Positive interactions among competitors can produce species-rich communities

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Abstract

Although positive interactions between species are well documented, most ecological theory for investigating multispecies coexistence remains rooted in antagonistic interactions such as competition and predation. Standard resource competition models from this theory predict that the number of coexisting species should not exceed the number of factors that limit population growth. Here I show that positive interactions among resource competitors can produce species-rich model communities supported by a single limiting resource. Simulations show that when resource competitors reduce each others' per capita mortality rate (e.g., by ameliorating an abiotic stress), stable multispecies coexistence with a single resource may be common, even while the net interspecific interaction remains negative. These results demonstrate that positive interactions may provide an important mechanism for generating species-rich communities in nature. They also show that focusing on the net interaction between species may conceal important coexistence mechanisms when species simultaneously engage in both antagonistic and positive interactions.

Introduction

Evidence of positive interactions between species in nature abounds (Margulis 1981, Hunter & Aarssen 1988, Bertness & Callaway 1994, Bronstein 1994, Callaway 1995, Stachowicz 2001, Bruno *et al.* 2003, Brooker *et al.* 2008). In addition to classic textbook examples of mutualisms and symbioses (e.g., coral-zooxanthellae associations, mycorrhizal networks, nutritional rewards for pollinators and seed dispersers), ecologists now recognize that facilitative or positive non-trophic interactions can also occur between species simultaneously competing for resources (Hunter & Aarssen 1988, Callaway & Walker 1997). These interactions are particularly well documented in plant communities, and examples are plentiful (e.g., Hunter & Aarssen 1988, Callaway 1995, Brooker *et al.* 2008). For instance, nurse plants can enhance heterospecific seedling establishment by reducing thermal and evaporative stresses or stabilizing substrate (Went 1942, Bertness & Callaway 1994, Bruno 2000), and unpalatable species can reduce herbivory on more palatable competitors nearby (associational defenses, Hay 1986). Examples of non-trophic positive interactions between competing animals are less common, but do occur. For example, hummingbirds transport hummingbird flower mites among flowers while competing with them for nectar (Colwell 1995), and caddisfly larvae enhance the feeding success of interspecific competitors by increasing topographical complexity of streambeds (Cardinale *et al.* 2002).

Despite this empirical evidence, the consequences of positive interactions for species diversity are poorly understood (Stachowicz 2001). Indeed, ecological theory used to explore questions of species coexistence remains rooted in antagonistic interactions such as predation and competition (Holt 2001). Over twenty-five years ago, May (1981) bemoaned the dearth of attention paid to positive interactions in ecological theory relative to that given to competition and predation, and implored the field to rectify this imbalance. While some progress has been made towards integrating positive interactions into contemporary theory (Hacker & Gaines 1997, Bruno *et al.* 2003, Bascompte *et al.* 2006, Michalet *et al.* 2006), competition and predation still dominate ecological thinking about interspecific interactions. Indeed, with regard to their coverage of positive interactions, the similarities between May's text and contemporary texts are striking (e.g., Roughgarden 1998, Gotelli 2001, May & McLean 2007).

In this paper, I use mathematical consumer-resource models to ask how positive interactions or facilitation between resource competitors affects species coexistence. The consumer-resource models that I use have a long history in the ecological literature, and form the backbone of the modern theory of exploitative resource competition (León & Tumpson 1975, Tilman 1982, Grover 1997). A central result from this literature is that in closed, homogeneous environments, the number of species coexisting at a fixed equilibrium cannot exceed the number of limiting resources (MacArthur & Levins 1964) or limiting factors (Levin 1970, McGehee & Armstrong 1977). Although these models clearly oversimplify the natural world, they have motivated a long and intensive search for mechanisms capable of explaining why species-rich communities supported by few limiting resources commonly appear in nature (Hutchinson 1961, Chesson 2000, Holt 2001). Many such mechanisms have been proposed, including spatial processes (Abrams & Wilson 2004), environmental variability (Tilman 1982), fluctuating population densities (Armstrong & McGehee 1980, Huisman & Weissing 1999), and intraguild predation (Holt & Polis 1994, Amarasekare 2002). Despite this progress, the search for mechanisms of species coexistence remains one of contemporary ecology's richest puzzles (Chesson 2000, Clark *et al.* 2007).

The models examined in this paper incorporate positive interactions by supposing that the per capita mortality or maintenance requirement of a resource competitor can be reduced by the presence of another species. While the mathematical formulation is intentionally abstract, it is motivated by empirical examples in which one species confers a non-trophic benefit that increases the fitness of another species. There are numerous examples of this type of interspecific interaction in the literature and in nature, including those mentioned above (Hay 1986, Colwell 1995, Bruno 2000, Cardinale *et al.* 2002). Often, the positive interaction occurs because one species ameliorates a physical, physiological, or trophic stress that otherwise compromises the fitness of a resource exploiter. Like many mathematical models in ecology, the models in this paper omit substantial biological detail in order to preserve generality and transparency.

The primary goal of this analysis is to show that a network of positive interactions among exploitative competitors can provide a potent mechanism for generating multispecies coexistence. This coexistence does not require either spatial heterogeneity or oscillating dynamics, and can even operate when exploitative competition outweighs positive interactions, resulting in net negative interspecific interactions. I develop the model in stages, investigating a two-species model first and a multi- (>2) species model second. The two-species model, which is structurally similar to the models used by Amarasekare (2002) to investigate trade-offs between interference and exploitative competition, permits extensive mathematical analysis. The multi-species model is more complex and is investigated through simulation.

Two-species model

I first consider a standard model for two species exploiting a single resource, modified so that species may confer benefits upon each other. Let n_1, n_2, and R denote the abundances of the two competing consumers and their shared resource, respectively. Dynamics are governed by the equations

$$\begin{aligned} \frac{1}{n_1}\frac{dn_1}{dt} &= f_1(R) - m_1(n_2) \\ \frac{1}{n_2}\frac{dn_2}{dt} &= f_2(R) - m_2(n_1) \\ \frac{dR}{dt} &= g(R) - \sum_i c_i f_i(R) n_i \end{aligned} \tag{1}$$

In this model, the net per-capita growth rate of species i is determined by the resource-dependent growth rate, $f_i(R)$, and the mortality or maintenance rate, $m_i(n_j)$. The growth rate $f_i(R)$ increases as resources become more abundant, while the mortality rate $m_i(n_j)$ may depend of the density of species j. To keep the terminology clear, I refer to a reduction [increase] in one species' mortality rate caused by another species as a positive [negative] effect or interaction. Per capita growth and mortality rates are not subject to intraspecific density dependence; instead, species limit their own densities indirectly by depleting the resource.

Resource dynamics in eq. (1) are determined by the balance between the net supply rate of the resource $g(R)$ and consumption. I assume that $g(R)$ is a declining function of R, which suggests that this model is most applicable to an abiotic resource. The parameters c_i represent the amount of resource consumed for each unit of biomass produced by species i. To facilitate the analysis, it is helpful define the baseline mortality rate m_i^0 as the mortality rate that species i experiences when it occurs alone (i.e., $m_i^0 = m_i(n_j = 0)$), R_i^* as the resource level at which species *i*'s net growth rate is 0 when that species occurs alone (i.e., $f_i\left(R_i^*\right)=m_i^0$), and n_i^0 as the density that species *i* attains in the absence of other species.

When mortality rates of both species are constant (i.e., $m_i\left(n_j\right)=m_i^0$), eq. (1) is a standard model for exploitative competition that has been thoroughly studied (Volterra 1928, Tilman 1982, Grover 1997). It yields the well-known result that if the dynamics approach a point equilibrium, only the superior exploitative competitor (the species with the smallest R^*) can persist, and the inferior competitor will go extinct (Volterra 1928, Tilman 1982). However, positive interactions can allow both species to persist simultaneously. To see this, suppose that species 1 is the superior exploitative competitor in the absence of positive effects (i.e., $R_1^*<R_2^*$; this designation holds throughout the article). Suppose also that the presence of species 1 makes the environment more hospitable to species 2, so that the per capita mortality rate of species 2 decreases as the density of species 1 increases. Using an invasion analysis, it is straightforward to show that both species can coexist if the benefit conferred by species 1 on species 2 is sufficient to allow species 2 to invade a community consisting solely of species 1, i.e., $f_2\left(R_1^*\right)>m_2\left(n_1^0\right)$ (fig. 1). This is true regardless of whether species 2 provides a reciprocal benefit for species 1 (proofs are provided in Appendix S1 in Supplementary Material).

To illustrate, fig. 2 shows several simulations with a specific version of eq. (1) that uses a Monod growth equation $f_i\left(R\right)=r_iR/\left(K_i+R\right)$ (Monod 1950) and a linear resource renewal equation $g\left(R\right)=a\left(S-R\right)$ (Tilman 1982). Here, r_i is the maximum per capita growth rate of species *i*, K_i is the resource level at which species *i*'s growth is one-half of its maximum, *a* scales the resource turnover rate, and *S* is the resource equilibrium without consumers. Mortality rates obey

$$m_i = m_i^{o} - d_i\left(1 - \exp\left\{-\theta_{ij} n_j\right\}\right) \quad (2)$$

where d_i is the maximum amount by which facilitation can reduce mortality, and θ_{ij} scales the rate at which species *j* decreases the mortality of species *i*. Figure 2a,b show cases where species 1 has a positive effect on species 2, but not vice versa, while fig. 2c,d show cases where both species have a positive effect on each other.

To understand how this coexistence arises, consider a case where species 1 reduces the mortality rate of species 2, but species 2 does not provide a reciprocal benefit for species 1 (fig. 2a,b). Suppose species 2 invades a community that consists solely of species 1. Initially, species 2's abundance increases because of the positive effect of species 1. Increased consumption by species 2 then depletes the resource, and decreased resources in turn reduce the growth rate of both species. Consequently, species 1's net growth rate becomes negative, and its density declines. Losses of species 1 reduce the benefit species 2 obtains from species 1, resulting in an increased mortality rate of species 2. Thus, species 2's net growth rate declines both because resources are diminishing and because the positive effect of species 1 is weakening. Reductions in both species' growth rates lead to reduced resource consumption, allowing the resource to rebound. Eventually, one of two possible dynamics results: if the resource renews itself quickly relative to the rate at which losses of species 1 diminish the benefit to species 2, then the dynamics approach a stable equilibrium (fig. 2a,c,d). Alternatively, if the resource renews itself slowly, then population cycles may result (fig. 2b). Figure 3 shows how interspecific facilitation and the resource renewal rate interact to determine whether populations cycle or approach an equilibrium.

Several comments about this two-species model deserve mention. (Formal mathematical justification for these comments is provided in Appendix S1.) First, although positive interactions are incorporated into eq. (1) through species' mortality rates, models incorporating positive interactions in species' growth rates ($f(R)$) yield similar results. Second, positive interactions can drive coexistence even if interspecific benefits only partially counteract exploitative resource competition. The net interspecific interactions may be either positive (fig. 2d) or negative (fig. 2a,c), in the sense that the presence of either species may increase or decrease the abundance of the other relative to the density that species would achieve alone. Thus, classifying interspecific interactions solely on the basis of the net effect may obscure the mechanism driving coexistence.

Third, it is not merely the additional interspecific interaction *per se* that drives coexistence in eq. (1), but the addition of a positive interspecific effect. For comparison, consider an alternative scenario where species 2's mortality rate is constant, but species 2 increases the mortality rate of species 1, perhaps through interference competition. In this case, coexistence is impossible, but the outcome of competition will depend on initial conditions if the interference competition is sufficiently strong (i.e., priority effects; Amarasekare 2002). Fourth, and finally, this model shares some similarities with Amarasekare (2002), who showed that interference competition via intraguild predation or parasitism could allow two exploitative competitors to coexist. Comparing these models shows that the key for coexistence is that the inferior resource exploiter benefits from the presence of the superior resource exploiter, regardless of whether the mechanism generating the benefit brings a concomitant cost to the superior resource exploiter.

Multispecies model

The model in eq. (1) can be easily modified to accommodate an arbitrary number of consumers. A model with *S* consumer species is

$$\begin{aligned}
&\frac{1}{n_1}\frac{dn_1}{dt} = f_1(R) - m_1(n_2, n_3, \ldots n_S) \\
&\frac{1}{n_2}\frac{dn_2}{dt} = f_2(R) - m_2(n_1, n_3, \ldots n_S) \\
&\ldots \\
&\frac{1}{n_S}\frac{dn_S}{dt} = f_S(R) - m_S(n_1, n_2, \ldots n_{S-1}) \\
&\frac{dR}{dt} = g(R) - \sum_{i=1}^{S} c_i f_i(R) n_i
\end{aligned} \qquad (3)$$

Here, each consumer's mortality rate may depend on the densities of the other consumers. Although the model in eq. (3) is difficult to analyze, it is possible to determine conditions that guarantee the existence of a feasible equilibrium point for an arbitrarily large number of consumer species. These conditions are somewhat technical, and are detailed in Appendix S2. Knowing these conditions, however, makes it possible to write down specific models with a feasible equilibrium point for an arbitrarily large number of species. One simple example of such a model uses eq. (3) with $f_1(R) = f_2(R) = \ldots = f_S(R)$, $c_1 = c_2 = \ldots = c_S$, and $m_i = m_i^{\mathrm{o}} - d_i\left(1 - \exp\left\{-\theta\sum_{j<i} n_j\right\}\right)$, where both the baseline mortalities m_i^{o} and the minimum achievable mortalities $m_i^{\mathrm{o}} - d_i$ are ordered so that (with the exception of m_1) the graphs of the mortality curves do not intersect (fig. 4a). In this model, species are arranged in a hierarchy by their ability to exploit the resource, and superior resource exploiters confer benefits on inferior resource exploiters, but not vice versa. The simulation in fig. 4b shows S=50 species coexisting at a point equilibrium for this model.

Three caveats are in order here. First, although it is difficult to establish conditions for the stability of the equilibrium point analytically, simulations show that the equilibrium is likely to be stable if the resource renews itself quickly enough (fig. 4b and simulations below). Second, although a strict hierarchy of positive interactions is not a necessary condition for the equilibrium point to exist, community assembly considerations suggest that such a hierarchy makes species-rich communities more likely (Appendix S2 and simulations below). Third, the focus on unidirectional benefits here is not meant to suggest that reciprocal benefits impede coexistence; instead, models with reciprocal benefits are just more difficult to analyze.

In lieu of analytical results, I used simulations to study the ability of positive interactions to generate multispecies communities. In this simulation species could either increase or decrease the mortality rate of other species. Specifically, mortality rates followed

$$m_i = m_i^{\mathrm{o}} + d_i - 2d_i\left(\exp\left\{\sum_{j\neq i}\theta_{ij}n_j\right\}\right)\Big/\left(1+\exp\left\{\sum_{j\neq i}\theta_{ij}n_j\right\}\right). \qquad (4)$$

Here, interspecific interactions increase ($\theta_{ij}<0$) or decrease ($\theta_{ij}>0$) mortality by a maximum amount d_i. Simulations used Monod growth equations and linear resource renewal equations as before. I investigated five different scenarios: constant mortality rates, both positive and negative effects on mortality rates, only positive effects, only negative effects, and positive effects structured so that superior resource exploiters conferred benefits on inferior resource exploiters, but not vice versa. For each scenario, 100 species pools of 25 species each were constructed by drawing species' parameter values from appropriate probability distributions. (Full methods appear in Appendix S3.) All species were equally abundant initially, and simulations were run long enough for initial transients to dissipate. Species were declared extinct if their density fell below .001% of their initial density. At the end of each simulation, the number of species remaining was recorded. (A second set of simulations in which species were introduced one at a time produced nearly identical results; data in Appendix S3.)

Consistent with established theory, when mortality rates were constant, the superior resource competitor always eliminated every other species (data not shown). With both positive and negative effects on mortality rates, multiple species persisted in 90 of the 100 simulations (fig. 5a), with an average of 2.62 (± standard error = 0.10) species. Simulations with only negative or only positive effects clearly demonstrate that this coexistence is attributable to positive interactions (fig. 5b,c; average species richness = 3.12 ± 0.11 in fig. 5b). Finally, simulations in which positive interactions were structured so that superior resource exploiters conferred benefits on inferior resource exploiters produced the most species rich communities (fig. 5d, average species richness = 5.31± 0.17). In the vast majority (99%) of simulations in which multiple species persisted, coexistence occurred at a stable equilibrium, and only occasionally involved more complicated dynamics. These simulations clearly demonstrate that positive interactions can drive multispecies coexistence in these models.

Discussion

Ecological theory has struggled to offer satisfying explanations for the diverse communities observed in nature. In part, this may be because the core models that form the foundation of ecological theory emphasize antagonistic interactions such as competition and predation, and rarely consider positive interactions (May 1981, Chesson 2000). However, empirical evidence for the importance of positive, non-trophic interspecific interactions in ecological communities is compelling (Stachowicz 2001, Bruno *et al.* 2003, Brooker *et al.* 2008). The models analyzed in this paper suggest that positive interactions among exploitative competitors may provide a potent mechanism for multispecies coexistence, especially when superior resource exploiters confer benefits on inferior resource exploiters. This coexistence does not require either spatial heterogeneity or oscillating species densities, although the interplay between exploitative competition and positive interactions can lead to population cycles. Although it is almost certain that a variety of coexistence mechanisms operate in nature (Tilman 1999), these modeling results together with mounting empirical evidence suggest that positive interactions may play a considerable role in structuring ecological communities.

From a theoretical standpoint, it is well established that the number of species coexisting at an attracting point equilibrium cannot exceed the number of limiting factors (Levin 1970, McGehee & Armstrong 1977). It is also well appreciated that a variety of entities can serve as limiting factors, such as accessible habitat (Hastings 1980) and predators or parasites (Holt 1984). The models here show that when resource exploiters engage in positive interactions, consumer species themselves can serve as limiting factors for other consumer species. If consumer species can serve as limiting factors for each other, then there is apparently no mathematical limit on the number of consumers that can persist on a small number of abiotic resources. Thus, although species coexistence via positive interactions fits within the classical framework of limiting factors, it also expands that framework to new encompass new terrain.

Importantly, positive interactions can support multispecies coexistence even when the net effect of interspecific interactions is negative (e.g., fig. 2a,c). While it may seem intuitive that positive interactions should enhance biodiversity when they generate net increases in species densities, positive interactions can also drive coexistence when they only partially counteract exploitative competition. This latter effect is more subtle, but may be more common in nature. The fact that these more subtle positive interactions could go undetected if interactions are classified only by their net effect emphasizes the need to understand all the components of an interaction between species (Callaway & Walker 1997). Even in communities that appear to be predominantly structured by resource competition, positive interactions may provide a key to explaining how many different species coexist.

Among other reasons, elucidating the role of positive interactions in natural communities is important because it impacts our understanding of how communities will respond to compositional change (Stachowicz 2001, Gross & Cardinale 2005). In strictly competitive communities, the loss of a competing species will reduce competition for resources, allowing the remaining species to partially compensate for the lost biomass. In communities where positive interactions are important, the loss of benefit to remaining species may partially or wholly counteract relaxed resource competition, and may in fact trigger cascading species loss. In the same vein, positive interactions may also impact community assembly when new species arrive or invade. Studies of sequential community assembly in competitive communities have found that communities tend to acquire certain characteristics (e.g., increasing resistance to invasion) as they are built up from single arrivals (Law & Morton 1996, Law 1999). Unfortunately, current mathematical techniques for studying community assembly are difficult to extend to positive non-trophic interactions. Developing a theory of community assembly that incorporates positive interactions would permit a more complete understanding of how facilitation affects natural communities.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Coexistence and priority effects in the two-species model
Appendix S2: Sufficient conditions for the existence of a feasible fixed point in the multispecies model
Appendix S3: Simulation details and community assembly simulation

Figure Legends

Figure 1. Coexistence criterion for two species competing for the same resource. Both species will coexist if facilitation by the superior resource exploiter (species 1) reduces the mortality rate of the inferior resource exploiter (species 2) enough to make species 2’s net growth rate positive when it invades a community consisting solely of species 1, i.e., $f_2\left(R_1^*\right) > m_2\left(n_1^0\right)$.

Figure 2. Dynamics of two species competing for a single resource under various scenarios. The solid line shows the dynamics of the superior exploitative competitor (species 1), and the dashed line shows the dynamics of the inferior exploitative competitor (species 2). Dotted lines show the equilibrium densities of each species occurring alone. **A**: Species 1 reduces the per capita mortality rate of species 2, but not vice versa, and dynamics approach a point equilibrium. **B**: Unidirectional benefits as in **A**, but the resource renews slowly relative to the rate at which positive effects accrue, leading to population cycles. **C**: Both species reduce each other’s mortality rate, but the net effect of each species on the other is negative. **D**: Reciprocal benefits as in **C**, but the net effect of each species on the other is positive. Common parameter values for all panels are S=5, r_1= r_2=2, K_1= K_2=1, c_1= c_2=1, $m_1^{\mathrm{o}} = 1$, d_1=0.5, $m_2^{\mathrm{o}} = 1.5$, and d_2=1. Parameter values that vary among panels are A: a=1, θ_{12}=0, θ_{21}=0.2; B: a=0.1, θ_{12}=0, θ_{21}=20, C: a=1, θ_{12}=0.2, θ_{21}=0.2, and D: a=1, θ_{12}=0.5, θ_{21}=0.5.

Figure 3. Regions of parameter space generating attracting point equilibria and limit cycles in a model with unidirectional benefits. Limit cycles occur when the resource renews slowly (a is small) and interspecific facilitation acts quickly (θ_{21} is large). In the region labeled “Species 1

only", the positive effect of species 1 on species 2 is not strong enough to allow species 2 to persist. Parameters other than a and θ_{21} are as in fig. 2b.

Figure 4. **A**: Mortality functions for a version of the multispecies model that permits a feasible equilibrium point with an arbitrary number of species. Species are ordered in terms of their R^* values ($R_1^* < R_2^* < ... < R_S^*$), the mortality rate of species *i* is a decreasing function of the sum density of species $j < i$, and (with the exception of species 1) the graphs of these mortality rate functions do not cross. In this model, the total biomass at the fixed point, $\sum_{i=1}^{S} n_i^* = n_1^0$, is independent of the number of species, *S*. A feasible equilibrium will exist if $m_S\left(n_1^0\right) < m_1$. At the fixed point, all species experience the same per capita mortality rate m_1, and fixed-point densities can be determined directly from the inverses of the mortality functions, i.e., $n_1^* = m_2^{-1}\left(m_1\right)$, $n_2^* = m_3^{-1}\left(m_1\right) - m_2^{-1}\left(m_1\right)$, etc. **B:** Dynamics of 50 species coexisting on a single resource. Each line indicates a separate species. Parameter values are $r_i = 2$, $K_i = 1$, $c_i = 1$, $m_i^0 = 1 + .02 * i$, $d_i = .5 + .02 * i$, $\theta = .28$, $a = 1$, and $S = 5$.

Figure 5. Species richness in simulated communities. Each panel shows a frequency histogram for 100 simulated communities. **A**: Species can either increase or decrease other species' mortality rates. **B**: Species either decrease or have no effect on each other species' mortality rates. **C**: Species either increase or have no effect on other species' mortality rates. **D**: Superior resource exploiters decrease the mortality rates of inferior resource exploiters, but not vice versa.

Figure 1.

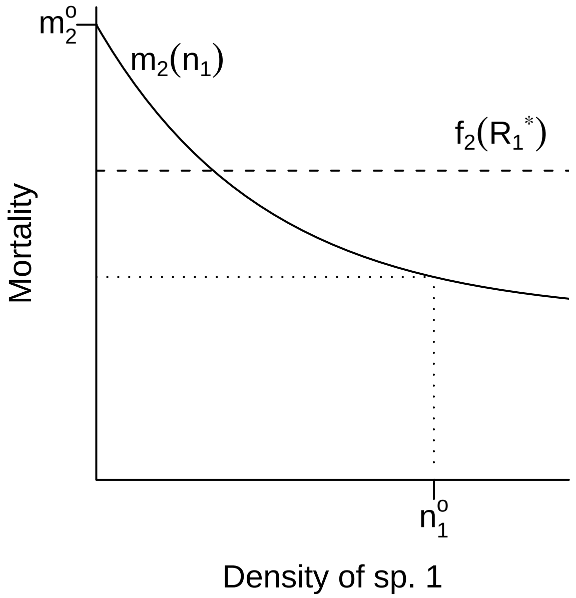


Figure 2.

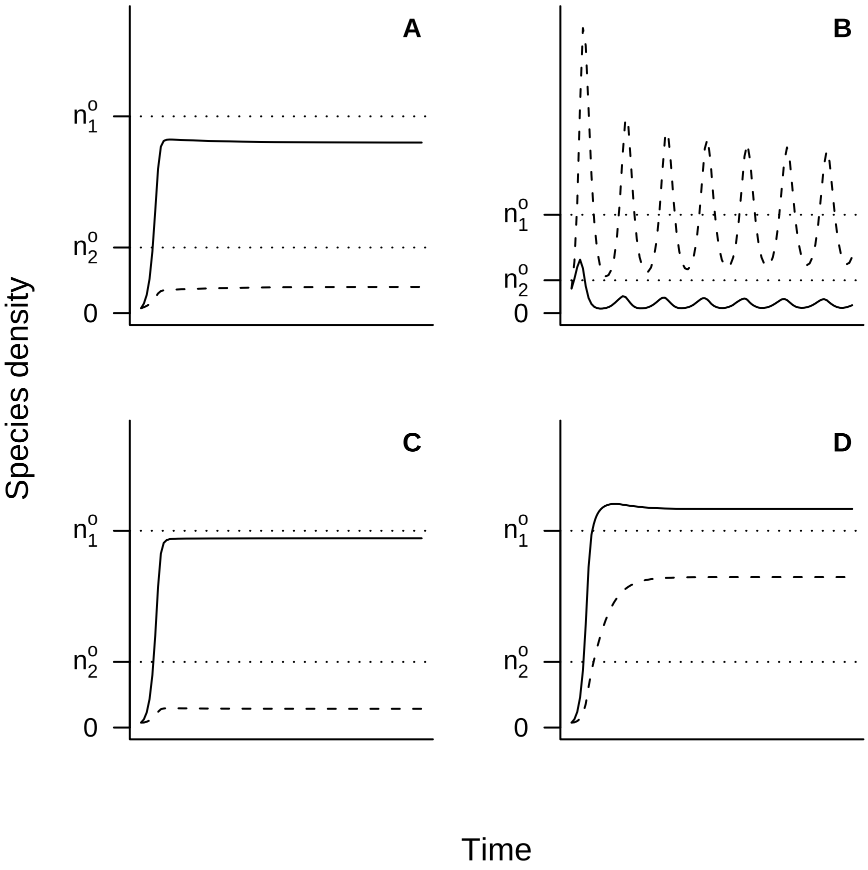


Figure 3.

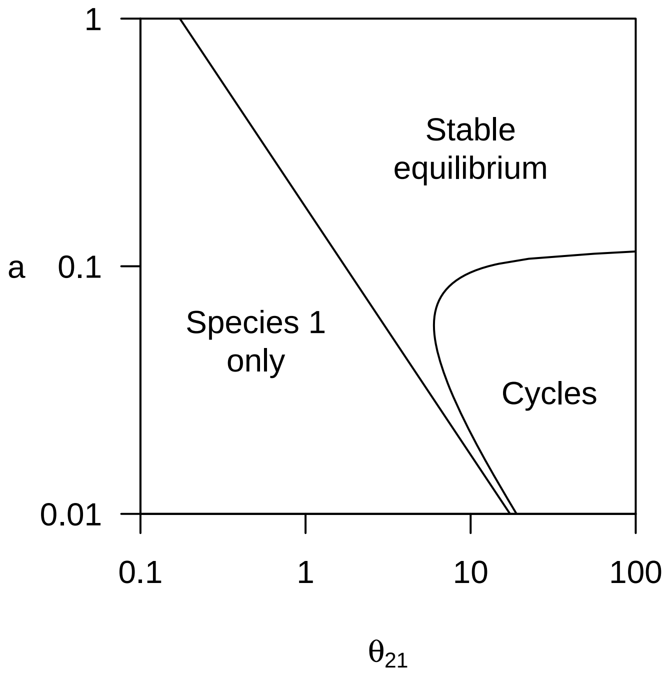

1
a
0.1
0.01
0.1
1
10
100
θ_{21}
Stable equilibrium
Species 1 only
Cycles

Figure 4.

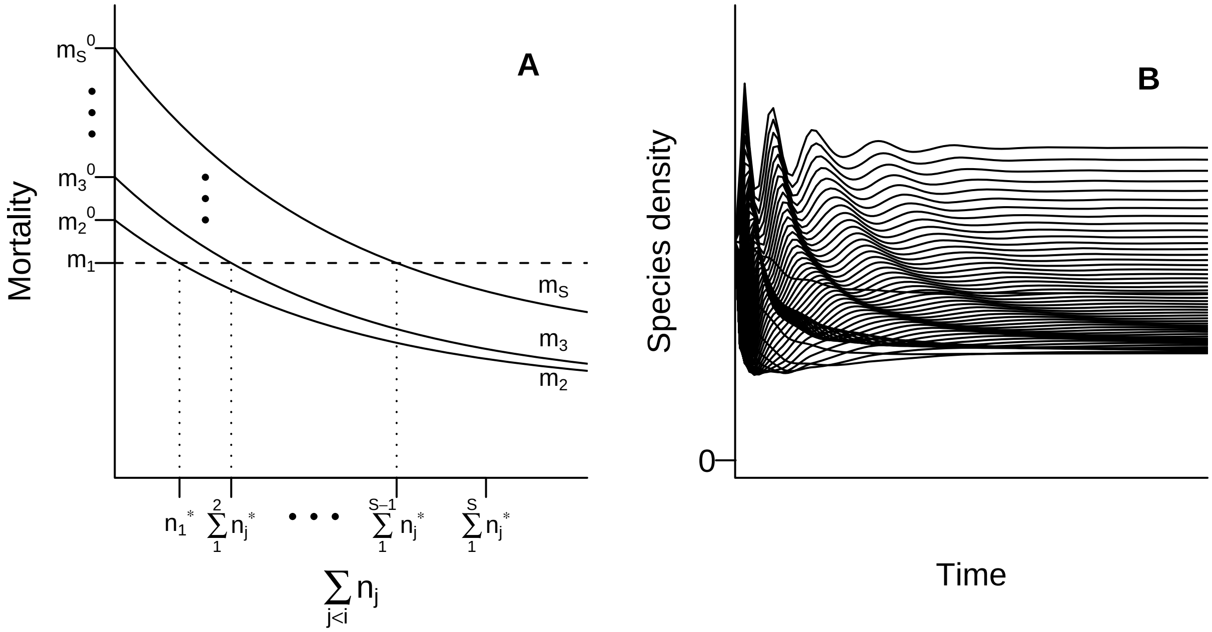
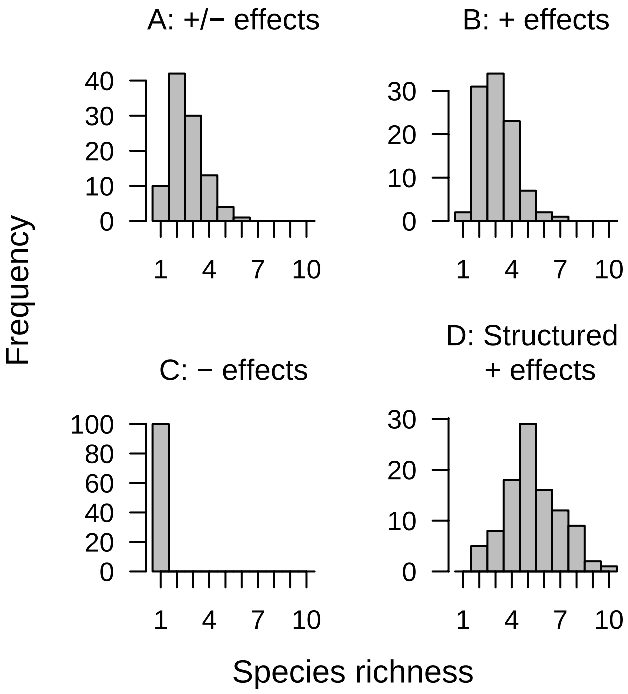

A
m_S^0
m_3^0
m_2^0
m_1
Mortality
m_S
m_3
m_2
n_1^*
$\sum_1^2 n_j^*$
$\sum_1^{S-1} n_j^*$
$\sum_1^S n_j^*$
$\sum_{j<i} n_j$
B
Species density
0
Time

Figure 5.


A: +/− effects
40
30
20
10
0
1
4
7
10
B: + effects
30
20
10
0
1
4
7
10
Frequency
C: − effects
100
80
60
40
20
0
1
4
7
10
D: Structured
+ effects
30
20
10
0
1
4
7
10
Species richness

Appendix S1: Coexistence and priority effects in the two-species model

Here I use an invasion analysis to derive sufficient conditions for the coexistence of two species in eq. (1). I assume the following conditions:

(i) $f_i(R)$, $m_i(n_j)$, and $g(R)$ are continuous functions whose first derivatives exist and satisfy the following conditions: $df_i/dR > 0$, $dm_i/dn_j \leq 0$, and $dg/dR < 0$.

(ii) Each species is able to persist by itself, i.e., if R^0 is the resource equilibrium in the absence of either species ($g(R^0) = 0$), then $f_1(R^0) > m_1^0$ and $f_2(R^0) > m_2^0$. Without loss of generality, $R_1^* < R_2^*$, so that species 1 eliminates species 2 in the absence of facilitation.

(iii) Species 2 can invade when species 1 is present and has attained its single-species equilibrium, i.e., $f_2(R_1^*) > m_2(n_1^0)$.

To show that both species can persist, it suffices to show that each species can invade when the other species persists alone. Because either species alone will approach a stable point equilibrium, it then suffices to show that $f_2(R_1^*) > m_2(n_1^0)$ and $f_1(R_2^*) > m_1(n_2^0)$. The first of these inequalities is true by assumption. The second is a direct consequence of assumptions (i) and (ii): $f_1(R_2^*) > f_1(R_1^*) = m_1^0 \geq m_1(n_2^0)$. It follows immediately that the above assumptions are also sufficient even if m_1 is independent of n_2.

To show that positive interactions mediated through the per-capita growth terms have similar effects, consider the model

$$\begin{aligned}\frac{1}{n_1}\frac{dn_1}{dt} &= f_1\left(R,n_2\right)-m_1\\ \frac{1}{n_2}\frac{dn_2}{dt} &= f_2\left(R,n_1\right)-m_2 \qquad . \\ \frac{dR}{dt} &= g\left(R\right)-\sum_i c_i f_i\left(R,n_j\right)n_i\end{aligned} \tag{1.1}$$

Suppose that increases in the density of species *i* can increase the per-capita growth tern of species *j*, i.e., $\partial f_i / \partial n_j \geq 0$, and that species 1 is the superior competitor in the absence of facilitation. An invasion argument similar to the one above can be used to show that both species can coexist if $f_2\left(R_1^*, n_1^0\right) > m_2$.

Priority effects and interference competition

Consider the model in eq. (1), but now suppose that $dm_i / dn_j > 0$. For mutual invisibility, we need $f_1\left(R_2^*\right) > m_1\left(n_2^0\right)$ and $f_2\left(R_1^*\right) > m_2\left(n_1^0\right)$. Suppose $f_1\left(R_2^*\right) > m_1\left(n_2^0\right)$. Now $m_1\left(n_2^0\right) > m_1^0 = f_1\left(R_1^*\right)$, which implies $f_1\left(R_2^*\right) > f_1\left(R_1^*\right)$, which then implies $R_2^* > R_1^*$. Now suppose $f_2\left(R_1^*\right) > m_2\left(n_1^0\right)$. By similar reasoning, it follows that $R_1^* > R_2^*$. Thus we have a contradiction, and so mutual invisibility is impossible.

Appendix S2: Sufficient conditions for the existence of a feasible fixed point in the multispecies model

Consider a version of eq. (3) where species are arranged in a hierarchy, such that species confer benefits on species lower in the hierarchy by reducing their mortality rates:

$$\begin{aligned}
&\frac{1}{n_1}\frac{dn_1}{dt} = f_1(R) - m_1 \\
&\frac{1}{n_2}\frac{dn_2}{dt} = f_2(R) - m_2(n_1) \\
&\ldots \\
&\frac{1}{n_S}\frac{dn_S}{dt} = f_S(R) - m_S(n_1, n_2, \ldots n_{S-1}) \\
&\ldots \\
&\frac{dR}{dt} = g(R) - \sum_{i=1}^{S} c_i f_i(R) n_i
\end{aligned} \tag{2.1}$$

This argument proceeds by induction to derive sufficient conditions for the existence of a feasible fixed point with an arbitrary number of consumers. (Here, "feasible" means that the equilibrium densities of all species and the resource are positive.) It is trivial to show that there exists a feasible fixed point with $S = 1$ consumer. Now suppose there exists a feasible fixed point with S consumers. It suffices to show that there exists a feasible fixed point with S+1 consumers. For the remainder of this argument, I use *'s to denote the fixed point of the system with S consumers, and **'s to denote the fixed point of the system with S+1 consumers. This fixed point of the system with S consumers satisfies

$$\begin{aligned}
f_1(R^*) &= m_1 \\
f_2(R^*) &= m_2(n_1^*) \\
&\ldots \\
f_S(R^*) &= m_S(n_1^*, n_2^*, \ldots n_{S-1}^*) \\
g(R^*) &= \sum_{i=1}^{S} c_i f_i(R^*) n_i^*
\end{aligned} \tag{2.2}$$

The fixed point of the system with *S*+1 consumers must satisfy

$$\begin{aligned} f_1\left(R^{**}\right) &= m_1 \\ f_2\left(R^{**}\right) &= m_2\left(n_1^{**}\right) \\ &\dots \\ f_S\left(R^{**}\right) &= m_S\left(n_1^{**}, n_2^{**}, \dots n_{S-1}^{**}\right) \\ f_{S+1}\left(R^{**}\right) &= m_{S+1}\left(n_1^{**}, n_2^{**}, \dots n_S^{**}\right) \\ g\left(R^{**}\right) &= \sum_{i=1}^{S+1} c_i f_i\left(R^{**}\right) n_i^{**} \end{aligned} \tag{2.3}$$

The first *S* equations of (2.2) and (2.3) are identical. Therefore, it follows immediately that $R^* = R^{**}$, $n_1^* = n_1^{**}$, $n_2^* = n_2^{**}$, …, $n_{S-1}^* = n_{S-1}^{**}$. Equating the last equations of (2.2) and (2.3) then implies that $c_S f_S\left(R^*\right) n_S^* = c_S f_S\left(R^*\right) n_S^{**} + c_{S+1} f_{S+1}\left(R^*\right) n_{S+1}^{**}$. Thus, because $c_i > 0$ and $f_i\left(R^*\right) > 0$, to show that $n_{S+1}^{**} > 0$, it suffices to show that $n_S^{**} < n_S^*$. Because m_{S+1} is a decreasing smooth function of n_S, it then suffices to show that (i) $f_{S+1}\left(R^{**}\right) > m_{S+1}\left(n_1^{**}, n_2^{**}, \dots, n_S = n_S^*\right)$ and (ii) $f_{S+1}\left(R^{**}\right) < m_{S+1}\left(n_1^{**}, n_2^{**}, \dots, n_S = 0\right)$. Condition (i) is the expected invasion criterion: the positive effect of species 1,…,*S* must be strong enough to allow species *S*+1 to invade the *S*-species community at its fixed point. Condition (ii) is more subtle. Roughly, it states that when species *S*+1 invades, it must reach n_{S+1}^{**} before driving species *S* extinct. If both of these conditions are satisfied for all *S*, then the feasible fixed point of eq. (2.3) exists, and thus there can be a feasible fixed pint with an arbitrarily large number of consumers.

It is easiest to understand condition (ii) in the context of a model with 3 consumers, with the simplifications that all consumers share the same growth rates $f\left(R\right)$, the same consumption parameter *c*, and that the mortality rate of species 3 depends on species 1 and 2 only through their combined abundance, i.e., m_3 is a decreasing function of $n_1 + n_2$. Thus, the model is

$$\begin{aligned} \frac{1}{n_1}\frac{dn_1}{dt} &= f\left(R\right) - m_1 \\ \frac{1}{n_2}\frac{dn_2}{dt} &= f\left(R\right) - m_2\left(n_1\right) \\ \frac{1}{n_3}\frac{dn_3}{dt} &= f\left(R\right) - m_3\left(n_1 + n_2\right) \\ \frac{dR}{dt} &= g\left(R\right) - cf\left(R\right)\sum_{i=1}^{3} n_i \end{aligned} \tag{2.4}$$

Note that in this particularly simple case, $f\left(R^*\right) = m_1$ implies $m_2\left(n_1^*\right) = m_1$ and $m_3\left(n_1^* + n_2^*\right) = m_1$. The four conditions that imply the existence of a fixed point are: (2i) $m_1 > m_2\left(n_1^0\right)$ (condition (i) for species 2; species 2 can invade a community consisting solely of species 1); (2ii) $m_1 < m_2^0$ (condition (ii) for species 2); (3i) $m_1 > m_3\left(n_1^0\right)$ (condition (i) for species 3; note that in this model when species 1 and 2 occur together but without species 3, their total density is n_1^0); and (3ii) if n_1^+ denotes the density of species 1 when it occurs together with species 2, then $m_1 < m_3\left(n_1^+\right)$. Note that conditions (2ii) and (3ii), together with the monotonicity of $m_3\left(n_1 + n_2\right)$ imply $m_1 < m_3^0$. (If condition (3ii) is not true, then $m_1 > m_3\left(n_1^+\right)$. Let n_1^*, n_2^* be the densities of species 1 and 2 at the fixed point in the 3-species system. Then $m_1 = m_3\left(n_1^* + n_2^*\right)$ and $n_1^+ = n_1^*$ imply $m_3\left(n_1^* + n_2^*\right) > m_3\left(n_1^*\right)$, which in turn implies $n_1^* + n_2^* < n_1^*$, which then implies $n_2^* < 0$, and thus the fixed point is not feasible.) Note also that, for the existence of the fixed point, it is irrelevant whether or not $m_2^0 < m_3^0$.

Note that the only assumption necessary about species' R^* values is that species 1 must have the lowest R^*, but the rank order of the R^* values for all the other species is irrelevant, at least for determining of the existence of the fixed point. However, from the perspective of community assembly, successful species additions are more likely if positive interaction rank does correspond to R^* rank. Again, the three-species case is informative. If $R_3^* < R_2^*$, then species 2 will not be able to invade a community consisting solely of species 3. Instead, species 2 can only invade if species 1 is present. If instead $R_2^* < R_3^*$, then there are (in general) no such restrictions on the order in which species must arrive.

Appendix S3: Simulation details and community assembly simulation

For each species, r_i was drawn randomly from a normal distribution with parameters $\mu = 3$ and $\sigma = 0.1$, K_i was drawn from a normal distribution with $\mu = 1$ and $\sigma = 0.1$, m_i^{o} was drawn from a (shifted) exponential distribution with minimum value 1 and mean 1.5, and $d_i = 0.5$. Values of θ_{ij} were drawn from a normal distribution with $\mu = 0$ and $\sigma = 0.4$, and then positive and/or negative values of θ_{ij} were re-set to 0 in the scenarios with only positive or negative effects. In the scenario with structured positive effects, θ_{ij}'s were set equal to either their absolute value or to 0 depending on which species was the superior resource exploiter. In this way, the frequency of positive interactions was roughly constant for all scenarios that included them. Simulations were run from t=0 to t=10^4.

Community assembly simulations

I repeated the simulations reported in fig. 5 of the main text, with the modification that species were introduced one at a time instead of all at once. At every t=10 time units, one of the species in the species pool was selected at random and introduced with a density of .01. After 100 such introductions, the simulation was allowed to run to time t=6000. Species were declared extinct if their density fell below .1% of their introduced density. Individual species pools were identical to those used in the main text. Table S3.1 summarizes the average number of species that persisted for each of the five simulated scenarios. Note that these simulations use the same collection of species pools as fig. 5, which is why the results are more similar than one would expect given the standard errors.

Table S3.1. Species richness in simulated communities (mean ± s.e.)

	Introductions	
Scenario	All at once	One at a time
No interactions	1 ± 0	1 ± 0
+ and – interactions	2.62 ± 0.10	2.60 ± 0.09
Pos. interactions only	3.12 ± 0.11	3.20 ± 0.12
Neg. interactions only	1 ± 0	1 ± 0
Structured pos. interactions	5.31 ± 0.17	5.33 ± 0.17