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# Does Species Richness Drive Community Production or Vice Versa? Reconciling Historical and Contemporary Paradigms in Competitive Communities

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ABSTRACT: Studies examining the relationship between species richness and the productivity of ecological communities have taken one of two opposite viewpoints, viewing either productivity as a primary driver of richness or richness as a driver of productivity. Recently, verbal and graphical hypotheses have been proposed that attempt to merge these perspectives by clarifying the causal pathways that link resource supply, species richness, resource use, and biomass production. Here we present mathematical models that formalize how these pathways can operate simultaneously in a single ecological system. Using a metacommunity framework in which classic consumer-resource competition theory governs species interactions within patches, we show that the mechanisms by which resource supply influences species richness are inherently linked to the mechanisms by which species richness controls resource use and biomass production. Unlike prior hypotheses, our models show that resource supply can affect species richness and that richness can affect productivity simultaneously at a single spatial scale. Our models also reproduce scale-dependent associations between species richness and community biomass that have been reported elsewhere. By detailing the pathways by which resource supply, species richness, biomass production, and resource use are connected, our models move closer to resolving the nature of causality in diversityproductivity relationships.

Keywords: biodiversity, community productivity, ecological theory, metacommunity, resource competition.

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One of the oldest questions in ecology is that of how species diversity relates to the productivity of ecosystems. Researchers have pursued this question from two fundamentally different viewpoints. Historically, differences in productivity among communities or ecoregions have been viewed as drivers of differences in biodiversity (Rosenzweig and Abramsky 1993). In this perspective, variation in species richness among sites is thought to result from differences in the supply of vital resources. In these investigations, a variety of patterns have emerged. Two of the most common have been a hump-shaped (i.e., unimodal) relationship, where species richness is highest at intermediate levels of productivity, and a monotonically increasing relationship, where richness increases as productivity increases. The mechanisms of coexistence that underlie these relationships (Tilman and Pacala 1993; Abrams 1995), the scales at which those mechanisms operate (Gross et al. 2000; Chase and Leibold 2002), and the generality of the patterns observed (Waide et al. 1999; Mittelbach et al. 2001) all continue to be the subjects of considerable research.

In recent years, ecologists have begun to view the relationship between diversity and productivity from a fundamentally different angle (Naeem 2002), examining how biodiversity controls, rather than responds to, biomass production. A growing number of experiments have assembled communities that differ in species richness and examined how this aspect of diversity affects the efficiency by which those communities capture resources and convert them into new tissue (e.g., Naeem et al. 1994; Tilman et al. 1997; Hector et al. 1999). Recent reviews of this body of work have shown surprising generality across a wide variety of trophic groups and ecosystems (Schwartz et al. 2000; Schmid et al. 2001; Covich et al. 2004; Cardinale et al. 2006b; Srivastava and Vellend 2006). When species richness has been experimentally manipulated, the average effect of increasing richness is to increase both the production of biomass and the depletion of resources. However, the dominant mechanism(s) underlying these diversity ef-

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fects continues to be a topic of controversy (Huston 1997; Loreau et al. 2001; Cardinale et al. 2006*b*; Srivastava and Vellend 2006).

The contrast between the historical and contemporary perspectives on diversity-productivity relationships has engendered a lively debate about whether species richness is a cause or consequence of ecosystem productivity (Huston 1997; Grime 1998; Loreau et al. 2001; Fridley 2002; Schmid 2002; Worm and Duffy 2003). As this debate has progressed, several researchers have hypothesized that diversity and productivity must feed back somehow to influence each other. For example, Loreau et al. (2001) and Schmid (2002) both proposed that the supply of vital resources (or "fertility" in Schmid's terminology) determines the maximum number of species that a landscape can support, but the actual richness present determines how efficiently available resources are converted to biomass. Loreau et al. (2001) suggested that these two perspectives operate at different spatial scales—differences in the supply of vital resources drive differences in species diversity across habitats or ecosystems, while biodiversity affects resource use and biomass production within habitats or ecosystems. Hypotheses such as these that embody both perspectives of causality in diversity-productivity relationships have begun to take heuristic form and to be empirically tested in simple model systems (Cardinale et al. 2006a). However, clear mathematical theory is currently lacking.

Here we present mathematical models that simultaneously embody the effect of resource supply on species richness and the effect of species richness on resource use and biomass. Our models use the metacommunity framework that has become increasingly popular in recent years (Amarasekare et al. 2004; Leibold et al. 2004; Holyoak et al. 2005). In this framework, species grow and interact as a local community within patches, and these patches are connected to each other by dispersal. The entire collection of dispersal-connected patches is called the metacommunity (Wilson 1992; Leibold et al. 2004). In our models, species compete for two resources within each patch, and competition for resources is governed by classic consumerresource models of competition (Tilman 1982, 1988; others). The power of this modeling approach is that it allows us to manipulate the supply of limiting resources directly and then relate this to species richness and biomass at both local (single patch) and regional (entire metacommunity) scales. Embedding explicit resource competition within a metacommunity framework is an idea that has recently proved useful for examining other ecological phenomena, such as how resource heterogeneity and dispersal affect species coexistence (Loreau et al. 2003; Abrams and Wilson 2004; Shurin et al. 2004; Mouquet et al. 2006).

In what follows, we analyze our models in two stages. In the first stage, we examine relationships between resource supply, species richness, and the production of biomass at the scale of single patches (i.e., species competing within local communities) embedded in a single metacommunity. In the second stage, we scale up our analyses to a regional perspective, examining how these relationships change as a function of resource supply and species richness in entire metacommunities. For clarity as well as mathematical tractability, we begin with the simplest possible metacommunity—one that contains two species (species 1 and 2) that interact and compete for two essential resources (resources 1 and 2). This is obviously an oversimplification of nature, but it is useful because it provides the clearest illustration of mechanisms that are likely to be broadly applicable. We then extend this two-species model by adding a species that persists regionally via a competition-colonization trade-off (Levins and Culver 1971; Hastings 1980; Tilman 1994). Adding more species and resources to these models is conceptually straightforward but mathematically taxing and unlikely to change our primary conclusions. Our models formalize Loreau et al.'s (2001) and Schmid's (2002) hypotheses that productivity can drive diversity and diversity can drive productivity simultaneously, and they generate new insights by merging historical and contemporary paradigms into a single mathematical framework.

# Metacommunity Models with Local Competition for Two Resources

## Conceptual Overview

These metacommunity models consist of an infinite collection of patches that vary in their supplies of two essential resources. We define a patch to be a locality that can support multispecies communities with many individuals (Leibold et al. 2004). The models are spatially implicit, in the sense that patches are not assigned spatial coordinates, and thus dispersal is no more likely between one pair of patches than it is for any other pair. Within patches, species compete for and consume resources and convert these resources to biomass. Classic resource-ratio theory determines which species can exist or coexist within a patch. Among-patch dynamics are determined by the balance between colonization and extinction. Colonization occurs via propagules that are produced and disperse at a constant per capita rate, while extinctions are caused either by abiotic disturbances or by the arrival of a superior competitor.

We consider two different scenarios in which resource supply varies among patches. In one scenario, we assume that the supply of one resource is the same everywhere, while the supply of a second resource varies among patches. This scenario might, for example, represent a collection of patches that differ in the supply of a single limiting resource (e.g., nitrogen to a grassland), perhaps as the result of human activity (e.g., fertilization), while the supply of all other important resources does not vary. Some have suggested that such a scenario is unrealistic because an increase in the supply of one resource often causes another resource to become limiting (Tilman 1982; Huston and DeAngelis 1994). Thus, our second scenario assumes a trade-off between the two resources, where the total resource supply is the same everywhere but patches differ in the relative supply of the two resources. This might, for example, mimic the case where nitrogen additions stimulate the production of biomass to the extent that light becomes a limiting resource to grassland plants. We refer to these as the "no-trade-off" and "trade-off" scenarios, respectively.

Like many other metacommunity models (Hastings 1980; Tilman 1994; Leibold et al. 2004 and references therein), our models assume a separation of timescales between the within-patch (local resource consumption and competition) and among-patch (disturbance and dispersal) dynamics. That is, we assume that the within-patch consumer-resource dynamics are sufficiently fast that they achieve equilibrium instantaneously relative to the amongpatch colonization and extinction dynamics. One consequence of separating timescales in this manner is that when local coexistence does occur, it arises purely from local niche partitioning. This distinguishes our models from those with source-sink dynamics (Loreau et al. 2003; Mouquet and Loreau 2003), where an inferior competitor can persist in a patch with a superior competitor because its population is continually replenished by propagules from a source population.

Mathematical Development of the Model with Two Species

To build the equations for a model with two species, we start by considering resource competition in a single patch. Let  $n_i(t)$  be the density of species i in a single patch, i = 1, 2, and let  $R_j(t)$  be the amount of resource j available in that patch, j = 1, 2. The equations governing  $n_i(t)$  and  $R_j(t)$  are

$$\frac{1}{n_i} \frac{dn_i}{dt} = f_i(R_1, R_2) - m_i, 
\frac{dR_j}{dt} = a(S_j - R_j) - \sum_i c_{ij} f_i(R_1, R_2) n_i.$$
(1)

In equation (1),  $f_i(R_1, R_2)$  and  $m_i$  are the per capita growth and mortality rates of species i, respectively; a is a constant that scales the resource turnover rate;  $S_j$  is the supply of resource j (equal to the equilibrium amount of resource j when no consumers are present); and  $c_{ij}$  is the amount

of resource j consumed for each unit of biomass produced by species i. The specific functional form of  $f_i(R_1, R_2)$  does not influence our conclusions as long as  $f_i$  is continuous and increasing in  $R_1$  and  $R_2$ . However, to be concrete, we make  $f_i(R_1, R_2)$  the standard combination of Monod equations (Monod 1950) and von Liebig's (1840) law of the minimum, that is,

$$f_i(R_1, R_2) = \min_{i} \left\{ \frac{r_i R_j}{K_{ii} + R_i} \right\}.$$
 (2)

In equation (2),  $r_i$  is the maximum per capita growth rate of species i and  $K_{ij}$  is the amount of resource j at which growth of species i is one-half of its maximum when all other resources are available in excess.

The model in equations (1) and (2) is well known in the ecological literature and has been exhaustively analyzed for two species competing for two resources (e.g., León and Tumpson 1975; Huisman and Weissing 2001 and references therein). The outcome of interspecific competition depends on the location of the competitors' zero net growth isoclines in  $R_1$ - $R_2$  phase space, their relative consumption of the two resources, and the supply of resources 1 and 2. In all of our simulations, parameter values are chosen such that coexistence is possible for some values of  $S_1$  and  $S_2$  (fig. 1; specifically, a = 1,  $r_1 = 2$ ,  $r_2 = 3$ ,  $m_1 = 1$ ,  $m_2 = 1.5$ ,  $c_{11} = c_{22} = 2$ ,  $c_{12} = c_{21} = 1$ ,  $K_{11} = K_{22} = 2$ , and  $K_{12} = K_{21} = 1$ ). With these parameter values, species differ in both their resource preferences (species 1 consumes more of resource 1, and species 2 consumes more of resource 2) and their rates of population turnover (species 2 has larger growth and mortality rates than species 1).

To facilitate analysis of this model, it is helpful to classify patches into six types based on whether resource supplies allow one or both species to exist within the patch at equilibrium (fig. 1). In type Z patches, resources are insufficient for either species to exist. In type A patches, species 1 can exist, but species 2 cannot. In type B patches, either species can exist when alone, but species 1 eliminates species 2 when both are present. Type C patches have resource supplies that allow both species to stably coexist. In type D patches, either species can exist when alone, but species 2 eliminates species 1 when both are present. Finally, in type E patches, species 2 can exist, but species 1 cannot.

To model the metacommunity dynamics, it is necessary to keep track of the proportion of patches occupied by one or both species. Because these proportions depend on the resource supply in a given patch, we use  $P_i(S_1, S_2, t)$  to denote the fraction of patches with resource supplies  $S_1$  and  $S_2$ , that are occupied by species i. For type C patches,

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 $P_{12}(S_1, S_2, t)$  is the fraction of patches with resource supplies  $S_1$  and  $S_2$  occupied by both species. Because of the separation of timescales, species densities within a patch are determined by the equilibria of equations (1) and (2). In notation, let  $n_i^*(S_1, S_2)$  denote the equilibrium density of species i in a patch with resource supplies  $S_1$  and  $S_2$  when only species i is present. In type C patches, let  $n_{12}^*(S_1, S_2)$ denote the equilibrium abundance of species 1 when species 2 is also present in the patch, and define  $n_{21}^*(S_1, S_2)$ similarly. The distribution of  $S_1$  and  $S_2$  among patches in the metacommunity is described by the density  $\phi(S_1, S_2)$ , which can be thought of as the joint probability density function of  $S_1$  and  $S_2$  for a randomly chosen patch. With these pieces in place, the total density of species i in the entire metacommunity, denoted  $N_i(t)$ , can be found by integrating the product of equilibrium densities and the proportion of patches occupied over  $\phi(s_1, s_2)$ :

$$N_{1}(t) = \iint_{s_{1}, s_{2}} P_{1}(s_{1}, s_{2}, t) n_{1}^{*}(s_{1}, s_{2}) \phi(s_{1}, s_{2}) ds_{2} ds_{1}$$

$$+ \iint_{s_{1}, s_{2} \in C} P_{12}(s_{1}, s_{2}, t) n_{12}^{*}(s_{1}, s_{2}) \phi(s_{1}, s_{2}) ds_{2} ds_{1},$$

$$N_{2}(t) = \iint_{s_{1}, s_{2}} P_{2}(s_{1}, s_{2}, t) n_{2}^{*}(s_{1}, s_{2}) \phi(s_{1}, s_{2}) ds_{2} ds_{1}$$

$$+ \iint_{s_{1}, s_{2} \in C} P_{12}(s_{1}, s_{2}, t) n_{21}^{*}(s_{1}, s_{2}) \phi(s_{1}, s_{2}) ds_{2} ds_{1}.$$

$$(3)$$

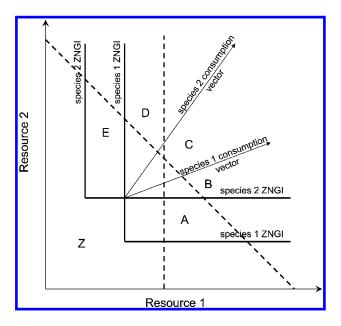
In equation (3), the notation  $s_1, s_2 \in C$  indicates that the second integral in each equation is taken over the values of  $S_1$  and  $S_2$  that correspond to type C patches.

Equipped with equation (3), we can write equations that describe how  $P_1(S_1, S_2, t)$ ,  $P_2(S_1, S_2, t)$ , and  $P_{12}(S_1, S_2, t)$  (for type C patches) change over time for each combination of  $S_1$ ,  $S_2$ . For example, in type A patches, the rate of change of  $P_1(S_1, S_2, t)$  is given by

$$\frac{dP_{1}(S_{1},S_{2},t)}{dt}=\alpha_{1}N_{1}(t)[1-P_{1}(S_{1},S_{2},t)]-\beta_{1}P_{1}(S_{1},S_{2},t)\quad S_{1},S_{2}\in\mathcal{A},$$

(4

where  $\alpha_1$  is the per capita colonization rate of species 1 and  $\beta_1$  is the rate at which abiotic disturbances cause single-patch extinctions. Equation (4) states that the colonization rate of type A patches by species 1 is equal to the per capita colonization rate,  $\alpha_1$ , times the total density of species 1,  $N_1(t)$ , times the proportion of patches that



**Figure 1:** Zero net growth isoclines (ZNGIs) and consumption vectors of two species competing for two resources. The dashed lines represent the two scenarios of environmental variation modeled, either the trade-off (*diagonal line*) or no-trade-off (*vertical line*) scenarios. Letters (A–E, Z) show the different patch types for each S<sub>1</sub>, S<sub>2</sub> supply point. Boundaries between patch types are determined by the ZNGIs and consumption vectors.

are eligible to be colonized. For type A patches, species 2 cannot exist, so the proportion of invasible patches is the proportion of vacant patches,  $1 - P_1(S_1, S_2, t)$ . Equation (4) holds for type B patches as well because the type B patches that are invasible by species 1 are the unoccupied patches plus the patches occupied by species 2, which is the same as  $1 - P_1(S_1, S_2, t)$ . Differential equations similar to equation (4) can be developed for  $P_1(S_1, S_2, t)$  in type C and D patches,  $P_2(S_1, S_2, t)$  in type B–E patches, and  $P_{12}(S_1, S_2, t)$  in type C patches. A full listing of equations is provided in appendix A.

Fortunately, this model can be simplified substantially by recognizing that equation (4) and related equations in appendix A are the same for all  $S_1$ ,  $S_2$  combinations that correspond to the same patch type. Therefore, if initial patch occupancy is the same for all patches of a given patch type, then the dynamics of those patches will be identical for all time. Consequently, it is not necessary to model patch occupancy for every  $S_1$ ,  $S_2$  pair; instead, it is necessary to model patch occupancy only for each patch type. Thus, the metacommunity model simplifies to one that has nine state variables:  $P_{A1}$ ,  $P_{B1}$ ,  $P_{C1}$ , and  $P_{D1}$ , the proportion of type A–D patches occupied by species 1;  $P_{B2}$ ,  $P_{C2}$ ,  $P_{D2}$ , and  $P_{E2}$ , the proportion of type B–E patches occupied by species 2; and  $P_{C12}$ , the proportion of type C

patches occupied by both species. The full set of equations for this metacommunity model is then (the time dependence of the P's and N's is suppressed for clarity):

$$\begin{split} \frac{dP_{A1}}{dt} &= \alpha_{1}N_{1}[1 - P_{A1}] - \beta_{1}P_{A1}, \\ \frac{dP_{B1}}{dt} &= \alpha_{1}N_{1}[1 - P_{B1}] - \beta_{1}P_{B1}, \\ \frac{dP_{C1}}{dt} &= \alpha_{1}N_{1}[1 - P_{C1} - P_{C2} - P_{C12}] \\ &+ \beta_{2}P_{C12} - [\beta_{1} + \alpha_{2}N_{2}]P_{C1}, \\ \frac{dP_{D1}}{dt} &= \alpha_{1}N_{1}[1 - P_{D1} - P_{D2}] - [\beta_{1} + \alpha_{2}N_{2}]P_{D1}, \\ \frac{dP_{B2}}{dt} &= \alpha_{2}N_{2}[1 - P_{B1} - P_{B2}] - [\beta_{2} + \alpha_{1}N_{1}]P_{B2}, \quad (5) \\ \frac{dP_{C2}}{dt} &= \alpha_{2}N_{2}[1 - P_{C1} - P_{C2} - P_{C12}] \\ &+ \beta_{1}P_{C12} - [\beta_{2} + \alpha_{1}N_{1}]P_{C2}, \\ \frac{dP_{D2}}{dt} &= \alpha_{2}N_{2}[1 - P_{D2}] - \beta_{2}P_{D2}, \\ \frac{dP_{E2}}{dt} &= \alpha_{2}N_{2}[1 - P_{E2}] - \beta_{2}P_{E2}, \\ \frac{dP_{C12}}{dt} &= \alpha_{1}N_{1}P_{C2} + \alpha_{2}N_{2}P_{C1} - [\beta_{1} + \beta_{2}]P_{C12}. \end{split}$$

Both  $N_1$  and  $N_2$  are given by equation (3). Equation (3) also simplifies, as shown in appendix A.

We investigated the behavior of the above model via simulations with various parameter combinations. In all simulations, we assume that both species had the same per capita colonization rate ( $\alpha_1 = \alpha_2 = 0.1$ ) and the same extinction rate ( $\beta_1 = \beta_2 = 0.01$ ). For the no-trade-off scenario, we assume that  $S_1 = 3$  for all patches but that patches differ in  $S_2$  (fig. 1, vertical dashed line). In the tradeoff scenario,  $S_1 + S_2 = 6$  for all patches (fig. 1, diagonal dashed line). In both cases, the values of  $S_1$  and  $S_2$  in a single patch are determined entirely by  $S_2$ , and so for brevity, we use only  $S_2$  to describe resource heterogeneity among patches. Although we cannot show analytically that this model has a unique nontrivial point equilibrium, all of our simulations rapidly approached a point equilibrium. We ran some of our simulations with multiple starting conditions and did not find any evidence of multiple equilibria.

## The Local Perspective: Comparing Patches within a Single Metacommunity

Our first set of simulations with this model examines how resource supply, species richness, resource use, and biomass are related at the scale of individual patches in a single metacommunity. For this analysis, we assumed that S<sub>2</sub> ranged from 0 to 6 among patches in the metacommunity and that the shape of its distribution among patches  $(\phi)$  was symmetric and triangular (i.e., a "tent" distribution, whose graph looks like an isosceles triangle resting on its base). We chose this distribution because it avoids the mathematical annoyances of a distribution that has infinitely long tails, such as a Gaussian distribution.

Figure 2A and 2B shows local species richness as a function of S<sub>2</sub> for a random sample of 100 patches selected from the metacommunity. Local richness is highest for patches with intermediate resource supply, indicating a hump-shaped or unimodal relationship between resource supply and richness. The discontinuous "stair-step" changes in richness in figure 2A and 2B occur because there are only two species in this model, and thus potential variation in richness is limited. With more species and resources, the pattern would appear more like a continuous curve. In figure 2, the hump-shaped pattern appears because both species can coexist in the same patch only when intermediate levels of resource supply allow niche partitioning to occur.

To determine how species diversity affects resource use and biomass production in this model, we simulated a typical diversity experiment where patches are planted with species 1 alone, species 2 alone, or both species together in polyculture. In these hypothetical experiments, diversity manipulations are preserved by buffering patches against the arrival of other propagules and extinction-causing disturbances. In each experimental plot, we allow competitive dynamics to proceed to equilibrium and then examine how the initial number of species planted in a patch (one vs. two) affects total resource use (defined as  $S_1 + S_2$  –  $R_1^* - R_2^*$ , where  $R_i^*$  is an equilibrium of eq. [1]) and aggregate biomass (defined as  $n_1^*$ ,  $n_2^*$ , or  $n_{12}^* + n_{21}^*$  as appropriate). We conduct these hypothetical diversity manipulations for patches spanning the entire range of resource supply values in the metacommunity.

Our results show that when resource supplies are too low or too high for species to coexist in the same patch (type A, B, D, and E patches), the more productive species planted in a patch outcompetes the less productive species. Consequently, the productivity of the patch planted as a polyculture ultimately comes to equal the productivity of the patch planted with the most productive species in a monoculture (fig. 2C-2F). This results in a pattern that is often called nontransgressive overvielding-the biomass

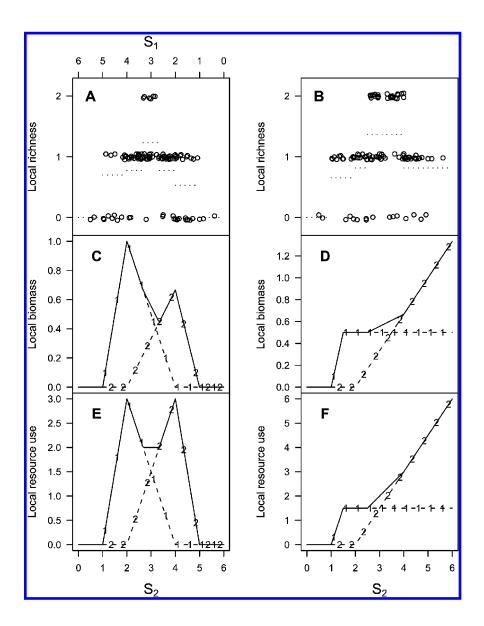


Figure 2: Species richness, biomass, and resource use for the two-species model at the patch (i.e., local community) scale as a function of resource supply. *A, B,* Richness versus resource supply for 100 patches sampled from the trade-off (*A*) and no-trade-off (*B*) metacommunities. A small amount of vertical jitter has been added to each data point for clarity. Dotted lines show the expected richness for each patch type. *C–F,* Local biomass (*C, D*) and resource use (*E, F*) versus local resource supply for patches initiated with one (*dashed lines*; numbers on lines indicate the species planted) or both (*solid line*) species. Left panels show the trade-off scenario, and right panels show the no-trade-off scenario.

and resource use of the two-species polyculture exceeds the average biomass and resource use of the two monocultures but is no greater than that of the most productive monoculture (see reviews by Fridley [2001] or Vandermeer [1989]). The mechanism driving this trend is the sampling effect of diversity, where increasing species richness increases the probability that the most productive species will be included in and ultimately come to dominate biomass and resource use in a patch (Huston 1997; Loreau and Hector 2001). Different results are observed in patches

with intermediate resource supplies (type C patches) where species are able to stably coexist within a patch via resource partitioning. In these patches, the biomass and resource use of the two-species patches exceeds the biomass and resource use of either species monoculture, resulting in transgressive overyielding. This pattern appears in both the trade-off and the no-trade-off scenarios.

Thus, at the scale of single patches where species compete directly for resources, resource supply mediates species richness by controlling the potential for niche parti-

tioning. Simultaneously, resource supply also indirectly controls the effect that species richness has on resource use and biomass. Indeed, both the magnitude of the effect of local diversity on resource use and biomass production (nontransgressive vs. transgressive overyielding) and the mechanism responsible for these effects (sampling effect vs. resource partitioning) depend on the resource supply in that patch. Thus, our model suggests that there is a fundamental connection between productivity-drivesdiversity and diversity-drives-productivity paradigms, as the niche partitioning mechanism that produces a humpshaped resource supply-diversity curve also determines the nature of the diversity-productivity relationship.

## The Regional Perspective: Comparing Different Metacommunities

Spatial scale has figured prominently in recent productivity-diversity research. Several recent studies have suggested that the effect of productivity on diversity depends on the scale at which productivity and diversity are measured (Waide et al. 1999; Gross et al. 2000; Mittelbach et al. 2001; Chase and Leibold 2002; Steiner and Leibold 2004). Similarly, recent mathematical models suggest that the effect of species richness on resource use and biomass production should be greater at regional as opposed to local scales (Loreau et al. 2003; Cardinale et al. 2004). In light of the potential importance of scale, we also use our model to investigate relationships between resource supply, species richness, resource use, and biomass at regional scales by comparing entire metacommunities to each other.

In these simulations, we compare metacommunities that differ in their distributions of resource supply among patches. In each metacommunity, we assume that  $S_2$  (and consequently  $S_1$  in the trade-off scenario) has a uniform distribution among patches. The average value of  $S_2$ , denoted  $S_2$ , varies from 1.5 to 4.5 among metacommunities, while the range of  $S_2$  among patches in a metacommunity is always 3. For example, metacommunities with the least regional supply of resource 2 ( $\overline{S}_2 = 1.5$ ) contain patches with S<sub>2</sub> ranging from 0 to 3, while metacommunities with the greatest regional supply of resource 2 ( $\overline{S}_2 = 4.5$ ) contain patches with  $S_2$  ranging from 3 to 6. In this way, we vary resource supply to all patches in a metacommunity without altering the degree of resource variation among patches.

To begin, we ask how regional resource supply affects regional diversity by finding the values of  $\overline{S}_2$  that allow both species to persist in the metacommunity. As figure 3A and 3B shows, both species can persist in the metacommunity only at intermediate values of  $\overline{S}_2$ . This occurs despite the fact that for all values of  $\overline{S}_2$  considered, there are always some type C patches present that provide possible habitat for both species. Only at intermediate values of  $S_2$  are both species able to produce enough propagules to offset patch-scale extinctions caused by abiotic disturbance. As a result, there is a unimodal relationship between resource supply and potential species richness at the scale of the entire metacommunity.

To determine how regional diversity affects regional biomass and resource use, we compared a metacommunity in which all patches were initiated with both species to metapopulations where all patches were initiated with each species in monoculture (fig. 3C-3F). At low or high values of  $\overline{S}_{2}$ , metacommunities initiated with both species ultimately become dominated by a single species, and the sampling effect of diversity again produces nontransgressive overyielding at the regional scale. At intermediate levels of  $\overline{S}_{2}$ , when both species are able to persist in the metacommunity, regional biomass and resource use of the metacommunity exceeds that of either metapopulation. Thus, at the regional scale of entire metacommunities, resource partitioning leads to transgressive overyielding whenever the balance of local colonization and extinction allows both species to persist in the metacommunity. Once again, both the form and the cause of diversity effects on resource use and biomass production depend on resource supply.

# Extending the Model: Three Species with a Competition-Colonization Trade-Off

To extend our model, we added a third fugitive species (species 3) that is an inferior competitor in all patches but that can persist in a metacommunity by being a superior colonizer of vacant patches. We assume that this species is equally limited by both resources ( $K_{31} = K_{32} = 2$ ), uses both resources equally ( $c_{31} = c_{32} = 1.5$ ), and has growth and mortality rates that are intermediate between species 1 and 2 ( $r_3 = 2.5$ ,  $m_3 = 1.25$ ). The per capita colonization rate of species 3 is 100 times that of species 1 or 2  $(\alpha_3 = 10)$ , while its extinction rate is the same  $(\beta_3 =$ 0.01). A more complete description of the three-species model can be found in appendix B in the online edition of the American Naturalist.

We analyzed the three-species model for both the tradeoff and the no-trade-off scenarios in the same manner that we analyzed the two-species model. Results for the tradeoff scenario are shown in figure 4, while results for the no-trade-off scenario (which are similar) are shown in appendix B. In the three-species model, a hump-shaped relationship between resource supply and species richness is again observed at both local and regional scales (fig. 4A, 4B; note that all three species can coexist in the same metacommunity but cannot coexist in a single patch). However, the effect of species richness on biomass and



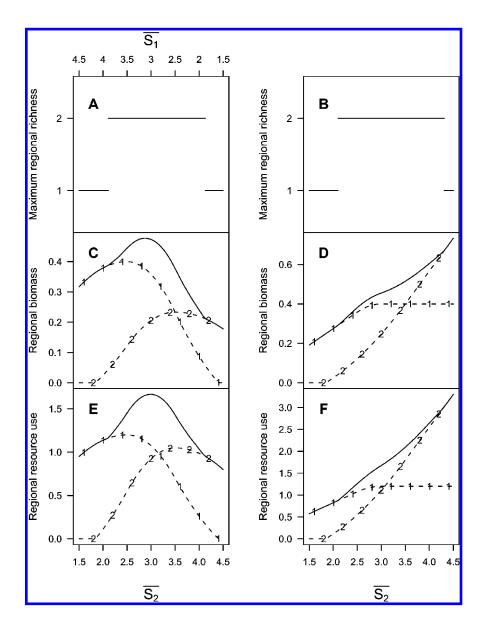


Figure 3: Species richness, biomass, and resource use for the two-species model at the metacommunity (i.e., regional) scale as a function of resource supply. *A, B,* Maximum regional richness versus regional resource supply. Both species can persist in the metacommunity only at intermediate values of regional resource supply, despite the fact that type C patches suitable for both species are always present. *C, D,* Regional biomass versus regional resource supply for metacommunities initiated with one (*dashed lines*) or both (*solid line*) species. *E, F,* Regional resource use versus regional resource supply for metacommunities initiated with one (*dashed lines*) or both (*solid line*) species. Left panels show the trade-off scenario, and right panels show the no-trade-off scenario.

resource use is subtly different. At the patch scale, there is a positive effect of richness on biomass and resource use in all patches, and transgressive overyielding occurs in nearly all patches with intermediate resource supply (fig. 4C, 4E). At the metacommunity scale, however, there is transgressive overyielding for all levels of resource supply (fig. 4D, 4F). Transgressive overyielding occurs at the metacommunity scale because when species 3 is present,

a larger fraction of the patches in the metacommunity are occupied, leading to greater biomass production and resource use.

Comparison between Local and Regional Scales and between Two- and Three-Species Models

In both two- and three-species models, there are similarities between the patterns that appear at the scale of an

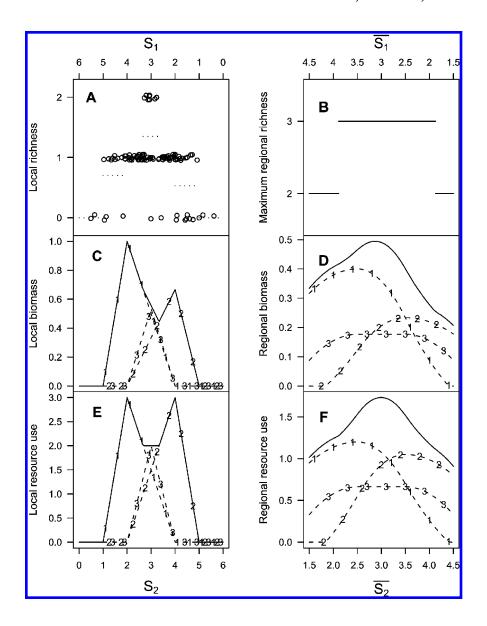


Figure 4: Species richness, biomass, and resource use for a three-species model that includes the two species from the two-species model plus a third species (species 3) that persists regionally by a competition-colonization trade-off. All panels are for a resource trade-off (results for the notrade-off scenario appear in app. B in the online edition of the American Naturalist). A, Local richness versus local resource supply for 100 randomly selected patches. Dotted lines show the expected richness for each patch. B, Maximum regional richness versus regional resource supply for metacommunities. C-F, Local biomass (C), regional biomass (D), local resource use (E), and regional resource use (F) for patches or metacommunities planted with all three species (solid lines) or one individual species (dashed lines) versus resource supply.

individual patch (figs. 2, 4) and patterns that appear at the larger scale of entire metacommunities (figs. 3, 4). At both scales and in both models, there is a hump-shaped relationship between resource supply and species richness and a positive effect of species richness on biomass and resource use. Also, the magnitude of diversity effects on biomass and resource use and the mechanisms that underlie these effects are mediated by resource supply in all cases. In the two-species model, diversity manipulations produce transgressive overyielding at resource supply levels where both species can coexist but produce nontransgressive overyielding at resource supply levels where only one species can persist. With a fugitive species, the same pattern holds at the scale of a single patch, but at the metacommunity scale, transgressive overyielding occurs for all resource supply levels.

In both two- and three-species models, there is a key difference between the patch and metacommunity scales. At the scale of individual patches, the most productive patches are those dominated by single species, regardless of whether there is a resource trade-off (figs. 2, 4). However, at the metacommunity scale, the most productive metacommunities also possess the greatest regional richness when there is a resource trade-off (figs. 3, 4). As a consequence, when species richness is plotted against biomass, an increasing pattern appears at the metacommunity scale in the trade-off scenario, while a hump-shaped pattern appears in all other cases (fig. 5; see app. B for the three-species model with no resource trade-off). Here, as before, the limited variation in species richness in these simple models creates a stair-step appearance to the plots that would disappear with more species and more resources.

The associations between diversity and biomass shown in figure 5 mimic studies that have used community biomass as a proxy for determining how resource supply affects species diversity (Waide et al. 1999; Mittelbach et al. 2001). The associations between species richness and biomass in our trade-off scenario are also strikingly similar to recent empirical data suggesting the shape of richness versus productivity relationship is unimodal at local scales and monotonically increasing at regional scales (Waide et al. 1999; Mittelbach et al. 2001; Chase and Leibold 2002). In our model, although richness and biomass are clearly associated with each other, these associations do not imply that biomass is determining richness. Instead, both biomass and richness are responding to variation in resource supply, and so the association between biomass and richness is correlative, not causal. Moreover, plots of richness versus biomass do not necessarily yield the same patterns as plots of richness versus resource supply (cf. increasing richness vs. biomass relationship in fig. 5D, 5F to the

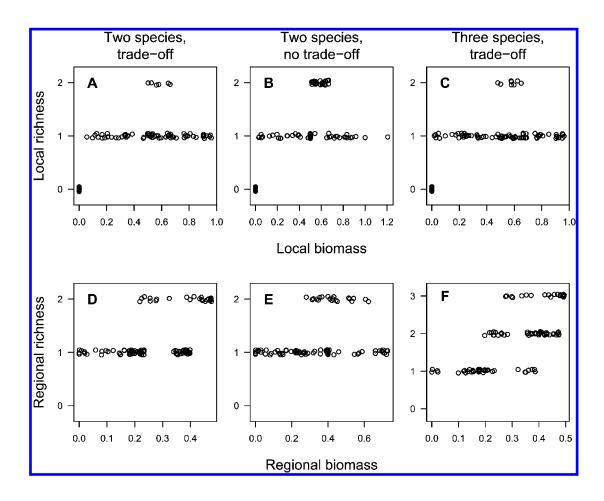


Figure 5: Associations between species richness and biomass in model communities. A-C, One hundred patches sampled from a single metacommunity. D-F, One hundred metacommunities or metapopulations. Data in A-C are from the metacommunities used to generate figure 2A and 2B and figure 4A, respectively. D-F were generated by picking 100 values of  $\overline{S}_2$  from a uniform distribution between 1.5 and 4.5 and then (D, E) initiating the metacommunity with species 1 only, species 2 only, or both species together, each with a probability of one-third, or (F) initiating the metacommunity with one, two, or three species, each with a probability of one-third.

hump-shaped richness vs. resource supply relationship in figs. 3A, 4B). These results suggest that caution is warranted in using biomass as a surrogate measure of resource supply.

We speculate that in these models two separate mechanisms are responsible for the increasing richness versus biomass patterns at the regional scale. First, we suspect that increasing richness versus biomass patterns are more likely when there is a greater degree of heterogeneity in resource ratios (i.e.,  $S_1/S_2$ ) within sampling units (i.e., patches in fig. 5A-5C; metacommunities in fig. 5D-5F). In metacommunities with a resource trade-off, the ratio  $S_1/S_2$  varies widely among patches within the metacommunity, and no single species' niche is broad enough to use the available resources as effectively as multiple species can. Consequently, the metacommunities with the greatest biomass are those that contain the most species. In all other cases, the ratio  $S_1/S_2$  varies less within a sampling unit, and so a single, well-adapted species can be more productive than a mix of species. Second, fugitive species that persist regionally by superior colonization also promote increasing richness versus biomass patterns at the regional scale but not at the local scale. This occurs because fugitive species can increase both the richness and the biomass of metacommunities that contain a superior competitor but cannot increase the richness and biomass of a single patch that is already occupied by a superior competitor.

## Discussion

The juxtaposition of productivity-drives-diversity and diversity-drives-productivity perspectives presents a major conceptual challenge for community ecology. The models developed here show that species richness can be both a cause of realized biomass production and a consequence of resource supplies that limit the potential productivity of a system. This possibility has received much recent attention by authors who have developed heuristic hypotheses about how such relationships might operate simultaneously in the same system (Loreau et al. 2001; Schmid 2002; Worm and Duffy 2003); our models formalize these ideas mathematically. At the least, the development of formal models that embody both historical and contemporary perspectives on diversity-productivity relationships shows that the two perspectives are not contradictory. That said, showing that resource supply can drive diversity and that diversity can drive resource use and biomass production simultaneously is but a small step toward ultimately merging the two perspectives into a single conceptual framework. It is, perhaps, more useful that our models show that there is a rich network of pathways by which resource supply, resource use, and species diversity are mutually dependent at both local and regional scales. Our analyses emphasize at least three primary points.

First, when communities are structured by resource competition, there is a fundamental connection between the shape of the resource supply-species richness curve and the effect of species richness on biomass and resource use. The hump in the resource supply-species richness curve appears in these models because species are able to coexist only via niche partitioning at intermediate levels of resource supply. As resource supply mediates species coexistence, it simultaneously determines the form and cause of the effect that species richness has on resource use and biomass. When resource supply does not permit local coexistence, richness can influence resource use and biomass only via the sampling effect where local communities initiated or colonized with many species ultimately come to be dominated by the competitively superior species. In our models, we assumed that the competitive superior was always the more productive species, and hence the sampling effect leads to nontransgressive overyielding (the most common pattern reported in experiments; see Cardinale et al. 2006b). In contrast, when resource supplies do allow local coexistence, resource partitioning among species results in transgressive overvielding where more species-rich communities achieve higher biomass and greater resource use than could be achieved by any single species (Tilman et al. 1997; Loreau 2004). Thus, these models suggest that the mechanism by which resource supply mediates species richness is fundamentally connected to the mechanism by which species richness controls resource use and biomass production.

Second, although notions of scale are clearly important in the interpretation of diversity-productivity relationships, our models suggest that it is too simplistic to claim that the direction of causality among resource supply, species richness, and biomass is simply a matter of scale. Both heuristic arguments (Loreau et al. 2001) and results from simplified experiments (Cardinale et al. 2006a) have been used to argue that species richness should respond to resource supply at one spatial scale, while resource capture and/or biomass production responds to diversity at another spatial scale. In contrast, our models show that resource supply can influence species richness and simultaneously mediate the effect that richness has on resource use and biomass production at the same spatial scale. Although scale may ultimately prove to be important in resolving productivity-drives-diversity and diversitydrives-productivity paradigms, our models show that these paradigms are compatible without invoking arguments of scale.

Third, at both local and regional scales, richness and biomass may be associated with each other, but this association may be correlative and does not imply that biomass determines species richness. In our models, biomass and richness are associated with each other because both are responding to variation in resource supply. Variation in resource supply affects community biomass and resource use directly by determining the amount of resources that are available to be converted to biomass and indirectly by setting an upper boundary on species diversity. The balance between these two effects determines the apparent association between richness and biomass. Among other things, these results call into question any mechanistic interpretations of empirical relationships that present species richness as a function of community biomass. Caution may be warranted when using biomass as a proxy for resource supply because biomass and resource supply are not mechanistically interchangeable variables.

Clearly, the models presented in this article omit a wealth of biological detail that is likely to be important in real systems. Trophic structure, facilitative or mutualistic interactions, larger numbers of species and resources, stoi-

chiometric considerations, and/or behavioral or physiological adaptations for reducing resource competition may all modify key details of the relationships among resource supply, species richness, biomass production, and resource use in real systems. The models here have their roots in work inspired by algal (e.g., Tilman 1977; Huisman and Weissing 2001) and terrestrial plant communities (e.g., Tilman 1982; Tilman et al. 1997, 2001; Hector et al. 1999) and are most directly applicable to these systems. Whether the addition of increasing ecological complexity changes the fundamental patterns observed in these models remains an open question and an area in need of future work.

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#### APPENDIX A

## Mathematical Details of the Two-Species Metacommunity Model

The equations for the full two-species metacommunity model are as follows:

$$\frac{dP_{1}(s_{1},s_{2},t)}{dt} = \begin{cases} \alpha_{1}N_{1}(t)[1-P_{1}(s_{1},s_{2},t)] - \beta_{1}P_{1}(s_{1},s_{2},t) & s_{1},s_{2} \in A,B \\ \alpha_{1}N_{1}(t)[1-P_{1}(s_{1},s_{2},t) - P_{2}(s_{1},s_{2},t) - P_{12}(s_{1},s_{2},t)] & s_{1},s_{2} \in C \\ + \beta_{2}P_{12}(s_{1},s_{2},t) - [\beta_{1}+\alpha_{2}N_{2}(t)]P_{1}(s_{1},s_{2},t) & s_{1},s_{2} \in C \end{cases}, \\ \alpha_{1}N_{1}(t)[1-P_{1}(s_{1},s_{2},t) - P_{2}(s_{1},s_{2},t)] - [\beta_{1}+\alpha_{2}N_{2}(t)]P_{1}(s_{1},s_{2},t) & s_{1},s_{2} \in D \end{cases}$$

$$\frac{dP_{2}(s_{1},s_{2},t)}{dt} = \begin{cases} \alpha_{2}N_{2}(t)[1-P_{1}(s_{1},s_{2},t) - P_{2}(s_{1},s_{2},t)] - [\beta_{2}+\alpha_{1}N_{1}(t)]P_{2}(s_{1},s_{2},t) & s_{1},s_{2} \in B \\ \alpha_{2}N_{2}(t)[1-P_{1}(s_{1},s_{2},t) - P_{2}(s_{1},s_{2},t) - P_{12}(s_{1},s_{2},t)] & s_{1},s_{2} \in C \\ + \beta_{1}P_{12}(s_{1},s_{2},t) - [\beta_{2}+\alpha_{1}N_{1}(t)]P_{2}(s_{1},s_{2},t) & s_{1},s_{2} \in D,E \end{cases}$$

$$\frac{dP_{12}(s_{1},s_{2},t)}{dt} = \alpha_{1}N_{1}(t)P_{2}(s_{1},s_{2},t) + \alpha_{2}N_{2}(t)P_{1}(s_{1},s_{2},t) - (\beta_{1}+\beta_{2})P_{12}(s_{1},s_{2},t) & s_{2} \in C. \end{cases}$$

$$(A1)$$

When occupancy rates are the same for all  $S_1$ ,  $S_2$  pairs within a given patch type, then the expression for  $N_1(t)$  in equation (3) simplifies to

$$N_{1}(t) = P_{A1}(t) \iint_{A} n_{1}^{*}(s_{1}, s_{2}) \phi(s_{1}, s_{2}) ds_{2} ds_{1} + P_{B1}(t) \iint_{B} n_{1}^{*}(s_{1}, s_{2}) \phi(s_{1}, s_{2}) ds_{2} ds_{1}$$

$$+ P_{C1}(t) \iint_{C} n_{1}^{*}(s_{1}, s_{2}) \phi(s_{1}, s_{2}) ds_{2} ds_{1} + P_{C12}(t) \iint_{C} n_{12}^{*}(s_{1}, s_{2}) \phi(s_{1}, s_{2}) ds_{2} ds_{1}$$

$$+ P_{D1}(t) \iint_{D} n_{1}^{*}(s_{1}, s_{2}) \phi(s_{1}, s_{2}) ds_{2} ds_{1}.$$
(A2)

The equation for  $N_2(t)$  simplifies similarly. The integrals in equation (A2) are constant over time and thus need to be evaluated only once.

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