

## Alternative stable states and regional community structure

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### Abstract

Many models of local species interactions predict the occurrence of priority effects due to alternative stable equilibria (ASE). However, few empirical examples of ASE have been shown. One possible explanation for the disparity is that local ASE are difficult to maintain regionally in patch dynamic models. Here we examine two possible mechanisms for regional coexistence of species engaged in local ASE. Biotically generated heterogeneity (e.g., habitat modification that favors further invasion by conspecifics) results in regional exclusion of one species at equilibrium. In contrast, abiotic heterogeneity due to spatial variation in resource supply ratios generates local-scale ASE and ensures regional coexistence with sufficiently broad environmental gradients. Abiotic heterogeneity can result in a species that is the dominant competitor over some of its range being excluded if the area where it is dominant is too small. Biotic heterogeneity can lead to alternative stable landscapes or regional priority effects, while abiotic heterogeneity results in regional determinism. Broad environmental gradients in resource supply favor regional coexistence of species that exhibit local ASE.

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### 1. Introduction

A continuing challenge in ecology is disentangling the relative role of deterministic processes from chance, historical factors in structuring ecological communities (Ricklefs and Schluter, 1993). The contingencies of history are likely to be most important when species interactions lead to alternative stable equilibria (ASE), where different steady-state, non-invasible community configurations arise in identical environments based on the order of colonization. A rich array of inter-specific interactions can generate ASE. The classical example is the Lotka–Volterra model of direct competition, where

competitive exclusion occurs and the identity of the winner depending on initial conditions (Gilpin and Case, 1976). Models of competition with explicit resource dynamics predict similar phenomena if each species has a greater impact on the resource that most limits its own growth (Tilman, 1988). Apparent competition coupled with an Allee effect can lead to ASE where either of two prey species sharing a generalist predator excludes the other (Holt, 1977). Intraguild predation, where a predator shares a common resource with its prey, can also generate ASE depending on system productivity (Holt and Polis, 1997; Diehl and Feissel, 2000; Mylius et al., 2001). ASE also occur in food web models when prey achieve a size refuge from predators and are highly tolerant of predation (Paine, 1974; Sutherland, 1974; Holt et al., 1994; Chase, 1999; Chase et al., 2000). Finally, species-specific modification of the physical environment, for instance through increasing fire frequency or suppression by litter, can

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also produce site pre-emption and priority effects (Bergelson, 1990; Dublin et al., 1990; Laycock, 1991; D'Antonio and Vitousek, 1992; Knowlton, 1992; Gragnani et al., 1999; Gunderson, 2000; Scheffer et al., 2001, 2003). Because many types of local interactions can lead to ASE, it may be reasonable to expect ASE to be commonly found in nature.

Local-scale ASE result in site pre-emption where the first species to colonize a patch excludes all subsequent invaders. The long-term persistence of local ASE therefore depends on the ability of each species to maintain populations within the broader landscape that provide propagules for colonizing local sites. The key issue with respect to long-term maintenance of ASE is in understanding the mechanisms that allow species to coexist regionally and thus maintain ASE locally. Investigating such mechanisms requires simultaneous consideration of local interactions leading to ASE and regional colonization–extinction dynamics. Although a great deal of theory exists on how ASE occur locally, very few studies have investigated the phenomena that allow their regional persistence. The relative lack of empirical examples of ASE may be due to the problem of maintaining such interactions regionally. Considering the consequences of regional dynamics for local-scale ASE may provide insight into the conditions that allow persistence of such interactions, as well as their broader influence on regional community structure.

Here we present simple mathematical models that combine local priority effects or ASE with colonization–extinction dynamics to identify conditions for coexistence of species whose interactions lead to local ASE. We begin by showing that local ASE can persist regionally if each species has a refuge external to the system (a form of spatial heterogeneity). We then consider two mechanisms that may lead to ASE in the presence of such heterogeneity. First, we investigate how biotically generated heterogeneity (e.g., species-specific habitat modification that favors further invasion by conspecifics) and colonization–extinction dynamics influence regional coexistence. Second, we extend Tilman's (1988) theory of competition for multiple limiting resources to ask how spatial variation in resource supply ratios generates local ASE and influences regional coexistence. The key result is that spatial heterogeneity per se does not necessarily lead to coexistence. Biotic heterogeneity does not allow regional coexistence of multiple species whose interactions lead to ASE since species are identical in their use of space and response to one another. Spatial variation in resource supply rates allows coexistence with local ASE depending on species traits (colonization and extinction rates) and the breadth of the environmental gradient. Finally, local ASE driven by biotically generated heterogeneity can lead to regional priority effects or alternative stable landscapes,

while abiotic heterogeneity leads to deterministic outcomes at the regional scale.

### 1.1. Model 1—metapopulation and island–mainland models of ASE

Consider a landscape consisting of two scales, a patch (which could be either local populations or individuals at specific spatial locations) and a region, a collection of patches connected by dispersal. Patches undergo stochastic extinction and are recolonized by species via global dispersal from the region. Stochastic extinction of local populations occurs via extrinsic factors such as disturbance, but not through exclusion by colonizing species. When occupied, patches obey priority rules whereby the first species to colonize a site excludes subsequent invaders. A patch may be occupied by no more than one species (or individual).

Given a local priority effect, the only patches available for colonization at a given time are those not occupied by other species. If species colonize local sites in proportion to their regional abundance, a simple model of two species engaged in pre-emptive competition is

$$\frac{dP_i}{dt} = c_i P_i (1 - P_i - P_j) - e P_i \quad (1)$$

where  $P_i$  is the fraction of patches occupied by species  $i$ , and  $c_i$  and  $e_i$  are species-specific colonization and extinction rates ( $i, j = 1, 2$ ).

As has been shown before (Taneyhill, 2000; Yu and Wilson, 2001), pre-emptive competition in a spatially homogeneous environment prevents regional coexistence of multiple species. The isocline for each species  $i$  is given by

$$P_i = 1 - P_j - \frac{e_i}{c_i} \quad (2)$$

The two isoclines are parallel, and the species with the lower value of  $e_i/c_i$  excludes the other (Fig. 1A). Thus, Model 1 predicts that, in a spatially homogeneous environment, species engaged in pre-emptive competition will not coexist at the regional scale at equilibrium. Although the identity of the species that dominates at the local scale is determined by priority rules, at the regional scale one species deterministically excludes the other. The winning species is the one that reduces the availability of empty patches to the lower level. Regional coexistence fails in a spatially homogeneous environment because it provides no opportunities for spatial niche partitioning. Since all species compete for empty patches and no species can displace another from occupied patches, there is complete niche overlap between competing species.

Next consider an island–mainland model where both species have a constant supply of colonists from somewhere within the region. In this case, the

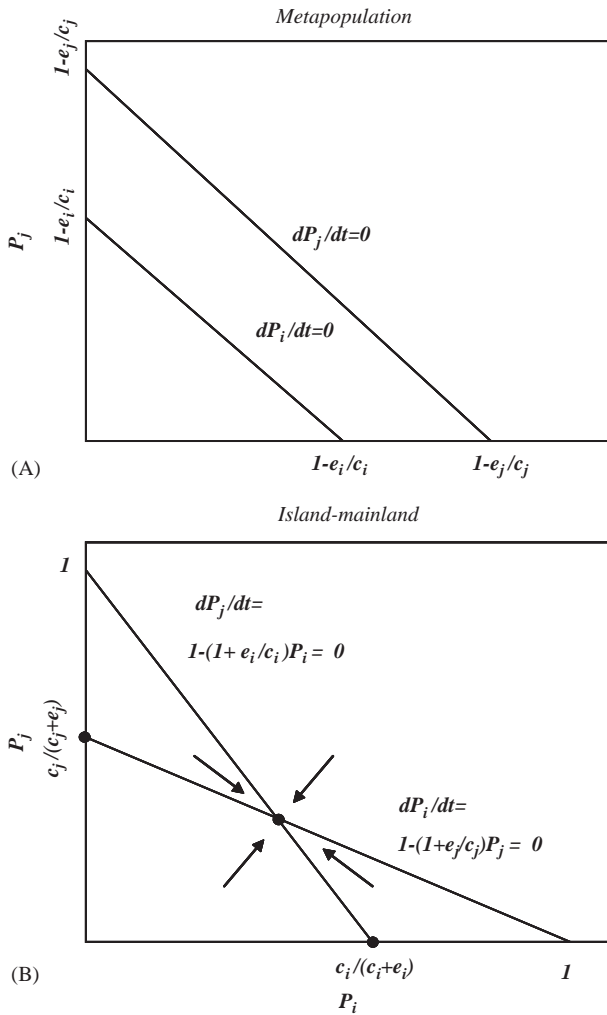


Fig. 1. Isoclines for Model 1, the regional model of bistable competition in (A) a simple, Levins-type metapopulation, and (B) an island-mainland model with a persistent refuge for each species. The island-mainland model has a persistent, stable equilibrium with both species present, while the metapopulation model does not.

probability of colonization is independent of regional abundance as the mainland provides a constant source of propagules. The equations for such a system are

$$\frac{dP_i}{dt} = c_i(1 - P_i - P_j) - e_iP_i. \quad (3)$$

In this case, a stable equilibrium with both species present is given by

$$P_i^* = \frac{c_i e_j}{c_j e_i + e_j(c_i + e_i)}. \quad (4)$$

A spatial refuge that is external to the system thus permits regional coexistence of both species, and the persistence of ASE in different patches. Fig. 1B shows a phase diagram for this system.

The island-mainland model represents an extreme case of spatial heterogeneity where every species has a refuge and its abundance inside the refuge (mainland) is unaffected by that in the islands. Such a situation may

not be biologically realistic for all systems in that it is unlikely that individuals move only from the mainland to the island, or that the source population is invulnerable to extinction (Harrison and Taylor, 1997). We next explore two realistic forms of spatial heterogeneity that may give rise to ASE in natural communities. We ask whether colonization-extinction dynamics combined with different forms of spatial heterogeneity allow the regional coexistence of species whose interactions lead to local ASE.

### 1.2. Model 2—metapopulation with biotically generated heterogeneity

Several proposed cases of ASE involve positive feedbacks where species modify the environment in ways that favor conspecifics. For instance, grasses in semi-arid rangelands are more flammable than woody plants and also recover more quickly following burning (Dublin et al., 1990; Laycock, 1991; D’Antonio and Vitousek, 1992; Gunderson, 2000). Removal of herbaceous plants by grazing has been proposed to favor woody plants, which in turn decrease the likelihood and severity of fires and further facilitate the transition to woody thickets. As another example, litter of *Poa annua* suppresses invasion by other species and allows regrowth of *Poa* in previously occupied sites (Bergelson, 1990). Finally, if species compete for heterogeneous resources, the resource level in a patch may recover slowly following extinction of a resident species. A recently vacated patch may be uninhabitable if the previous occupant reduced resource levels below what is required for invasion by another species. Thus, species may alter the local environment in ways that favor later colonization by conspecifics.

To consider the dynamics of such a system, we modified Model 1 to include a latency period after a species becomes extinct during which the empty patch can only be invaded by its conspecifics. The model represents a system where patches are more likely to return to their previous state following extinction than to make a transition to another state. In this case, there are five patch types: empty, occupied by either of two species, and latent or previously occupied by either species. The equations for this system are as follows:

$$\frac{dP_i}{dt} = c_i P_i (1 - P_i - P_j - L_i) - e_i P_i, \quad (5a)$$

$$\frac{dL_i}{dt} = e_i P_i - L_i (r_i + c_i P_i), \quad (5b)$$

where  $P_i$  is the fraction of patches occupied by species  $i$ .  $L_i$  is the fraction of “latent” patches from which species  $i$  has recently become extinct and are only invulnerable by its conspecifics ( $i, j = 1, 2$ ). The parameter  $r$  is the recovery rate of latent patches; when a patch “recovers” it becomes invulnerable by either species.

Sustained regional coexistence requires that each species is able to invade when rare. Species  $j$  can invade when species  $i$  is at its equilibrium abundance, provided the dominant eigenvalue of the Jacobian matrix evaluated at the edge equilibrium (i.e., with  $P_j = 0$  and  $L_j = 0$ ,  $L_i^*$  and  $P_i^*$  set at the single-species equilibrium) is positive. Evaluating this leads to the following invasion criterion for species  $j$  (see the appendix):

$$\frac{r_i(c_j e_i - c_i e_j) + c_i e_j (e_i - c_i)}{c_i(c_i + r_i - e_i)} > 0. \tag{6}$$

In order for a species to maintain positive abundance when alone, its colonization rate must be greater than its extinction rate ( $c_i > e_i$ ). Hence, the denominator must always be positive. The second term of the numerator is always negative. Hence, a necessary (but not sufficient) condition for invasion is that  $c_j e_i - c_i e_j > 0$ . Switching the indices  $i$  and  $j$  in Eq. (6) gives the invasion criterion for species  $i$ , when species  $j$  is present and at its equilibrium. This leads to a symmetrical necessary inequality for invasion, namely  $c_i e_j - c_j e_i > 0$ . Clearly, the invasion criteria for both species cannot be met at the same time. There are no mutually invulnerable combinations of parameter values, so sustained regional coexistence is impossible in Model 2.

To determine the identity of the winner in this system, we constructed phase diagrams for Model 2 (Fig. 2). The equilibrium fraction of latent patches for species  $i$  is

$$L_i^* = \frac{e_i P_i}{c_i P_i + r_i}. \tag{7}$$

The zero growth isocline for species  $i$  (by substituting Eq. (7) into Eq. (5a) and solving for  $P_j$ ) is then

$$P_j = \frac{-c_j e_i - (A + c_i(e_j + r_j)) + \sqrt{-4c_i r_j (A + c_j e_i) + (A + c_j e_i + c_i(e_j + r_j))^2}}{2c_i c_j}, \tag{8}$$

where

$$A \equiv c_i c_j (P_i - 1), \tag{9}$$

By solving the equation for  $P_j$ , we find the expression for species  $j$ 's isocline

$$P_j = 1 - \frac{e_j}{c_j} - P_i \left( \frac{e_i}{c_i P_i + r_i} + 1 \right). \tag{10}$$

Fig. 2 shows the isoclines for two species. When either the colonization rates ( $c$ 's) or recovery times ( $r$ 's) are very asymmetrical, the system shows regional competitive dominance, with one species deterministically excluding the other (Fig. 2A). However, when the species have similar traits, the system shows an unstable equilibrium that is a saddle point. This case results in a priority effect at the regional scale where either species can exclude the other depending on their initial densities

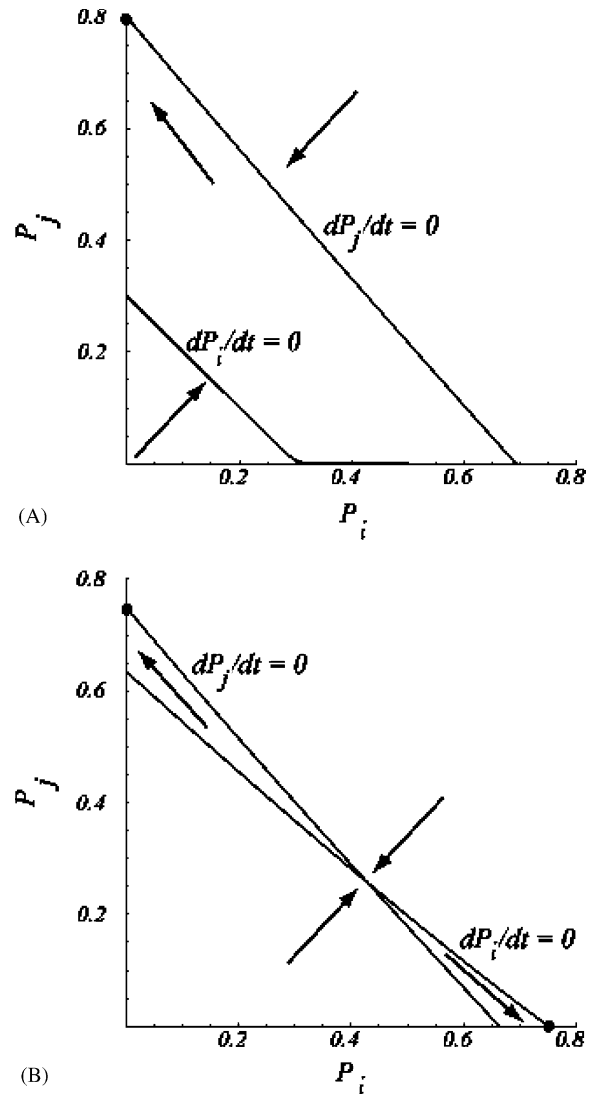


Fig. 2. Isoclines for the model of ASE with biotically generated heterogeneity (Model 2). The two panels show the situations where the recovery times are (A) very asymmetric ( $c_i = 0.2$ ,  $c_j = 0.5$ ,  $e_i = e_j = 0.1$ ,  $r_i = 0.5$ ,  $r_j = 0.0001$ ) and (B) more symmetric ( $c_i = c_j = 0.4$ ,  $e_i = e_j = 0.1$ ,  $r_i = 0.5$ ,  $r_j = 0.3$ ). In the first case, species  $j$  deterministically excludes species  $i$  (the black dot on the  $y$ -axis is the only stable, non-invasible equilibrium). In the second case (B), there is a stable, non-invasible equilibria on both axes. Each is an attractor in a different part of the phase space. The arrows indicate the trajectory of the system from different starting points. The same results obtain whether we make the colonization, extinction or recovery rates symmetric vs. asymmetric; unstable equilibria (priority effects) only occur when all parameter values are similar.

(Fig. 2B). Incorporating biotically generated heterogeneity does not permit regional coexistence of ASE. Unlike the spatially homogeneous case (Model 1), Model 2 predicts competitive dominance when species differ strongly in either colonization rates or the recovery times of latent patches, and alternative stable landscapes when species are more similar.

1.3. Model 3—abiotically generated spatial heterogeneity

Spatial heterogeneity can arise via processes external to the species themselves. One well-known example comes from mechanistic resource competition models (Tilman, 1988; Grover, 1997). The two consumer species require a minimum amount of each of two essential resources. The line representing the minimum amount of each resource that a species needs to maintain zero net growth at equilibrium is referred to as the zero net growth isocline (ZNGI, Fig. 3). The intersection of two species' ZNGIs represents a potential equilibrium where the stability of the equilibrium is determined by the relative positions of the consumption vectors. In this case, we represented the situation where each species has a relatively greater consumption vector on the resource it finds most limiting; thus, the equilibrium is bistable and priority effects occur. However, bistability only occurs when the supply of the two resources falls at ratios intermediate between the slopes of the consumption vectors (e.g., area C in Fig. 3). When resources are supplied in either high or low ratios (areas A and B in Fig. 3), the species with the lowest requirement for the least abundant resource deterministically excludes the other.

If the entire range of resource supply points among all patches within the region falls in area C in Fig. 3 (the

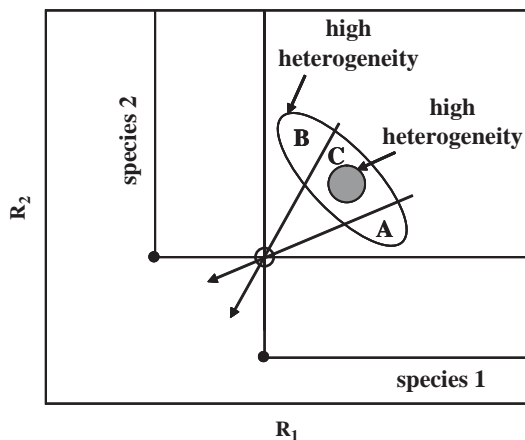


Fig. 3. Isoclines for two species showing bistable local competition for two essential resources. Species 1's impact vector is the arrow with the shallower slope. In the region between the two impact vectors, the densities of the two resources will be drawn to the unstable equilibrium (the open circle where the isoclines cross). Any small perturbation from this equilibrium leads the densities to one of the two stable equilibria (solid dots) where either species one or two excludes the other. ASE occur only in patches where the resource supply point falls in area C. In a region with low spatial heterogeneity in the supply of the two resources, all patches will have supply points within area C (the shaded circle), and the system obeys the dynamics of simple bistable competition (Model 1). With greater spatial heterogeneity, some patches fall into regions A and B where species 1 and 2, will dominate, respectively. Here, regional coexistence becomes possible, but only with sufficient numbers of patches in each region.

area between the supply vectors), then priority effects occur in every patch and the dynamics are described by the simple metapopulation (Model 1). However, if some patches fall within areas A or B, then each species has some proportion of the habitat where it is the dominant competitor. Each species can persist in patches where it is the weaker competitor (e.g., species 2 can invade patches with supply points in area A), but only if the dominant competitor is absent. Thus, the species display dominance competition (e.g., Levins and Culver, 1971) in patches with high or low resource supply ratios (areas A and B), and pre-emptive competition in patches with intermediate ratios (area C). Since each species has an area in the landscape where it is the dominant competitor and can displace the other species from occupied patches, spatial variation in resource supply ratios creates the potential for spatial niche partitioning. However, the degree of partitioning depends on the distribution of habitat among the three patch types (A, B, and C) and the species' colonization and extinction rates. Spatial heterogeneity alone may be insufficient to insure regional coexistence if the population in the refuge is influenced by the supply of colonists outside the refuge (e.g., if all patch types A, B and C exchange colonists). In this case, the amount of refuge available to each species may affect its ability to persist. Here we ask how the distribution of habitat among the three patch types A, B, and C influences coexistence of the two competitors.

The dynamics of two species (1 and 2) in patch types A, B, and C (Fig. 3) where species 1 is dominant in A patches, 2 in B patches, and priority effects take place in C patches, are described by the following model:

$$\frac{dP_{1A}}{dt} = c_1s_1(h_A - P_{1A}) - eP_{1A}, \tag{11a}$$

$$\frac{dP_{2A}}{dt} = c_2s_2(h_A - P_{1A} - P_{2A}) - eP_{2B} - c_1s_1P_{2A}, \tag{11b}$$

$$\frac{dP_{1B}}{dt} = c_1s_1(h_B - P_{1B} - P_{2B}) - eP_{1B} - c_2s_2P_{1B}, \tag{11c}$$

$$\frac{dP_{2B}}{dt} = c_2s_2(h_B - P_{2B}) - eP_{2B}, \tag{11d}$$

$$\frac{dP_{1C}}{dt} = c_1s_1(h_C - P_{1C} - P_{2C}) - eP_{1C}, \tag{11e}$$

$$\frac{dP_{2C}}{dt} = c_2s_2(h_C - P_{1C} - P_{2C}) - eP_{2C}, \tag{11f}$$

where  $h_A$ ,  $h_B$  and  $h_C$  are the proportions of habitat of types A, B and C, respectively ( $h_A + h_B + h_C = 1$ ) and  $s_1$  and  $s_2$  are the total number of patches containing species 1 and 2 (i.e.,  $s_1 = P_{1A} + P_{1B} + P_{1C}$  and  $s_2 = P_{2A} + P_{2B} + P_{2C}$ ). The model assumes that the different patch types are well mixed across the landscape so that colonists originate from each patch state at a rate proportional to its regional abundance. It also assumes

that the rate of production of colonizing propagules is independent of the habitat type; relaxing these assumptions makes the algebra cumbersome, even in single species cases (Holt, 1997). For simplicity, we assume that extinction rates ( $e$ ) are uniform among habitats and species. Relaxing this assumption does not alter the qualitative results that follow.

If species 1 is present alone in the region, its equilibrium abundance in any patch type  $i$  is

$$P_{1i} = h_i \left( 1 - \frac{e}{c_i} \right). \quad (12)$$

Proceeding with the invasion analysis as before (see the appendix), we find that species 1 can invade when rare with species 2 at equilibrium if

$$h_B < \frac{c_2(c_1 - c_2)}{c_1(c_2 - e)} + \frac{c_2 h_A}{e} \quad (13)$$

and that species 2 can invade species 1 when

$$h_B > \frac{e(c_1 - c_2)}{c_2(c_1 - e)} + \frac{e h_A}{c_1}. \quad (14)$$

When inequalities (13) and (14) are both satisfied, the system is mutually invulnerable and coexistence is possible. The invasion criteria define the degree of spatial niche overlap between species.

Fig. 4 shows the parameter space where exclusion and coexistence take place. The key result is that abiotic heterogeneity allows regional coexistence of competitors that would otherwise exclude each other if neither had a refuge where it is the dominant competitor. The critical amount of refuge habitat for each species is a linear function of the amount of refuge for the other (Eqs. (13) and (14), Fig. 4A) and a nonlinear function of the two species' colonization and extinction rates (Eqs. (13) and (14), Fig. 4B). If the two species' colonization rates are equal, the conditions for mutual invasibility are  $h_B < c_2 h_A / e$  and  $h_B > e h_A / c_1$ . Coexistence is therefore possible when the species have identical colonization–extinction dynamics as long as  $h_A$  and  $h_B$  are greater than zero (e.g., both species have some refuge habitat available, Fig. 4A). When species are dissimilar in their extinction and colonization rates however, spatial niche overlap may be too large (i.e., refuge size is too small; e.g., near the axes in Fig. 4A) and competitive exclusion results. The presence of refuge habitat by itself is insufficient to insure coexistence. That is, a species may be dominant in some patches but still be excluded regionally (e.g., in the upper-left and lower-right of Fig. 1A).

To determine whether alternative stable landscapes occur with spatial variation in resource supply ratios, we searched for combinations of parameter values where neither species could invade the other at equilibrium (where the dominant eigenvalues of the Jacobian matrix with one species at equilibrium and the other absent were both negative, see the appendix). Over a wide range

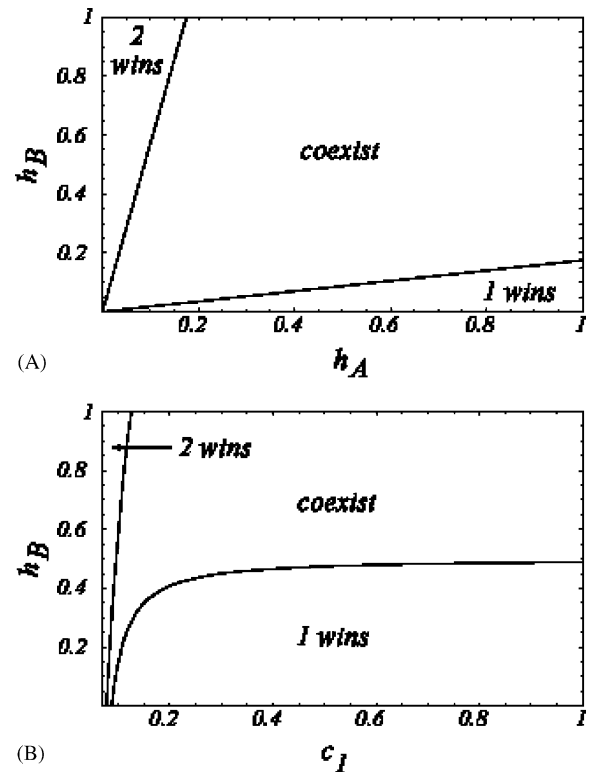


Fig. 4. Invasibility boundary for the model of priority effects and dominance competition with spatial heterogeneity (Model 3). The lines show the combinations of parameter values where the dominant eigenvalue of the Jacobian matrix is zero for the invasion of both species. (A) The value of  $h_B$  where each species is able to invade the other as a function of  $h_A$ . (B) The critical value of  $h_B$  as a function of  $c_1$ , the colonization rate of species 1.

of parameter values, we found no situations where both eigenvalues were negative. Thus, competitive exclusion is deterministic when spatial niche overlap is large and regional priority effects are not possible.

## 2. Discussion

Theory has identified many mechanisms that give rise to ASE at the local scale. However, long-term persistence of ASE requires that competing species coexist regionally. Few models to date have examined the mechanisms that allow regional coexistence of species engaged in local ASE. We found that spatial heterogeneity per se cannot guarantee regional coexistence, and hence long-term persistence of ASE. Spatial heterogeneity has to create opportunities for spatial niche partitioning or differential responses of species to one another or the abiotic environment. Biotic heterogeneity cannot lead to regional coexistence because it provides no opportunities for spatial niche partitioning. In the language of Chesson (2000), biotic heterogeneity is not a stabilizing force, which is a required condition for long-term coexistence. Abiotic heterogeneity through

variation in resource supply ratios, by contrast, allows regional coexistence through spatial niche partitioning or variable dominance mediated by abiotic conditions.

Several of the best-studied empirical examples of ASE involve situations where species alter the physical environment in ways that drive positive feedbacks that favor conspecifics. For example, many grasses are both more flammable than woody plants and more tolerant of burning. Replacement of shrubs by grasses therefore promotes fire which further favors invasion by grasses (Laycock, 1991; D'Antonio and Vitousek, 1992). Similar situations have been proposed for plants whose litter suppresses competitors (Bergelson, 1990; Foster and Gross, 1997), in competition between corals and macroalgae (Knowlton, 1992), between intertidal algae and invertebrates (Petraitis and Dudgeon, 1999), with diatoms in mudflats (Van De Koppel et al., 2001), and between floating and submerged plants (Scheffer et al., 2003). Positive feedbacks driven by plant–water interactions in semi-arid ecosystems may also lead to spatial pattern formation (Rietkerk et al., 2002). Model 2 represents the case of biotically generated environmental heterogeneity, and indicates that such situations lead to regional exclusion in the absence of mitigating factors. This result suggests that, if the above cases indeed represent ASE, then some other process must be present that allows regional coexistence of the two states. For instance, abiotic environmental heterogeneity may create refugia or sites where one or another state dominates. The example of Scheffer et al. (2003) illustrates this situation. They found that floating plants dominate at high nutrients and submerged macrophytes at low nutrients in shallow lakes, and that alternative states occurred at intermediate productivity. Another possible explanation is that alternative stable *ecosystem* states often involve dominance by one or another suite of species without complete exclusion of the other. Thus, some degree of local coexistence between the alternate states may facilitate regional coexistence (Taneyhill, 2000).

We found that spatial variation in resource supply ratios can allow regional coexistence by producing preemptive competition in some patches and dominance competition in others. The breadth of the resource supply gradient determines the degree of spatial niche overlap between species and the likelihood of regional coexistence. Thus, the extension of resource ratio theory to incorporate the regional processes of colonization–extinction dynamics provides a quantifiable measure of regional niche overlap or limiting similarity. Niche overlap is determined by the interplay between the breadth of the environmental gradient and the species' colonization rates (Fig. 4). Spatial heterogeneity in resource ratios is not sufficient to insure regional coexistence. It is interesting to note that a species that is the dominant competitor for some part of its range

can be excluded if the amount of habitat where it is dominant is too small (e.g., near the axes in Fig. 4A). Competition for multiple resources is one commonly proposed mechanism for local scale ASE, and is analogous to Lotka–Volterra models of direct competition with explicit resource dynamics. Our results indicate that spatial heterogeneity in resource supply at the regional scale is critical to the persistence of such interactions.

An interesting contrast between biotic and abiotic heterogeneity is that ASEs through habitat modification (Model 2) can lead to alternative stable landscape configurations, while abiotic heterogeneity cannot (Model 3). This is a direct result of the degree of spatial niche overlap. With complete spatial niche overlap, as in the case of biotic heterogeneity (Model 2), ASE at the local scale produce alternative states at regional scales. In the case of abiotic heterogeneity, niche overlap is incomplete because species can displace one another and respond differently to the physical environment. In this case, the only outcomes at the regional scale are coexistence (if niche overlap is small) or deterministic exclusion of one species by the other (if niche overlap is large). Relatively few mechanisms for generating alternative stable landscapes have been demonstrated theoretically. Other examples include sink effects where local dynamics are affected by migration (the core-satellite hypothesis, Hanski, 1982) and spatial food chain interactions where predators stabilize local dynamics among species at lower trophic levels (Holt, 2002).

In Model 3, we showed how bistable resource competition at intermediate resource supply ratios can allow long-term, regional persistence of local ASE. This mechanism may be generalizable to other local interactions that produce ASE depending on the position of sites along environmental gradients, particularly productivity. For instance, in a model of size-structured predation and competition, Chase (1999) showed that ASE only occurred at intermediate productivity (see also Holt, 1997; Chase et al., 2000). One species dominated at higher rates of productivity and the other at low productivity. The presence of ASE at intermediate productivity has received experimental support (Chase, 2003). Similarly, models of intra-guild predation predict ASE involving pre-emptive exclusion of either the intermediate or top predator only at intermediate productivities (Holt and Polis, 1997; Diehl and Feissel, 2000; Mylius et al., 2001). A similar situation occurs in competition between floating and submerged aquatic plants (Scheffer et al., 2003). In each of these examples, one species dominates at either end of the gradient. Our model suggests that local-scale ASE among localities connected by colonization occur only if there is sufficient spatial heterogeneity in environmental conditions among sites that ASE do not occur in all patches. If the conditions of all sites falls within the range where

ASE occur locally, then spatial niche overlap is complete and one species excludes the other. Broader gradients in local conditions increase the likelihood of coexistence in the portion of the habitat where ASE occur. Although our model was motivated by models of competition (Fig. 3), the above examples suggest that they may apply more generally to a range of different local interactions giving rise to ASE.

Although abiotic spatial heterogeneity is required for the persistence of ASE in the models we examined, other model formulations would likely reveal additional situations under which ASE can persist regionally. For instance, we assumed separation of local and regional time-scales, i.e., a species achieves its local equilibrium population density immediately upon colonizing a site. Taneyhill (2000) showed that incorporating transient phases of local coexistence could produce stable regional coexistence in a system with local ASE. If competitive exclusion takes place slowly relative to colonization and extinction, then patches containing both species may temporarily persist. If these patches produce colonists, then regional coexistence may be possible with preemptive competition even though local exclusion eventually takes place. In addition, we only considered situations where species could coexist at equilibrium. In non-equilibrium systems, priority effects can persist for long periods before species eventually become extinct (Hubbell, 2001). However, in order for new species to invade such a system, dispersal must be localized so that new species sometimes encounter areas with many vacant patches where they are able to increase. In a well-mixed system with ASE, new species can only invade by having a larger ratio of  $c/e$  than the species already present, and will then deterministically exclude the resident species. However, the local dispersal model approximates the one with global dispersal in that, in the absence of input of new species, one species eventually excludes all others from the region. Finally, temporal fluctuations and storage effects can promote regional coexistence in models with local-scale priority rules (Chesson and Warner, 1981; Kelly and Bowler, 2002). Our model assumes that all species and environmental properties are constant through time.

The prevalence of ASE in communities has long been a topic of debate in ecology (Connell and Sousa, 1983; Petraitis and Latham, 1999; Scheffer et al., 2001; Bertness et al., 2002). A number of plausible theoretical mechanisms have been shown to give rise to ASE. Bertness et al. (2002) proposed that ASE are “an interesting theoretical idea without a definitive empirical example.” Our models indicate that regional persistence of ASE depends on spatial niche partitioning between species among patches. This result may help to explain why ASE are difficult to maintain, and point to situations where they may be more likely to be observed (e.g., along environmental gradients). Many proposed examples involve biotically generated heterogeneity and habitat modification. Interestingly, Model 2 predicts that such a case does not allow regional coexistence, but does produce alternative stable landscapes or regional-scale priority effects. Such effects are impossible in spatially homogeneous models. Our results indicate that local ASE driven by competition for multiple resources can persist provided there is sufficient spatial heterogeneity in resource supply for niche partitioning to take place. Interestingly, several of the best-studied empirical examples of ASE involve situations where priority effects occur along some, but not all portions of an environmental gradient (e.g., only at intermediate productivity). Our predictions indicate that local-scale ASE should most likely occur where broad environmental gradients protect each of the states from the other.

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### Appendix

The Jacobian matrix for Model 2 is

	$P_1$	$P_2$	$L_1$	$L_2$
$P_1$	$c_1(1 - 2P_1 - P_2 - L_2) - e_1$	$-c_2P_2$	$e_1 - c_1L_1$	0
$P_2$	$-c_1P_1$	$c_2(1 - 2P_2 - L_1 - P_1) - e_2$	0	$e_2 - c_2L_2$
$L_1$	0	$-c_2P_2$	$-r_1 - c_1P_1$	0
$L_2$	$-c_1P_1$	0	0	$-r_2 - c_2P_2$



Species *i* can invade when rare if the dominant eigenvalue of the Jacobian (Eq. (4)) is positive when evaluated at the equilibrium with species *j* present without species *i*. In this equilibrium, the density of patches with species *j* ( $P_j$ ) is  $1 - e_j/c_j$  and the density of latent patches is given by Eq. (5). The equilibrium is unstable to invasion by species *i* if the dominant eigenvalue (Eq. (4)) is negative. In the main text, we show that the invasion criteria for both species cannot occur simultaneously, therefore mutual invasion is impossible.

The Jacobian matrix for Model 3 is:

	$P_{1A}$	$P_{2A}$	$P_{1B}$	$P_{2B}$	$P_{1C}$	$P_{2C}$
$P_{1A}$	$c_1(h_A - s_1 - P_{1A}) - e$	$-c_1P_{2A} - c_2s_2$	$c_1(h_B - P_{1B} - P_{2B})$	0	$c_1(h_C - P_{1C} - P_{2C})$	0
$P_{2A}$	0	$c_2(h_A - P_{1A} - P_{2A} - s_2) - c_1s_1 - e$	$-c_2P_{1B}$	$c_2(h_B - P_{2B})$	0	$c_2(h_C - P_{1C} - P_{2C})$
$P_{1B}$	$c_1(h_A - P_{1A})$	$-c_1P_{2A}$	$c_1(h_B - s_1 - P_{1B} - P_{2B}) - e - c_2s_2$	0	$c_1(h_C - P_{1C} - P_{2C})$	0
$P_{2B}$	0	$c_2(h_A - P_{1A} - P_{2A})$	$-c_2P_{1B} - c_1s_1$	$c_2(h_B - s_2 - P_{2B}) - e$	0	$c_2(h_C - P_{1C} - P_{2C})$
$P_{1C}$	$c_1(h_A - P_{1A})$	$-c_1P_{2A}$	$c_1(h_B - P_{1B} - P_{2B})$	0	$c_1(h_C - s_1 - P_{1C} - P_{2C}) - e$	$-c_2s_2$
$P_{2C}$	0	$c_2(h_A - P_{1A} - P_{2A})$	$-c_2P_{1B}$	$c_2(h_B - P_{2B})$	$-c_1s_1$	$c_2(h_C - P_{1C} - P_{2C} - s_2) - e$

Species *i* can invade when rare if the dominant eigenvalue of the Jacobian is positive when evaluated at the equilibrium with species *j* by itself. Here, the density of species *j* in each patch type is  $h_Q(1 - e/c_j)$  where  $h_Q$  is the proportion of patches of type *Q* ( $Q=A, B$  or  $C$ ). The equilibrium is unstable to invasion by species *i* if the dominant eigenvalue (Eqs. (13) and (14)) is negative. This leads to the invasion criteria shown in Fig. 4.

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