Fusing spatial resource heterogeneity with a competition-colonization trade-off in model communities

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Abstract

Two commonly cited mechanisms of multispecies coexistence in patchy environments are spatial heterogeneity in competitive abilities caused by variation in resources and a competition-colonization trade-off. Here, a model that fuses these mechanisms together is presented and analyzed. The model suggests that spatial variation in resource ratios can lead to multispecies coexistence, but this mechanism by itself is weak when the number of resources for which species compete is small. However, spatial resource heterogeneity is a powerful mechanism for multispecies coexistence when it acts synergistically with a competition-colonization trade-off. The model also shows how resource supply can control the competitive balance between species that are weak competitors but superior colonizers and strong competitors / inferior colonizers. This provides additional theoretical support for a possible explanation of empirically observed hump-shaped relationships between species diversity and ecological productivity.

keywords: biodiversity, dispersal, resource competition, spatial dynamics

Introduction

A longstanding goal of community ecology is to elucidate the mechanisms that allow competing species to coexist. Broad classes of mechanisms proposed to explain coexistence include niche partitioning, neutral theory (Caswell 1976, Bell 2000, Hubbell 2001), and high dimensional explanations (Clark et al. 2004, 2007). Among niche partitioning explanations, recent theoretical and empirical work has focused on the interplay among spatial heterogeneity, dispersal, and trade-offs in species traits (reviewed in Amarasekare 2003 and Kneitel and Chase 2004). Two well-established ideas permeate this literature. First, if species differ in their requirements for resources that limit population growth (e.g., nutrients, light, predator-free space), and if the availability of these resources differs in space such that different species are favored at different localities, then it is thought that many species may be able to persist regionally even though only a small number of species can persist in a single locality at any given time. Tilman (1982) articulated this idea in the context of his resource ratio hypothesis, using verbal and graphical models to argue that if spatial locations differ in the supply of two different resources, then different pairs of species could persist at different locations in space (fig. 36 in Tilman 1982; see also fig. 2.2 in Tilman and Pacala 1993, fig. 7.1 in Grover 1997, or fig. 6.2 in Chase and Leibold 2003). While this idea is intuitively appealing, verifying it in mathematical models that include spatial processes such as dispersal has proved challenging (Chesson 2000). In recent years, some progress has been made on this front (Amarasekare and Nisbet 2001, Codeco and Grover 2001, Shurin et al. 2004, Abrams and Wilson 2004, Mouquet et al 2006). However, the complexity inherent in modeling both resource competition and dispersal simultaneously has limited most of these models to only a small number of species and/or spatial localities.

A second idea that has permeated the spatial coexistence literature is that of a competition-colonization trade-off (CCTO; Levins and Culver 1971, Hastings 1980, Tilman 1994). In a CCTO, species are arranged in a strict competitive hierarchy that is the same everywhere, and inferior competitors persist by being superior colonizers of vacant space. In fact, a CCTO can theoretically lead to the coexistence of an infinite number of species (Tilman 1994). While patch occupancy models that have been used to investigate CCTOs are straightforward to build and to analyze, the phenomenological way in which they model within-patch competition raises questions about their biological realism. These questions have sparked a debate in the literature about whether CCTO models provide an appropriate representation of nature (e.g., Adler and Mosquera 2000, Yu and Wilson 2001, Levine and Rees 2002, Kisdi and Geritz 2003, Calcagno et al. 2006).

In this paper, I develop and analyze a model that embeds standard consumer-resource theory within a patch occupancy framework, and thus fuses together spatial variation in resources with a CCTO. The model aims for the "best of both worlds" by striking a balance between the biological appeal of consumer-resource models and the mathematical tractability of patch occupancy models. There are two primary motivations for developing this model. First, I use the model to investigate whether or not spatial variation in resource supply can lead to the coexistence of more than a handful of species in a formal spatial model, and to investigate the properties of the communities that emerge. Second, I investigate if and how the predictions of CCTO models are altered by using mechanistic consumer-resource models instead of a phenomenological competitive hierarchy to determine the outcome of within-patch competition. A previous version of this model of was used in Gross and Cardinale (2007) to investigate relationships between resource supply, species richness, and ecological productivity. However, the version of the model used there considered only three species, and thus was not well-suited to investigate questions of species coexistence.

This paper is organized into two main parts: a one-resource model and a two-resource model. The one-resource model is simpler and serves as a natural precursor to the two-resource model, and so I present it first. The one-resource model is most useful for investigating the effect of adding mechanistic resource competition to a CCTO model, and the two-resource model is then used to investigate the effect of spatial resource heterogeneity on multispecies coexistence. For brevity, both models are sketched in the main text while additional details are provided in the appendix.

One-resource model

To lay the groundwork for what follows, I briefly restate the standard patch occupancy model used to embody a CCTO. The presentation here follows Grover (1997). Assume that there exist an infinite number of identical patches, and that these patches are not assigned explicit spatial locations. For lack of better terms, I will refer to the entire collection of patches as the "landscape" or "region". Assume the species pool consists of N species arranged in a competitive hierarchy, and assign species labels to indicate competitive strength, e.g., species 1 outcompetes all other species, species 2 outcompetes all species except species 1, etc. Patches are either vacant or occupied by a single species. Let p_i denote the proportion of patches occupied by species i. The dynamics of the system are governed by the equation

$$\frac{dp_i}{dt} = c_i p_i \left(1 - \sum_{j \le i} p_j\right) - \left(e_i + \sum_{j<i} c_j p_j\right) p_i, \quad i = 1, \ldots, N \,. \tag{1}$$

In eq. (1), c_i sets the rate at which species i colonizes accessible patches (i.e., vacant patches or patches occupied by competitively inferior species) and e_i is the rate at which abiotic disturbances cause patches occupied by species *i* to become vacant. Typically, e_i is assumed to be the same for all species. This model can support an arbitrarily large number of species at a stable equilibrium given by

$$p_i^* = \left(1 - \sum_{j<i} p_j^* - \frac{e_i + \sum_{j<i} c_j p_j^*}{c_i} \right) \vee 0. \tag{2}$$

(In eq. (2), the symbol $\vee$ denotes maximum, i.e., $x \vee y = \max(x, y)$.) A more intuitive way to view eq. (2) is that species *i* can persist if

$$c_i \left(1 - \sum_{j<i} p_j^* \right) > e_i + \sum_{j<i} c_j p_j^* . \tag{3}$$

Eq. (3) is an invasion criterion — it says that species *i* can persist if, when its density is very low, the rate at which it colonizes accessible patches exceeds the rate at which it loses patches, either by extinction or by being displaced by a superior competitor. Eq. (3) shows that any species, no matter how poor a competitor it may be, can persist if its colonization rate is large enough.

In this paper, I replace the phenomenological competitive hierarchy of the standard model with explicit models of resource competition. To model resource competition within a patch, let $n_i(t)$ be the density of species *i* in a patch, and let $R(t)$ be the amount of resource available in the patch. Within-patch dynamics are governed by the consumer-resource equations (Tilman 1980, 1982)

$$\begin{aligned} \frac{1}{n_i}\frac{dn_i}{dt} &= f_i(R) - m_i, \quad i = 1, \ldots N \\ \frac{dR}{dt} &= a(S - R) - \sum_i b_i f_i(R) n_i \end{aligned} . \tag{4}$$

In eq. (4), $f_i(R)$ is the per capita growth rate of species *i*, m_i is the per capita mortality rate of species *i*, *a* is a constant that scales the resource turnover rate, *S* is the supply of the resource (equal to the equilibrium amount of the resource when no consumers are present), and b_i is the amount of the resource consumed for each unit of biomass produced by species *i*. The specific functional form of $f_i\left(R\right)$ does not matter as long as f_i is continuous and increasing in *R*.

To analyze the model, I assume that resource competition within a patch occurs much more rapidly than the among-patch processes of colonization and disturbance. This “separation of time scales” assumption is standard in CCTO models (eq. 1) which assume that competitive displacement within a patch occurs instantaneously relative to among-patch dynamics. With this assumption, all we need to know about eq. (4) is its long-run behavior. Let $n_i^*\left(S\right)$ be the equilibrium density of species *i* in a patch with resource supply *S*

$$n_i^*\left(S\right)=\frac{a(S-R_i^*)}{b_i m_i}\vee 0\,. \tag{5}$$

In eq (5), R_i^* is the resource level at which the species *i*’s net growth rate is zero, i.e., $f_i\left(R_i^*\right)=m_i$. When multiple species are initially present in a patch, the competitively superior species is the one with the smallest R^* value (Tilman 1982). Thus, with competition for a single resource, species can still be arranged in a strict competitive hierarchy based on R^* values.

To embed this resource competition model in a patch occupancy framework, suppose that patches differ in their resource supplies, and use $\phi(S)$ to denote the distribution of *S* among patches. Let $p_i(S,t)$ denote the proportion of patches with resource supply *S* occupied by species *i* at time *t*. The total density of species *i*, denoted $N_i(t)$, can be found by integrating the product of equilibrium densities and the proportion of patches occupied over $\phi(S)$:

$$N_i(t)=\int_S p_i\left(S,t\right)n_i^*\left(S\right)\phi\left(S\right)dS\ . \tag{6}$$

Now assume that species *i* produces potential colonizers at a rate equal to its total density, $N_i(t)$, times a constant per capita rate α_i. The same logic as eq. (1) leads to an equation that governs how $p_i(S,t)$ evolves over time:

$$\frac{dp_i(S,t)}{dt} = \alpha_i N_i\left(1-\sum_{j\le i} p_j(S,t)\right) - \left(e_i + \sum_{j<i}\alpha_j N_j\right)p_i(S,t). \tag{7}$$

Like eq. (1), eq. (7) says that the proportion of patches with resource supply *S* occupied by species *i* increases from colonization of accessible patches, but decreases by abiotic disturbances or colonization by superior competitors. Eq. (7) only holds for $S > R_i^*$, because a species cannot occupy a patch with insufficient resources ($p_i(S,t)=0$ if $S \le R_i^*$).

In the appendix, I show that the model in eqq (5)-(7) behaves much like its phenomenological counterpart, eq. (1). In fact, if we define $\langle n_i^* \rangle$ as the average equilibrium abundance for species *i* across patches

$$\langle n_i^* \rangle = \int_S n_i^*(S)\phi(S)\,dS \tag{8}$$

then the explicit resource-consumption model behaves exactly like the phenomenological model with $c_i = \alpha_i \langle n_i^* \rangle$. It can be shown (appendix) that if a species persists, its equilibrium $p_i^*(S)$ will be constant for $S > R_i^*$. These equlilibria are (compare with eq. (2)):

$$p_i^*(S) = \left(1-\sum_{j<i} p_j^* - \frac{e_i + \sum_{j<i}\alpha_j \langle n_j^* \rangle p_j^*}{\alpha_i \langle n_i^* \rangle}\right) \vee 0 \qquad S > R_i^*. \tag{9}$$

In analogy to eq. (3), a species can persist in the explicit resource competition model if

$$\alpha_i \langle n_i^* \rangle \left(1-\sum_{j<i} p_j^*\right) > e_i + \sum_{j<i}\alpha_j \langle n_j^* \rangle p_j^*. \tag{10}$$

Thus, the explicit resource competition model can support an arbitrarily large number of species, just like the phenomenological model, as long as poor competitors (species with large R_i^* values) can compensate with superior colonization ability (large α_i).

Unlike the phenomenological model, a species' total colonization rate in eqq. (5) – (7) is proportional to the species' abundance, which in turn is controlled by resource supply. Consequently, the effect of changing the distribution of resource supply among patches is not immediately obvious. For example, consider the persistence criterion in eq. (10) from the perspective of species *i*. Increasing resource supply across all patches will increase species *i*'s average equilibrium abundance, $\left\langle n_i^* \right\rangle$, which will in turn increase its colonization ability, $\alpha_i \left\langle n_i^* \right\rangle$. However, the colonization ability of species *i*'s competitors, $\alpha_j \left\langle n_j^* \right\rangle$, will also increase, and the fraction of accessible patches ($1 - \sum_{j<i} p_j^*$) will decrease. Will the net effect of these changes be to increase or decrease species richness?

To address this question, I conducted the following simulation. (Details about the simulation appear in the appendix.) A species pool of 100 species was created by first assigning R^* values to species by random draws from a normal distribution, and species were then sorted by their R^* values to determine their competitive rank. Per capita colonization rates (α's) were drawn from a lognormal distribution, and were assigned so that the best competitor for the resource was the worst colonizer, the second best competitor was the second worst colonizer, and so on. Species were identical in all other respects. I then created a collection of patches where the distribution of resources among patches, $\phi(S)$, was uniformly distributed with mean $\left\langle S \right\rangle$. Species were introduced to the landscape in the order of their competitive rank, and eq. (10) was used to determine if the species could persist. (Because the invasion criterion for a given species only depends on the equilibrium densities of superior competitors, introducing species in the order of their competitive rank produces the same final community as introducing all species at once.) After all species had been introduced, I recorded species richness (the number of species persisting in the landscape) and species evenness (measured by the Shannon diversity index $H = -\sum_{i=1}^{N} p_i \ln p_i$, where p_i is the relative density of species *i* [not the proportion of patches occupied]). I also measured the characteristics of the species present by calculating the average values of α and R^* for those persisting species, weighted by species' densities. I then repeated this procedure for several values of $\langle S \rangle$, in each case keeping a uniform distribution for $\phi(S)$ with the same range. I repeated this process for 20 different species pools, and then repeated the entire procedure twice more, once with a five-fold increase in the disturbance rate, and once with a spatially homogeneous landscape in which all patches had the same value of *S*.

As fig. 1 shows, resource supply controlled the competitive balance between strong competitors / weak colonizers and weak competitors / strong colonizers, resulting in a unimodal or "hump-shaped" relationship between species richness and resource supply. At low levels of resource supply, only strong colonizers were able to persist. Superior competitors / weak colonizers were absent when resources were scarce because they were unable to achieve high enough colonization rates to offset patch extinctions caused by disturbance. In contrast, when resources were abundant, the community was dominated by the superior competitor. With increasing resources, the superior competitor occupied an increasing fraction of the available habitat, leaving too little habitat for many of the remaining species (fig. 2). Only at intermediate levels of resource supply was there competitive balance between strong competitors / weak colonizers and weak competitors / strong colonizers. The unimodal richness vs. resource supply pattern observed (fig. 1) matches empirical diversity vs. productivity curves sometimes observed in nature (Rosenzweig and Abramsky 1993, Waide et al. 1999, Mittelbach et al. 2001, Chase and Leibold 2002).

The shifting competitive balance between superior competitors / weak colonizers and weak competitors / superior colonizers depends on the disturbance rate. When the disturbance rate is larger, the peak in the richness vs. resource supply curve is shifted towards larger values of resource supply (compare the left and center columns of fig. 1). However, even if disturbance is high, if resource supply is increased enough superior competitors will dominate the landscape eventually and eliminate inferior competitors. Lastly, the presence or absence of spatial variation in resource supply had little effect in the one-resource model (compare the left and right columns of fig.1).

The behavior of the one-resource model echoes previous analyses of the phenomenological CCTO (eq. 1). For example, Kondoh (2001) studied a version of eq. (1) in which species' colonization rates were proportional to a parameter describing productivity. His model also produced hump-shaped relationships between richness and productivity, and demonstrated that the peak of the richness vs. productivity curve shifted to the right as disturbance became more frequent. The one-resource model here almost matches these results exactly because colonization rates are proportional to average abundance, and average abundance is proportional to average resource supply $\langle S \rangle$ when all patches have enough resources for species to grow. (To see this, plug eq. (5) into eq. (8) to yield $\langle n_i^* \rangle = \left\langle \frac{a\left(S - R_i^*\right)}{b_i m_i} \vee 0 \right\rangle = \frac{a\left(\langle S \rangle - R_i^*\right)}{b_i m_i}$ if and only if $S > R_i^*$ for all patches in the landscape.)

Also, Kinzig et al. (1999) used eq. (1) to show that dominant competitors cast "niche shadows" that limit the similarity of coexisting species. The pattern of bands and gaps in fig. 2 show that the size of these niche shadows depends on resource supply when resources, species abundances and colonization rates are linked together. Thus, adding resource competition to a CCTO provides additional theoretical support for both Kondoh's and Kinzig et al.'s results by establishing a mechanism for the dependence of species richness on productivity and disturbance.

Two-resource model

I now modify the model so that species compete for two resources. Here, I give these resources the generic labels "resource 1" and "resource 2", although to make the discussion concrete these resources can be thought of as two different abiotic nutrients, such as nitrogen and phosphorous. In the terminology of Tilman (1980, 1982), we consider these resources to be "essential", in the sense that a species cannot compensate for a lack of one resource by consuming more of the other. In the two-resource model, within-patch dynamics are given by the equations

$$\begin{aligned} \frac{1}{n_i}\frac{dn_i}{dt} &= f_i\left(R_1, R_2\right) - m_i, \quad i = 1,\ldots,N \\ \frac{dR_j}{dt} &= a\left(S_j - R_j\right) - \sum_i b_{ij} f_i\left(R_1, R_2\right) n_i \quad j = 1,2 \end{aligned} . \qquad (11)$$

In eq. (11), S_j is the supply of the resource j, and b_{ij} is the amount of resource j consumed for each unit of biomass produced by species i. All other parameters are the same as they are in the one-resource model, eq. (4). Again, the specific functional form of $f_i\left(R_1, R_2\right)$ does not matter, as long as it satisfies the standard properties for essential resources. Specifically, $f_i\left(R_1, R_2\right)$ is continuous and non-decreasing in both R_1 and R_2, and each species has values R_{i1}^* and R_{i2}^* for which the net growth rate is positive ($f_i\left(R_1, R_2\right) > m_i$) when $R_1 > R_{i1}^*$ and $R_2 > R_{i2}^*$, and is negative ($f_i\left(R_1, R_2\right) < m_i$) when either $R_1 < R_{i1}^*$ or $R_2 < R_{i2}^*$. Graphically, the "zero net-growth isocline" (ZNGI; the set of R_1, R_2 values for which $f_i\left(R_1, R_2\right) = m_i$) forms a right-angle in resource space (fig. 3a). Models of this sort have been thoroughly analyzed in the ecological literature (e.g., León and Tumpson 1975; Tilman 1980, 1982; Huisman and Weissing 2001 and references therein). The key result is that two species can coexist in the same patch if the following conditions are met: (i) the species' ZNGIs cross, (2) each species consumes more of the resource that limits it at the two-species equilibrium, and (3) the "supply point" S_1, S_2 falls within a region bounded by the consumption or impact vectors of the two species (fig. 3a).

In theory, it is possible to use a separation of time scales assumption to derive a multi-species patch occupancy model analogous to eqq (5)-(7) when species compete for two-resources. (Gross and Cardinale [2007] present an example of such a model for two and three species communities, although the disturbance rate is defined slightly differently.) An important difference between this model and most other patch-occupancy models used for a CCTO is that in this model two different species can occupy the same patch at the same time if the supplies of the two resources allow it. However, in part because of the possibility of two species occupying the same patch, even a modest number of species makes the model prohibitively complex and writing the model equations down is difficult. Instead, it is easier to construct and simulate a stochastic version of the model. I have constructed and simulated such a model and used it to test the idea that spatial variation in resources can lead to multi-species coexistence (Tilman 1982, Tilman and Pacala 1993). The simulation is sketched here, and additional details are provided in the appendix.

In the simulation, I first construct a species pool of 100 species. Species were assigned R_1^* and R_2^* values by independent draws from a normal distribution. Consumption rates (the b_{ij}'s) were determined by setting $b_{i1} / b_{i2} = R_{i1}^* / R_{i2}^*$ while constraining total consumption to be equal for all species ($b_{i1} + b_{i2} = 1$). Calculating consumption rates in this way ensures that two species whose ZNGIs cross will be able to coexist in the same patch for at least some values of S_1 and S_2. Per capita colonization rates (α's) were again drawn from a lognormal distribution, and were assigned so that the best resource competitor was the worst colonizer of vacant patches, etc. Model landscapes of 10^5 patches were then constructed by assigning S_1 and S_2 values to each patch. Four different scenarios were modeled (fig. 3b): independent variation in resources (S_1 and S_2 drawn from a uniform distribution), no variation in resources ($S_1 = S_2 =$ constant for all patches), variation in resource ratios (S_1/S_2) with constant total resources ($S_1 + S_2$), and variation in total resources with constant resource ratios. After seeding the landscape with all species in the species pool, simulations were run for a long time to allow initial transients to disappear. Species richness, species evenness, and weighted averages of the colonization rates and resource requirements of the persisting species were then measured. Simulations were repeated for 20 separate pools, for different average resource supplies and for low and high disturbance rates. All simulations were repeated with species pools that eliminated differences in colonization rates among species.

With two resources, resource supply again controls the competitive balance between superior competitors / weak colonizers and weak competitors / superior colonizers (Kondoh 2001). Consequently, species richness (fig. 4) and evenness (not shown) are hump-shaped functions of average resource supply across all model scenarios. When resources are scarce, communities are dominated by species that are weak resource competitors but superior colonizers of vacant patches. When resources are abundant, communities are dominated by species that are superior resource competitors but weak colonizers. When disturbance rates are higher, the richness vs. resource supply curve is stretched and shifted to the right, so that peak richness occurs for larger values of resource supply. The shifting competitive balance between superior competitors / weak colonizers and weak competitors / superior colonizers is illustrated for a single representative species pool in fig. 5. In addition, average colonization rates and R^* values of persistent species decline as resource supply increases for all model scenarios. These patterns (not shown) are similar to those observed in the one-resource model (fig. 1).

With two resources, the effect of spatial variation in resources on species richness is substantial. Without spatial variation in resource supply, only a handful of species are able to persist. Fig. 5 shows that the species that do persist are those whose resource requirements match the particular resource ratio found in the landscape. (For comparison, fig. 6 shows how the identity of the persisting species changes when resource 1 is only 75% as abundant as resource 2.) When resource supply varies among patches, a variety of species are able to persist in the community (fig. 4-6). Peak species richness is more than twice as large when resources vary compared to when resources are constant. Moreover, the effect of spatial variation on species richness is driven primarily by variation in resource ratios, not by variation in total resource supply (fig. 4). This explains why variation in resources has almost no effect in the one-resource model, where there is no resource ratio to vary.

However, spatial heterogeneity in resource ratios by itself is not sufficient to support the persistence of many species. Eliminating differences in colonization rates among species greatly reduced the effect of resource heterogeneity for all levels of average resource supply. This suggests that spatial variation in resource ratios alone is a relatively weak mechanism for generating multispecies coexistence, at least when species are competing for a small number of resources. Instead, species that are poorer resource competitors still require a colonization advantage to access the subset of patches that provide a more suitable combination of resources. Thus, spatial variation in resource supply is a much more powerful mechanism for generating multispecies coexistence when it acts synergistically with a CCTO.

Finally, figs. 1 and 4 appear to suggest that peak richness in the spatially homogeneous case is greater in the one-resource model than the two-resource model. There are two reasons for this, both of which can be considered model artifacts. First, increasing the number of resources increases the range of species' competitive abilities. Without a concomitant increase in the range of colonization abilities, many species in the two-resource, spatially homogeneous model are eliminated automatically simply because their resource requirements do not match the resource ratio available in the landscape. (The increased range in competitive abilities also explains why increasing the disturbance rate increases peak richness more in the two-resource model than the one-resource model.) Second, because the two-resource model is stochastic, some rare species are simply lost because of chance events. All rare species persist in the one-resource model because the model is deterministic.

Discussion

In this paper, I have presented and analyzed a patch occupancy model that uses standard consumer-resource equations to determine the outcome of interspecific competition within a patch. In some respects, the model behaves similarly to well-studied phenomenological CCTO models (Hastings 1980, Tilman 1994). However, by connecting colonization rates to species abundances, and by connecting species abundances to resource supply, this model predicts that the competitive balance between superior competitors / weak colonizers and weak competitors / superior colonizers is controlled by resource supply and the disturbance rate. This is true in both one- and two-resource models. These results provide additional theoretical support for Kondoh's (2001) explanation of the unimodal richness vs. productivity patterns that sometimes appear in nature (Rosenzweig and Abramsky 1993, Waide et al. 1999, Mittelbach et al. 2001, Chase and Leibold 2002). This explanation can be tested by evaluating the prediction that the community composition of less species communities should depend on whether resources are scarce or abundant. Species adapted to compete for vacant space should predominate when resources are scarce, while species adapted for direct resource competition should predominate when resources are abundant.

In the one-resource model, spatial heterogeneity in resource supply had a negligible effect on community composition. In the two-resource model, however, spatial variation in resource supply ratios leads to more diverse communities. Thus, this model provides mathematical evidence that spatial variation in resource ratios can lead to multispecies coexistence (Tilman 1982, Tilman and Pacala 1993). However, the effect of spatial heterogeneity alone on multispecies coexistence is weak when species are competing for a small number of resources. In the model here, when differences in colonization abilities among species were eliminated, species richness dropped dramatically. Consequently, this model suggests that a synergy between a CCTO and spatial heterogeneity in resource supply ratios is a much more powerful mechanism for generating species diversity than spatial heterogeneity alone.

While these results appear to suggest that a CCTO may be more likely to generate multispecies coexistence than resource variation, two additional observations must be kept in mind. First, the species pools in these models were constructed to ensure a strict trade-off between the ability to compete for resources and the ability to produce colonizing propagules. However, whether or not strict trade-offs in species traits exist in nature is a matter of debate (Clark et al. 2004), and breaking the strict trade-off between competitive and colonizing abilities reduces the number of persisting species relative to the strict trade-off simulations shown here (data not shown; see also Banks 1997). Second, and perhaps more intriguingly, the models here suggest that the effect of spatial resource heterogeneity on multispecies coexistence grows when species compete for a greater number of resources. Spatial heterogeneity by itself may be a weak mechanism for generating coexistence when only one or two resources limit species growth, but it may be a more powerful coexistence mechanism when species compete for a handful of resources instead of just one or two. Competition for these multiple resources combined with a mild (though not strict) CCTO could lead to the coexistence of many species under very reasonable biological conditions.

Lastly, there are two important caveats to the structure of this model. First, the separation of timescales assumption dictates that the within-patch resource competition plays out very fast relative to the among-patch processes of colonization and disturbance. Although this may be a reasonable assumption for some communities, recent work by Amarasekare and Nisbet (2001), Abrams and Wilson (2004), and Mouquet et al. (2006) suggests that the effect of dispersal on coexistence is more subtle and complex if resource competition and dispersal occur on the same time scale. Consequently, it appears that the effect of dispersal on multispecies coexistence depends on the relative rates at which dispersal and resource competition occur, and that the results here apply most directly to communities where dispersal happens slowly relative to resource competition. A second caveat to this model is that by modeling space implicitly, all patches are equally accessible to potential colonizers. In reality, resource supply is apt to change smoothly in space, so that nearby patches are apt to be more similar than distant patches. Higgins and Cain (2002) suggested that localized dispersal promotes coexistence in spatially explicit CCTO models when all patches are identical, but it is not clear whether the same will be true when patches vary in their resource supply. The interaction between spatial correlation in resources and local dispersal could have appreciable impacts on coexistence and merits further study.

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Appendix. Additional details and analysis for the one- and two-resource models

I first show that the model in eq. (5)-(7) behaves identically to the phenomenological model in eq. (1). First, I show that if there is a fixed point of eq. (7), then the fixed point is of the form $p_i^*\left(S\right)$ = constant for $S > R_i^*$. To keep the math simple I present only the analysis for the competitively superior species, species 1. Altering the analysis for other species is straightforward. Suppose there exists a fixed point $p_1^*\left(S\right)$ that may vary as a function of *S*. Let $N_1^* = \int_S p_1^*\left(S\right) n_1^*\left(S\right) \phi\left(S\right) dS$. Setting $dp_1\left(S,t\right)/dt = 0$ for all *S* (eq. (7)) implies that $p_1^*\left(S\right) = \alpha_1 N_1^* / \left(\alpha_1 N_1^* + e_1\right)$ for $S > R_1^*$. Plugging this expression back into $N_1^* = \int_S p_1^*\left(S\right) n_1^*\left(S\right) \phi\left(S\right) dS$ yields $N_1^* = p_1^* \left\langle n_1^* \right\rangle$ which in turn yields $p_1^*\left(S\right) = 1 - e_1 / \alpha_1 \left\langle n_1^* \right\rangle$ for $S > R_1^*$.

I now use an invasibility analysis to show that if $p_1^*\left(S\right) > 0$ then the boundary $p_1^*\left(S\right) = 0$ is repelling. Again, extensions to competitively inferior species are straightforward. Without loss of generality, suppose $p_1\left(S\right) = \varepsilon > 0$ for $S > R_1^*$. Then the overall change of the population size N_1 is

$$\begin{aligned}
\frac{dN_1}{dt} &= \frac{d}{dt}\int_S p_1\left(S\right) n_1^*\left(S\right) \phi\left(S\right) dS \\
&= \int_S \frac{dp_1\left(S\right)}{dt} n_1^*\left(S\right) \phi\left(S\right) dS \\
&= \int_{S>R_1^*} \left[\alpha_1 \varepsilon \left\langle n_1^* \right\rangle (1-\varepsilon) - e_1 \varepsilon\right] n_1^*\left(S\right) \phi\left(S\right) dS \\
&\approx \varepsilon\left[\alpha_1 \left\langle n_1^* \right\rangle - e_1\right] \left\langle n_1^* \right\rangle
\end{aligned}$$

which is >0 if and only if $\alpha_1 \left\langle n_1^* \right\rangle > e_1$.

Spatial heterogeneity matters in the two-resource model but not the one-resource model because in the two-resource model the competitive hierarchy can vary among patches depending on the resource ratio. The simplest setting in which to see this is a two-resource, two-species model where all patches have sufficient resources to support either species, and there are no patches where both species can coexist simultaneously. Let $\mathcal{S}_1$ denote the set of patches in which species 1 outcompetes species 2, and let $\mathcal{S}_2$ denote the set of patches in which species 2 outcompetes species 1. In the absence of species 2, an argument similar to the one above shows that species 1 comes to an equilibrium occupancy p_1^* that is constant for all $\vec{S}=(S_1,S_2)$ pairs and an equilibrium density $N_1^* = p_1^*\left\langle n_1^*\right\rangle$. Now suppose $p_2\left(\vec{S}\right)=\varepsilon>0$ everywhere. The invasion criterion that must be satisfied in order for species 2 to invade is:

$$\int_{\vec{S}\in\mathcal{S}_1}\left[\alpha_2\left\langle n_2^*\right\rangle\left(1-p_1^*\right)-\left(e_2+\alpha_1 N_1^*\right)\right]n_2^*\left(\vec{S}\right)\phi\left(\vec{S}\right)d\vec{S}+\int_{\vec{S}\in\mathcal{S}_2}\left[\alpha_2\left\langle n_2^*\right\rangle-e_2\right]n_2^*\left(\vec{S}\right)\phi\left(\vec{S}\right)d\vec{S}>0\,.$$

Clearly, this invasion criterion depends on the distribution $\phi\left(\vec{S}\right)$.

Simulation details for the one-resource model

R^* values were assigned to species by independent random draws from a normal distribution with mean 5 and variance 1. α values were drawn from a lognormal distribution with parameters $\mu=0$ and $\sigma=1$ (thus the average value of α was $e^{1/2}\approx 1.65$). The species with the smallest R^* value was assigned the smallest α value, and so on. Other parameter values that were identical for all species were $m=1$ and $b=1$ (eq. 4). The resource turnover rate a was equal to 1 (eq. 4). The patch extinction rate e was 1 in the low disturbance simulations, and 5 in the high disturbance simulations. The range of $\phi(S)$ was 10 in the spatially heterogeneous simulations and 0 in the spatially homogeneous simulations.

Simulation details for the two-resource model

R_1^* and R_2^* values were assigned to species by independent draws from a normal distribution with mean 0 and variance 1. α values were drawn from a lognormal distribution with parameters $\mu=0$ and $\sigma=1$. Each species' competitive ability was measured by the probability that the species' R_1^* and R_2^* values would be smaller than the R_1^* and R_2^* values, respectively, of a new, randomly chosen species. The species with the greatest competitive ability (measured in this way) was assigned the smallest colonization rate, and so on.

At the beginning of each simulation, each of the 10^5 patches were assigned S_1 and S_2 values by randomly drawing S_1 and S_2 from uniform probability distributions (spatially heterogeneous simulations) or by assigning each patch the same S_1 and S_2 values (spatially homogeneous simulations). (To generate figure 6, the limits of the distribution of S_1 were 0.75 times the limits of the distribution of S_2.) Patches were populated by drawing species randomly and with equal probability from the species pool. Thus, each species occupied approximately 10^3 patches at the beginning of the simulation. Simulations were run as a generalized birth-death process, with the following types of events: either a species could attempt to colonize another patch, or a disturbance would strike a patch. Attempted colonizations happened with rate $\alpha_i N_i$, where N_i was the total density of species i summed over all patches. Here, rates are stochastic rates in the sense that if an event occurs with rate β, then the probability that event occurs in an infinitesimal time interval Δt is $\beta\Delta t + o(\Delta t)$, and the probability of more than one event occurring in Δt is $o(\Delta t)$ (Ross 2003). Disturbances occurred with rate e times the total number of patches, 10^5. If species i attempted to colonize a patch, one target patch was picked at random from all the patches in the landscape. If species i already occupied the target patch, no changes occurred. Otherwise, the consumer-resource model (eq. 11) was used to determine the outcome of resource competition within that patch. If a disturbance event occurred, one patch was selected at random from all the patches in the landscape. If the selected patch was already vacant, no changes occurred. Otherwise, any species present in that patch were eliminated from the patch.

Time was recorded in units of epochs, were one epoch was equal to a total of 10^5 attempted colonizations or disturbances striking occupied patches (note that disturbances striking unoccupied patches were not included in the calculation of epochs). Thus, on average each patch in the landscape would be the target of one attempted colonization or disturbance per epoch. After 500 epochs, the average per patch density of each species was recorded.

Figure legends

Figure 1. Species richness, species evenness (measured by the Shannon diversity index), average colonization rate (α), and average R^* among species for the one-resource model as a function of the average resource supply among patches, $\langle S \rangle$. Points show averages for 20 different species pools, and vertical lines span +/- 1 SE. Left column: low disturbance (e=1) and resource variation among patches. Middle column: High disturbance (e=5) and resource variation (note the different scale of the horizontal axis). Right column: low disturbance (e=1) without spatial resource variation. In all cases, species richness is maximized at intermediate levels of resource supply, although the resource supply at which this maximum occurs is larger when disturbance is greater. At low levels of resource supply, communities are dominated by weak competitors / superior colonizers, while at high levels of resource supply communities are dominated by strong competitors / weak colonizers.

Figure 2. Community composition as a function of average resource supply in the one-resource model. Each vertical column of points shows the species that persist in a community with a given average resource supply. The size of each point is proportional to each species' average per patch density. When resource supply is low, only weak competitors / superior colonizers persist. As average resource supply increases, communities become increasingly dominated by the single most competitive species. The distribution of resource supply values among patches is a uniform distribution with range = 10 in all cases.

Figure 3. (A): Graphical analysis of a two-species consumer-resource model, after Tilman (1982). Zero net-growth isoclines (solid lines) and consumption vectors (dashed lines) are shown for two hypothetical species, “X” and “Y”. The outcome of competition between the two species depends on the numbered region in which the supply point S_1, S_2 falls. If it falls in region 1, neither species can survive. In region 2, only species Y can survive. In region 3, both species can survive alone, but species Y will eliminate species X if both species occur together. In region 4, both species can coexist. Regions 5 and 6 are analogous to regions 3 and 2, respectively. (B): Distributions of resource supply points among patches for the stochastic simulations of the two-resource model. Boxes show the range of resource supply points when resources vary independently, and different boxes correspond to simulations with different average resource supply. Dashed diagonal lines show the locus of supply points when the resource ratio varies but total resource supply is constant, and dotted diagonal lines (which all run together) show the locus of supply points when total resource supply varies but the resource ratio is constant. Points at the center of the boxes show the resource supply point shared by all patches for different spatially homogeneous simulations.

Figure 4. Species richness for the two-resource model as a function of the average supply of resource 1 among patches, $\langle S_1 \rangle$. In all cases, both resources have the same average supplies, so $\langle S_1 \rangle = \langle S_2 \rangle$. Circles show averages for 20 different species pools, and vertical lines span +/- 1 SE. x’s (and associated error bars) show species richness and evenness for species pools where all species share the same colonization rate (error bars are sometimes too small to be visible). Left column: low disturbance (e=1). Right

column: high disturbance (*e*=5). Different rows correspond to (top to bottom) independently varying resources, no resource variation, variation in resource ratios (S_1/S_2) without variation in total resources, and variation in total resources ($S_1 + S_2$) without variation in resource ratios. In all cases, species richness is maximized at intermediate levels of resource supply, although the resource supply at which this maximum occurs is larger when disturbance is greater.

Figure 5. Community composition for different levels of average resource supply, spatial heterogeneity, and disturbance. In each panel, points show the R_1^* and R_2^* values of all the species in the species pool (leftmost panels), or the species that persist in the community (all other panels). These points are the vertices of each species' ZNGI. The size of the plot symbol indicates the colonization ability of each species (larger species are stronger colonizers); note that plot symbol size does not correspond to species abundance as it does in fig. 2. Diagonal dotted lines show where $R_1^* = R_2^*$. Top row: low disturbance with independent variation in resource supply among patches. When resources are scarce, communities are dominated by weak competitors / superior colonizers, while the reverse occurs when resources are abundant. Middle row: high disturbance with independent variation in resource supply among patches. Bottom row: low disturbance with no variation in resource supply among patches.

Figure 6. Community composition for different levels of average resource supply when resource 1 is only 75% as abundant as resource 2. Each panel shows the R_1^* and R_2^* values of all the species in the species pool (leftmost panels), or the species that persist in the

community (all other panels). Plot symbol size indicates the colonization ability of each species. Diagonal dotted lines indicate $R_1^* = 0.75 R_2^*$. Top row: independent variation in resource supply among patches. Bottom row: no variation in resource supply among patches. All simulations use the low disturbance rate (*e*=1).

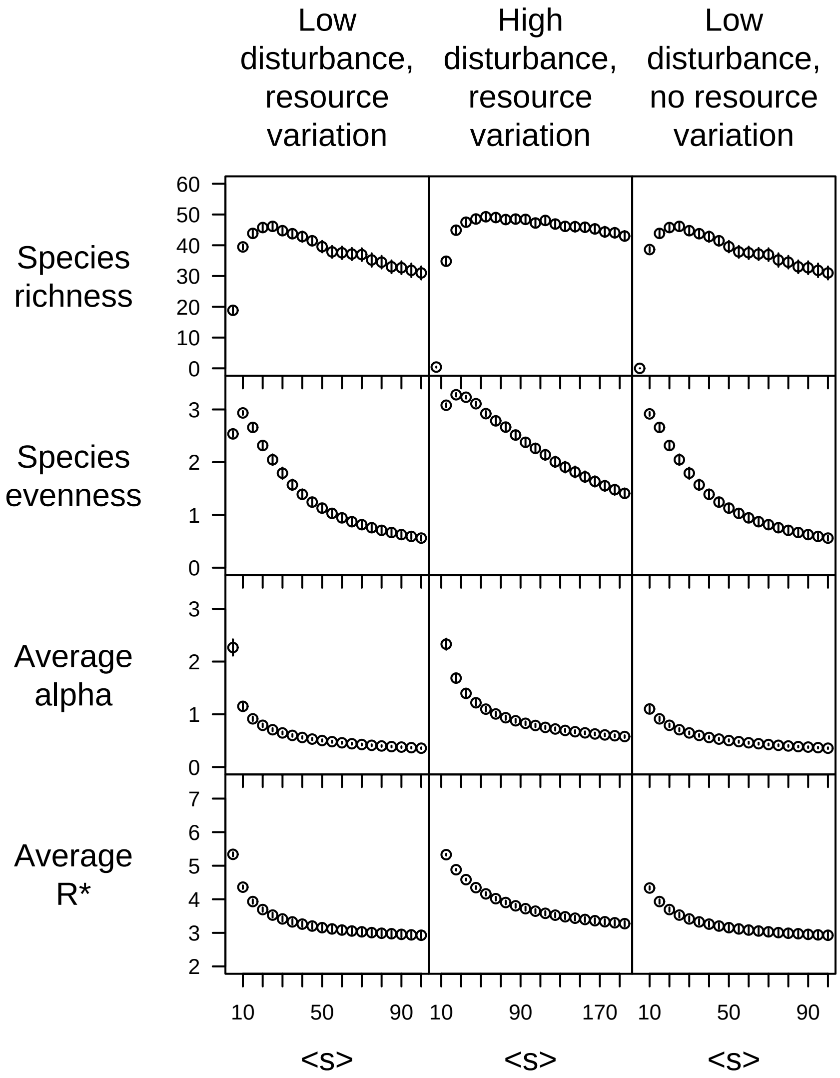
Low disturbance, resource variation
High disturbance, resource variation
Low disturbance, no resource variation
Species richness
Species evenness
Average alpha
Average R*
60
50
40
30
20
10
0
3
2
1
0
3
2
1
0
7
6
5
4
3
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Figure 1.

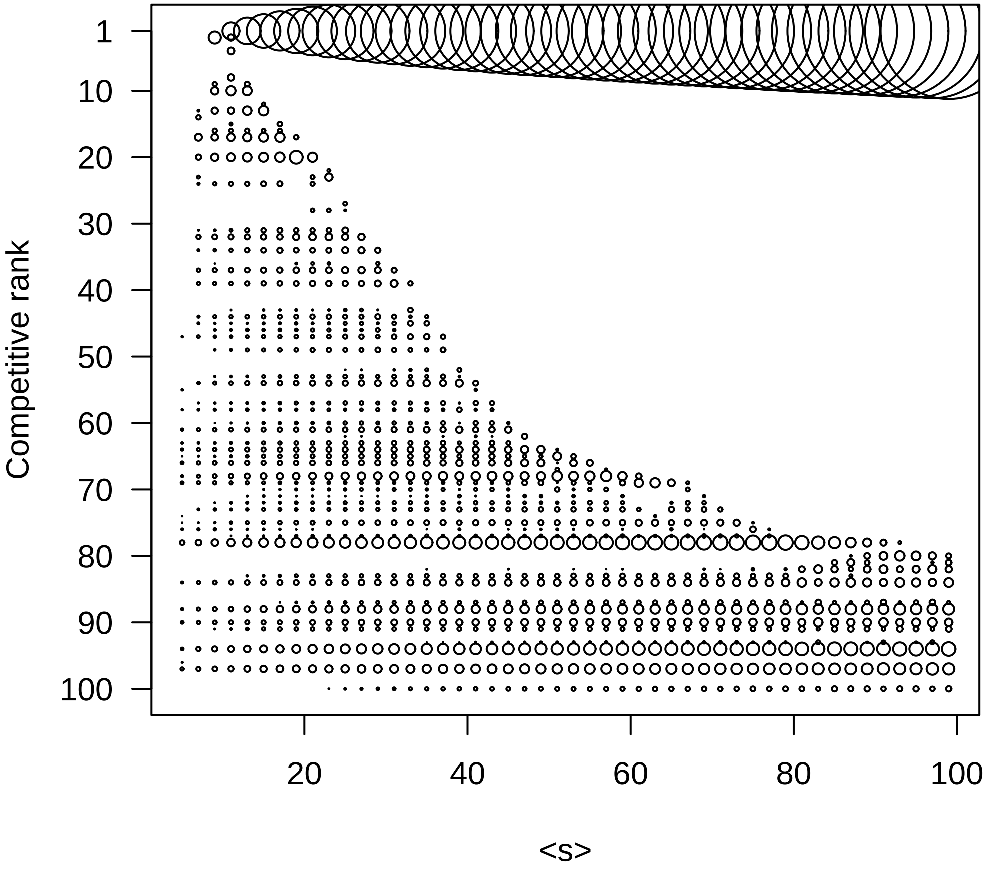


Figure 2.

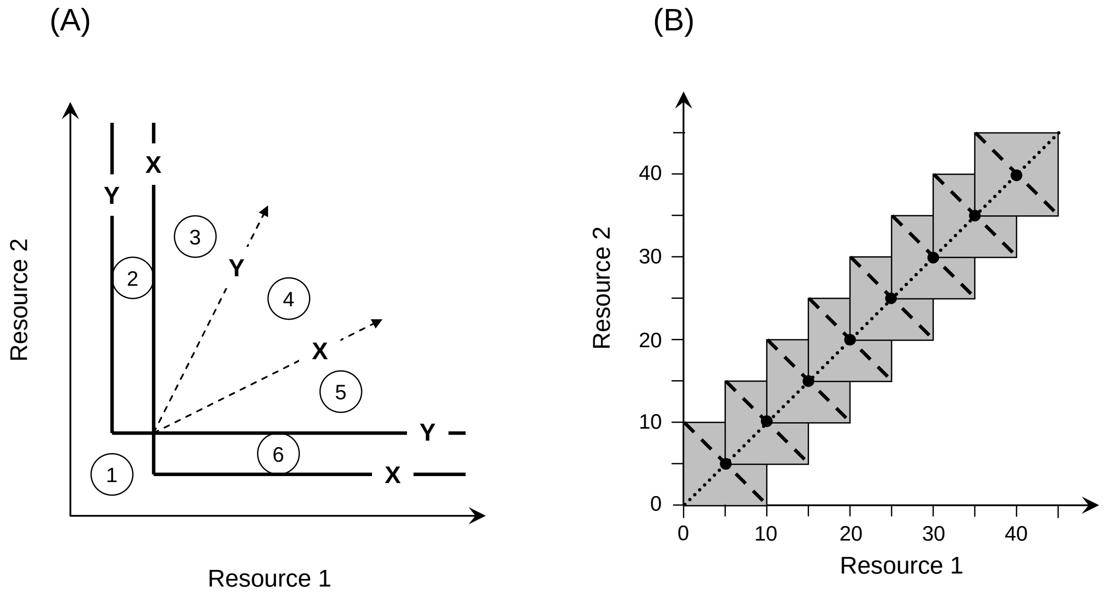

(A)
Resource 2
Resource 1
Y
X
Y
X
Y
X
1
2
3
4
5
6
(B)
Resource 2
Resource 1
0
10
20
30
40
0
10
20
30
40

Figure 3.

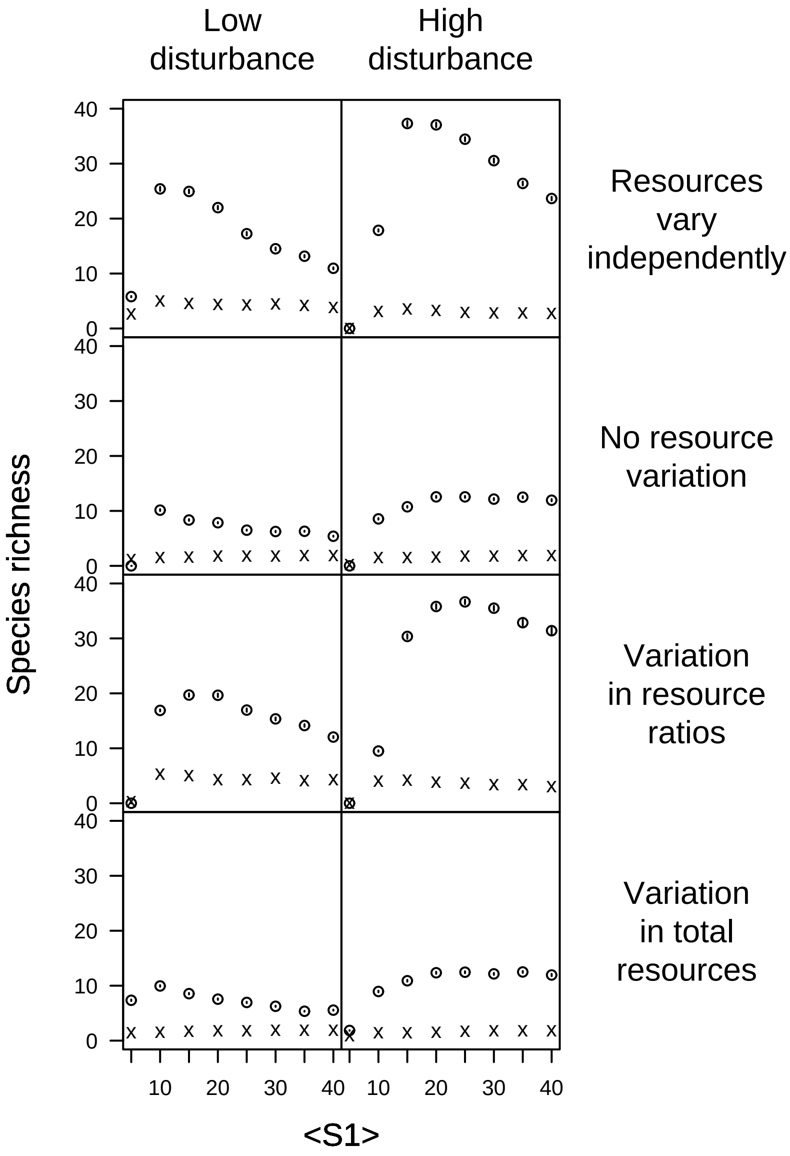
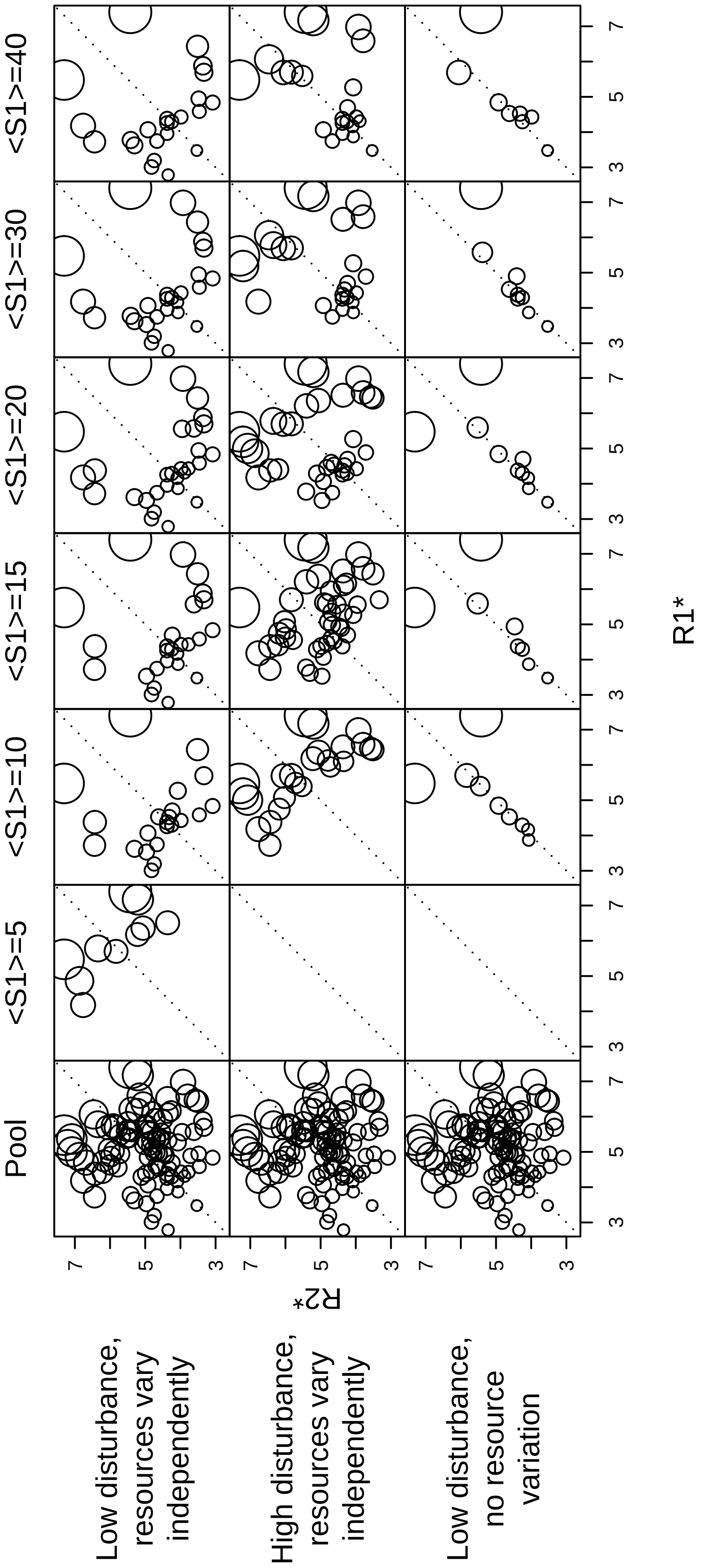

Low disturbance
High disturbance
Resources vary independently
No resource variation
Variation in resource ratios
Variation in total resources
Species richness
0
10
20
30
40
10
20
30
40
<S1>

Figure 4.


Pool
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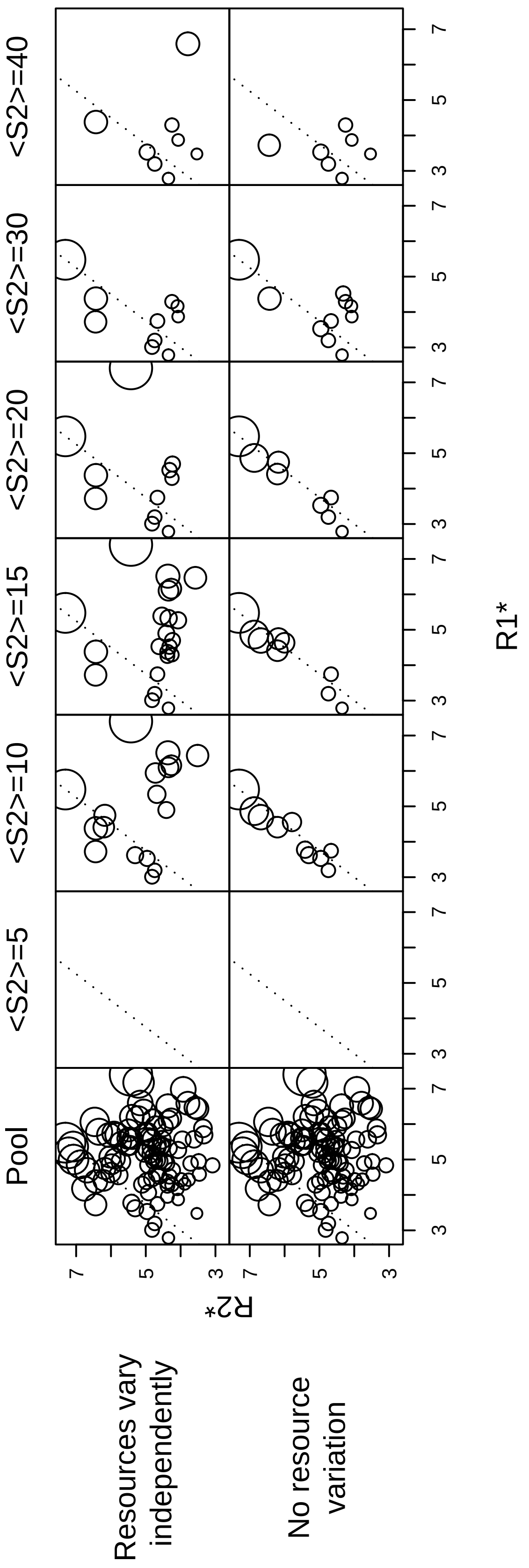
Low disturbance, resources vary independently
High disturbance, resources vary independently
Low disturbance, no resource variation
R2*
R1*
3
5
7

Figure 5.


Pool
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<S2>=30
<S2>=40
Resources vary independently
No resource variation
R2*
R1*
7
5
3

Figure 6.