Competition and the Effect of Spatial Resource Heterogeneity on Evolutionary Diversification

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ABSTRACT: A model is presented to explore how the form of selection arising from competition for resources is affected by spatial resource heterogeneity. The model consists of a single species occupying two patches connected by migration, where the two patches can differ in the type of resources that they contain. The main goal is to determine the conditions under which competition for resources results in disruptive selection (i.e., selection favoring a polymorphism) since it is this form of selection that will give rise to the evolutionary diversification of resource exploitation strategies. In particular, comparing the conditions giving rise to disruptive selection when the two patches are identical to the conditions when they contain different resources reveals the effect of spatial resource heterogeneity. Results show that when the patches are identical, the conditions giving rise to disruptive selection are identical to those that give rise to character displacement in previous models. When the patches are different, the conditions giving rise to disruptive selection can be either more or less stringent depending upon demographic parameters such as the intrinsic rate of increase and the migration rate. Surprisingly, spatial resource heterogeneity can actually make forms of evolutionary diversification such as character displacement less likely. It is also found that results are dependent on how the resource exploitation strategies and the spatial resource heterogeneity affect the population dynamics. One robust conclusion however, is that spatial resource heterogeneity always has a disruptive effect when the migration rate between patches is low.

Keywords: character displacement, frequency-dependent selection, density-dependent selection, competition, resource exploitation, Lotka-Volterra.

Much of the early work in theoretical ecology centered on trying to determine the importance of competition for resources in the structuring of communities. One of the

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first organizing principles to emerge from this research was the principle of limiting similarity (e.g., see MacArthur and Levins 1967; May 1974; Abrams 1975). This principle postulates that there is a limit to how similar species can be and still coexist. Although this is primarily an ecological principle, there has been considerable interest in related evolutionary processes as well. Brown and Wilson (1956), and later Hutchinson (1959), initiated study of the evolutionary consequences of competition by introducing putative examples of what they termed "character displacement." In these examples, species that coexist in some geographic regions and not in others, differ to a greater extent where they occur in sympatry than where they occur in allopatry. They suggested that such patterns might have arisen from evolutionary character divergence because competition for resources in areas of sympatry should result in each species specializing on different resources.

Since Brown and Wilson's paper, the plausibility of evolutionary character divergence has been examined theoretically in a number of different ways. Initially, MacArthur and Levins (1964, 1967) and Levins (1968) investigated the idea in terms of fitness sets. Subsequent to these investigations, several authors have explored character displacement using more explicit accounts of consumer (and resource) population dynamics, as well as more explicit accounts of evolutionary change (Bulmer 1974; Crozier 1974; Lawlor and Maynard Smith 1976; Roughgarden 1976, 1983; Fenchel and Chistiansen 1977; Slatkin 1980; Case 1981, 1982; Matessi and Jayakar 1981; Pacala and Roughgarden 1982; Lundberg and Stenseth 1985; Milligan 1985; Taper and Case 1985, 1992; Abrams 1986, 1987*a*, 1987*b*, 1990*a*, 1990*b*; Brown and Vincent 1987; Gotelli and Bossert 1991; Vincent et al. 1993; Doebeli 1996; Law et al. 1997). This list is undoubtedly incomplete, but most such theoretical research builds on previous models by exploring the effects of additional biological factors such as asymmetric competition, different types of genetic architecture, nonequilibrium population dynamics, temporally fluctuating environments, multidimensional resource spaces, and the importance of absolute versus relative resource abundances. This research has centered on deter-

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mining the conditions that favor evolutionary divergence as opposed to convergence.

An important biological factor that is conspicuously absent from the above list is the effect of spatial resource heterogeneity (SRH). In particular, if different resources are found in different spatial locations, is character displacement more or less likely to occur? Many organisms forage under such resource heterogeneity. For example, some freshwater fish species forage in both the limnetic and the benthic regions of lakes, and these regions contain very different suites of prey (Mittlebach 1981). There is considerable evidence that character displacement has occurred in some of these systems as well (Schluter and McPhail 1992; Robinson and Wilson 1994; Schluter 1994), but there are few theoretical results available to predict when we expect such divergence and when we do not if SRH is present. The initial theoretical work on character displacement by Levins (1962, 1968) and MacArthur and Levins (1964) clearly considered such SRH to be important, but the large body of theory on competition for resources and character displacement that followed essentially ignored this issue. Although the flavor of spatial heterogeneity is present in the foraging time trade-offs in many of the above models (e.g., Lawlor and Maynard Smith 1976), the movement of individuals between different resource patches is usually not explicitly considered. Consequently, it is not possible from these results to determine how factors such as the propensity of individuals to move mediates the effects of spatial heterogeneity.

Of the few spatial models of character displacement that have been examined, none to my knowledge has examined how the incorporation of SRH alters predictions. For example, Pacala (1988) explored a model in which there is spatially local resource use by sedentary individuals, and he showed that the extent of resource partitioning decreases as resource use becomes more local. His model did not, however, explore the effect of SRH, and he identified this as an important area for future research. Similarly, Kawata (1996) constructed a spatial simulation model of character displacement based on a two-consumer, two-resource model of competition. Resource use was again local, but both resources were randomly distributed throughout space and, thus, there was no consistent, coarse-grained SRH. Last, Brown and Pavlovic (1992) considered a two-patch model that did explicitly involve SRH. They analyzed it in terms of fitness sets, however, and because their model is quite different from most of the aforementioned models of character displacement, it is difficult to draw any clear comparisons.

The purpose of this article is, therefore, to determine how the predictions from previous models change when there is spatial resource heterogeneity. In particular, is character divergence more or less likely to occur under these conditions? There are a number of ways in which this question might be addressed, and I take what is probably the simplest possible approach. I consider competition for resources among individuals of a single species and determine the conditions necessary for there to be a single, evolutionarily stable resource exploitation strategy. What is of most interest, however, is when these conditions are not satisfied. In such instances, selection will be disruptive, favoring an evolutionary diversification of strategies, and it is under these conditions that phenomena like character divergence will occur.

It should be stressed that I do not model character displacement per se. I simply examine the conditions under which competition for resources results in disruptive selection within a single species. The reasoning is that, if selection favors a diversity of strategies within a single species, then it will also favor a diversity of strategies among species when there is more than one present. In this sense, disruptive selection is a necessary condition for the occurrence of evolutionary diversification via natural selection. Making any predictions about evolutionary diversification would require knowledge about the number of competing species as well as their underlying genetic architectures. Because understanding the form of selection is a first step toward understanding evolutionary change, I restrict my attention to this more limited goal. The advantage is that my results should have a much broader scope of applicability. Of course, it is possible to construct models of character displacement in which disruptive selection is sufficient for evolutionary divergence. In fact, this is true of many previous models of character displacement, and it is these models that are most easily compared to my results.

My approach is to consider two spatially distinct resource patches connected by migration and to ask how the conditions for disruptive selection change as the resources in each patch become more different. At first glance, it would seem that this should effectively broaden the available resource base. As a result, it should lead to increased disruptive selection and, thereby, make character displacement (or other forms of evolutionary diversification) more likely. It turns out, however, that this is not always the case. The form of selection depends critically on demographic parameters such as the migration rate and the intrinsic rate of increase. Furthermore, the form of selection is dependent on the specifics of competition such as how the resource exploitation strategies and the spatial resource heterogeneity affect the population dynamics. Nevertheless, some general conclusions can still be drawn.

The Model

There are two main approaches in the literature for constructing evolutionary models of competition for resources. One uses the explicit consumer-resource equations of theoretical ecology (e.g., Lawlor and Maynard Smith 1976; Taper and Case 1985; Abrams 1986, 1987*a*, 1987*b*). The other is more phenomenological and is based on the Lotka-Volterra competition equations or similar equations (e.g., Bulmer 1974; Slatkin 1980; Case 1981, 1982; Milligan 1985; Taper and Case 1985; Brown and Vincent 1987; Doebeli 1996; Law et al. 1997). The Lotka-Volterra approach is followed here. This approach assumes that the available resources can be indexed along a single axis such as size (but see Pacala and Roughgarden 1982). The available resources can then be depicted by a plot of resource abundance versus size (fig. 1*A*). To introduce SRH into this framework, I consider two discrete patches coupled by migration, where each patch has a different distribution of resources (fig. 1*B*). For simplicity, I assume that the resource distribution in each patch is symmetric and unimodal and that the shape of the distribution does not differ between patches. Therefore, with the size example, the two patches can differ in the mean size of resources available and in the total resource abundance. Without loss of generality, I choose a scale such that the means of the resource distributions are symmetric about 0 at $\pm\theta$ (fig. 1*B*). With this formulation, θ is a measure of spatial heterogeneity, and $\theta = 0$ corresponds to no heterogeneity. Therefore, I can replicate the results of nonspatial models by setting $\theta = 0$.

The Lotka-Volterra approach also assumes that the resource exploitation strategies of consumers can be mapped onto the resource axis. If the resources are indexed by size, for example, then the exploitation strategies must also be indexed by size. A strategy, *u*, would be a strategy that primarily consumes resources of size *u*. Of course, this strategy will consume resources of different sizes as well, and this is why different strategies compete. The Lotka-Volterra approach supposes that this effect of competition decreases as the strategies become more different, reflecting the fact that very different strategies are less likely to consume the same resources than very similar strategies.

The next step is to specify how the frequency of different strategies in the population will be modeled. Here the Lotka-Volterra approach has been handled using two different types of models: quantitative-genetic (QG) models and the game-theoretic (GT) models (Taper and Case 1992). Quantitative-genetic models assume that the strategies in the population are present according to some continuous frequency distribution (usually Gaussian), while GT models assume that the population is monomorphic for a resident strategy and consider the fate of rare mutant
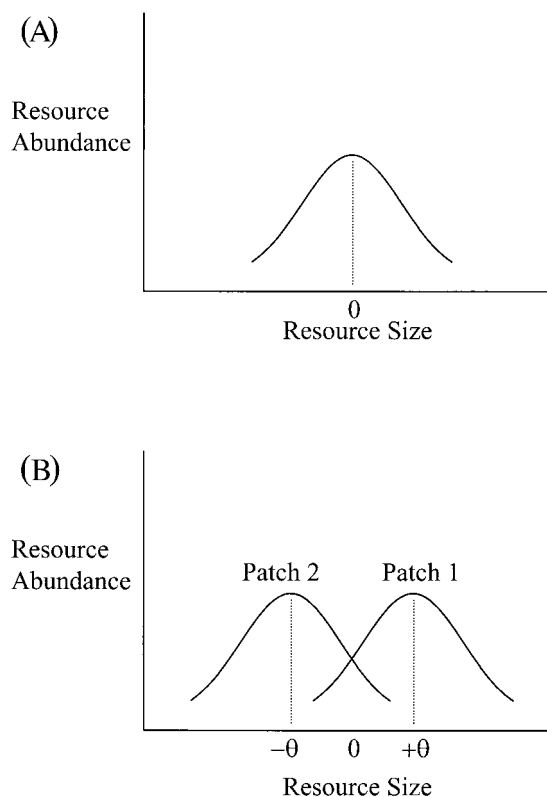

Figure 1: Plot of resource abundance against resource size. The abundance axis is arbitrary. Size is one example of how the available resources might be indexed. *A*, Plot depicting the qualitative features of the abundance distribution for a single habitat, with the size axis scaled so that the peak of the abundance graph coincides with zero. *B*, Plot depicting the qualitative features of the abundance distributions in the model presented here that has two patches connected by dispersal. The size axis is again scaled so that the two abundance graphs have peaks that are symmetric around 0 at $\pm\theta$.

strategies that arise. It turns out that these two approaches are mathematically very similar (Iwasa et al. 1991; Abrams et al. 1993; Taylor 1996; Taylor and Day 1997), and they give similar results under a very wide range of conditions, particularly for character displacement models (Taper and Case 1992). Therefore, I use a GT model because it is easier to obtain analytical results.

With this background, I now describe the model more explicitly. Let $\hat{u}$ denote the resident resource exploitation strategy. I will assume that reproduction (which is both density and frequency dependent) takes place within each patch, followed by dispersal, and that the population size is regulated independently within each patch. Thus, the number of resident individuals in patches 1 and 2 (denoted N_1^* and N_2^*) are governed by the system

$$N_1^*(t + 1) = \tilde{R}_1^* N_1^*(t)(1 - \delta) + \tilde{R}_2^* N_2^*(t)\delta,$$

$$N_2^*(t + 1) = \tilde{R}_1^* N_1^*(t)\delta + \tilde{R}_2^* N_2^*(t)(1 - \delta), \qquad (1)$$

where

$$\tilde{R}_i^* = 1 + \rho_i\left(1 - \frac{N_i^*}{K_i(\hat{u})}\right), \qquad (2)$$

where ρ_i is the intrinsic rate of increase in patch i, δ is the probability of an individual migrating to the other patch $(0 < \delta < 1/2)$, and $K_i(\hat{u})$ is the carrying capacity of the resident population in patch i. The expected number of offspring produced by a resident individual in patch i is $\tilde{R}_i^*$. Notice that, although the probability of migration is symmetric between the two patches, the number of migrants per generation need not be symmetric because each patch can have a different total number of individuals.

I assume that the resource distribution in each patch is reflected by the carrying capacity functions K_i, such that a strategy specializing on an abundant resource type will have a high carrying capacity. Thus, the K_i are symmetric and unimodal, with peaks at $\pm\theta$. I follow previous models by using a Gaussian form for K_i:

$$K_1(u) = \kappa_1 \exp\left[-\frac{1}{2\sigma_k^2}(u - \theta)^2\right], \qquad (3)$$

$$K_2(u) = \kappa_2 \exp\left[-\frac{1}{2\sigma_k^2}(u + \theta)^2\right]. \qquad (4)$$

The shape of these functions is similar to those of the resource abundance curves depicted in figure 1*B*. The breadth of resources available in each patch is represented by σ_k^2, and the parameter κ_i gives the maximal possible carrying capacity in patch i.

Equations (1) describe the population dynamics of the resident strategy in isolation, and to determine the fate of a rare mutant strategy, u, system (1) is augmented to incorporate the mutant's dynamics:

$$N_1^*(t + 1) = R_1^* N_1^*(t)(1 - \delta) + R_2^* N_2^*(t)\delta,$$

$$N_2^*(t + 1) = R_1^* N_1^*(t)\delta + R_2^* N_2^*(t)(1 - \delta),$$

$$N_1^m(t + 1) = R_1^m N_1^m(t)(1 - \delta) + R_2^m N_2^m(t)\delta, \qquad (5)$$

$$N_2^m(t + 1) = R_1^m N_1^m(t)\delta + R_2^m N_2^m(t)(1 - \delta).$$

The number of mutants in patch i is denoted by N_i^m and the expected number of offspring produced by each type

(denoted by R_i^* and R_i^m) is given by the Lotka-Volterra competition equations,

$$R_i^* = 1 + \rho_i\left[1 - \frac{N_i^* + \alpha(u, \hat{u})N_i^m}{K_i(\hat{u})}\right], \qquad (6)$$

$$R_i^m = 1 + \rho_i\left[1 - \frac{N_i^m + \alpha(\hat{u}, u)N_i^*}{K_i(u)}\right]. \qquad (7)$$

Notice that $\tilde{R}_i^* = R_i^*$ when the mutants are absent (i.e., $N_i^m = 0$). Thus, when mutants are present, the dynamics of the resident population (i.e., [1]) change due to competition, which affects the expected number of offspring produced in each patch. The function $\alpha(u, \hat{u})$ is the competition coefficient from the Lotka-Volterra equations, and it specifies the intensity of competition between an individual with strategy u and one with strategy $\hat{u}$ relative to the intensity of competition between two identical individuals. There are several possible choices for the function α, and again I follow previous models by using the Gaussian form:

$$\alpha(u, \hat{u}) = \exp\left[-\frac{1}{2\sigma_\alpha^2}(u - \hat{u})^2\right]. \qquad (8)$$

The parameter σ_α specifies how quickly the intensity of competition falls off with increasing phenotypic distance.

Method of Analysis

In all analyses, I restrict attention to values of ρ satisfying $0 < \rho < 2$ so that the resident population dynamics reach a stable equilibrium. Suppose there is a single, evolutionarily stable strategy. When it is the resident strategy, no mutant strategy will be able to invade. The ability of a mutant to invade is described by the stability of the equilibrium $N_1^* = \hat{N}_1^*$, $N_2^* = \hat{N}_2^*$, $N_1^m = 0$, and $N_2^m = 0$ of system (5), where $\hat{N}_1^*$, $\hat{N}_2^*$ is the equilibrium obtained by the resident strategy in the absence of the mutant. A linear stability analysis (app. A) shows that this stability depends on the magnitude of the eigenvalue

$$\lambda[u, \hat{u}, \hat{N}_1^*(\hat{u}), \hat{N}_2^*(\hat{u})] = \frac{1}{2}\Big[(1 - \delta)(R_1^m + R_2^m)$$

$$+ \sqrt{(1 - \delta)^2(R_1^m + R_2^m)^2 - 4R_1^m R_2^m(1 - 2\delta)}\Big].$$

I refer to expression (9) as the fitness of a mutant using strategy u in a population using $\hat{u}$ because it is the mutant's

initial multiplication rate. A mutant will invade if and only if its fitness is >1 because invasion requires that it more than replace itself. Notice that the arguments of the fitness function λ in (9) display the fact that selection is both frequency and density dependent, but for shorthand, I will simply write $\lambda(u, \hat{u})$. Therefore, if there is a single, evolutionarily stable strategy (an ESS), u^*, we have

$$\lambda(u, u^*) \leq \lambda(u^*, u^*), \tag{10}$$

$$\lambda(u^*, u^*) = 1 \tag{11}$$

for all mutant strategies, $u \neq u^*$. Condition (10) expresses the fact that, if the population is at an ESS, then a mutant's fitness will be maximized by using the same resource exploitation strategy as the resident (i.e., $u = u^*$). In other words, if u^* is an ESS, then no other strategy provides a larger fitness in a population dominated by this strategy. The equality in (11) follows from the fact that the mutant will be completely neutral if its resource exploitation strategy is the same as that of the resident.

It is difficult to characterize u^* using condition (10) directly, so local conditions are employed instead. Since condition (10) implies that $\lambda(u, u^*)$ is maximized in u at $u = u^*$, an ESS must satisfy

$$\left.\frac{\partial \lambda}{\partial u}\right|_{u=\hat{u}=u^*} = 0. \tag{12}$$

This is simply a first-order necessary condition for λ to be maximized in u at $u = u^*$, and I refer to it as the evolutionary equilibrium condition. This reflects the fact that directional selection ceases to act when (12) holds ($\partial \lambda/\partial u|_{u=\hat{u}}$ is a measure of the strength of directional selection).

The crux of my analysis rests upon an examination of the sign of the second derivative,

$$\left.\frac{\partial^2 \lambda}{\partial u^2}\right|_{u=\hat{u}=u^*}. \tag{13}$$

If (13) is negative, then $u = u^*$ represents a local maximum of λ as a function of u, and therefore, nearby strategies cannot invade because their fitness is <1. If, however, (13) is positive, then $u = u^*$ represents a local minimum of λ as a function of u, and therefore, nearby strategies will invade because they have a fitness >1. In such cases, selection favors extreme phenotypes, and this is when we expect evolutionary diversification. This is what will be referred to as "disruptive selection" in what follows (see Christiansen 1991 for a more detailed explanation of this approach). Notice, however, that this type of analysis is meaningful only if directional selection near the evolu-

tionary equilibrium actually drives the population toward it since it is only such equilibria that the population will experience. This means that we require directional selection to be positive (favoring larger values of u) when $\hat{u} < u^*$ and for it to be negative (favoring smaller values of u) when $u^* < \hat{u}$. This implies that the derivative of $\partial \lambda/\partial u|_{u=\hat{u}}$ with respect to $\hat{u}$ is negative at $\hat{u} = u^*$; that is,

$$\frac{d}{d\hat{u}}\left\{\left.\frac{\partial \lambda}{\partial u}\right|_{u=\hat{u}}\right\}\Bigg|_{\hat{u}=u^*} < 0. \tag{14}$$

I refer to condition (14) as the "convergence stability condition" (Eshel 1983; Taylor 1989). The sign of (13) will be examined only for those evolutionary equilibria that satisfy this condition. Incidentally, it turns out that there is always at least one evolutionary equilibrium in the model presented, and numerical results suggest that when there is only one evolutionary equilibrium, it always satisfies condition (14).

Results

Explicit expressions for (12) and (13) are presented in appendix B for two different levels of generality. The most general expressions (given by [B2] and [B5]) allow for any function R_i^m for the number of offspring produced by a mutant individual in patch i. The next level of generality is more specific and substitutes the Lotka-Volterra form of R_i^m (i.e., [7]) into these expressions but allows for arbitrary parameter values (see [B6] and [B9]). The results presented here are more specific yet and assume certain restrictions on the parameter values. Throughout the results below, I simplify the notation by defining $\eta = \delta/(1 - \delta)$ as an index of migration. Since the migration rate δ is between 0 and 1/2, η is between 0 and 1. The value $\eta = 0$ corresponds to perfect site fidelity ($\delta \to 0$) and $\eta = 1$ corresponds to random mixing ($\delta \to 1/2$).

No Spatial Resource Heterogeneity

By setting $\theta = 0$ and $\rho_1 = \rho_2 = \rho$, I recover a model that is similar to many previous models of character displacement that lack spatial resource heterogeneity. In this case $u^* = 0$ (and $\hat{N}_1^* = K_1(0)$, $\hat{N}_2^* = K_2(0)$) is the only value of u^* that satisfies (B6), and therefore, it is the only evolutionary equilibrium. This equilibrium also always satisfies the convergence stability condition (14). Using this evolutionary equilibrium in (B9) shows that (13) has the same sign as

$$\sigma_k^2 - \sigma_\alpha^2. \tag{15}$$

Disruptive selection occurs if (15) is positive, whereas sta-

bilizing selection occurs when (15) is negative. This is identical to results from many previous models of character displacement (Roughgarden 1976, 1983; Brown and Vincent 1987; Vincent et al. 1993). Biologically, it means that more than one consumer species (or strategy) can be supported by the available resources (i.e., disruptive selection occurs) if the diversity of resource types (as measured by σ_k^2) is greater than the diversity of resources used by any single type of consumer (as measured by σ_α^2). In other words, the spectrum of available resources must be broader than any single consumer's niche. This is a well-known result in the character displacement literature, and it provides a benchmark against which results that incorporate spatial resource heterogeneity can be compared.

The Effect of Spatial Resource Heterogeneity

Habitat Symmetry. With habitat symmetry (i.e., $\rho_1 = \rho_2$ and $\kappa_1 = \kappa_2$), $u^* = 0$ (and $\hat{N}_1^* = K_1(0)$, $\hat{N}_2^* = K_2(0)$) is again one possible evolutionary equilibrium. This is not surprising since the two habitats are identical except that their resource distributions have peaks that are symmetric around 0. With the approach outlined in appendix B, it can be shown that the convergence stability condition (14) at this evolutionary equilibrium requires that

$$\frac{\sigma_k^2}{\theta^2} > \frac{-2(\eta + \eta\rho - \rho)}{2 + (1 - \eta)(\rho - 2)}. \tag{16}$$

Numerical results suggest that this condition is satisfied if and only if $u^* = 0$ is the only evolutionary equilibrium.

Restricting attention to parameter values for which (16) is satisfied, we can determine the conditions necessary for this evolutionary equilibrium to exhibit disruptive selection. Substituting $u^* = 0$ (and $\hat{N}_1^* = K_1(0)$, $\hat{N}_2^* = K_2(0)$) into (B9) shows that (13) has the same sign as

$$(\sigma_k^2 - \sigma_\alpha^2) + \frac{\sigma_\alpha^2}{\sigma_k^2} \theta^2 \left(\frac{\rho - \eta\rho - \eta}{\eta} \right). \tag{17}$$

Disruptive selection occurs when (17) is positive, and stabilizing selection occurs when it is negative. Note that setting $\theta = 0$ reduces this expression to the nonheterogeneous expression (15) as it should.

This makes clear the effect of spatial resource heterogeneity. In particular, spatial heterogeneity (having $\theta \neq 0$) will have a disruptive effect if $(\rho - \eta\rho - \eta)/\eta > 0$, and it will have a stabilizing effect if $(\rho - \eta\rho - \eta)/\eta < 0$. Therefore, for a given rate of increase, ρ, selection tends to be stabilizing for large migration rates and disruptive for small migration rates. If the migration rate becomes small

enough, however, condition (16) may no longer be satisfied (fig. 2).

The migration rate at which the form of selection switches from disruptive to stabilizing depends on the value of the intrinsic rate of increase. For example, a larger intrinsic rate of increase allows for a larger range of migration rates that result in disruptive selection (fig. 2). Notably, if migration is high enough ($\eta \to 1$), (16) is always satisfied, and (17) shows that heterogeneity always has a stabilizing effect. Conversely, if migration rate is low enough ($\eta \to 0$), condition (16) requires that $\sigma_k^2 > 2\theta$ and heterogeneity always has a disruptive effect (fig. 3).

The fact that SRH can result in stabilizing selection and, therefore, can hinder the evolutionary diversification is somewhat surprising. To gain more insight into this phenomenon, consider the specific parameter values $\delta = 1/2$ and $\rho = 1$, in which case SRH always has a stabilizing effect. The fitness expression (9) reduces to

$$\lambda(u, 0) = \frac{1}{2}(R_1^m + R_2^m), \tag{18}$$

a mutant's fitness is simply the average of its rate of growth in each patch, with each patch weighted equally. Substituting expressions (7) for the R's gives
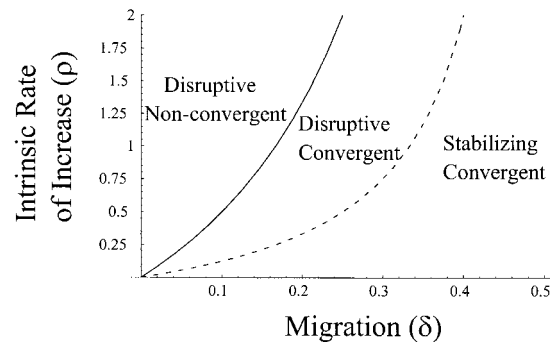

Figure 2: Range of migration rates that result in heterogeneity having a disruptive versus a stabilizing effect on the equilibrium, $u^* = 0$. Spatial heterogeneity has a disruptive effect when $\delta < \rho/(1 + 2\rho)$ and a stabilizing effect when the reverse inequality holds. Dashed line is the boundary between these two types of behavior (i.e., it is defined by $\delta = \rho/(1 + 2\rho)$). The parameter combinations that result in $u^* = 0$ being convergent stable (*convergent*) and convergence unstable (*nonconvergent*) are also depicted. The solid line is the boundary between these two types of behavior and is defined by $\delta = \rho/(4 + 2\rho)$. Results are for the parameter values $\sigma_k = 1$, and $\theta = 1$.
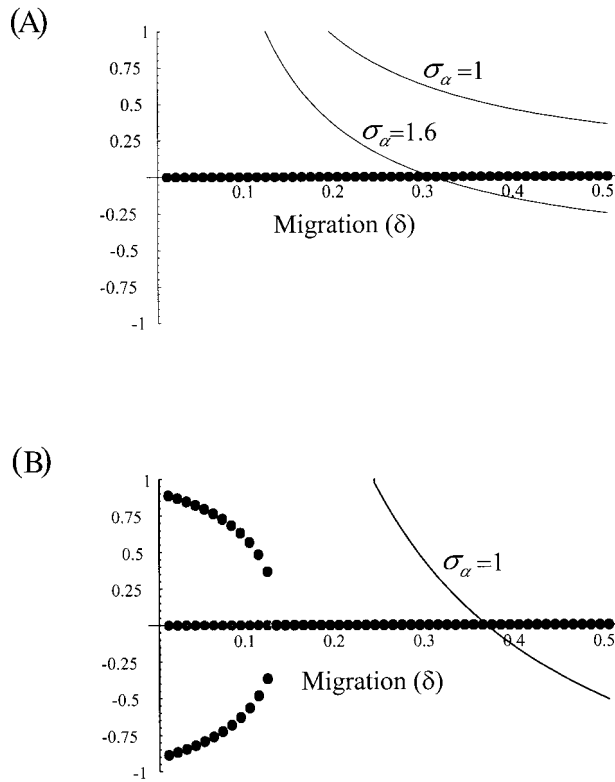
Figure 3: Plot of evolutionary equilibria and expression (13) against migration rate. Circles are evolutionary equilibria, and curves are expression (13) different values of σ_α (note: changes in σ_α do not affect the evolutionary equilibria). Where the curves are above the δ-axis, expression (13) is positive, and therefore, selection at the equilibrium is disruptive (negative values imply stabilizing selection). Black circles represent convergence stable equilibria, and grey circles represent convergence unstable equilibria. *A*, Parameter values $\sigma_k = 1.5$, $\rho = 1$, $\theta = 1$, $\kappa_1 = \kappa_2 = 1,000$. For these values, condition (16) holds for all values of δ, and the only evolutionary equilibrium is $u^* = 0$. *B*, Parameter values $\sigma_k = 1.1$, $\rho = 1$, $\theta = 1$, $\kappa_1 = \kappa_2 = 1,000$. For these values, condition (16) fails when the migration rate is low enough, at which point two additional evolutionary equilibria appear, both of which are convergence stable, and $u^* = 0$ becomes convergence unstable. Only one value of σ_α is shown in panel *B*.

$$\lambda(u, 0) = \frac{1}{2}\left\{4 - \left[\frac{\alpha(u, 0)}{K_1(u)} + \frac{\alpha(u, 0)}{K_2(u)}\right]\hat{N}\right\} \qquad (19)$$

$$= 2 - \alpha(u, 0)\frac{1}{2}\left[\frac{1}{K_1(u)} + \frac{1}{K_2(u)}\right]\hat{N} \qquad (20)$$

$$= 2 - \alpha(u, 0)\frac{1}{\tilde{K}(u)}\hat{N}, \qquad (21)$$

where $\tilde{K}(u)$ is the harmonic mean carrying capacity for a mutant using resource exploitation strategy u and $\hat{N} = K_1(0) = K_2(0)$.

First consider the case where heterogeneity is absent (i.e., $\theta = 0$). Then $K_1(u) = K_2(u) = K(u)$. A mutant using strategy $u > 0$ (or $u < 0$) will benefit from reduced competition through a decrease in α, but it will pay the cost of specializing on a resource type that is less abundant through a decrease in K. It will invade only if the benefits outweigh the costs, and this is more likely to be the case if the resource distribution, K, is broad. This condition is embodied in expression (15) being positive.

Now consider the case where $\theta \neq 0$. Here $K_1(u) \neq K_2(u)$ except in the case where $u = 0$. A mutant using strategy $u > 0$ will again benefit from reduced competition through a decrease in α. Now however, we need to compare this benefit to the cost that results from a change in $\tilde{K}$. Although having $u > 0$ will increase K_1, it will decrease K_2 substantially, and because it is the harmonic mean of the two that is relevant, the smaller K dominates. Therefore, spatial heterogeneity inhibits the evolutionary diversification of strategies. Biologically, a specialist strategy (one that uses $u \neq 0$) loses much more in the "wrong" habitat than it gains in the "right" habitat. In general, however, the migration rate at which selection switches from being disruptive to stabilizing depends on the intrinsic rate of increase. If this is high, then a specialist strategy is better able to make up for the heavy loss in the wrong habitat, so that there is a greater range of migration rates for which selection is disruptive.

Habitat Asymmetry. Most of the qualitative effects of SRH are exhibited by the symmetric case. There are some differences under asymmetry, however, and I present these results here. All results in this section were obtained numerically.

Asymmetric Intrinsic Rates of Increase ($\rho_1 > \rho_2$). The most obvious effect of having asymmetric intrinsic rates of increase is that $u^* = 0$ is no longer an evolutionary equilibrium. Instead, it seems that there is always an evolutionary equilibrium that is positive when $\rho_1 > \rho_2$ and that this equilibrium is larger for lower migration rates (fig. 4). Unlike in the symmetric case, however, this equilibrium is always convergence stable for all migration rates. This reflects the fact that directional selection drives the population to a strategy that is best adapted to the habitat with the highest intrinsic rate of increase.

As with the symmetric case, this positive equilibrium experiences stabilizing selection when the migration rate is high enough, and the form of selection switches to disruptive once the migration rate drops below a critical threshold (fig. 4). For certain parameter values, however, two additional equilibria form when the migration rate becomes low enough (fig. 4). Unlike the symmetric case,
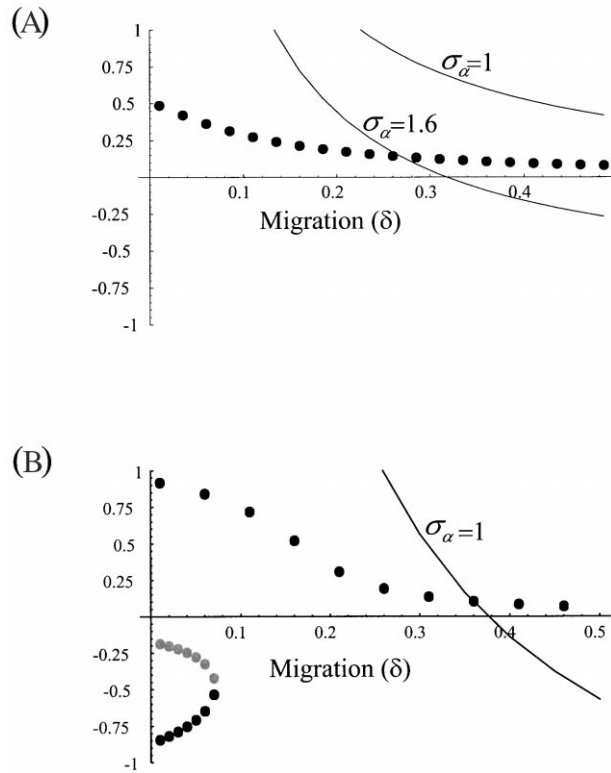
population toward being adapted to the habitat with the highest maximal carrying capacity when the migration rate is low.

This can be understood with reference to the previous arguments involving the harmonic mean carrying capacity. When the migration rate is high, natural selection favors a strategy that is adapted to the habitat with the lowest maximal carrying capacity, thereby minimizing adverse effects when in the wrong habitat.

As with the case when $\rho_1 \neq \rho_2$, for some parameter values, two new equilibria appear when the migration rate gets low enough. The original equilibrium appears to remain convergence stable, and again one of the two new equilibria is convergence unstable while the other is convergence stable.

The Form of Selection Can Also Depend on the Specifics of Competition

One of the most surprising results of the above analysis is that spatial resource heterogeneity can cause selection to be stabilizing for a single resource exploitation strategy and can, therefore, hinder evolutionary diversification. It is, therefore, of interest to determine whether or not this result is dependent upon the underlying details of competition for resources. Here, I demonstrate that this is the case by using a different choice of R_i^m.

Although many alternative forms of R_i^m might be used, the simplest is perhaps

Figure 4: Plot of evolutionary equilibria and expression (13) against migration rate for asymmetric intrinsic rates of increase ($\rho_1 = 1.25$ and $\rho_2 = 1$). Circles are evolutionary equilibria, and curves are expression (13) for different values of σ_α. Where the curves are above the δ-axis, expression (13) is positive, and therefore, selection at the equilibrium is disruptive (negative values imply stabilizing selection). Black circles represent convergence stable equilibria, and grey circles represent convergence unstable equilibria. *A*, Parameter values: $\sigma_k = 1.5$, $\theta = 1$, $\kappa_1 = \kappa_2 = 1,000$. For these values, there appears to be only one evolutionary equilibrium, and it is always convergence stable. *B*, Parameter values: $\sigma_k = 1.1$, $\theta = 1$, $\kappa_1 = \kappa_2 = 1,000$. For these values, two new equilibria appear when the migration rate is low enough. At this point the initial equilibrium remains convergence stable, and one of the new equilibria (the middle equilibrium) is convergence unstable and the second new equilibrium is convergence stable. Only one value of σ_α is shown in panel *B*.

the original equilibrium remains convergence stable, but one of the two new equilibria is convergence unstable while the other is convergence stable.

Asymmetric Maximal Carrying Capacities ($\kappa_1 > \kappa_2$). In this case, again $u^* = 0$ is no longer an evolutionary equilibrium; instead, there is an equilibrium that is positive for low migration rates, and it becomes negative as the migration rate increases (fig. 5). This equilibrium appears to always be convergence stable as well. Therefore, with high migration rates, directional selection drives the population toward being adapted to the habitat with the lowest maximal carrying capacity, but it switches to driving the
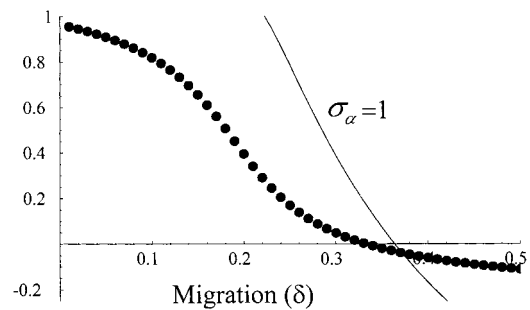
Figure 5: Plot of evolutionary equilibria and expression (13) against migration rate for asymmetric maximal carrying capacities ($\kappa_1 = 1,500$ and $\kappa_2 = 1,000$). Circles are evolutionary equilibria, and curves are expression (13). Where the curves are above the δ-axis, expression (13) is positive, and therefore, selection at the equilibria is disruptive (negative values imply stabilizing selection). Parameter values: $\sigma_k = 1.1$, $\rho = 1$, $\theta = 1$. For these values, there appears to be only one evolutionary equilibrium, and it is always convergence stable. For other parameter values, it is again possible for there to be more than one evolutionary equilibria (not shown).

$$R_i^m = 1 + \tilde{\rho}_i[K_i(u) - N^m - \alpha(u, \hat{u})\hat{N}^*]. \qquad (22)$$

Expression (22) is related to the Lotka-Volterra form used earlier in that the carrying capacity for this type of population dynamic is again given by $K_i(u)$. The difference lies in the fact that the intrinsic rate of increase, $\tilde{\rho}_i K_i(u)$, is now also a function of the resource exploitation strategy, u. To see how this type of population dynamic compares to the Lotka-Volterra version used earlier, I examine the case where $\tilde{\rho}_1 = \tilde{\rho}_2$ and $\kappa_1 = \kappa_2$.

From (B2) and (B5) of appendix B, $u^* = 0$ (and $\hat{N}_1^* = K_1(0)$, $\hat{N}_2^* = K_2(0)$) is again an equilibrium, and expression (5) now has the same sign as

$$(\sigma_k^2 - \sigma_\alpha^2) + \frac{\sigma_\alpha^2}{\sigma_k^2}\theta^2\left[\frac{\eta + (1 - \eta)\tilde{\rho}K(0)}{\eta}\right], \qquad (23)$$

where $K(0) = K_1(0) = K_2(0)$ (cf. [17]). This shows that, when heterogeneity is absent ($\theta = 0$), the condition for disruptive selection is the same as in the other model (i.e., [15] must be positive), but now heterogeneity always has a disruptive effect ($[\eta + (1 - \eta)\rho K(0)]/\eta$ is always positive).

Discussion

The purpose of the model analyzed here was to explore the effects of coarse-grained spatial resource heterogeneity on the evolutionary diversification of resource exploitation strategies. In particular, I examined how the conditions for phenomena such as character displacement change when spatial heterogeneity is introduced. Surprisingly, it was found that spatial heterogeneity can cause selection to be either disruptive or stabilizing, depending upon the balance between the intrinsic rate of increase and the migration rate. Additionally, the form of selection can also depend on how the resource exploitation strategy and the spatial resource heterogeneity affect the population dynamics. Previous models by Abrams (1986, 1987a, 1987b, 1990a, 1990b) have demonstrated that competition for resources can result in nonintuitive evolutionary outcomes as well. His models were based on explicit consumer and resource dynamics rather than on the Lotka-Volterra approach used here, however, and therefore, a comparison of the two is difficult. It would be very useful to explore the correspondence between these two modeling approaches.

The results presented here are closely related to those of Brown and Pavlovic (1992). They studied a model similar to that studied here, but they used a continuous-time formulation with a different type of population dynamic, and they framed their analysis in the context of Levins's (1968) ideas of fitness sets. They obtained similar results in that, for the two types of competition that they explored (a Lotka-Volterra type and a consumer-resource type), high migration rates resulted in stabilizing selection, and low migration rates resulted in disruptive selection. My results complement their findings in two ways. First, I have explicitly tied my approach to previous models of character displacement, and therefore, I am able to examine directly how conditions that favor character displacement change when spatial heterogeneity is introduced. This is useful because, as mentioned earlier, many organisms probably forage under such spatial resource heterogeneity. Expression (17) is a generalization of previous character displacement results, and it reveals how spatial resource heterogeneity affects the conditions for divergence. It shows that factors such as the intrinsic rate of increase, in addition to the migration rate, can influence whether selection will be stabilizing or disruptive. Second, Brown and Pavlovic (1992) analyzed two quite different models of competition and found that both displayed a range of migration rates for which selection was stabilizing, although the exact migration rate at which the form of selection switched was different for each. Thus, they suggested that different formulations of competition could have nontrivial effects on model predictions. My results reiterate and strengthen this claim by showing that qualitatively different predictions can be made depending on how the resource exploitation strategy and the spatial resource heterogeneity affect the population dynamics.

All of the findings presented here make it clear that simple, general predictions will often be difficult, but they do not necessarily imply that "anything goes." There is some regularity to all of the predictions found here as well as to those found by Brown and Pavlovic (1992). In particular, if the migration rate between resource patches is low, then spatial resource heterogeneity always has a disruptive effect. This conforms to our intuition that selection should favor specialization on each resource patch. The surprise comes when the migration rate is high. Under these conditions, it is possible for selection to be either stabilizing or disruptive depending on the specifics of the situation. Of course, this does not mean that no predictions can be made but rather that more information regarding the underlying biology is necessary before this will be possible. This should not be surprising. Indeed, it would be more surprising if general predictions could be made that are independent of the underlying form of competition for resources and of the population dynamics.

Biological Implications

Given the diversity of predictions that can be made when there is SRH, how can such models be used to understand better the evolutionary diversification of resource exploi-

tation strategies? To answer this question, it is helpful to return to a specific example of freshwater fish alluded to in the introduction, three-spine sticklebacks. Many lakes inhabited by sticklebacks can be thought of as two resource patches, the benthic and the limnetic. One of the primary differences between the prey found in each of these two habitats is their size, the benthic habitat generally containing larger prey (Mittlebach 1981). Furthermore, it has been shown that certain morphological characteristics are required to forage efficiently in each of the two habitats (Larson 1976; Bentzen and McPhail 1984; Lavin and McPhail 1986; Schluter 1993), and therefore, resource exploitation strategies can be mapped onto a prey size axis reasonably well. What is not known is the extent of migration between the two habitats. The above model assumes that individuals forage in a single habitat during any given season, and there is some circumstantial evidence suggesting that this is true of sticklebacks. For example, some solitary species appear to partition the lake along the benthic-limnetic axis such that individuals found in the benthic habitat tend to be morphologically distinct from those found in the limnetic habitat (Lavin and McPhail 1985; Schluter and McPhail 1992). This might result from habitat choice or habitat-induced morphological plasticity (Day et al. 1994), but in either case it suggests relatively consistent habitat use since diet-induced morphological change occurs only over a long period of time (Day and McPhail 1996).

Given that the model's assumptions are adequately met for this system, what predictions does it make? First, if habitat preferences are highly heritable, then the effective migration rate between the habitats will be low. In this case, we would expect strong disruptive selection, and this should result in a diversification of resource exploitation strategies. This might be realized simply as an increased variance in trophic morphology or, perhaps, a trophic polymorphism. Alternatively, if there is very little correlation between parents and offspring in their foraging habitats, then selection can be strongly stabilizing or strongly disruptive.

Comparisons across lakes with different amounts of benthic and limnetic habitat might also be understood by looking at the model's predictions when the two habitats have different carrying capacities. Figure 5 shows that the resource exploitation strategy (i.e., the trophic morphology) should more closely match the most abundant habitat. This makes perfect sense, but there are some comparisons across lakes that can result in counterintuitive predictions. For example, fish from a lake in which the size distribution of benthic prey is very similar to that of limnetic prey might well experience greater disruptive selection than those from a lake in which the size distributions are very different. Mathematically, the first lake

has a smaller θ than the second, and if the standard Lotka-Volterra model is adequate, then expression (17) shows that this can result in greater disruptive selection. Therefore, in some circumstances, it might not be surprising to see a smaller variance in the trophic morphology of fish inhabiting lakes with very different sized benthic and limnetic prey than in fish inhabiting lakes in which these two types of prey have very similar sizes.

In closing, it is perhaps useful to take a broader perspective and ask how the results presented here might be altered when other biological details are incorporated. In particular, all of the present results assume that migration is passive. This is not unreasonable for some organisms, but often individuals exhibit adaptive behavior either by "choosing" not to migrate if migration is likely to result in a fitness disadvantage or by exhibiting some type of habitat choice when migrating. Such behavior might be a facultative response (e.g., habitat choice) or a constant response that has become fixed through evolution (e.g., a low migration rate). In either case, for organisms that exhibit this type of adaptive behavior, spatial resource heterogeneity will likely have a disruptive effect most of the time. Without adaptive behavior, resources can be partitioned only through individuals specializing on different resource types. With adaptive behavior, however, resources can be partitioned spatially as well. This suggests some tentative general predictions about the effects of spatial resource heterogeneity: SRH will tend to have a disruptive effect and, thereby, favor a diversification of resource exploitation strategies if migration is passive and the migration rate is low or if individuals can exhibit some form of adaptive migratory behavior; SRH will have a stabilizing effect and, thereby, hinder the diversification of resource exploitation strategies only when migration is passive and the migration rate is high; SRH can have a disruptive effect in this context as well, however, and therefore more information about the biological details of competition is necessary before more definite predictions can be made.

Acknowledgments

APPENDIX A

Linear Stability Analysis

A linear stability analysis of the equilibrium shows that stability is determined by the leading eigenvalue of an upper-triangular matrix:

$$\begin{bmatrix} \mathbf{R} & \mathbf{U} \\ 0 & \mathbf{M} \end{bmatrix}_{N_1^* = \hat{N}_1^*,\, N_2^* = \hat{N}_2^*,\, N_1^m = 0,\, N_2^m = 0}, \tag{A1}$$

where $\mathbf{R}$, $\mathbf{U}$, and $\mathbf{M}$ are 2×2 submatrices. Thus, stability is determined by the largest eigenvalue (in modulus) of the two submatrices:

$$\mathbf{R} = \begin{bmatrix} \left(\dfrac{\partial R_1^*}{\partial N_1^*} N_1^* + R_1^* \right)(1 - \delta) & \left(\dfrac{\partial R_2^*}{\partial N_2^*} N_2^* + R_2^* \right)\delta \\[3mm] \left(\dfrac{\partial R_1^*}{\partial N_1^*} N_1^* + R_1^* \right)\delta & \left(\dfrac{\partial R_2^*}{\partial N_2^*} N_2^* + R_2^* \right)(1 - \delta) \end{bmatrix}_{N_1^* = \hat{N}_1^*,\, N_2^* = \hat{N}_2^*,\, N_1^m = 0,\, N_2^m = 0} \tag{A2}$$

and

$$\mathbf{M} = \begin{bmatrix} R_1^m(1 - \delta) & R_2^m \delta \\ R_1^m \delta & R_2^m(1 - \delta) \end{bmatrix}_{N_1^* = \hat{N}_1^*,\, N_2^* = \hat{N}_2^*,\, N_1^m = 0,\, N_2^m = 0}. \tag{A3}$$

Notice that $\mathbf{R}$ is the matrix obtained from conducting a linear stability analysis of the pure resident system (1) at the equilibrium $N_1^* = \hat{N}_1^*$, $N_2^* = \hat{N}_2^*$, and because this equilibrium is stable by assumption, both eigenvalues of $\mathbf{R}$ are <1 in magnitude. Thus, stability is completely determined by the leading eigenvalue of the mutant submatrix, $\mathbf{M}$. These are

$$\frac{1}{2}\left[(1 - \delta)(R_1^m + R_2^m) \pm \sqrt{(1 - \delta)^2 (R_1^m + R_2^m)^2 - 4 R_1^m R_2^m (1 - 2\delta)} \right]. \tag{A4}$$

It can be shown that the second term in these eigenvalues is always real, and thus, assuming $R_1^m + R_2^m \geq 0$, (9) of the text is the leading eigenvalue.

APPENDIX B

Equilibrium Conditions

Here I calculate conditions (12) and (13) at two levels of generality. First, I allow any functions R_i^m, and simply calculate these conditions using the leading eigenvalue (9). The next level of (reduced) generality then substitutes the Lotka-Volterra form of R_i^m (i.e., [7]) into these expressions but allows for arbitrary parameter values. Last, I also demonstrate how (14) is calculated although I do not present these results here.

Condition (12)

Writing (9) as $1/2[(1 - \delta)(R_1^m + R_2^m) + \sqrt{S}]$, where $S = (1 - \delta)^2 (R_1^m + R_2^m)^2 - 4 R_1^m R_2^m (1 - 2\delta)$, we get

$$\frac{\partial \lambda}{\partial u} \propto (1 - \delta)\left(\frac{\partial R_1^m}{\partial u} + \frac{\partial R_2^m}{\partial u} \right) + \frac{1}{2\sqrt{S}} \frac{\partial S}{\partial u}. \tag{B1}$$

Now, because $\lambda(u^*, u^*) = 1$, we have that $\sqrt{S} = 2 - (1 - \delta)(R_1^m + R_2^m)$ when at $u = u^*$ (recall that $\sqrt{S}$ is always real) and therefore, (B1) evaluated at $u = u^*$ is proportional to

$$(1 - \delta)\left(\frac{\partial R_1^m}{\partial u} + \frac{\partial R_2^m}{\partial u}\right) - (1 - 2\delta)\left.\left(\frac{\partial R_1^m}{\partial u} R_2^m + R_1^m \frac{\partial R_2^m}{\partial u}\right)\right|_{u=\hat{u}=u^*}. \tag{B2}$$

Condition (13)

Calculating (13) from (B1) we get

$$\frac{\partial^2 \lambda}{\partial u^2} \propto (1 - \delta)\left(\frac{\partial^2 R_1^m}{\partial u^2} + \frac{\partial^2 R_2^m}{\partial u^2}\right) + \frac{1}{2}\left[-\frac{1}{2}\left(\frac{\partial S/\partial u}{\sqrt{S}}\right)^2 \frac{1}{\sqrt{S}} + \frac{\partial^2 S/\partial u^2}{\sqrt{S}}\right]. \tag{B3}$$

Now, because the definition of an ESS sets (B1) equal to 0 at $u = u^*$, we have

$$\left(\frac{\partial S/\partial u}{\sqrt{S}}\right)^2 = 4(1 - \delta)^2\left(\frac{\partial R_1^m}{\partial u} + \frac{\partial R_2^m}{\partial u}\right)^2, \tag{B4}$$

and using the simplification for $\sqrt{S}$ above at $u = u^*$, shows that (B3) evaluated at $u = u^*$ is proportional to

$$(1 - \delta)\left(\frac{\partial^2 R_1^m}{\partial u^2} + \frac{\partial^2 R_2^m}{\partial u^2}\right) - (1 - 2\delta)\left.\left(\frac{\partial^2 R_1^m}{\partial u^2} R_2^m + 2\frac{\partial R_1^m}{\partial u}\frac{\partial R_2^m}{\partial u} + R_1^m\frac{\partial^2 R_2^m}{\partial u^2}\right)\right|_{u=\hat{u}=u^*}. \tag{B5}$$

Next, I substitute the Lotka-Volterra form of R_i^m (i.e., [7]) into these expressions. In this case, setting (B2) equal to 0 gives (12) as

$$\frac{u^*}{\theta} = \frac{\tilde{\Gamma}}{\Gamma}, \tag{B6}$$

where

$$\tilde{\Gamma} = \eta(\rho_1 \hat{N}_1^* K_2 - \rho_2 \hat{N}_2^* K_1) + (1 - \eta)\rho_1\rho_2[\hat{N}_1^*(\hat{N}_2^* - K_2) - \hat{N}_2^*(\hat{N}_1^* - K_1)] \tag{B7}$$

$$\Gamma = \eta(\rho_1 \hat{N}_1^* K_2 + \rho_2 \hat{N}_2^* K_1) + (1 - \eta)\rho_1\rho_2[\hat{N}_1^*(\hat{N}_2^* - K_2) + \hat{N}_2^*(\hat{N}_1^* - K_1)]. \tag{B8}$$

Similarly, substituting (7) into (B5) shows that (13) has the same sign as

$$\Gamma\left\{(\sigma_k^2 - \sigma_\alpha^2) + \frac{\sigma_\alpha^2}{\sigma_k^2}(u^{*2} - \theta^2)\left[1 - \frac{2\rho_1\rho_2(1 - \eta)\hat{N}_1^*\hat{N}_2^*}{\Gamma}\right]\right\}. \tag{B9}$$

The derivation of this expression is tedious and is therefore omitted (it is available upon request).

Calculating (14) is more difficult because we need to differentiate with respect to the resident's strategy $\hat{u}$, but the equilibrium population size of the resident in each patch is also a function of $\hat{u}$. In other words, the derivative in (14) can be written more explicitly as

$$\frac{d}{d\hat{u}}\left\{\left.\frac{\partial \lambda}{\partial u}\right|_{u=\hat{u}}\right\}\Bigg|_{\hat{u}=u^*} = \frac{\partial^2 \lambda}{\partial u^2} + \frac{\partial^2 \lambda}{\partial \hat{u}\partial u} + \frac{\partial^2 \lambda}{\partial \hat{N}_1^*\partial u}\frac{d\hat{N}_1^*}{d\hat{u}} + \frac{\partial^2 \lambda}{\partial \hat{N}_2^*\partial u}\frac{d\hat{N}_2^*}{d\hat{u}}\Bigg|_{u=\hat{u}=u^*}. \tag{B10}$$

Unfortunately, it is not possible to obtain $\hat{N}_1^*$ and $\hat{N}_2^*$ as a function of $\hat{u}$ explicitly in any simple form. Therefore, the derivatives of the equilibrium population size in each patch with respect to $\hat{u}$ are calculated most easily by implicitly differentiating system (1) with respect to $\hat{u}$, and evaluating at $u = \hat{u} = u^*$. This gives two equations that can then be solved for the two unknowns, $d\hat{N}_1^*/d\hat{u}$ and $d\hat{N}_2^*/d\hat{u}$.

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