
The influence of species diversity on ecosystem productivity: how, where, and why?

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The effect of species diversity on ecosystem productivity is controversial, in large part because field experiments investigating this relationship have been fraught with difficulties. Unfortunately, there are few guidelines to aid researchers who must overcome these difficulties and determine whether global species losses seriously threaten the ecological and economic bases of terrestrial ecosystems. In response, I offer a set of hypotheses that describe *how* diversity might influence productivity in plant communities based on three well-known mechanisms: complementarity, facilitation, and the sampling effect. Emphasis on these mechanisms reveals the sensitivity of any diversity-productivity relationship to ecological context (i.e., *where* this relationship should be found); ecological context includes characteristics of the surrounding environment, temporal and spatial scales of observation, and the intensity of human management. In particular, the legitimacy of the sampling effect as a mechanism of productivity enhancement is dependent upon the degree to which stochastic events influence immigration and extinction processes in a given ecosystem. A mechanistic approach also requires that the three mechanisms be separated and quantified in diversity experiments, and I examine the most appropriate analyses for doing so, focusing on the overyielding technique. Finally, I question *why* productivity per se is a relevant management concern in non-agricultural systems once relationships among diversity, productivity, and the qualities of the surrounding environment are considered.

Ecosystem productivity, the rate of whole-ecosystem biomass production, is influenced by the identities of the species that compose an ecosystem. But does the number of species in an ecosystem affect productivity? Researchers studying plant communities of artificial microcosms (Naeem et al. 1994, 1995, Symstad et al. 1998) and semi-natural grasslands (Naeem et al. 1996, Tilman et al. 1996, 1997a, Hector et al. 1999) have asserted that species diversity influences ecosystem properties, especially productivity (Loreau 1998a, Naeem et al. 1999, Tilman 1999a). However, these studies have generated a considerable amount of criti-

cism based upon their experimental methodology (Huston 1997, Hodgson et al. 1998, Wardle 1999), analyses (Aarssen 1997, Huston et al. 2000), and general conclusions (Grime 1998, Wardle et al. 2000). As a result, the nature of the relationship between species diversity and ecosystem productivity remains unclear.

One cause of the diversity-productivity debate, and a reason that this relationship remains controversial, is the lack of clear hypotheses to guide experimental hypothesis testing. For example, what qualifies as an effect of diversity? Inevitably, in experiments of treatments of varying species richness levels, those plots initially more diverse are more likely to contain certain species whose presence more greatly affects plot productivity than others in the species pool – a phenomenon called the “sampling effect”. Should the sampling effect qualify as a diversity effect, or is it an undesired artifact of experimental methodology? As a genuine mechanism of a diversity effect, the sampling effect has been both defended (Tilman et al. 1997b, Naeem et al. 1999, Tilman 1999a) and disputed (Aarssen 1997, Garnier et al. 1997, Huston 1997, Wardle 1999, Wardle et al. 2000). If the sampling effect is regarded as an experimental artifact, how should this artifact be removed? This too has been debated (Garnier et al. 1997, Hector 1998, Loreau 1998b, Huston et al. 2000) and the measurement of overyielding, which seeks to quantify the true extent of crop mixture advantage (de Wit 1960, Trenbath 1976, Vandermeer 1989), has emerged as a valuable analysis tool. Nevertheless, researchers are still lacking criteria to decide whether there are some cases where sampling effects may be relevant in natural ecosystems.

The difficulties involved in testing hypotheses of a diversity-productivity relationship are compounded by

the shortage of specific mechanistic models describing how a greater number of species might enhance productivity, given the obvious roles of species identity and the qualities of the surrounding environment. Without such models, researchers are stuck trying to fit general phenomenological models to systems of a wide variety of ecological contexts. It will almost certainly be more profitable for researchers to focus on ways in which certain ecological circumstances allow species diversity to govern ecosystem productivity rather than pursue a single, universal relationship between diversity and productivity. In other words, by providing researchers with potential mechanisms by which diversity may affect productivity, and specifying the ecological contexts in which these mechanisms may operate, a pluralistic perspective allows experimenters to more robustly test hypotheses of the relationship between diversity and productivity. This approach also better suits the needs of ecosystem managers who operate under a particular set of environmental and ecological contexts.

In response to the need for a more mechanistic framework describing the diversity-productivity relationship, I suggest that the processes governing species interaction and community assembly, including competition and facilitation, allow diversity to promote productivity by means of three general mechanisms: complementarity, facilitation, and the sampling effect. I briefly summarize what is known about complementarity and facilitation and recast the sampling effect as a complex phenomenon that is closely tied to the degree to which stochastic events influence species immigration and extinction. This reformulation of the sampling effect allows ecological context (e.g., environmental conditions, spatial and temporal scales of observation, human management intensity) to enter the discussion of whether to include the sampling effect as a legitimate effect of diversity on productivity. Because the realized effect of these mechanisms on productivity is dependent upon ecological context, it is necessary to separate their effects in diversity experiments. Appropriate analyses for separating these mechanisms have been suggested, but no consensus has emerged (Loreau 1998b, Huston et al. 2000); I advocate a method for detecting mechanisms of enhanced mixture productivity and attempt to clarify semantic issues concerning the measurement of overyielding. Finally, after exploring the importance of each of the three mechanisms along selected ecological gradients, I explore the general consequences of these hypotheses: In what context does diversity affect productivity? Are species diversity and overyielding related? Does ecological context provide a basis for deciding where ecosystem productivity is a legitimate management concern?

How species diversity may influence productivity

Species diversity may promote ecosystem productivity in three general ways. Complementarity occurs when competition from interspecific neighbors is lower than that from conspecifics as a result of differences in resource requirements, which may lead to more complete use of environmental resources by a more species-rich community (Hooper 1998, Loreau 1998a). Facilitation occurs when an individual attains greater biomass in the presence of interspecific neighbors because of their beneficial effects on an intermediary resource (defined broadly to include resource enhancement or alleviation of stress or disturbance) (Vandermeer 1989). The sampling effect comprises the greater probability of including more productive species (or combinations of species) in more species-rich communities (Huston 1997, Tilman et al. 1997b). In addition, the sampling effect can involve the greater probability of complementary and facilitative interactions in more species-rich communities. In the following summary of these three potential mechanisms of the diversity effect, I argue that there is little empirical support for a necessary relation between high levels of diversity and complementarity or facilitation, but there is a potential relation between diversity and the sampling effect.

Complementarity

Because it is presumed that competition is the predominant interaction among plant species, an explanation of how species coexist and how they might act concomitantly to influence ecosystem function must focus on how competitive exclusion is avoided. Several influential models of plant species coexistence suggest that coexistence is the result of niche partitioning, or differences in resource requirements among species. Partitioning may include species using different types of resources (e.g., chemical forms of nitrogen), different ratios of amounts of resource types needed (e.g., light-water tradeoffs), or different times or spaces of exploitation of the same resource (e.g., phenology, rooting zones). More generally, coexisting plants are thought to complement each other in traits related to resource foraging (Tilman 1982, Smith and Huston 1989), life-history strategy (Grubb 1977), or both (Grime 1977). Complementarity is the reduction of interaction due to differences in species traits, or, more specifically, reduced competition between interspecific neighbors, one or each of which would be more greatly suppressed by a conspecific neighbor. Species may “control” productivity via complementarity because resource partitioning enhances total resource use, and thus often a greater amount of energy is harvested in plant mixtures compared to their monocultures (Tren-

bath 1974, Jolliffe 1997). Indeed, complementarity is the principal basis for the science of intercropping and evidence in support of complementary species associations in agriculture is extensive (Ewel 1986, Willey 1990).

Complementarity is a central principle behind the “functional group” approach in which species diversity is broken down into its most obvious functional components (Tilman et al. 1997a, Hooper 1998). But is complementarity related to species diversity beyond what is expected from the inevitable correlation of functional diversity and species diversity? Though theoretically attractive (e.g., Tilman et al. 1997b), there is no empirical support for a necessary relationship between diversity and complementarity. Complementarity has been found to be the product of particular species combinations, not random species combinations (Hooper and Vitousek 1997, Tilman et al. 1997a, Hooper 1998). Naeem et al. (1994, 1995), describing a trend of enhanced light capture in more diverse plant assemblages, argued that increased diversity produced a greater variety of leaf forms and plant canopies within the community, which led to greater packing of photosynthetic tissues. While this possibility is intuitively appealing, these studies have been criticized for confounding species richness levels with particular species compositions (Huston 1997); it is possible that more efficient light use in the highest diversity treatments was caused by a certain densely-foliated species or, more likely, canopy packing of only a few complementary species. The efficiency of light capture is indeed a common principle in the design of intercropping systems (Allen et al. 1976), but there is little evidence that such light partitioning occurs among all species in communities of more than three or four species. Thus, species composition, and that of relatively few species, is likely the best predictor of resource partitioning among plant species, not the number of local species (Schwartz et al. 2000). Because few diversity-productivity studies have been constructed to test mechanistic hypotheses, however, these relationships require further exploration.

Facilitation

A robust, mechanistic definition of facilitation for intercropping studies was suggested by Vandermeer (1989), who defined it as the circumstance where a species modifies the environment in a way favorable to a co-occurring species. This definition highlights the typical nature of plant interaction, through an intermediate entity, which could be a resource (e.g., nitrogen, water), a regulation factor (e.g., temperature, wind stress), space, or interactions with other species or trophic levels (e.g., weeds, herbivores). Examples of facilitative processes in intercropping are numerous (Vandermeer

1989). Requiring facilitation to occur via an intermediate material conceptually separates it from complementarity. Theoretically, this also gives researchers the potential to separate occurrences of the two mechanisms because intermediate materials can be manipulated independently of the effects of neighboring plants.

Current perspectives on the significance of facilitation in structuring plant communities often include beneficial effects among neighboring species of different life stages (Callaway and Walker 1997). For example, large desert perennials or “nurse plants” often aid in the establishment of younger neighbors by alleviating thermal and water stresses (Turner et al. 1966, Fowler 1986). These relationships are also important in managed ecosystems. In Britain, for example, spruce production is enhanced by growing spruce seedlings under the canopy of pines and larches (Morgan et al. 1992). The importance of facilitative relationships via the “nurse plant” mechanism has yet to be addressed in diversity-productivity experiments, however, because experimenters have grown only one cohort of plants. The juxtaposition of several life stages should become a component of future experiments.

The only facilitative mechanism addressed in diversity-productivity experiments is nutrient enrichment by N-fixers, despite evidence for several other facilitative processes in natural communities, such as water sharing via hydraulic lift (Caldwell et al. 1998) and nutrient sharing via mycorrhizal networks (Read 1997). Although the presence of N-fixers in certain N-limited habitats is undoubtedly an important mechanism of plant control over ecosystem productivity, the use of N-fixers in experiments may actually confound attempts to explore the relationship between diversity and productivity. For example, Hector et al. (1999) claimed that the number of functional groups (including N-fixing legumes, grasses, and non-leguminous forbs) present was a significant predictor of ecosystem productivity in their experimental grassland plots. However, their data are consistent with an interpretation based on simply the presence or absence of one functional group – N-fixers (Huston et al. 2000). Thus, their claim may be an artifact of legume inclusion (an important sampling effect component; see below) rather than an indication of complementarity among functional groups. Indeed, nearly all plant community experiments investigating the functional significance of diversity have included N-fixers as a functional group (e.g., Tilman et al. 1997a, Symstad et al. 1998), leaving open the possibility that the perceived significance of plant functional group diversity for ecosystem function is actually overestimated due to a sampling effect for the N-fixing group. At this point, using N-fixers in experiments appears to create more confusion than understanding of diversity-productivity relations, and there is dire need to perform experiments on the role of functional groups without the confounding presence of N-

fixers. Thus, as for the case of complementarity, there is currently no unambiguous evidence suggesting that random increases in species diversity enhance the strength or frequency of facilitative interactions.

The sampling effect

Although the sampling effect has been discussed primarily in terms of differentially including species of greatest inherent productivity in more diverse plots, it is actually an amalgam of at least four separate phenomena, of which inherent productivity is but one component. These four phenomena can be separated into two that focus exclusively on the traits of the species being selected and two that depend both on these species traits and those of the community to which the species are being added. Concerning traits of the introduced species, the sampling effect can be separated into the greater likelihood of selecting a species 1) better adapted to the particular site conditions, or 2) of higher potential growth rate or larger mature size. The first process – the habitat sampling effect – is that of finding a “match” between species and environment, in the sense of an “environmental filter” (Wilson 1999). “Habitat” is meant to emphasize niche breadth (Fig. 1), or the range of a species distribution along a resource gradient (*sensu* Whittaker et al. 1973). The ability of a species to tolerate a range of conditions along a resource gradient has been hypothesized to negatively relate to its maximum potential productivity, or niche amplitude, due to trade-offs between growth rate and stress tolerance (Grime 1977, Chapin 1980, Austin and Smith 1989, Smith and Huston 1989). The second process – the performance sampling effect – is a prop-

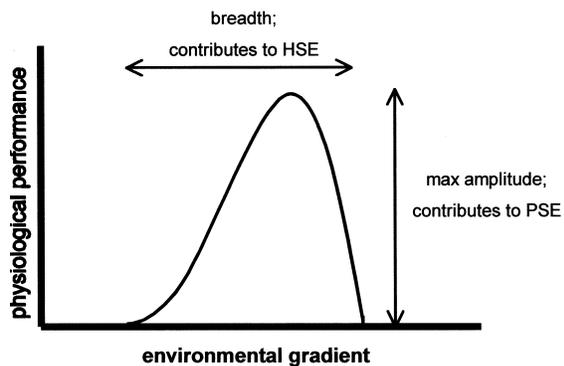


Fig. 1. Two dimensions of species niche distributions play a role in sampling effects – the habitat sampling effect (HSE) and performance sampling effect (PSE) – and their importance is determined by environmental conditions. Species tolerant of low resource levels typically perform better over a larger range of the gradient but have smaller maximum niche amplitudes; species of fertile habitats have high amplitudes but a narrower range of resource level tolerance (Smith and Huston 1989).

erty of the maximum size or growth rate of an individual, reflected in its maximum niche response (or amplitude) (Fig. 1). Here “performance” refers specifically to vegetative growth of an individual, and thus may not necessarily correlate with fitness. Often growth rate or mature size and competitive ability are correlated, particularly in fertile sites (Grime 1979; but see Newman 1973); the performance sampling effect is thus related to selecting species of greater competitive ability, at least for terrestrial plants. For organisms or habitats in which competitive ability and growth rate are negatively correlated and sufficient competitive exclusion occurs, ecosystem productivity may be reduced by diversity via a similar sampling phenomenon (Tilman 1999b).

The other two sampling effect components are functions of both the traits of the selected species and the community to which species are added. As such, they compose “biotic filters”, important aspects of community assembly rules (Wilson 1999). If two species within a species pool highly complement each other, for example, then a mixture that includes these two species might be expected to lead to enhanced productivity and they should stably coexist. The likelihood of pairing these species in mixture increases with the number of species drawn from the species pool (Hooper and Vitousek 1997) – a sampling effect for complementarity. In a similar manner, if a certain species in the species pool has a large facilitative effect on a few or all of the other community members, such as a N-fixer, the likelihood of including this species in a community increases with the number of species drawn (Wardle 1999, Huston et al. 2000) – a sampling effect for a facilitator.

Is the sampling effect an artifact or the analogue of an important natural process?

The crux of the debate over the validity of the sampling effect as a mechanism of the diversity effect is whether the methods of random species addition or deletion used in most diversity experiments are relevant to how species are added or deleted in non-experimental ecosystems. Obviously, species are not randomly added to agroecosystems or other such managed systems. Natural communities are also not assembled randomly – Watt (1947), Whittaker (1956), and many others illustrated the predictability of community composition along broad successional and environmental gradients long ago (Kershaw 1973). However, it is equally apparent that chance events sometimes play an important role in both species addition processes (immigration) and species deletion processes (extinction) (MacArthur and Wilson 1967, Roughgarden 1989). This is not to say that deterministic and stochastic processes have equal control over vegetation pattern; rather, commu-

nity composition in a particular ecosystem at a given time is predictable within certain bounds, but this precision varies among ecosystems. If, as an extreme example, future composition (constrained from a species pool) were completely unpredictable, one would wish to include all species to maximize productivity even if one species eventually came to dominate. It is this issue of compositional uncertainty that allows the sampling effect to be a mechanism of productivity enhancement in natural ecosystems. It then follows that the relevance of the sampling effect as a legitimate mechanism of the diversity effect is related to the degree to which immigration and extinction processes are stochastic for an ecosystem of specific environmental position and scale of observation.

Factors that influence the degree to which communities are deterministically or stochastically assembled are not well known and a complete discussion of this topic is not merited here. However, several researchers have explored the predictability of community composition along specific ecological gradients. It is thus appropriate to consider these examples and how the influence of the sampling effect might also be described along these gradients.

Variation in sampling effect importance with natural gradients of stochastic community assembly

One example of a natural gradient in the relevance of the sampling effect as a mechanism of the diversity effect is that stochastic events influence immigration and extinction processes to a greater degree in smaller areas than in larger areas. It has been empirically shown that the compositional predictability of plant communities increases from small to large sampling areas (Reed et al. 1993). Moreover, van der Maarel and Sykes (1993) introduced the "carousel model" in which many local species in a chalk grassland community colonized available microsites without apparent pattern, and composition in small plots (e.g., 2.5 m²) was unpredictable and highly unstable from year to year. Indeed, the plot size at which composition appears to have an important stochastic component in herbaceous plant communities is the scale at which nearly all diversity-productivity studies have been conducted (ca m²). Therefore, processes akin to sampling effects in experiments appear to be operating in some natural ecosystems, at least for small areas.

A similar gradient of stochasticity appears to be operative along a temporal continuum, whether in terms of biotic change (e.g., succession) or environmental fluctuation. Several researchers, for example, have suggested that the predictability of species composition increases with time after the onset of succession (Margalef 1963, Kershaw 1973, Peet 1992). For example, del

Moral and Wood (1993) reported that composition was largely unpredictable in the first years of primary succession on Mount St. Helens. Given suitably constant environmental conditions, greater compositional predictability through time suggests that the sampling effect will influence plot productivity to a greater extent in earlier measurements of yield, and less so as plot composition converges on a predictable yet dynamic assemblage (Peet 1992). On the other hand, the variance of observed conditions increases with time, and in a fluctuating environment that causes corresponding fluctuations in composition, the sampling effect should become a greater influence on total productivity as the duration of observation increases (and is the opposite of that predicted for increases in spatial area). Thus, in a time interval of relatively stable environment, the role of the sampling effect should decrease with time, but in scenarios of greater environmental fluctuation, the role of the sampling effect should depend upon the relative influences of compositional convergence (from succession) and stochastic environmental change.

Ecosystems can also be placed along a gradient of human management intensity, and stochastic processes are greatly reduced in intensively managed systems. The sampling effect plays little to no role in agricultural systems where the abundances of crop species are highly regulated and random assembly processes are all but eliminated from the management regime. The same is true, although to a lesser degree, in foraged grasslands and forests managed for timber production. It is incorrect, however, to assume that agricultural management precisely regulates species performance, as agroecosystems vary widely in their complexity and natural autonomy (Swift and Anderson 1993). There are conditions in which a sampling effect process may be significant. For example, crop diversification, and agricultural diversification in general, is deemed enormously important in terms of risk minimization (Vandermeer et al. 1998), and this results from future environment unpredictability – an argument very similar to those involving the importance of biodiversity for buffering productivity in natural ecosystems (Tilman 1999a, Yachi and Loreau 1999). Thus, although the influence of the sampling effect on ecosystem productivity may be small in managed ecosystems in general, it may be more informative to place a given system along a gradient of management intensity, from highly managed ecosystems to relatively stable natural ecosystems to communities generally regarded as highly unstable.

The necessary emphasis on ecological scale in deciding whether the sampling effect is relevant in non-experimental ecosystems becomes especially apparent in the examination of the interaction of regional and local processes governing both species diversity and local ecosystem productivity. At the local or neighborhood scale (say, m²) and at small temporal scales, productivity may indeed be highly dependent upon which species

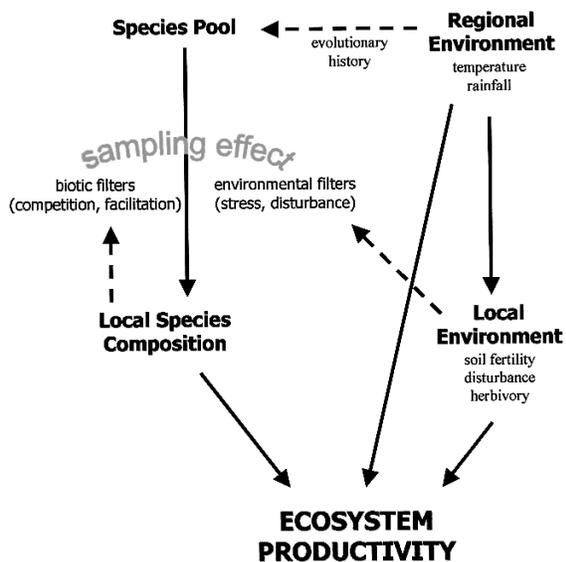


Fig. 2. Factors that influence ecosystem productivity. Main controls of productivity include regional and local environmental conditions, such as temperature, rainfall, and soil fertility. Species also control ecosystem productivity, and species composition is determined by the diversity and composition of the species pool, which is then “filtered” by the local environment and biota (indicated by dashed lines). In this way, species diversity, at least in terms of the size of the species pool, may influence ecosystem productivity (a “natural” sampling effect).

are there, not how many are there (Aarssen 1997, Garnier et al. 1997, Huston 1997). Which species are present at this scale is a function of environmental conditions, including resource availability and disturbance regime, and the nature and intensity of local biotic interactions (which in turn are strongly influenced by environment) (Grime 1973, Huston 1979, Grace 1999) (Fig. 2). Importantly, however, the composition and diversity of the pool of potential colonizing species (“species pool”) also affects local species composition and diversity (Cornell and Lawton 1992, Pärtel et al. 1996, Cornell 1999, Huston 1999 but see Austin 1999). (As used here, “species pool” is defined as the set of species that may potentially survive in and disperse to a particular community, defined as the “local pool” in Pärtel et al. 1996.) Thus, at the scales at which nearly all diversity experiments have been conducted, there may be little reason to expect local diversity to enhance productivity, but the size and composition of the species pool may affect local production by controlling which species are available for colonization – a process analogous to the experimental sampling effect. By using experimental species richness treatments as treatments of species pool size, however, small-scale diversity-productivity studies have the potential to provide insight into natural “sampling” processes.

The distinction between local diversity and species pool diversity

Species diversity has been most often modeled as responding to site productivity, not affecting it (Grime 1973, Huston 1979, Tilman 1982), and abundant evidence supports a unimodal (“hump-backed”) relationship between local species diversity and standing biomass (Grace 1999). The general model illustrated in Fig. 2, however, potentially resolves this paradox by recognizing that the two opposite pathways of causation are actually employing two different scales of diversity – local diversity in the case of the hump-backed model and the diversity of the species pool in the case of the diversity-productivity effect. This is because local diversity is largely a function of local environmental conditions, most notably fertility and disturbance levels as predicted by the hump-backed model. However, a proportion of the variance in total productivity levels among habitats is explained by *which* species are present, and this is in turn a function of the composition and diversity of the species pool. Therefore, a large portion of the variance in local species diversity among habitats is explained by site conditions, manifest as productivity; a smaller portion of the variance in local habitat productivity is explained by local species composition, determined in part by the size of the species pool via the sampling effect. High species pool diversity provides a greater array of species (and species traits) that environments and communities may “select” from; all else equal, diverse species pools are more likely to contain species of higher growth rates than smaller pools and are more likely to contain species better adapted to a greater array of environmental conditions. Therefore, by reducing species pool diversity, global species extinctions weaken the ability of the sampling effect to regulate local productivity (and ecological processes in general), and especially in response to global environmental change that is forcing local biotic communities to quickly adapt to radically new local environments (Bazzaz 1996).

Rather than describe the relationship between local diversity and productivity, diversity-productivity experiments conducted to date appear to better address the relationship between local productivity and species pool diversity. Nearly all diversity-productivity studies have constructed diversity treatments using seeded diversity, and several do not report measurements of “realized” diversity (e.g., Naeem et al. 1994, 1995, 1996, Tilman et al. 1997a, Symstad et al. 1998, van der Heijden et al. 1998, Hector et al. 1999). This is partially because most of these studies were conducted over short durations (Naeem et al. 1996, 2 months; Symstad et al. 1998, 4 months; Naeem et al. 1994, 206 days) and a “final” diversity measurement may not have indicated equilibrium species diversity. In this context, “species richness” in these experiments closely resembled a seed

influx from a species pool, from which the local environment and biota “sampled” to achieve a realized diversity level. (In several experiments, however, species composition was artificially constrained by weeding, e.g., Tilman et al. 1996, Hooper 1998.) To explore the relationship between local diversity and productivity, one would first have to construct different levels of realized diversity – that is, levels reasonably stable over the life span of the component species.

Given the important natural role for the sampling effect via species pool diversity and local filtering processes, how can this be best reflected in the design of artificial experiments? First, experimental treatments of seeded species diversity should be viewed as treatments of varied species pool sizes. The most diverse treatments represent the case where all species are available to colonize a site, and the most species-poor plots represent the most depauperate species pools. By monitoring species composition through the course of the experiment, it can then be determined to what extent the local environment and biota select from the immigrants, and to what extent competitive or facilitative relationships among species affect realized composition. This local assembly process will influence species composition, local diversity, and plot productivity. Second, although experiments at small spatial scales may best reflect scales at which assembly processes in nature are more stochastic than deterministic, this may be trivial because species composition at these scales is often unstable at the scale of a year or more. Moreover, composition may strongly vary with different rates of propagule supply (e.g., via mass effects; Schmid and Ellner 1984) and experiments should be performed that compare single seed additions with a constant rate of seed addition. Finally, the strong interaction between local biotic and environmental controls of ecosystem productivity suggests that there is a compelling need to perform diversity experiments among a range of environmental conditions both among and within plots.

Separating the sampling effect and other mechanisms: the use and misuse of overyielding

Because the influence of the sampling effect on ecosystem productivity is sensitive to ecological context, it is necessary to separate its effect from the biological interactions of a realized diversity level. Such interactions may be grouped as either those complementary or facilitative, and their net effect quantified as “overyielding”. In general, if a plant mixture performs better than its monocultures, it overyields, but there is confusion over which quantities to compare in its calculation. For example, one might compare the absolute yields of mixtures and monocultures, and define overyielding as either: 1) the event where a crop mixture produces greater yields per unit area than the average yield of its

component monocultures (Tilman 1999a); or 2) the event where a crop mixture outperforms its most productive component monoculture per unit area (Garnier et al. 1997, Hector 1998, Hector et al. 1999), also referred to as “transgressive overyielding” (Trenbath 1974). The distinction between these two types of overyielding is illustrated in Fig. 3. In addition, one might instead compare “relative yields” by dividing a species yield in mixture by its monoculture yield, either at equal total densities (as in a replacement series; de Wit 1960) or equal specific densities among richness treatments (as in an additive design; Harper 1977). The sum of relative yields for all species in mixture is an indicator of complementarity and facilitation (e.g., values over unity in replacement series designs; Vandermeer 1989). Because the quantification of overyielding is crucial to mechanistically explore the influence of species diversity on productivity, the most appropriate operational definition of overyielding must be resolved.

Any investigation of overyielding must first state the goal of the analysis, because different hypotheses are tested depending upon which yield values are compared among treatments. For example, from a farmer’s perspective, it may be most profitable to compare the absolute yields of all crop treatments, and statistically determine the assemblage with the highest total yield per unit area. In this case, transgressive overyielding appears the best candidate for measuring yield advantage – unless a mixture yields transgressively, an “all-knowing” manager could maximize productivity with the most productive monoculture (Tilman et al. 1997b). Indeed, several researchers have argued that transgressive overyielding is the most appropriate indicator of enhanced productivity in more diverse assemblages

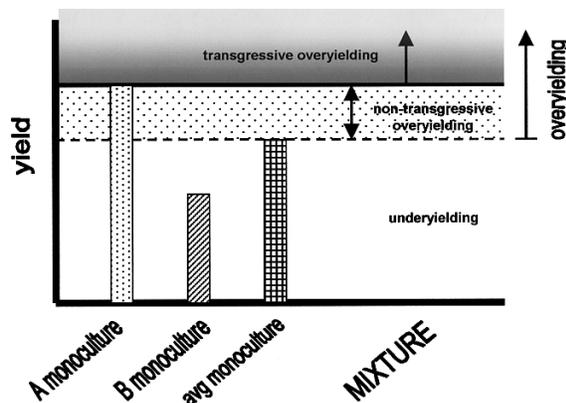


Fig. 3. Illustration of the two types of overyielding (adapted from Hector 1998). Two monocultures of different total yields are plotted, A and B, and their average yield is indicated. If a mixture of A and B at the same total density yields between the maximum yielding monoculture (in this case A) and the average monoculture yield, it overyields but non-transgressively. If the mixture yield is greater than that of the most productive monoculture, it transgressively overyields (Trenbath 1974). Underyielding is also possible.

Table 1. Illustration of the species size-disparity dependence of transgressive and non-transgressive overyielding. The degree of complementarity is the same in both scenarios.

Scenario 1:	species A achieves 10% greater biomass in mixture						
	monoculture size of A individuals = 100 g						
	monoculture size of B individuals = 50 g						
	constant density of 10 plants per plot in replacement series						
A mono	B mono	A poly	B poly	avg(mono)	max(mono)	mixture yield	RYT
1000 g	500 g	550 g	250 g	750 g	1000 g	800 g	0.55+0.5 = 1.05
Scenario 2:	species A achieves 10% greater biomass in mixture						
	monoculture size of A individuals = 100 g						
	monoculture size of B individuals = 95 g						
	constant density of 10 plants per plot in replacement series						
A mono	B mono	A poly	B poly	avg(mono)	max(mono)	mixture yield	RYT
1000 g	950 g	550 g	475 g	975 g	1000 g	1025 g	0.55+0.5 = 1.05

(Garnier et al. 1997, Loreau 1998b, Huston et al. 2000), and it is obvious that if a mixture yields more than the most productive monoculture, a mechanism other than simply including the most productive species must be operating.

In diversity-productivity experiments, however, it is important to identify the mechanisms by which diversity may influence productivity, and there are several reasons why comparison of absolute yields among treatments, as performed in the calculation of transgressive overyielding, is not the most accurate method for exploring mechanisms of a putative diversity effect. Indeed, it is well-appreciated by agronomists that although there are myriad ways to compare yields in mixture experiments, relative yields, and particularly use of the Relative Yield Total (RYT; equivalently, the Land Equivalent Ratio), are the most robust estimators of overyielding mechanisms (de Wit 1960, de Wit and van den Bergh 1965, Trenbath 1976, 1978), although even RYT is not without its problems (e.g., allelopathy; Trenbath 1976, Loreau 1998b).

One major problem with using absolute yields to quantify overyielding is that the difference between non-transgressive and transgressive overyielding can be caused entirely by the size difference between species, independent of the degree of complementary resource use (or facilitative interaction). This point is illustrated in Table 1 by comparing two scenarios in which the level of niche complementarity between two species is held constant and only the mature size difference is altered. In both scenarios, species A attains 10% greater biomass per individual in mixture compared to monoculture because it can exploit, for example, additional organic nitrogen in the soil. Individuals of species B, however, attain the same biomass in mixtures as in monocultures. In Scenario 1, individuals of species A have an average monoculture size of 100 g; individuals of species B, 50 g. Because A and B are slightly complementary in their use of soil N, species A overyields in mixture and the RYT of the mixture is above unity (1.05) (Vandermeer 1989). The mixture yield, however, is only slightly above the average yield of the two component monocultures (800 g compared

to 750 g) – far from the transgressive boundary of 1000 g. In Scenario 2, however, the level of complementarity is the same but the monoculture average sizes of the species are similar: 100 g and 95 g for A and B, respectively. In this case, though the complementary use of resources is the same (the RYT is still 1.05), the mixture yields transgressively (1025 g). Thus, the difference between transgressive and non-transgressive overyielding may be due entirely to the size disparity of component species, not the degree of complementary resource use or facilitative interaction.

Instead, to best estimate complementarity or facilitation and remove the influence of certain species asserting dominance in mixtures, one must show that the enhanced response of one species in mixture is not compensated for by a proportional decrease in another. This indicates that additional resources used by one species in mixture are not completely denied to others (Trenbath 1974). This can happen by means of resource partitioning (complementarity) or supply of new resources by neighboring species (facilitation). Such non-compensatory responses are obscured when comparing absolute yields among diversity treatments, but are exposed with the use of relative yields (such as RYT), which were designed for the purpose of robustly estimating complementary and facilitative species interactions (de Wit and van den Bergh 1965, Vandermeer 1989).

Another potential hazard in the assessment of relationships between species diversity and mechanisms that cause overyielding is inevitable sampling effects for certain species or combinations that are complementary or facilitative. More diverse mixtures make the inclusion of such species or combinations more probable, and the resulting productivity increase is not the result of a particular realized diversity level but rather the presence of one or a few species from the initial species pool. The problem is especially troublesome because overyielding metrics will (correctly) indicate the occurrence of complementarity or facilitation in assemblages containing the special facilitator or complementary pair but not necessarily be able to identify its cause. The few diversity studies that have quantified overyielding have

apparently not appreciated the significance of this problem – again consider the analysis of Hector et al. 1999 where the significant effect of functional richness was likely a sampling effect for legume inclusion. The problem could be corrected by a technique similar to that of single-species relative yields; instead of comparing single-species yields among diversity treatments, the mixture yields could be compared to specific biculture yields. However, this would require growing plots of all possible bicultures, which may be impossible in experiments of high diversity (e.g., 190 unique biculture assemblages in an experiment of 20 species), and does not account for the role of special facilitators whose effect may not be species-specific. In these cases, it would be advantageous for the most diverse mixtures to include all species except one, including replicates for all one-species removals.

In what context does diversity or composition influence ecosystem productivity?

Given the dominant role of environmental factors as regulators of both ecosystem productivity and local diversity, it is surprising that several researchers have suggested the expectation of a single, universal relationship between diversity and productivity, regardless of environmental position (e.g., Hector et al. 1999). The recognition that the nature and intensity of species interactions change with environmental context has a long history in ecology (DeCandolle 1820, cited in Clements et al. 1929). Because these same processes underlie the functional response of ecosystems to varied levels of species diversity, it is reasonable to predict that the influence of diversity on productivity is also sensitive to attributes of the surrounding environment.

A good illustration of the interaction between mechanisms of the diversity effect and local environmental conditions is the hypothesized sensitivity of the magnitude of facilitative plant interactions along gradients of environmental stress. It has been suggested that the outcome of plant interaction is the net result of competitive and facilitative processes, with facilitation most important in more stressful habitats such as deserts and salt marshes (Bertness and Callaway 1994). This suggests that, if facilitative relationships among species are a potential means by which diversity influences productivity, such an influence would be most apparent in stressful or resource-poor environments, and particularly those of severe water stress (Fowler 1986). Diversity-productivity experiments have generally not been conducted in such environments, and facilitation in stressful habitats as a diversity effect may be more significant than these studies have indicated.

The role of complementarity as a driver of the diversity effect should also be sensitive to local environmental conditions. Because the importance of complementarity is dependent upon the spatial and temporal heterogeneity of resources and other environmental factors (Tilman 1999a), the role of complementarity as a determinant of community structure and function should increase with environmental heterogeneity. For example, spatial resource heterogeneity should promote the ability of different species to partition resources (Tilman 1982), a process often invoked as a mechanism of species coexistence (Tilman 1982, Pacala and Tilman 1994) but similarly used to predict an increase in complementarity with the variance of resource conditions (Tilman et al. 1997b). This assumes heterogeneity exists at the scale of species response (Bell and Lechowicz 1994) and conditions do not lie outside the range of physiological tolerances of component species.

The relevance of the sampling effect as a mechanism of the diversity effect, described above, is dependent upon ecosystem scale and the degree of stochasticity in community assembly processes. Because sampling effect processes are affected by species interactions, certain aspects of the sampling effect may also be sensitive to environmental gradients. In particular, the influences of the performance and habitat sampling effects on ecosystem productivity may change along an environmental gradient, and in opposite directions. Consider the expected differences of species niche distributions along a resource gradient (Austin and Smith 1989) (Fig. 4A). All species enjoy high, non-toxic resource levels but relatively few have adapted tolerance to low resource levels (“stress” sensu Grime 1974). Under this scenario, randomly selecting a species that fits the environmental conditions of a plot should only be relevant at the lower end of the resource gradient and the upper end of toxicity. This suggests that the habitat sampling effect becomes a more important component of diversity’s role in ecosystem productivity as resource stress increases (Fig. 4B). At the stressful ends of the resource gradient, however, species have inherently low growth rates (Lambers et al. 1990), and the importance of selecting a species with higher inherent productivity (the performance sampling effect) should increase with resource levels (in the non-toxic region) (Fig. 4B). As apparent in Fig. 4B, these two facets of the sampling effect may mirror each other along a resource gradient due to the evolutionary trade-offs associated with stress tolerance versus growth rate and competitive ability (Grime 1977). Because niches should be distributed differently along regulator gradients (regulators being environmental factors that affect plant growth and survival but are not consumed; e.g., temperature, salinity, pH; Austin and Smith 1989), so too should the importance of the sampling effect (Fig. 5).

Conclusion: why worry about species diversity and productivity in non-agricultural ecosystems?

Within the context of the diversity-productivity debate, there has been surprisingly little discussion about the relevance of ecosystem productivity as an appropriate management concern. On the one hand, half of the terrestrial biosphere is managed for productivity (Pimentel and Kounang 1998). In these ecosystems, maximizing productivity is of obvious importance; it is necessary to meet the demands of the expanding human population and increase the efficiency of natural resource use by minimizing total land use and providing for long-term resource sustainability. In many of these ecosystems, however, species composition is tightly controlled by managers, and the only mechanism of enhanced productivity that appears to be directly attributable to species diversity, the sampling effect, is precluded by non-random human control of composition. Rather, species combinations that are facilitative

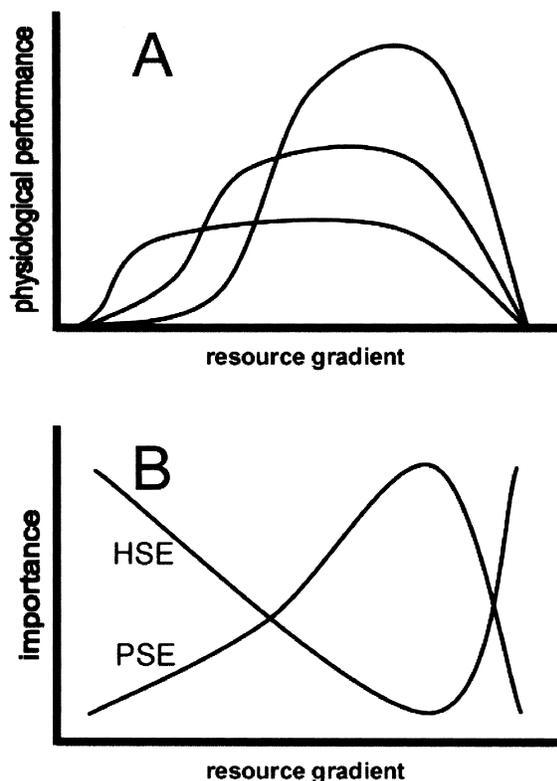


Fig. 4. A) Expected niche distributions of species along a resource gradient, adapted from Austin and Smith (1989). B) Predicted distributions of the importance of the habitat sampling effect (HSE) and the performance sampling effect (PSE) along a resource gradient in randomly assembled diversity experiments based on the niche distributions of figure A. Note that the two types of sampling effect may mirror each other along the gradient.

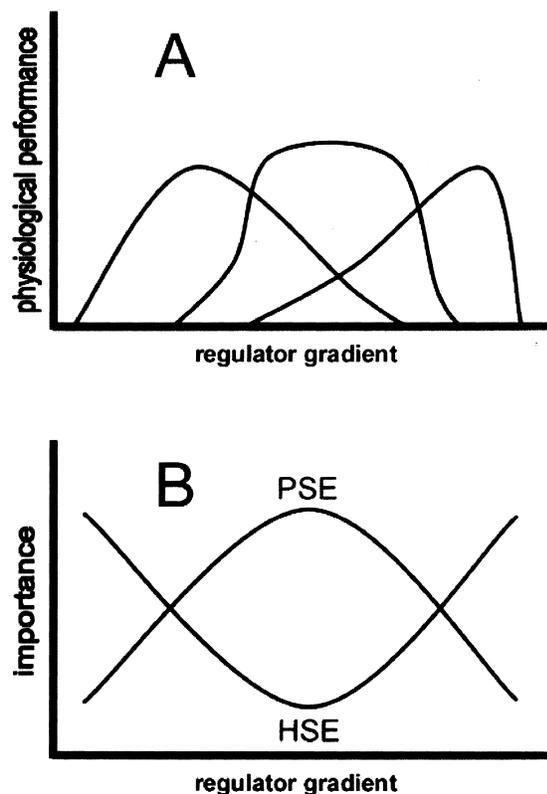


Fig. 5. A) Expected niche distributions of species along a regulator gradient, adapted from Austin and Smith (1989) and Huston (1994). B) Predicted distributions of the importance of the habitat sampling effect (HSE) and the performance sampling effect (PSE) along a regulator gradient in randomly assembled diversity experiments, based on the niche distributions of (A). Note that the two types of sampling effect may mirror each other along the gradient.

and complementary are selected to maximize production levels (Swift and Anderson 1993, Altieri 1999). Thus, in half of all terrestrial ecosystems, the ecosystems in which productivity is of overwhelming importance, diversity may play a negligible role in ecosystem productivity.

In the other half of the terrestrial world exist “natural” ecosystems that are managed (if at all) for species or habitat conservation. Productivity in these areas is typically lower and species diversity higher than in agricultural areas, because agriculture has been most successful in fertile areas and species diversity at the local scale is maximized at relatively low fertility levels (Huston 1993). Indeed, anthropogenic resource enrichment in historically unproductive habitats is a serious threat to biodiversity (Vitousek et al. 1997). It may be asked, then: To what extent is the maximization of productivity in these habitats desirable? Diversity may indeed play an important role in the regulation of productivity in these habitats, most notably via the sampling effect and the size of species pools, but is

productivity in these habitats an appropriate management concern? It may be that where ecosystem productivity is a relevant ecosystem property of applied concern, its dependence on diversity is largely made inoperative by intensive regulation of known, productive species assemblages; and where diversity may influence productivity (via the sampling effect), productivity is of little applied importance.

What then are the appropriate goals of experiments investigating diversity-productivity relationships? To start with, it would be beneficial to acknowledge at the outset of an experiment whether it is meant to inform intensely managed, human-dominated ecosystems or ecosystems in which composition is left to naturally fluctuate. This decision would then determine the most appropriate scales, environmental conditions, and species under which the experiment should be performed. For example, studies to inform agricultural systems can profitably be performed at small spatial and temporal scales (with of course advantages to larger scales), over a narrow range of fertile conditions, and with species most relevant to agriculture. In these studies, it is important to remove the sampling effect and quantify the overyielding of certain assemblages (although the sampling effect may still be important in highly fluctuating environments). Studies to inform natural systems are best performed at larger spatial and especially temporal scales, with species from a common species pool, and, most importantly, under a range of environmental conditions, incorporating resource heterogeneity both within and among experimental treatments.

It is also important to realize the limitations inherent in small-scale diversity-productivity studies that seriously hinder their ability to extrapolate to ecosystems of natural complexity. Such constraints may lead researchers to wrongly conclude that species diversity does not influence ecosystem productivity (and ecosystem function in general). If this is true, then experiments that employ larger amounts of environmental complexity (e.g., resource heterogeneity, environmental fluctuation) should more aptly demonstrate the relationship between diversity and function and perhaps help resolve the diversity-function debate. Indeed, there is emerging consensus that global environmental change is producing a significant role for biodiversity as a stabilizer of ecosystem processes (Schläpfer et al. 1999, Schwartz et al. 2000), largely because the nature of future environments is, for the most part, unknown (Mitchell and Hulme 1999). Stochasticity in community assembly and species composition is the driver of a diversity effect for static ecosystem properties via the sampling effect, and environmental heterogeneity promotes species complementarity as a diversity effect mechanism. Thus, the importance of biodiversity for the functioning of ecosystems appears closely coupled to environmental unpredictability and complexity, and there remains a great need for researchers to explore

these relationships by incorporating greater levels of environmental complexity in their experiments.

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