. 2004). The spatial heterogeneity that results from patchiness can be a crucial determinant of species coexistence (Paine and Levin 1981, Tilman and Kareiva 1997), and the partitioning of resources across patches is thought to be a key mechanism by which species diversity influences the primary productivity of ecosystems (Hooper 1998). Consequently, we asked “do conclusions about the diversity-productivity relationship depend on the spatial scale of observation?”

To address this question, we varied the number of species in the initial colonist pool (from $N_{\text{col}} = 1$ to 20) in ‘regions’ composed of 20 patch types (see below for a description of patch types). We again used 100 randomly selected species or species combinations in 100 identical regions. There were, therefore, 20 levels of initial species richness \times 100 randomly chosen species combinations, giving a total of 2000 experimental regions each with 20 patches.

Initial colonization of the patches was again standardized so that a biomass of $B(0)/N_{\text{col}}$ of each of the N_{col}

species was added to each patch at time $t=0$ of the experiment. Eq. 1 was modified to describe the dynamics of N_{col} species in the region of P patch types. If $b_{ip}(t)$ is the biomass of species i ($i = 1, \dots, N$) in a patch of type p ($p = 1, \dots, P$) at time t , then the dynamics of species i in the patch are given by

$$b_{ip}(t+1) = b_{ip}(t) \exp \left[r_i \left(1 - \frac{b_{ip}(t) + \alpha \sum_{j \neq i}^N b_{jp}(t)}{K_{ip}} \right) \right] \quad (8)$$

We assume as before that values of r_i are assigned so that the geometric mean for all $N=20$ taxa was 0.2 with values evenly spaced between $\log 0.2 - 0.1$ and $\log 0.2 + 0.1$.

We modeled two cases that were comparable to our prior simulations. For case I we assumed that all α 's = 1, implying that there was no resource partitioning by species within patches. For any given patch type, carrying capacities, K_{ip} , were the same as in Eq. 1, leading to strong competitive hierarchies in a patch (Fig. 1a). Among species, however, we set values of K_{ip} such that each species had a patch type for which it had the highest carrying capacity of any species (Fig. 3a). Thus, patch types were equivalent in that they had the same

distribution of K_{ip} among species, and species were equivalent in that they had the same distributions of K_{ip} among patches. For case II, we assumed that all species had the same carrying capacity for all patch types (Fig. 3d). However, $\alpha = 0.2$ so that species could coexist by partitioning resources within a patch.

At equilibrium, the mean relationship between N_{col} and biomass production for the entire region was very similar for case I and II, with both scenarios producing the same positive, and strongly curvilinear relationship (solid lines, Fig. 3b, e). The mean regional relationships were identical to the local relationships, differing only by a constant multiple (compare trend lines in 3b to 3c, and 3e to 3f). This is expected given that biomass in each patch still resulted from local processes of growth and interactions; thus, the production of biomass in a region was simply the summed biomass in all patch types. These results illustrate that spatial scale per se had no fundamental impact on mean values of the diversity-productivity relationship, which is important because it shows that the dynamics of the model did not change between the local and regional scales of observation. It is, therefore, interesting to note that in case I (Fig. 3a–c) the mechanism producing a positive diversity-productivity relationship changed between scales of observation.

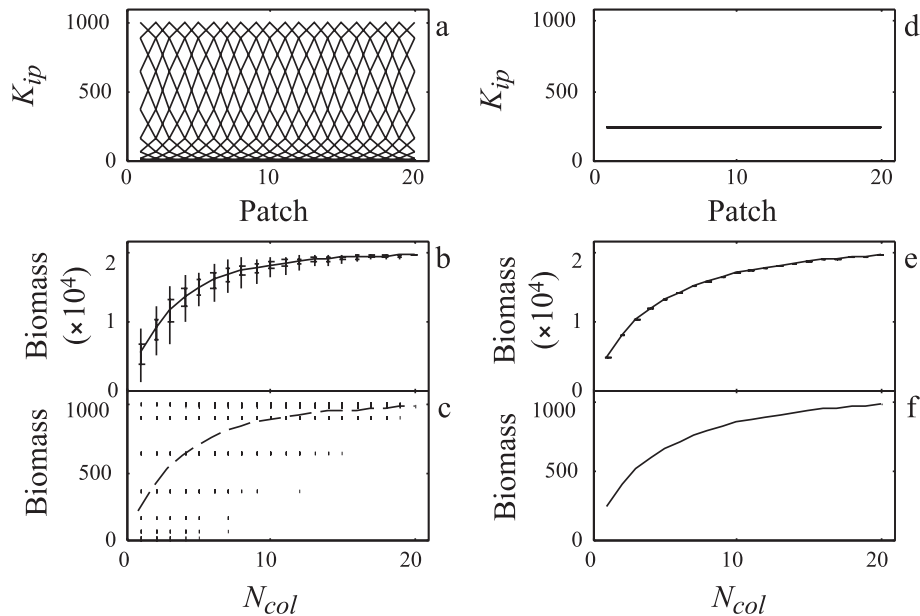


Fig. 3. The local vs regional relationship between the number of species in the colonist pool, N_{col} , and biomass at equilibrium. The distributions of K_{ip} for species i on patch p are shown for case I (a) where carrying capacities vary among species and $\alpha = 1$, and case II (d) where all species have the same carrying capacity and $\alpha = 0.2$. In panel (a) each line corresponds to a different species i . Panels (b) and (e) are the regional diversity-productivity relationships showing the summed biomass over all 20 patches of types $p = 1, \dots, 20$ as a function of N_{col} . Bars are standard deviations, vertical lines indicate the minimum and maximum values for 100 randomly chosen species combinations. Panels (c) and (f) show the local diversity-productivity relationship, which is the same for all patch types. Individual data points are the biomass of various species combinations, lines show the mean. The dashed line in panel (c) gives the biomass predicted from Eq. 5, and the line in panel (f) gives the biomass that coincides with that predicted by Eq. 7. Note in panels (e) and (f) there is almost no variation among species combinations.

At the local scale, a positive relationship resulted from sampling effects such that, in any given patch, productivity at equilibrium was dominated by the species having the K_{ip} most closely matched to $K_{(m)}$ (Fig. 3c, Eq. 5). At the regional scale, however, resource partitioning occurred across patches because the distribution of K_{ip} 's allowed different patches to dominate different patch types (Fig. 3a).

The similarity of the mean relationship at the local and regional scales of observation in case I (Fig. 3a–c), in spite of differing mechanisms, can be understood by further analysis of Eq. 5. We previously used Eq. 5 to describe how a sampling effect occurs within a patch, but the equation can also be used to describe how regional productivity changes with N_{col} when species partition resources across patch types. Note that when resource partitioning across patch types is great – for example, when species specialize on individual patch types – $K_{(m-1)}$ approaches zero and the mean biomass in a region increases linearly with number of species in the regional colonist pool (since mean total biomass = $(N_{col}/N)K_{(m)}$; Fig. 4a top line). If, however, $K_{(m-1)}$, $K_{(m-2)}$

etc. are greater than zero but not equal, then productivity is a positive, curvilinear function of diversity (Fig. 4a middle line). In the case where species are habitat generalists, the positive relationship disappears altogether (Fig. 4a bottom line). Thus, Eq. 5 shows that the sampling effect within patches and resource partitioning across patches can be manifestations of the same process operating at differing scales of resolution. Obviously, our assumption that the distributions of K_{ip} 's were the same for all patch types (Fig. 3a) served to highlight this conclusion. Nonetheless, the results are relevant whenever species have carrying capacities that are high in some patches and low in others.

Case I and II produced the same diversity-productivity relationship at the regional spatial scale (Fig. 3b, e) despite the fact that species were assumed to partition resources differently in the two cases. In case I, species coexisted by partitioning resources across patch types (paragraph above; Fig. 3a), whereas in case II (Fig. 3d) we assumed species coexisted by partitioning resources locally within a patch type ($\alpha < 1$). The similarity of these two modes of coexistence is evident from a

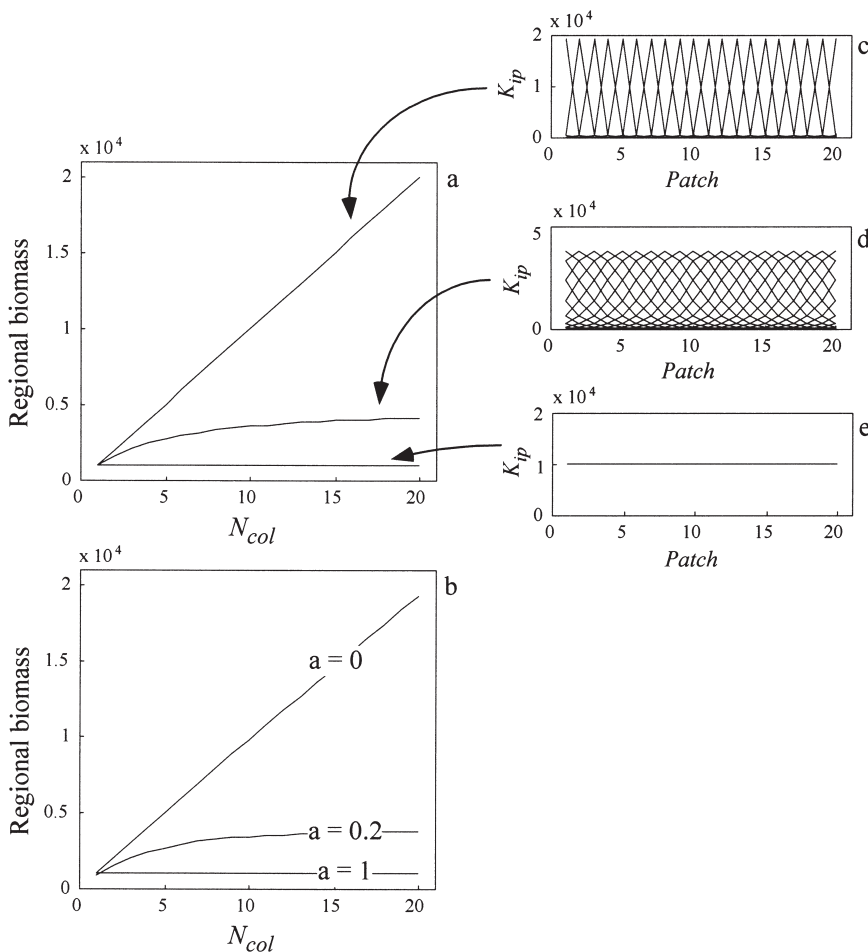


Fig. 4. Regional biomass vs initial species richness, N_{col} , for (a) resource partitioning among patch types (case I, Eq. 5) and (b) resource partitioning within patches (case II, Eq. 7). Panels (c–e) illustrate the distributions of species carrying capacities among patch types for case I. No overlap in K_{ip} (c) indicates that species specialize on patches while complete overlap (e) indicates generalization with no resource partitioning across patches. In panel (b), the degree of within-patch resource partitioning is given by values of α . In all cases, the values of K_{ip} were selected such that when there was only a single species ($N_{col} = 1$) the regional biomass was 1000. This differs from the simulations in Fig. 3 where values of K_{ip} were set so that the maximum patch biomass was 1000 when $N_{col} = 20$.

comparison of Eq. 5, which predicts trends for resource partitioning across patch types (Fig. 4a), to those of Eq. 7, which predicts trends for partitioning within patch types (Fig. 4b). When species exhibit no overlap in resource use (e.g. either complete partitioning of patch types or $\alpha = 0$), both equations predict that production of biomass at the regional scale will increase linearly with richness of the regional colonist pool. When species exhibit partial overlap of resource use (either partial partitioning of patch types or $0 < \alpha < 1$), regional production is expected to be a curvilinear function of N_{col} . When there is complete overlap in resource use (no partitioning of patch types or $\alpha = 1$), productivity is independent of N_{col} . This comparison shows that, while the magnitude and curvilinearity of the diversity-productivity relationship clearly depend on the degree of resource partitioning, the mean values of the diversity-productivity relationship are similar irrespective of whether resource partitioning occurs among or within patches.

Adding regional processes

All of our discussion so far has addressed communities that are isolated from the regional processes of dispersal and disturbance. Dispersal and patchily distributed disturbances can have a major influence on the persistence, distribution, and productivity of species (Paine and Levin 1981, Pickett and White 1985, Hanski 1989, Petraitis et al. 1989, Hastings 1991). Given this, we asked “does the diversity-productivity relationship change when local processes are augmented by regional processes?”

To examine the role of regional processes on the diversity-productivity relationship, we modified our model to incorporate disturbances that lead to extinction of all species from a patch, with subsequent recolonization from a pool of propagules that disperse among patches in a region. Although some natural systems experience such severe conditions (Pickett and White 1985), we adopted these assumptions only because they allowed us to evaluate the more extreme effects of regional processes on the diversity-productivity relationship. Here we consider only case I (i.e. those depicted in Fig. 3a) because we have already demonstrated in the last section that cases I and II produce similar results.

We modified Eq. 8 to include W replicate patches of each of the P types, and incorporated colonization to give

$$b_{ipw}(t+1) = b_{ipw}(t) \exp \left[r_i \left(1 - \frac{b_{ipw}(t) + \alpha \sum_{j \neq i}^N b_{jpw}(t)}{K_{ip}} \right) \right] + Q[cg_i(t)] \quad (9)$$

where $Q[cg_i(t)]$ is a random variable giving the number of colonists arriving to a patch between times t and $t+1$. We assumed that $Q[cg_i(t)]$ is Poisson distributed with a colonization rate equal to $cg_i(t)$, where $g_i(t)$ is the abundance of species i in the propagule pool at time t , and c is the per capita propagule colonization rate. While we treated the biomass of initial colonists as a continuous variable in previous sections of this paper, here we model colonization by individuals; thus, random colonization events determine which species occur in a given patch. For simplicity, we assumed that propagules are small so that their release into the propagule pool represents a negligible change in patch biomass. The number of propagules of each species i colonizing a patch at time t was converted into biomass assuming each propagule had a biomass of 1 ($0.001 \times$ the carrying capacity).

At each time step, species in a patch produce propagules that enter the regional propagule pool, with the dynamics of the pool governed by

$$g_i(t+1) = sg_i(t) + m \sum_{p=1}^P \sum_{w=1}^W b_{ipw}(t+1) \quad (10)$$

where s is the proportion of propagules surviving in the pool between time steps, and m is the per capita production of propagules by each species. We assumed that propagule production was proportional to the biomass of species i across all patches, and that propagule survival and per capita production were the same for all species. To impose disturbance on patches, we established a fixed probability, d , that any patch would be cleared of all biomass at a given time step. Disturbances affected patches independently, which created asynchrony in the temporal dynamic of patches leading to a spatial ‘mosaic’ of patches in differing stages of succession. By iterating the equations over 1500 time steps and eliminating the first 500 iterations to remove transient dynamics, a stochastic distribution was generated to give the average, long-term abundances of species among patches.

We modeled two ecological scenarios that contrast the relative importance of disturbance, colonization, and population growth rates. In the first scenario, disturbance rates were low ($d = 0.005$) allowing most patches to reach late stages of succession. In the second scenario, disturbance rates were relatively high ($d = 0.05$), forcing most patches to stay in early stages of succession. To standardize the colonization probabilities between these two disturbance scenarios, we selected values for the per capita propagule colonization rate, c , such that when $N_{col} = 1$, regions with both low and high disturbance rates had the same average colonization probabilities of 0.1. Without this standardization, either all species go extinct in the high-disturbance scenario, or all patches are instantaneously colonized by all species in the low-disturbance scenario. The standardization has no direct

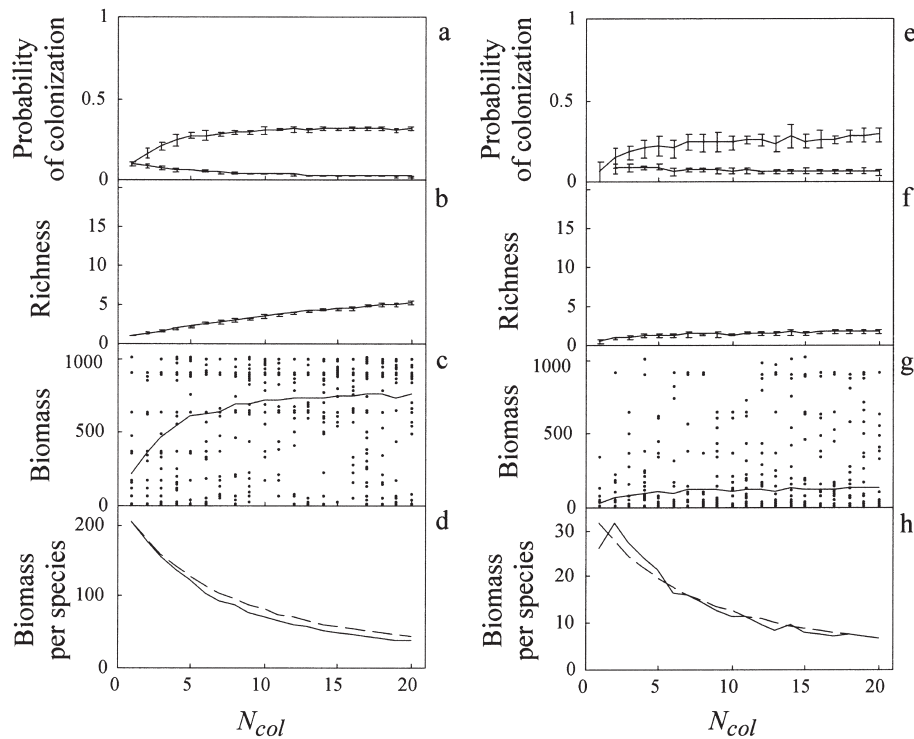


Fig. 5. Results of stochastic simulations for systems containing 20 patch types ($P = 20$) and 5 patches of each type ($W = 5$) subjected to low (a–d) and high (e–h) disturbance rates. For each value of species richness in the regional colonist pool, N_{col} , simulations were repeated for 10 randomly chosen species combinations. Panels (a) and (e) give the probability of patch colonization per unit time by any species (top line) and the probability of colonization per species (bottom line). Panels (b) and (f) give the number of species per patch for the 10 different species combinations. Data are means ± 1 SD. Solid lines in panels (c) and (g) give the mean biomass in a patch with dots showing biomass in individual patches. Panels (d) and (h) show the mean biomass per species as a function of N_{col} (solid lines). Dashed lines show the predicted decline in mean biomass due to competitive interactions (Eq. 5). The probabilities of patch disturbance were $d = 0.005$ and $d = 0.05$ for low and high disturbance frequencies, respectively. Values of per capita propagule colonization rates, c , were 11.5 and 2.5 for the high and low disturbance scenarios, respectively. Other parameter values were $s = 0.5$ and $m = 10^{-6}$.

effect on how regional biomass changes with N_{col} , so it does not influence conclusions about the diversity-productivity relationship.

In the low-disturbance scenario, the probability that a given species would colonize a patch per time step was low (Fig. 5a bottom line), and the probability that a patch would be colonized by any species increased from 0.1 (set for the case of $N_{col} = 1$) to roughly 0.3 when N_{col} was equal to 20 (Fig. 5a top line). The average number of species coexisting in a patch increased with the number of species in regional colonist pool, reaching roughly five when $N_{col} = 20$ (Fig. 5b). At any given time, the biomass in a patch ranged from zero to 1000 (individual data points in Fig. 5c), illustrating the spatial mosaic of patches in various stages of succession. Despite this variation, the average patch biomass increased from roughly 250 at $N_{col} = 1$ to a plateau of 750 per patch (Fig. 5c). This 3-fold increase in patch biomass with increasing N_{col} paralleled the 3-fold increase in the probability of patch colonization (Fig. 5a) because the production of propagules was directly proportional to

the total biomass of species in a region. The diversity-productivity relationship produced here, with local and regional processes coupled (Fig. 5c), was very similar to that observed in late successional patches where only local processes operated (Fig. 2c and 3c). This similarity is expected given that low disturbance rates allowed the majority of patches to reach mid- to late-stages of succession such that local competitive interactions largely determined patch biomass.

In the high-disturbance scenario, the probability that a patch would be colonized per time step also increased with increasing N_{col} (Fig. 5e, top line). In contrast to the low-disturbance scenario, however, there was a much smaller increase in the number of species coexisting in a patch (Fig. 5f) because the frequent disturbances did not allow enough time for species to colonize. Although patches in the high-disturbance scenario occasionally persisted long enough to reach high biomasses (individual data points in Fig. 5g), the majority of patches were held in early stages of succession with low total biomass (Fig. 5g solid line). In spite of this outcome, there was

roughly a 3-fold increase in the production of biomass with increasing N_{col} (from roughly 35 at $N_{\text{col}} = 1$ to a plateau of 105). This trend is noteworthy for two reasons. First, it contrasts with our prior simulations that showed local processes alone do not generate a positive relationship between N_{col} and the biomass of patches in early stages of succession (Fig. 2a, f, Eq. 4). The reason that diversity had a positive effect on productivity here is because, when local and regional processes were coupled, there was a positive feedback loop between the local production of biomass and the size of the regional propagule pool. The more species there were in the region, the more propagules were released into the regional pool. More propagules meant a greater probability of patch colonization, which ensured greater patch biomass, and therefore more propagule production.

The second point worth noting is that the 3-fold increase in productivity with N_{col} in the high-disturbance scenario (Fig. 5g) was the same proportional increase found in the low-disturbance scenario (Fig. 5c). This might, at first, seem surprising since (1) trends in the low disturbance scenario were largely driven by local competitive interactions (above), but (2) frequent disturbances that hold patches in early stages of succession might be expected to reduce the strength of competition. It is true that disturbance reduced the absolute magnitude of competitive interactions. This is evident in Fig. 5d and 5h, which show the average biomass of a species as a function of N_{col} . The declines in the average biomass of a species with increasing N_{col} (solid lines) were due to competitive interactions among species predicted by Eq. 5 (dashed lines). However, while the absolute magnitude of the decrease in biomass was less in the high-disturbance than low-disturbance scenario (compare y-axis scales in Fig. 5d, h), the proportional change in the biomass of a species was quite similar between the two scenarios. This is because species were more sensitive to competition when the disturbance rate was high (for the same reasons described by Chesson and Huntly 1997) and, as a result, weak competition within patches still had a large impact on the regional production of propagules. The net result was that the diversity-productivity relationship for the high-disturbance scenario depended on local competitive interactions in much the same way as described for the low-disturbance scenario.

The results above suggest that species diversity could play as important a role in frequently disturbed systems where communities are structured by processes of colonization as it does in less frequently disturbed systems where local species interactions are strongest. This finding contrasts with several recent studies having shown that disturbance can alter the diversity-productivity relationship by changing the strength of species interactions (Cardinale et al. 2000, Dukes 2001, Mulder

et al. 2001, Cardinale and Palmer 2002). To understand whether the results of these empirical studies apply at scales where regional processes operate, the key question that needs to be addressed is "how does regional species richness affect processes of colonization?" If richness has a positive effect on the probability of colonization, then our model predicts colonization processes will lead to a positive effect of diversity on productivity in systems disturbed frequently enough that dispersal dictates community structure. This result is not readily anticipated from experiments addressing local processes only.

Conclusions and implications

Our models lead us to a series of qualitative conclusions about how explicit consideration of spatial and temporal scales might influence our views of the functional consequences of biodiversity loss. These conclusions are not intended to explain patterns and processes observed in any particular natural ecosystem or experiment; they may, however, be useful for focusing questions and stimulating hypotheses that guide future research.

(1) *The duration of an experiment was a primary determinant of the effect of diversity on primary productivity.* We found that for the commonly used replacement-series experimental design, the production of biomass was independent of initial species richness in early successional communities (Fig. 2a, f). However, as communities were allowed to proceed into later stages of succession, productivity in a patch became an increasingly positive, curvilinear function of initial species richness (Fig. 2). When species exhibited a competitive hierarchy, a positive effect of diversity on productivity resulted from the sampling effect. In our model, an increasing probability that a species having the highest growth rate would dominate biomass was not sufficient to generate a sampling effect (Fig. 2). Rather, a positive diversity-productivity relationship only resulted when the sampled species differed in traits that had an influence on how resources were used under competitive conditions (Fig. 2c, Eq. 5). This suggests that positive diversity-productivity relationships documented in the early stages of prior experimental studies (Hector et al. 1999, Tilman et al. 2001) may have resulted from more than just interspecific differences in maximal growth rates, as has been proposed (Grime 1997, Huston 1997, Tilman et al. 2002).

We also found that resource partitioning within patches led to temporal changes in the diversity-productivity relationship quite similar to those resulting from sampling effects (Fig. 2). We confirmed analytically that both mechanisms converge to similar diversity-productivity relationships as communities approach late stages of succession and species reach equilibrium biomasses

(Eq. 5, 7). Collectively, these results suggest that temporal trends now being documented as empirical studies progress reflect more than just “a temporal transition from growth-rate-driven sampling effects to niche differentiation [that results from] the transient dynamics of competition” (Tilman et al. 2002). Rather, our model suggests the effects of diversity on productivity will grow stronger through successional time regardless of the underlying mechanism.

(2) *The form of the diversity-productivity relationship was independent of spatial scale, but the mechanism generating the relationship differed between scales of observation.* When local processes regulated species biomasses, increasing species richness in a regional colonist pool led to the same positive, curvilinear increase in biomass in individual patch types as it did in a region composed of many patch types (Fig. 3). Moreover, the diversity-productivity relationship was similar irrespective of whether species coexisted by local partitioning of resources in a set of spatially homogeneous patches, or whether they coexisted regionally by partitioning resources across different patch types (Fig. 4). These results suggest that the mean values of the diversity-productivity relationship (that is, the average across all possible species combinations) are insensitive to spatial scale. Note, however, that we were able to examine the diversity-productivity relationship in all patch types comprising a region; thus, “scaling-up” in our model did not lead to the incorporation of totally new habitat types. In any natural system, increases in spatial scale will certainly be coupled with the addition of new habitats that increase overall spatial heterogeneity. However, our focus on spatial scale per se is useful because it demonstrates that if experiments were conducted across the range of heterogeneity relevant for species coexistence, then small-scale experiments could provide qualitatively robust insight into the regional consequences of species loss for communities structured by local processes. This may not be so unrealistic given that many groups of organisms are thought to coexist because small-scale heterogeneity mediates interactions between immediate neighbors (Dayton 1971, Schoener 1983, Paine 1984, Tilman 1994, Connolly et al. 2000).

Our model further suggests that at a regional scale of observation, primary production is less sensitive to the regional composition of species (i.e. what species actually occur) than is productivity in any given patch type. Sampling effects that occur within individual patches produce considerable variation among different species or species combinations, but resource partitioning that occurs across patch types results in diversity explaining a greater fraction of total variation in regional productivity (for example, compare the variation in Fig. 3b, c). This result suggests that while the most productive species could maximize productivity at local spatial scales, no single species is likely to maximize productivity

at larger spatial scales. It also supports the expectation that different mechanisms will operate simultaneously to influence the diversity-productivity relationship at varying scales of observation (Loreau et al. 2001, Chesson et al. 2002, Mouquet et al. 2002). In fact, in our models, the sampling effect and resource partitioning simply represented the same biological processes operating at two different spatial scales of resolution.

(3) *Adding regional processes of dispersal and disturbance to the model did alter conclusions about the effect of diversity on productivity.* When we held disturbance rates low relative to the probability of colonization, the diversity-productivity relationship was similar to that already demonstrated for late successional communities regulated solely by local processes (compare Fig. 2c, 5c). This is because low rates of disturbance allowed for sufficient time to elapse that species could colonize a patch and grow to their carrying capacities; therefore, biomass in the average patch was primarily determined by local species interactions.

In contrast, when rates of disturbance were high, the coupling of local and regional processes produced a positive diversity-productivity relationship that did not occur when local processes acted alone (compare Fig. 2a–5g). This was because the probability of a patch being colonized, and thus the short-term production of biomass between disturbance events, was a function of the number species in the regional colonist pool. The contrast between models considering only local processes and those coupling local and regional processes has important implications for the interpretation of previous empirical studies. Most diversity-productivity experiments have focused on communities isolated from regional processes of dispersal and disturbance, and have imposed colonization experimentally (Loreau et al. 2001, Schmid et al. 2001). Our model suggests that the results of these experiments may have limited ability to predict the consequences of species loss in natural ecosystems where recruitment to disturbed sites is a function of regional diversity, and where community structure is limited by recruitment from the regional colonist pool.

There is growing recognition that the biomass of species in many ecosystems is influenced more by recruitment than by local species interactions (Townsend 1989, Underwood and Fairweather 1989, Sutherland 1990, Palmer et al. 1996, Lawton 1999, Srivastava 1999, Symstad and Tilman 2001). The relative impacts of local versus regional processes on community structure are also thought to differ among ecosystems (Ricklefs 1987, Hubbell 2001, Giller et al. 2004). Therefore, to understand differences in the diversity-productivity relationship between ecosystems, future research needs to address the effect of regional species richness on rates of colonization (a regional process) as well as the effect of richness on growth and species interactions in individual patches (local processes). In the meantime,

some caution may be warranted in extrapolating conclusions from past experimental studies to other systems, or to the regional scales at which disturbance and dispersal often allow natural communities to persist.

Acknowledgements – This work was motivated by discussions with our colleagues at the International Workshop on Aquatic Biodiversity and Ecosystem Functioning held in Ascona, Switzerland, in April, 2002. Generous support for the conference was provided by the European Science Foundation (LINKECOL/61), DIVERSITAS, the Swiss National Science Foundation (3101-067069.01/1), the Swiss Federal Institute for Environmental Science and Technology (EAWAG), and the U.S. National Science Foundation (NSF; DEB 0217338). Additional support was provided by NSF grants IBN 0104768 to BJC, and DEB 0108300 to ARI. We are indebted to Kevin Gross, Chad Harvey, Andy Forbes and Mark Gessner for comments that helped improve this manuscript.

References

- Aarssen, L. W. 1997. High productivity in grassland ecosystems: effected by species diversity or productive species? – *Oikos* 80: 183–184.
- Belyea, L. R. and Lancaster, J. 1999. Assembly rules within a contingent ecology. – *Oikos* 86: 402–416.
- Bengtsson, J., Engelhardt, K., Giller, P. et al. 2002. Slippin' and slidin' between the scales: the scaling components of biodiversity-ecosystem functioning relations. – In: Loreau, M., Naeem, S. and Inchausti, P. (eds), *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford Univ. Press, pp. 209–220.
- Cardinale, B. J. and Palmer, M. A. 2002. Disturbance moderates biodiversity-ecosystem function relationships: Experimental evidence from caddisflies in stream mesocosms. – *Ecology* 83: 1915–1927.
- Cardinale, B. J., Nelson, K. and Palmer, M. A. 2000. Linking species diversity to the functioning of ecosystems: on the importance of environmental context. – *Oikos* 91: 175–183.
- Cardinale, B. J., Palmer, M. A. and Collins, S. L. 2002. Species diversity increases ecosystem functioning through interspecific facilitation. – *Nature* 415: 426–429.
- Case, T. J. and Diamond, J. M. 1986. *Community ecology*. – Harper and Row.
- Caswell, H. and Cohen, J. E. 1991. Disturbance, interspecific interaction and diversity in metapopulations. – *Biol. J. Linn. Soc.* 42: 193–218.
- Chapin, F. S. III, Zavaleta, E. S., Eviners, V. T. et al. 2000. Consequences of changing biodiversity. – *Nature* 405: 234–242.
- Chesson, P. and Huntly, N. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. – *Am. Nat.* 150: 519–553.
- Chesson, P., Pacala, S. and Neuhauser, C. 2002. Environmental niches and ecosystem functioning. – In: Kinzig, A. P., Pacala, S. and Tilman, D. (eds), *The functional consequences of biodiversity: empirical progress and theoretical extensions*. Princeton Univ. Press, pp. 213–245.
- Connolly, J., Wayne, P. and Bazzaz, F. 2000. Interspecific competition in plants: how well do current methods answer fundamental questions? – *Am. Nat.* 157: 107–125.
- Dayton, P. K. 1971. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. – *Ecol. Monogr.* 41: 351–389.
- Diamond, J. M. 1975. Assembly of species communities. – In: Cody, M. L. and Diamond, J. M. (eds), *Ecology and evolution of communities*. Harvard Univ. Press, pp. 342–444.
- Drake, J. A. 1990. Communities as assembled structures: do rules govern pattern? – *Trends Ecol. Evol.* 5: 159–164.
- Dukes, J. S. 2001. Productivity and complementarity in grassland microcosms of varying diversity. – *Oikos* 94: 468–480.
- Fridley, J. D. 2002. Resource availability dominates and alters the relationship between species diversity and ecosystem productivity in experimental plant communities. – *Oecologia* 132: 271–277.
- Giller, P., Hillebrand, H., Berninger, U. G. et al. 2004. Biodiversity effects on ecosystem functioning: emerging issues and their experimental test in aquatic environments. – *Oikos* 104: 423–436.
- Grime, J. 1997. Biodiversity and ecosystem function: the debate deepens. – *Science* 277: 1260–1261.
- Hanski, I. 1989. Metapopulation dynamics: does it help to have more of the same? – *Trends Ecol. Evol.* 4: 113–114.
- Harper, J. 1977. *Population biology of plants*. – Academic Press.
- Hastings, A. 1991. Structured models of metapopulation dynamics. – *Biol. J. Linn. Soc.* 42: 57–71.
- Hector, A., Schmid, B., Beierkuhnlein, C. et al. 1999. Plant diversity and productivity experiments in European grasslands. – *Science* 286: 1123–1127.
- Holt, R. D. and Loreau, M. 2002. Biodiversity and ecosystem functioning: the role of trophic interactions and the importance of system openness. – In: Kinzig, A. P., Pacala, S. and Tilman, D. (eds), *The functional consequences of biodiversity: empirical progress and theoretical extensions*. Princeton Univ. Press, pp. 246–262.
- Hooper, D. 1998. The role of complementarity and competition in ecosystem responses to variation in plant diversity. – *Ecology* 79: 704–719.
- Hubbell, S. 2001. *The unified neutral theory of biodiversity and biogeography*. – Princeton Univ. Press.
- Huston, M. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. – *Oecologia* 110: 449–460.
- Johnson, K. H., Vogt, K. A., Clark, H. J. et al. 1996. Biodiversity and the productivity and stability of ecosystems. – *Trends Ecol. Evol.* 11: 372–377.
- Lawton, J. H. 1999. Are there general laws in ecology? – *Oikos* 84: 177–192.
- Loreau, M. 1998. Biodiversity and ecosystem functioning: a mechanistic model. – *Proc. Natl Acad. Sci. USA.* 95: 5632–5636.
- Loreau, M., Naeem, S., Inchausti, P. et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. – *Science* 294: 804–808.
- Mouquet, N., Moore, J. L. and Loreau, M. 2002. Plant species richness and community productivity: why the mechanism that promotes coexistence matters. – *Ecol. Lett.* 5: 56–65.
- Mulder, C. P. H., Uliassi, D. D. and Doak, D. F. 2001. Physical stress and diversity-productivity relationships: the role of positive interactions. – *Proc. Natl Acad. Sci. USA.* 98: 6704–6708.
- Naeem, S. 2002. Ecosystem consequences of biodiversity loss: the evolution of a paradigm. – *Ecology* 83: 1537–1552.
- Naeem, S., Thompson, L. J., Lawler, S. P. et al. 1994. Declining biodiversity can alter the performance of ecosystems. – *Nature* 368: 734–737.
- Paine, R. 1984. Ecological determinism in the competition for space. – *Ecology* 65: 1339–1348.
- Paine, R. and Levin, S. 1981. Intertidal landscapes: disturbance and the dynamics of patterns. – *Ecology* 62: 145–178.
- Palmer, M. A., Allan, J. D. and Butman, C. A. 1996. Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. – *Trends Ecol. Evol.* 11: 322–326.
- Petraitis, P., Latham, R. and Niesenbaum, R. 1989. The maintenance of species diversity by disturbance. – *Q. Rev. Biol.* 64: 393–418.
- Pickett, S. and White, P. (eds). 1985. *The ecology of natural disturbance and patch dynamics*. – Academic Press.

- Pimm, S. I., Russell, G. J., Gittleman, J. L. et al. 1995. The future of biodiversity. – *Science* 269: 347–350.
- Ricklefs, R. 1987. Community diversity: relative roles of local and regional processes. – *Science* 235: 176–181.
- Rosenzweig, M. L. 1999. Ecology – heeding the warning in biodiversity's basic law. – *Science* 284: 276–277.
- Sala, O. E., III, F. S. C., Armesto, J. J., Berlow, E. et al. 2000. Global biodiversity scenarios for the year 2100. – *Science* 287: 1170–1174.
- Schmid, B., Joshi, J. and Schlöpfer, F. 2001. Empirical evidence for biodiversity-ecosystem functioning relationships. – In: Kinzig, A., Pacala, S. and Tilman, D. (eds), *The functional consequences of biodiversity: empirical progress and theoretical extensions*. Princeton Univ. Press, pp. 120–150.
- Schoener, T. 1983. Field experiments on interspecific competition. – *Am. Nat.* 122: 240–283.
- Schwartz, M. W., Brigham, C. A., Hoeksema, J. D. et al. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. – *Oecologia* 122: 297–305.
- Srivastava, D. S. 1999. Using local-regional richness plots to test for species saturation: pitfalls and potentials. – *J. Anim. Ecol.* 68: 1–16.
- Sutherland, J. 1990. Recruitment regulates demographic variation in a tropical intertidal barnacle. – *Ecology* 71: 955–972.
- Symstad, A. J. and Tilman, D. 2001. Diversity loss, recruitment limitation, and ecosystem functioning: lessons learned from a removal experiment. – *Oikos* 92: 424–435.
- Symstad, A. J., Chapin, F. S. III, Wall, D. H. et al. 2003. Long-term and large-scale perspectives on the relationship between biodiversity and ecosystem functioning. – *BioScience* 53: 89–98.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. – *Ecology* 75: 2–16.
- Tilman, D. and Kareiva, P. (eds). 1997. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. – Princeton Univ. Press.
- Tilman, D., Wedin, D. and Knops, J. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. – *Nature* 379: 718–720.
- Tilman, D., Lehman, D. and Thompson, K. 1997. Plant diversity and ecosystem productivity: theoretical considerations. – *Proc. Natl Acad. Sci.* 94: 1857–1861.
- Tilman, D., Reich, P. B., Knops, J. et al. 2001. Diversity and productivity in a long-term grassland experiment. – *Science* 294: 843–845.
- Tilman, D., Knops, J., Wedin, D. et al. 2002. Experimental and observational studies of diversity, productivity, and stability. – In: Kinzig, A. P., Pacala, S. and Tilman, D. (eds), *The functional consequences of biodiversity: empirical progress and theoretical extensions*. Princeton Univ. Press, pp. 42–70.
- Townsend, C. R. 1989. The patch dynamics concept of stream community ecology. – *J. N. Am. Benthol. Soc.* 8: 36–50.
- Underwood, A. J. and Fairweather, P. G. 1989. Supply-side ecology and benthic marine assemblages. – *Trends Ecol. Evol.* 4: 16–20.
- Vitousek, P., Mooney, H., Lubchenco, J. et al. 1997. Human domination of Earth's ecosystems. – *Science* 277: 494–499.
- Waide, R. B., Willig, M. R., Steiner, C. F. et al. 1999. The relationship between productivity and species richness. – *Annu. Rev. Ecol. Syst.* 30: 257–300.
- Wardle, D. A. 1999. Is “sampling effect” a problem for experiments investigating biodiversity-ecosystem function relationships? – *Oikos* 87: 403–410.