

## Linking species diversity to the functioning of ecosystems: on the importance of environmental context

Brad J. Cardinale, Karen Nelson and Margaret A. Palmer

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.

There is currently much interest in understanding how loss of biodiversity might alter ecological processes vital to the *functioning* of ecosystems. Unfortunately, ecologists have reached little consensus regarding the importance of species diversity to *ecosystem functioning* because empirical studies have not demonstrated any consistent relationship between the number of species in a system and the rates of ecological processes. We present the results of a simple model that suggests there may be no single, generalizable relationship between species diversity and the productivity of an ecosystem because the relative contributions of species to productivity change with environmental context. The model determined productivity for landscapes varying in species diversity (the number of species in the colonist pool), spatial heterogeneity (the number of habitat types composing the landscape), and disturbance regimes (+/– a non-selective mortality). Linear regressions were used to relate species diversity and productivity for each of the environmental contexts. Disturbance changed the form of the diversity/productivity relationship by reducing the slope (i.e. the change in productivity per species added to the colonist pool), but spatial heterogeneity increased or decreased this slope depending on the particular habitat types composing the landscape. The cause of the diversity/productivity relationship also changed with environmental context. The amount of variation in productivity explained by species diversity always increased with spatial heterogeneity, while the amount of variation explained by species composition (i.e. the particular species composing the colonist pool) tended to increase with disturbance. These results lead us to conclude that the form and cause of the relationship between species diversity and productivity may be highly dynamic-changing over both time and space. Because the trends resulted from well-known mechanisms by which environmental variation alters the absolute and relative abundances of taxa, we suspect this conclusion may be applicable to many different systems.

*B. J. Cardinale, K. Nelson and M. A. Palmer, Dept of Biology, Univ. of Maryland, College Park, MD 20742, USA (bc84@umail.umd.edu).*

With the rate of species extinction rapidly increasing, there has been growing interest in determining how the loss of biodiversity might alter the rates of ecological processes that are vital to the functioning of ecosystems (e.g. productivity, decomposition, elemental cycling, etc.). Several studies have provided clear evidence that biological communities do indeed regulate ecological processes (Naeem et al. 1994, Tilman et al. 1996, 1997a, Hooper and Vitousek 1997, McGrady-Steed et al. 1997,

Wardle et al. 1997a, Symstad et al. 1998 and others), but these studies have often reached very different conclusions about the contribution that species diversity itself makes to ecosystem functioning. Disparate conclusions have fueled a long-standing debate focused on two fundamental questions: 1) What is the general *form* of the relationship between species diversity and ecosystem functioning, and 2) What *causes* the relationship – the number of species or the particular types of species?

---

Accepted 24 March 2000

Copyright © OIKOS 2000

ISSN 0030-1299

Printed in Ireland – all rights reserved

In this paper, we do not address the controversy over whether biodiversity governs the temporal stability of ecological processes, but instead focus on how species diversity influences the rate of a process at any point in time. Therefore, by form of the relationship between diversity and function we mean the direction and magnitude of the *slope* relating the number of species in a system to the rate of an ecological process. This form has varied greatly between different groups of organisms as well as between different systems that have been studied. A recent review by Johnson et al. (1996) emphasized the incongruity among empirical studies that have found positive, negative, or even no relationship at all between the number of species in a system and primary productivity – an ecosystem function of widespread interest. Even when studies have agreed on the direction of the diversity/productivity relationship, there has been considerable variation in the magnitude of change in productivity over levels of species diversity.

In addition to there being no consensus over the form of the diversity/function relationship, the cause of the relationship has been a topic of much debate (Aarssen 1997, Grime 1997, Huston 1997, Tilman 1997). The debate has generally focussed on the relative importance of two possible causes – species diversity and species composition. Early empirical evidence led some to conclude that species diversity itself was a primary contributor to ecosystem functioning (e.g. Naeem et al. 1994, Tilman et al. 1996). This conclusion was consistent with niche theory which predicts that species diversity will increase the rates of ecological processes when species coexist locally by niche differentiation (McNaughton 1993, Swift and Anderson 1993). Niche differentiation ensures that limiting resources are used in ‘complementary’ ways, and thus, more resources are used when more niches are filled. Unfortunately, few of the studies claiming to affirm the importance of species diversity have actually demonstrated complementary resource use among taxa, and this has left the cause of empirical results open to much debate.

It has also been argued that species composition (meaning the particular types and combinations of species present) may influence ecological processes to a much greater extent than the number of species (Naeem et al. 1996, Aarssen 1997, Hooper and Vitousek 1997, Huston 1997, Tilman et al. 1997a, Wardle et al. 1997a, Chapin et al. 1998, Symstad et al. 1998). Obviously, not all species are equivalent in their control over the rates of ecological processes. Interspecific differences in resource use and efficiency can interact with uneven distributions of species abundances to result in one taxon (or a select few taxa) having disproportionate influence on a process. Indeed, there are many examples where individual species such as competitive dominants, keystone species, ecosystem engineers, or taxa with

biologically unique traits control community and ecosystem-level processes (Schoener 1983, Paine 1984, Lawton 1994, Brown 1995, Power et al. 1996). Several authors have now pointed out that spurious relationships between species diversity and the rates of ecological processes can result when changing diversity alters the probability of including one of these important or unique species in the pool of potential colonists (e.g. the ‘selection probability’ effect sensu Huston 1997, or the ‘sampling’ effect sensu Tilman 1999).

Clearly, there is still much debate about the form and cause of the relationship between species diversity and the rates of ecological processes (Johnson et al. 1996, Grime 1997, Naeem et al. 1998). Given that we have more than 50 years of research on this topic (see Johnson et al. 1996, or Tilman 1999 for a more thorough historical review), why have so few generalities emerged? We argue that it is useful to recognize there may be no single, generalizable relationship between the number of species and the functioning of ecosystems because the relative contributions of species diversity and species composition to ecological processes change with environmental context. We are not the first to suggest that the relationship between species diversity and ecosystem functioning may be context dependent (see Risser 1995, Johnson et al. 1996, and Chapin et al. 1998); however, there have been few efforts by ecologists to delineate the circumstances under which species diversity should or should not matter. As a result, ecologists have rarely acknowledged the potential for context dependent relationships in their own systems (for an exception see van der Heijden et al. 1998).

The purpose of this paper is to show how common types of environmental variability (both spatial and temporal) can change both the form and cause of the relationship between species diversity and the productivity of an ecosystem. Integrating environmental variation into the diversity/productivity debate is important because variability can greatly influence the partitioning of resources among species in a system. For instance, spatial heterogeneity is generally thought to increase niche diversity leading to a greater number and/or evenness of species coexisting in a local area (Kolas and Pickett 1991). Spatial heterogeneity can, therefore, be a primary determinant of how resources are divided among species (Tilman and Kareiva 1997). Disturbance is another form of environmental variation that is well known to influence the number and evenness of species in a community. Disturbance can affect communities via a number of different mechanisms, but one of the most widely cited is the prevention of competitive exclusion of taxa that might occur if a system were allowed to proceed to an equilibrium (Pickett and White 1985, Petraitis et al. 1989). In communities where this mechanism operates, the frequency and/or magnitude of disturbance should regulate the distribution of resources among inferior and superior competitors. Be-

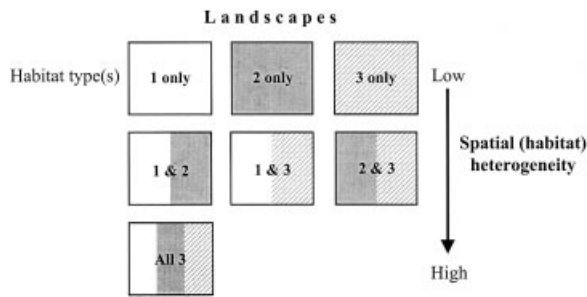


Fig. 1. A depiction of the seven different landscapes examined by the model.

cause spatial heterogeneity and disturbance potentially govern the distribution of resources among coexisting taxa, it seems likely that both forms of environmental variation have important consequences for the relationship between species diversity and productivity. Yet, we are not aware of any theoretical or empirical work that has explicitly examined this possibility.

We present the results of a simple model that illustrates how spatial heterogeneity and disturbance could alter the form and cause of the relationship between species diversity and productivity. We define species diversity as the number of taxa in a pool of colonists because this definition is equivalent to how most empirical studies have defined and manipulated diversity. Our model is based on a hypothetical system that is intentionally oversimplified, and thus, not meant to represent the reality of complex ecosystems. Instead, the model is meant to serve as a heuristic tool to demonstrate that the relationship between species diversity and ecosystem functioning may depend on the environmental context in which species interactions take place. Given the simplicity of the model and its unequivocal results, the qualitative conclusions reached are likely to pertain to many real ecosystems.

## The model

We used a simple model to investigate how productivity can change with the number of competing species inhabiting landscapes that differ in the number of available niches (i.e. habitat types) and disturbance regimes. We examined seven landscapes composed of either one, two, or three different types of habitats (Fig. 1). Landscapes with a greater number of habitat types were considered to be more spatially heterogeneous and have a greater number of available niches than landscapes with fewer habitat types. We assumed that each landscape had an equal carrying capacity ( $K$  was defined as maximum abundance) which was evenly divided among all habitat types composing a landscape (assumption 1, Table 1). Making this assumption ensured that increasing spatial heterogeneity in our model was never confounded with changes in carrying capacity such as might occur with increases in scale or with greater productivity.

The pool of potential colonists for the model included three species – A, B, and C. These species differed in their fundamental niches with A having the ability to establish in habitat type one, B being able to establish in habitat types one and two, and C able to establish in all three habitat types (assumption 2, Table 1). Thus, species A was a habitat specialist while B and C were more generalists. For simplicity, we assumed that when present in the colonist pool, each species had an excess of propagules such that population sizes were not recruitment limited (assumption 3, Table 1).

The three taxa composed a functional guild, and thus, they competed in habitats for which their fundamental niches overlapped *when their abundance approached  $K$* . When two species competed, we assumed that better competitors always excluded poorer competitors according to the dominance hierarchy  $A > B > C$  (assumption 4, Table 1). Disturbance, however,

Table 1. Six assumptions of the model with corresponding implications.

Assumption	Implication
1. Landscapes had an equal carrying capacity ( $K$ was defined as maximum abundance) which was equally divided amongst all habitat types composing the landscape.	Increases in spatial heterogeneity were independent of scale and productivity.
2. Species differed in their fundamental niches: A could establish in habitat type 1, B in types 1 and 2, C in 1, 2, and 3.	A was a habitat specialist, species C was a habitat generalist, species B was inbetween.
3. When present in the colonist pool, each species had an excess of propagules.	Population sizes were never limited by recruitment.
4. There was a strict dominance hierarchy amongst the taxa with $A > B > C$ .	When competing, better competitors always excluded poorer competitors from habitats for which niches overlapped.
5. Disturbance imposed a non-selective 50% mortality to individuals in the landscape.	Abundance in disturbed habitats was equally divided amongst taxa having overlapping niches (e.g. disturbance increased evenness).
6. The concentration to which a species reduced the limiting resource, $R^*$ , was inversely proportional to competitive ability ( $R_C^* > R_B^* > R_A^*$ ).	Superior taxa had greater per capita resource use than inferior taxa and were, therefore, more productive.

allowed species to locally coexist by reducing total abundance in the landscape to 0.5K individuals with abundance in post-disturbance habitats being equally divided among taxa having overlapping niches (assumption 5, Table 1). Although disturbance often acts selectively against particular organisms, the non-selective form we chose to model is similar to how disturbance acts in many systems (e.g. fires, tides, floods, grazing, etc.) to prevent competitive exclusion and increase the evenness of taxa in a habitat (Dayton 1971, Armstrong 1976, Grubb 1977, Connell 1978, Huston 1979, Sousa 1979, Hemphill and Cooper 1983, Paine and Levin 1981, Williamson and Black 1981).

Using the constraints of assumptions 1–5, we wrote a “rule-based” program (Mathematica v. 3.0) that calculated the abundance of each species,  $N_i$ , as:

$$N_i = f(\text{the fundamental niche of species } i, \text{ the available habitat types, species } i\text{'s realized niche in the presence of competitors, the presence/absence of disturbance}). \quad (1)$$

The program calculated  $N_i$  in a factorial design for systems representing all possible combinations of: species diversity (all combinations of 1, 2, or all 3 species in the colonist pool), spatial heterogeneity (all combinations of 1, 2, or 3 habitat types in the landscape), and disturbance regime (+/– a non-selective 50% mortality). For each combination, the ‘landscape-level’ productivity of a species in the colonist pool,  $P_i$ , was taken to be the biomass of the taxon summed across all habitat types composing the landscape. In this model, biomass (a standing stock) is equivalent to productivity (a rate) for any given time scale because there are no losses of tissue to other trophic levels or to the decomposer pool. As such, time is implicit in the model and all of the results we present are insensitive to temporal scale.

$P_i$  was calculated using a slight modification of the equation used by Tilman et al. (1997b):

$$P_i = \sum_{h=1}^3 N_{ih} z Q (S - R_i^*) \quad (2)$$

where  $N_{ih}$  is the abundance of species  $i$  in habitat type  $h$ ,  $z$  is the rate of resource mineralization,  $Q$  is the coefficient of resource conversion into biomass,  $S$  is the supply rate of the limiting resource in all habitat types, and  $R_i^*$  is the equilibrium concentration to which the limiting resource is reduced by a monoculture of species  $i$ . Because resource competition theory predicts that  $R^*$  is inversely proportional to competitive ability (the  $R^*$  principle, Tilman 1982) we assumed that  $R_C^* > R_B^* > R_A^*$  (assumption 6, Table 1). The particular values chosen for  $R_i^*$  did not influence our analyses since increasing or decreasing interspecific differences would only alter the magnitude, but not direction of the trends we

report. For our purposes,  $z$ ,  $Q$  and  $S$  were considered constants. In more realistic models, species might also differ in  $Q$ . This improvement would not change our conclusions, however, since the trends we present could only be magnified by the fact that superior competitors tend to have higher resource conversion efficiencies (Chapin 1980).

Total ‘landscape-level’ productivity,  $P_T$ , was then calculated as the sum of the productivity of each species in the colonist pool:

$$P_T = \sum_{i=A}^C P_i \quad (3)$$

$P_T$  was determined for all levels of species diversity and every combination of spatial heterogeneity and disturbance. This data set, used in the remainder of our analyses, is presented in Table 2.

We used 14 linear regressions to relate productivity to species diversity for the seven combinations of habitat types and two possible disturbance regimes (see Table 2). The slope of any given regression indicated the direction and average magnitude of change in productivity per species added to the colonist pool. Thus, the slope was used to summarize the *form* (direction and magnitude) of the diversity/productivity relationship for a particular environmental context. To assess the *cause* (species diversity vs species identity) of any given relationship, we examined the proportion of variance accounted for by the regression (i.e.  $R^2$ ). Given that there were no unknown variables in our model, productivity could only be influenced by species diversity and species composition. Therefore, the variance explained by a regression of diversity vs productivity ( $R^2$ ) was the variance in productivity attributable to species diversity itself for that particular environmental context. In turn, the residual variation of a regression of diversity vs productivity ( $1 - R^2$ ) could only be attributable to the effects of species composition on productivity. In this manner, we determined how the *form* (direction and magnitude of slope), and *cause* ( $R^2$  = effect of diversity,  $1 - R^2$  = effect of composition) of the relationship between species diversity and productivity changed with spatial heterogeneity and disturbance.

## Environmental variation and the form of the diversity/function relationship

The first question we addressed was: Does the form of the relationship between species diversity and productivity depend on environmental context? We found that the slope relating species diversity and productivity differed dramatically for landscapes with and without disturbance, but did not differ for landscapes varying in

Table 2. Data used to characterize the relationship between species diversity and productivity.

	Habitat type(s)	Spatial heterogeneity	Productivity (in relative units) of systems with species ...						
			A	B	C	A+B	A+C	B+C	A+B+C
No disturbance	1	1	2700	1800	900	2700	2700	1800	2700
	2	1	0	1800	900	1800	900	1800	1800
	3	1	0	0	900	0	900	900	900
	1+2	2	1350	1800	900	2250	1800	1800	2250
	1+3	2	1350	900	900	1350	1800	1350	1800
	2+3	2	0	900	900	900	900	1350	1350
+disturbance	1+2+3	3	900	1200	900	1500	1500	1500	1800
	1	1	1350	900	450	1125	900	675	900
	2	1	0	900	450	900	450	675	675
	3	1	0	0	450	0	450	450	450
	1+2	2	675	900	450	1013	675	675	788
	1+3	2	675	450	450	563	675	563	675
	2+3	2	0	450	450	450	450	563	563
	1+2+3	3	450	600	450	675	600	600	675

Species abundances were calculated for each environmental condition using a program based on the assumptions of our model. Abundances were then converted to productivity using eqs 2 and 3 in the text. Parameter values used to generate the above data set were  $K = 900$ ,  $S = 4$ ,  $Q = 1$ ,  $z = 1$ ,  $R_A^* = 1$ ,  $R_B^* = 2$ ,  $R_C^* = 3$ .

spatial heterogeneity. Disturbance always reduced the per species gain in productivity (i.e. the *slope* relating system-wide productivity,  $P_T$ , to species diversity, Fig. 2) for all levels of spatial heterogeneity and for all combinations of habitat types. This trend resulted from an interaction of two factors. First, disturbance reduced the overall abundance of organisms in the landscape by 50% (assumption 5, Table 1) so that the addition of species to the colonist pool of a disturbed landscape had, on average, less impact on productivity (i.e. a simple abundance phenomenon). In addition, disturbance increased the evenness of taxa in habitat types for which fundamental niches overlapped (assumption 5, Table 1). Without disturbance, superior competitors formed monocultures in habitat types they could establish in. Because superior competitors were also the most productive species (assumption 6, Table 1), the addition of these taxa to the colonist pool always ensured greater productivity. On the other hand, when disturbance prevented competitive exclusion, productivity was more evenly divided among species in the colonist pool. Disturbance, therefore, reduced the influence each species had on productivity by reducing overall abundance and by limiting dominance. These two effects interacted to reduce the average per species gain in productivity in systems with disturbance.

In contrast to the effects of disturbance, spatial heterogeneity had no *average* effect on the form of the diversity/productivity relationship. The average slope relating species diversity and productivity remained constant across all levels of spatial heterogeneity for systems with and without disturbance (Fig. 2). While counterintuitive at first glance, spatial heterogeneity did not change the per species gain in productivity because when averaged over all combinations of habitats, spatial heterogeneity neither altered total abundance nor changed the evenness of taxa in the landscape. Note,

however, that Fig. 2 shows considerable variation for landscapes composed of different habitat types (consider the error bars for landscapes composed of one or two habitat types). When the data are replotted to show each particular habitat combination (Fig. 3) it becomes apparent that spatial heterogeneity did alter the relationship between diversity and productivity, but the effect of spatial heterogeneity depended on the particular habitat types that composed the landscape because of differences in the species' fundamental niches (assumption 2, Table 1). Fig. 3 also reveals a clear interaction between multiple forms of environmental variation in this model. Note, there is no way to predict the per species gain in productivity (e.g. the slope relating

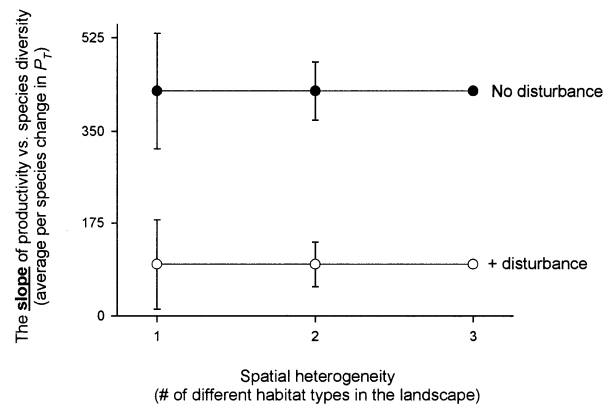


Fig. 2. The effects of spatial heterogeneity and disturbance on the *form* of the diversity/productivity relationship. Note that the y-axis is the *slope* relating productivity to the number of species in the colonist pool. This slope indicates the direction and average magnitude of change in 'landscape-level' productivity,  $P_T$ , per species added to the colonist pool. Data shown are the mean  $\pm$  SD of all possible combinations of habitat types from Table 2.

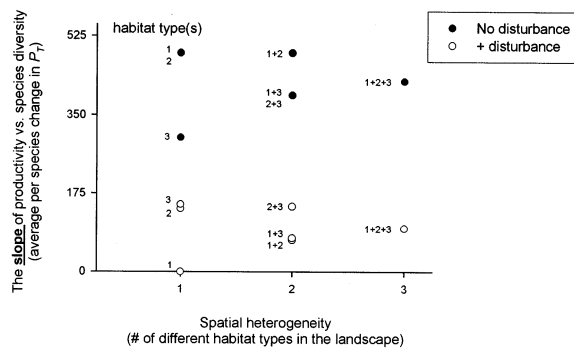


Fig. 3. Data from Fig. 2 replotted to emphasize the differences in individual habitat types and habitat combinations. Again, note that the *y*-axis is a *slope* indicating the change in productivity per species added to the colonist pool. The numbers shown next to each data point are the habitat type(s) composing the landscape for that particular value.

species diversity to productivity, Fig. 3) without knowing the spatial heterogeneity, particular habitat types, and disturbance regime of a system. Depending on the particular environmental conditions, there could be no relationship at all between diversity and productivity (note the data point at 0 on *y*-axis in Fig. 3), or any number of positive relationships that vary widely in magnitude. These results indicate that the form of the diversity/productivity relationship depended on how multiple types of environmental variability interactively determined the absolute and relative abundances of species in a system.

### Environmental variation and the cause of the diversity/function relationship

The second question addressed was: Does the cause of the relationship between diversity and productivity

depend on environmental context? We found that the diversity/productivity relationship was sometimes caused by the number of species in the colonist pool (i.e. species diversity) and other times caused by the particular types of species in the colonist pool (i.e. species composition). As spatial heterogeneity increased, the amount of variation explained by the number of species always increased (Fig. 4). Greater spatial heterogeneity reduced differences in the productivity of single species systems because inferior taxa were able to establish in a greater number of habitat types when they were available in the landscape (assumption 2, Table 1). In addition, spatial heterogeneity allowed competitors to coexist via classical niche partitioning which, in turn, led to spatial complementarity in resource use across habitat types. Together, these two factors ensured that abundance, and thus, productivity was more evenly divided among species in the colonist pool.

In contrast to the effects of spatial heterogeneity, disturbance tended to increase the contribution of species composition to the diversity/productivity relationship (Fig. 4). Interestingly, it was the competitively inferior taxa that contributed most to productivity when disturbance was present in the landscape. Inferior taxa were able to use a greater fraction of the total resources under these conditions because (1) disturbance increased the relative abundance of inferior competitors in habitats also occupied by superior taxa (assumption 5, Table 1), and (2) as generalists, inferior taxa had the ability to colonize more habitat types (assumption 2, Table 1). This result points to the often ignored possibility that competitively inferior taxa may, under some circumstances, be the 'drivers' of ecosystem functioning. This might occur, for example, in spatially subdivided landscapes where 'fugitive' species attain numerical dominance due to greater colonization and dispersal abilities (Tilman 1994, Nee et al. 1997).

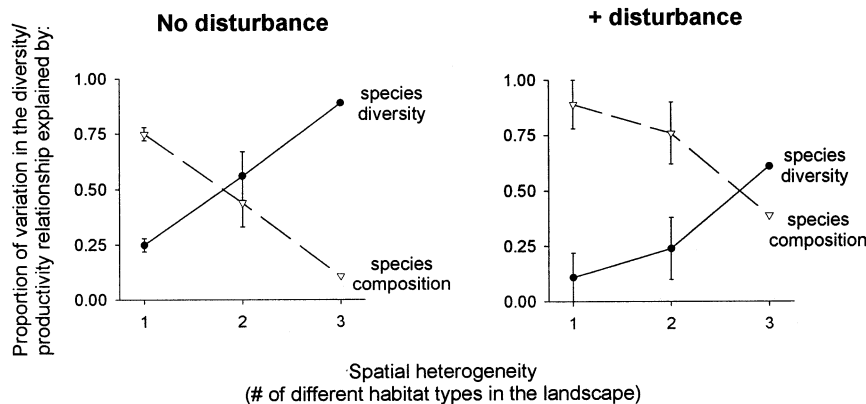


Fig. 4. The effects of spatial heterogeneity and disturbance on the *cause* of the diversity/productivity relationship (e.g. species diversity vs species composition). Data are the mean  $\pm$  SD of all possible combinations of habitat types. See text for a description of how variation was partitioned between these two possible causal factors. Because species diversity and composition were the only factors contributing to productivity in the model, values always sum to one.

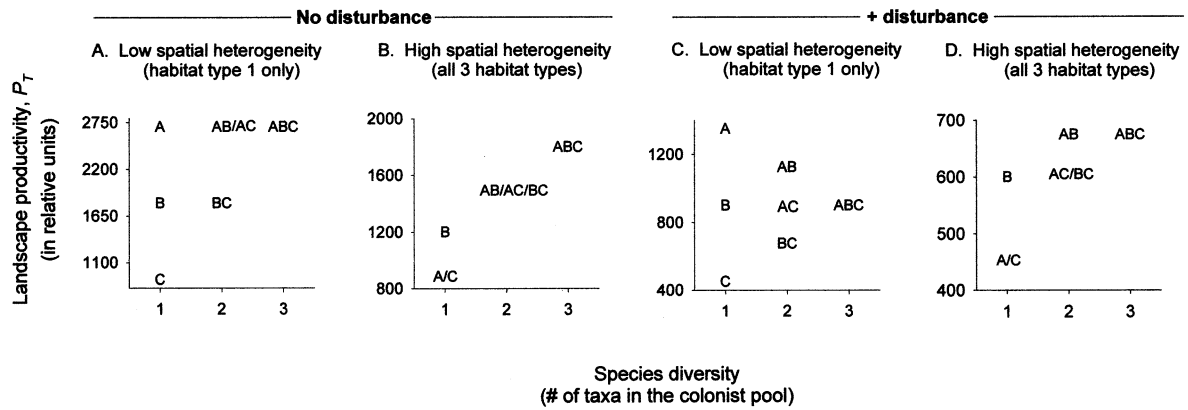


Fig. 5. The relationship between species diversity and productivity under four different environmental conditions. Note that data labels represent productivity for a system with that particular species or species combination. Slashes indicate different possible species combinations (e.g. AB/AC means species A + B result in the same productivity as species A + C).

## Relevance to other studies and implications

So far, we have shown that the form and cause of the diversity/productivity relationship can vary greatly with environmental context. Many of the theoretical relationships we found from our simple model are similar to those that have been demonstrated empirically. Consider the four examples shown in Fig. 5. In a spatially homogeneous landscape that did not experience disturbance, a positive relationship between diversity and productivity resulted almost entirely from the effects of species composition (Fig. 5A). Under these circumstances, diversity was only important because it increased the probability of including species A (the dominant competitor and most productive species) in the colonist pool. As a result, the presence/absence of species A was the primary determinant of ecosystem functioning. The relationship shown in Fig. 5A has been referred to as the ‘sampling’ or ‘selection probability’ effect of diversity (Huston 1997, Tilman 1999), and it is probably common when environmental conditions promote strong competition and dominance by one, or a select few, species.

In a spatially heterogeneous landscape with no disturbance, a positive relationship between species diversity and productivity resulted from the effects of species diversity itself (Fig. 5B). Spatial heterogeneity allowed resources to be used in spatially complementary ways because inferior taxa utilized habitats that would have otherwise been unused by superior competitors. This is the theoretical mechanism that underlies the long held belief that productivity should increase with species diversity (McNaughton 1993, Swift and Anderson 1993), and it is based on the concept of “limiting similarity” which suggests that co-occurring species must differ by some minimum amount and use limiting resources in complementary ways to coexist. While this is likely true, it seems trivial to point out that most rare species, by definition, make little *direct* contribution to

the productivity of ecosystems. Thus, species diversity should have the greatest influence on productivity when interspecific differences allow species to locally coexist *and* when environmental conditions encourage relatively even distributions of abundance among co-occurring taxa. While this seems intuitive, we point out that very few studies have used species evenness as an independent variable or as a covariate when trying to statistically attribute productivity to species diversity. Because a preoccupation with the species richness component of diversity could potentially hinder insights into how diversity regulates productivity, we suggest that future studies should pay much greater attention to the distribution of species abundances in a system.

Our model also identified conditions in which there was no relationship between species diversity and productivity. When disturbance was added to a spatially homogeneous system, productivity could increase, decrease, or remain constant with species diversity depending only on the particular taxa that were in the pool of colonists (Fig. 5C). This has been referred to as the “idiosyncratic” relationship between species diversity and ecosystem functioning (Lawton 1994) and it has been demonstrated empirically for several ecological processes including primary productivity (Hooper and Vitousek 1997, Hooper 1998), decomposition (Wardle et al. 1997b), and community metabolism (Mikola and Setälä 1998). Our model suggests this relationship may occur when all species utilize the same habitat but population sizes remain relatively even, perhaps because competition is not a structuring force.

Interestingly, in between the two extremes where the number of species or species composition were primary contributors to productivity (Fig. 5A, B), there were a variety of conditions where both factors were equally important. For example, when disturbance was added to a spatially heterogeneous system, a positive relationship between diversity and productivity resulted from

an interaction of species diversity and composition (Fig. 5D). Single species systems varied widely in productivity but disturbance resulted in taxonomic combinations being much more similar in this function. Consequently, the number of species explained 60% of the overall relationship while species composition explained 40%. This result supports the growing recognition that both species diversity and composition are likely to be important to the functioning of ecosystems (Chapin et al. 1997, 1998, Tilman et al. 1997a, b, Tilman 1999). Given that most systems are characterized by both spatial heterogeneity and disturbance, our results also suggest that dichotomizing systems as being controlled by either species diversity or species composition could be misleading under a wide set of environmental contexts.

## Conclusions

We have presented the results of a simple, heuristic model suggesting that there may be no single, generalizable relationship between species diversity and the rates of ecological processes. Rather, the form and cause of the relationship are likely to change as environmental context alters the relative contributions of species to ecological processes. The hypothetical system we modeled is unrealistic for most natural systems, and more complex treatments of this problem (e.g. more species, differential effects of disturbance, different types of spatial heterogeneity, etc.) are likely to produce quantitatively different results. Yet, it is unlikely that adding complexity and realism to the model would change the qualitative conclusion that any factor that alters the absolute abundance and/or evenness of species in a landscape will simultaneously change the relationship between diversity and productivity. It is difficult to imagine a system in which the absolute abundance and dominance of taxa do not change over time, space, scale, etc. Therefore, we should probably expect the relationship between species diversity and ecosystem functioning to be equally as dynamic, constantly changing over time and space. To the extent that this is true, there are likely to be many different relationships between diversity and function for the same organisms in the same system, for the same organisms in different systems, and for different organisms in the same/different system(s). We suggest this is one of many potential reasons why empirical studies have failed to show any consistent relationship between species diversity and the rates of ecological processes.

*Acknowledgements* – We are indebted to Richard Bardgett, Shane Brooks, LeRoy Poff, Chris Swan, Mark Toal, and Dave Wooster for their insightful comments on the manuscript. We also wish to thank all members of the Palmer lab for numerous discussions about this topic which greatly influenced our thinking, and ultimately led to this paper.

## References

- Aarssen, L. W. 1997. High productivity in grassland ecosystems: effected by species diversity or productive species? – *Oikos* 80: 183–184.
- Armstrong, R. A. 1976. Fugitive species: experiments with fungi and some theoretical considerations. – *Ecology* 57: 953–963.
- Brown, J. H. 1995. Organisms as engineers: a useful framework for studying effects on ecosystems? – *Trends Ecol. Evol.* 10: 51–52.
- Chapin III, F. S. 1980. The mineral nutrition of wild plants. – *Annu. Rev. Ecol. Sys.* 11: 233–260.
- Chapin III, F. S., Walker, B. H., Hobbs, R. J. et al. 1997. Biotic control over the functioning of ecosystems. – *Science* 277: 500–504.
- Chapin III, F. S., Sala, O. E., Burje, I. C. et al. 1998. Ecosystem consequences of changing biodiversity. – *BioScience* 48: 45–52.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. – *Science* 199: 1302–1310.
- 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.
- Grime, J. P. 1997. Biodiversity and ecosystem function: the debate deepens. – *Science* 277: 1260–1261.
- Grubb, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. – *Biol. Rev.* 52: 107–145.
- Hemphill, N. and Cooper, S. D. 1983. The effect of physical disturbance on the relative abundances of two filter-feeding insects in a small stream. – *Oecologia* 58: 378–382.
- Hooper, D. 1998. The role of complementarity and competition in ecosystem responses to variation in plant diversity. – *Ecology* 79: 704–719.
- Hooper, D. and Vitousek, P. 1997. The effects of plant composition and diversity on ecosystem processes. – *Science* 277: 1302–1305.
- Huston, M. 1979. A general hypothesis of species diversity. – *Am. Nat.* 113: 81–101.
- 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.
- Kolasa, J. and Pickett, S. T. A. (eds) 1991. Ecological heterogeneity. – Springer-Verlag.
- Lawton, J. H. 1994. What do species do in ecosystems? – *Oikos* 71: 367–374.
- McGrady-Steed, J., Harris, P. and Morin, P. 1997. Biodiversity regulates ecosystem predictability. – *Nature* 390: 162–165.
- McNaughton, S. 1993. Biodiversity and function of grazing systems. – In: Mooney, H. and Schulze, E. (eds), Biodiversity and ecosystem function. Springer-Verlag, pp. 361–383.
- Mikola, J. and Setälä, H. 1998. Relating species diversity to ecosystem functioning: mechanistic backgrounds and experimental approach with a decomposer food web. – *Oikos* 83: 180–194.
- Naeem, S., Thompson, L. J., Lawler, S. P. et al. 1994. Declining biodiversity can alter the performance of ecosystems. – *Nature* 368: 734–737.
- Naeem, S., Håkansson, K., Lawton, J. et al. 1996. Biodiversity and plant productivity in a model assemblage of plant species. – *Oikos* 76: 259–264.
- Naeem, S., Kawabata, Z. and Loreau, M. 1998. Transcending boundaries in biodiversity research. – *Trends Ecol. Evol.* 13: 134–135.
- Nee, S., May, R. M. and Hassell, M. P. 1997. Two-species metapopulation models. – In: Hanski, I. A. and Gilpin, M. E. (eds), Metapopulation biology: ecology, genetics, and evolution. Academic Press, pp. 123–147.

- Paine, R. T. 1984. Ecological determinism in the competition for space. – *Ecology* 65: 1339–1348.
- Paine, R. T. and Levin, S. A. 1981. Intertidal landscapes: disturbance and the dynamics of patterns. – *Ecology* 51: 145–178.
- Petraitis, P. S., Latham, R. E. and Neisenbaum, R. A. 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.
- Power, M. E., Tilman, D., Estes, J. A. et al. 1996. Challenges in the quest for keystones. – *BioScience* 46: 609–620.
- Risser, P. 1995. Biodiversity and ecosystem function. – *Conserv. Biol.* 9: 742–746.
- Schoener, T. W. 1983. Field experiments on interspecific competition. – *Am. Nat.* 122: 240–283.
- Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the non-equilibrium maintenance of species diversity. – *Ecology* 60: 1225–1239.
- Swift, M. J. and Anderson, J. M. 1993. Biodiversity and ecosystem function in agricultural systems. – In: Mooney, H. and Schulze, E. (eds), *Biodiversity and ecosystem function*. Springer-Verlag, pp. 240–283.
- Symstad, A., Tilman, D., Willson, J. and Knops, J. 1998. Species loss and ecosystem functioning: effects of species identity and community composition. – *Oikos* 81: 389–397.
- Tilman, D. 1982. *Resource competition and community structure*. – Princeton Univ. Press.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. – *Ecology* 75: 2–16.
- Tilman, D. 1997. Distinguishing between the effects of species diversity and species composition. – *Oikos* 80: 185.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. – *Ecology* 80: 1455–1474.
- 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., Knops, J., Wedin, D. et al. 1997a. The influence of functional diversity and composition on ecosystem processes. – *Science* 277: 1300–1302.
- Tilman, D., Lehman, D. and Thompson, K. 1997b. Plant diversity and ecosystem productivity: theoretical considerations. – *Proc. Natl. Acad. Sci. USA* 94: 1857–1861.
- van der Heijden, M. G., Klironomos, J. N., Ursic, M. et al. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. – *Nature* 396: 69–72.
- Wardle, D. A., Zackrisson, O., Hornberg, G. and Gallet, C. 1997a. The influence of island area on ecosystem properties. – *Science* 277: 1296–1299.
- Wardle, D. A., Bonner, K. I. and Nicholson, K. S. 1997b. Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. – *Oikos* 79: 247–258.
- Williamson, G. B. and Black, E. M. 1981. High temperature of forest fires under pines as a selective advantage over oaks. – *Nature* 293: 643–644.