

Hot Spots, Cold Spots, and the Geographic Mosaic Theory of Coevolution

Richard Gomulkiewicz,^{1,2,*} John N. Thompson,^{1,†} Robert D. Holt,³ Scott L. Nuismer,¹ and Michael E. Hochberg^{4,‡}

1. School of Biological Sciences, P.O. Box 644236, Washington State University, Pullman, Washington 99164;

2. Department of Pure and Applied Mathematics, P.O. Box 643113, Washington State University, Pullman, Washington 99164;

3. Department of Evolution and Ecology and Natural History Museum, University of Kansas, Lawrence, Kansas 66045;

4. Institute of Ecology, University of Paris VI, 7 quai St. Bernard, 75252 Paris Cedex 05, France

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ABSTRACT: Species interactions commonly coevolve as complex geographic mosaics of populations shaped by differences in local selection and gene flow. We use a haploid matching-alleles model for coevolution to evaluate how a pair of species coevolves when fitness interactions are reciprocal in some locations ("hot spots") but not in others ("cold spots"). Our analyses consider mutualistic and antagonistic interspecific interactions and a variety of gene flow patterns between hot and cold spots. We found that hot and cold spots together with gene flow influence coevolutionary dynamics in four important ways. First, hot spots need not be ubiquitous to have a global influence on evolution, although rare hot spots will not have a disproportionate impact unless selection is relatively strong there. Second, asymmetries in gene flow can influence local adaptation, sometimes creating stable equilibria at which species experience minimal fitness in hot spots and maximal fitness in cold spots, or vice versa. Third, asymmetries in gene flow are no more important than asymmetries in population regulation for determining the maintenance of local polymorphisms through coevolution. Fourth, intraspecific allele frequency differences among hot and cold spot populations evolve under some, but not all, conditions. That is, selection mosaics are indeed capable of producing spatially variable coevolutionary outcomes across the landscapes over which species interact. Altogether, our analyses indicate that coevolutionary trajectories can be strongly shaped by the geographic distribution of coevolutionary

hot and cold spots, and by the pattern of gene flow among populations.

Keywords: geographic mosaic, coevolution, hot and cold spots, hard and soft selection, mutualism, antagonism.

Interspecific interactions between pairs of species are often composed of collections of genetically differentiated populations connected by gene flow. Well-studied examples from natural populations include interactions between wild flax and flax rust (Burdon and Thrall 1999), snails and trematodes within New Zealand lakes (Lively 1999), wild *Drosophila melanogaster* populations and their parasitoids (Kraaijeveld and Godfray 1999), legumes and rhizobia (Parker and Spoerke 1998; Parker 1999), red crossbills and lodgepole pines (Benkman 1999), garter snakes and *Taricha* salamanders (Brodie and Brodie 1999), wild parsnips and parsnip webworms (Berenbaum and Zangerl 1998), yuccas and yucca moths (Leebens-Mack et al. 1998), and *Greya* moths and their saxifragaceous host plants (Thompson 1999). All these interactions show geographic differentiation in the genetic structure of the interacting populations and in the traits important to the association.

The geographic mosaic theory of coevolution argues that the overall coevolutionary dynamics of such interactions are driven by three components of geographic structure: selection mosaics, coevolutionary hot spots, and trait remixing (Thompson 1994; Thompson 1997). Selection mosaics occur when natural selection on interactions varies among different communities. Hot spots are communities in which interacting species have reciprocal effects on fitness and are often embedded within surrounding communities in which interspecific selection affects only one or neither species (cold spots). Finally, a combination of gene flow, random genetic drift, and extinction/colonization dynamics continually reshapes the genetic landscape over which future selection takes place (trait remixing). This tripartite coevolutionary process should produce three general ecological patterns: different combinations of coevolved traits in different regions, local

* To whom correspondence should be addressed; e-mail: gomulki@wsu.edu.

† Present address: Ecology and Evolutionary Biology Group, Department of Biology, University of California, Santa Cruz, California 95064.

‡ Present address: Institut des Sciences de l'Évolution, UMR-CNRS 5554, Université de Montpellier 2 (CC 065), 34095 Montpellier, France.

maladaptation within some interactions, and few geographically uniform coevolved traits.

There is now evidence for selection mosaics (e.g., Brodie and Brodie 1991; Ritland 1995; Travis 1996; Carroll et al. 1997; Radtkey et al. 1997), coevolutionary hot spots (Benkman 1999), and trait remixing (e.g., Dybdahl and Lively 1996; Burdon and Thrall 1999) in coevolving interactions. Formal theory exploring these components of the geographic mosaic is beginning to provide more precise predictions of how these components interact to shape coevolutionary dynamics. Two models have explicitly explored the development and dynamics of selection mosaics among coevolutionary hot spots. Hochberg and van Baalen (1998) showed that interactions between predators and prey along environmental gradients of prey productivity (i.e., prey birth rate) can produce gradients of coevolutionary hot spots that vary in selection intensity. Using a different approach, Nuismer et al. (1999) evaluated a genetic model in which interactions between two species varied from antagonism to mutualism among communities. They modeled an extreme selection mosaic (antagonism vs. mutualism) that included a pair of equal-sized coevolutionary hot spots connected by gene flow. Although the above models do not consider cold spots, their results hint at the importance of components of selection mosaics in shaping the overall coevolutionary trajectory of interacting species. Moreover, Nuismer et al.'s (1999) analyses indicated that local coevolutionary dynamics can depend strongly on geographically connected coevolutionary hot spots. Under some conditions (e.g., geographic asymmetries in the strength of reciprocal selection and moderate gene flow levels), the coevolutionary dynamics of a local interaction with mutualistic selection could actually resemble those of an isolated antagonistic interaction or vice versa. Minimization of local fitness was a common consequence of coevolution in this model.

Here, we analyze the scenario directly envisioned by the geographic mosaic theory in which coevolutionary hot spots exist within a broader geographic landscape that includes regions of coevolutionary cold spots, that is, regions in which there is no reciprocal selection. Specifically, we examine how the frequencies of hot and cold spots combined with various patterns of gene flow can shape coevolution for a pair of species distributed across a landscape containing hot and cold spots.

The goal of our analyses is to develop a formal understanding of how gene flow between hot and cold spots creates coevolutionary dynamics different from those that would be predicted for closed populations. We are especially interested in using the models as a step toward understanding three practical questions on how ongoing coevolution contributes to the organization of biodiversity. First, must hot spots be nearly ubiquitous for coevolution

to be important in shaping the overall evolution of species? Or, can cold spots have disproportionately strong effects on the overall evolution of interactions when rare? Second, how do asymmetric patterns of gene flow between species interact with spatially variable selection to shape the evolution of interactions? Examples of such asymmetries are growing as the evolutionary genetics of more interactions are studied in detail (Michalakis et al. 1993; Dybdahl and Lively 1996; Thrall and Burdon 1997; Althoff and Thompson 1999). Moreover, a recent metapopulation model suggests that asymmetric gene flow among hot spots can influence the potential for local adaptation in coevolving hosts and parasites (Gandon et al. 1996). Third, do selection mosaics, coevolutionary hot spots, and trait remixing tend to create spatially variable patterns of evolution across landscapes? If so, then coevolution is likely to be an important determinant of ecological interactions and dynamics within local communities.

We begin by developing a general model for the evolutionary dynamics of a pair of interacting species inhabiting a geographically variable landscape that includes hot and cold spots. Our general model can be applied to most any pattern of gene flow between hot spots and cold spots (fig. 1). Although biologically simple, the general model is mathematically cumbersome and difficult to analyze

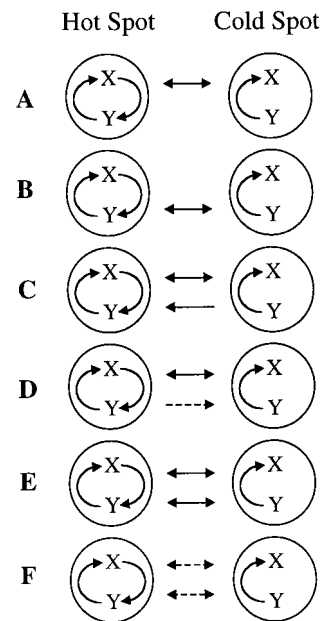


Figure 1: Types of coupled coevolutionary hot and cold spot habitats. Curved arrows indicate interspecific effects on fitness. The fitness of a species at the arrow tip is affected by the other species. Horizontal arrows indicate species-specific patterns of gene flow between hot and cold spots. Solid and dashed arrows indicate unlimited and limited levels of gene flow, respectively.

comprehensively. Instead, we analyze the coevolutionary dynamics of hot and cold spots for a series of relatively extreme, but biologically realistic, gene flow patterns and then use those analyses to understand the more intermediate cases.

A General Model

In this section, we describe a simple, general model for the evolutionary dynamics of two species named X and Y that can mutually affect one another's fitness, depending on the geographic location of the interaction. Variables and parameters of the model are listed in table 1. Although reciprocal selection can vary continuously across space, our model will recognize just two patch types: cold spots and hot spots. Cold spots are defined as regions in which the fitnesses of at most one of the two species depend on interactions with the second species. Hot spots, in contrast, are defined as areas in which the species have reciprocal effects on each other's fitnesses.

We assume that X and Y are both haploid with synchronous, discrete, and nonoverlapping generations. Fitnesses within each species depend on a single major gene with two alleles. In species X, the alleles are X_1 and X_2 , and in species Y, they are Y_1 and Y_2 . We assume that allele frequencies are censused after mating (reproduction). A fraction h of newly formed zygotes in both species are found in hot spots, while the remaining $1 - h$ occur in cold spots. We assume that hot and cold spots lack explicit spatial structure. In hot spots, the frequencies of alleles X_1 and Y_1 in newborns are denoted by x_H and y_H , respectively; corresponding frequencies in cold spots are x_C and y_C . Local frequencies of the "2" alleles can be obtained by subtracting the "1" allele frequency from 1 (e.g., the frequency of X_2 in cold spots is $1 - x_C$).

We assume that selection occurs before migration. (The order of these events has no qualitative effect on the results.) We posit that fitnesses in species X depend on the local allele frequencies of species Y in both hot and cold spots and that the form of frequency dependence is the same in both patches. We let $V_i(y)$ denote the fitness of allele X_i ($i = 1, 2$) when the local frequency of Y_1 is y . Note that fitnesses of X_i will vary spatially whenever allele frequencies in species Y differ between hot and cold spots. The notation $V_i(y)$ emphasizes that intraspecific-frequency dependence is assumed to be negligible.

We now turn to the fitnesses of species Y. In cold spots, by definition, the fitnesses of no more than one of the two species can be affected by the presence of the other species. Since fitnesses in species X depend on allele frequencies in Y in both cold and hot spots, the fitnesses of species Y in cold spots must be unaffected by species X. To emphasize this, we will let the fitness of allele Y_i in cold spots

be Ω_i , a constant. In hot spots, the fitness of Y_i , denoted $W_i(x_H)$, depends on the local allele frequencies in X. (Note that intraspecific effects on fitness are again ignored.) So species Y is, overall, less sensitive to allelic variation in species X than X is to allelic variation in Y.

Allele frequencies after selection in hot and cold spots are determined by standard formulas. If we indicate post-selection frequencies with an asterisk, then

$$x_H^* = x_H \frac{V_1(y_H)}{\bar{V}(x_H, y_H)}, \quad (1a)$$

$$x_C^* = x_C \frac{V_1(y_C)}{\bar{V}(x_C, y_C)}, \quad (1b)$$

$$y_H^* = y_H \frac{W(x_H)}{\bar{W}(x_H, y_H)}, \quad (1c)$$

$$y_C^* = y_C \frac{\Omega_1}{\bar{\Omega}(y_C)}, \quad (1d)$$

where

$$\bar{V}(x_H, y_H) = x_H V_1(y_H) + (1 - x_H) V_2(y_H), \quad (2a)$$

$$\bar{V}(x_C, y_C) = x_C V_1(y_C) + (1 - x_C) V_2(y_C), \quad (2b)$$

$$\bar{W}(x_H, y_H) = y_H W_1(x_H) + (1 - y_H) W_2(x_H), \quad (2c)$$

$$\bar{\Omega}(y_C) = y_C \Omega_1 + (1 - y_C) \Omega_2 \quad (2d)$$

are the mean fitnesses for each species in hot and cold spots.

Selection may also change the allocation of individuals in the two habitats (see, e.g., Nagylaki 1992). Let h_X^* and h_Y^* denote the respective proportions of species X and Y in hot spots after selection but before migration. We will consider two simplifications that represent extremes in how population size is regulated (Christiansen 1985): "soft selection" and "hard selection." With soft selection, the number of surviving adults in a particular patch is determined independently of local selection. This implies that population size is regulated independently within each habitat (Dempster 1955; see Christiansen 1985 for an explicit formulation). We assume that the postselection fractions of individuals in hot and cold spots are unchanged given soft selection:

$$h_X^* = h \text{ and/or } h_Y^* = h. \quad (3)$$

In contrast to soft selection, the proportion of adults in hot (and cold) spots under hard selection depends directly on local fitnesses:

Table 1: Variables and parameters used in the text

Notation	Description
$x_c(x_c^*)$	Frequency of X_1 in cold spots before (after) selection
$x_h(x_h^*)$	Frequency of X_1 in hot spots before (after) selection
$y_c(y_c^*)$	Frequency of Y_1 in cold spots before (after) selection
$y_h(y_h^*)$	Frequency of Y_1 in hot spots before (after) selection
$V_i(y)$	Fitness of X_i when the local frequency of $Y_1 = y$
$W_i(x)$	Fitness of Y_i in hot spots
Ω_i	Fitness of Y_i in cold spots
h	Fraction of new zygotes in hot spots
$h_x^*(h_y^*)$	Fraction of species X (Y) in hot spots after selection
$m_{C \rightarrow H}^X(m_{C \rightarrow H}^Y)$	Probability of migrating from cold to hot spots in species X (Y)
$m_{H \rightarrow C}^X(m_{H \rightarrow C}^Y)$	Probability of migrating from hot to cold spots in species X (Y)
$x(y)$	Shared frequency of X_1 (Y_1) allele in hot and cold spots
ψ_c	Fixed frequency of Y_1 allele in cold spots
s	Selection coefficient for Y_1 in cold spots = $\Omega_1 - \Omega_2$

$$h_x^* = h \frac{\bar{V}(x_H, y_H)}{h\bar{V}(x_H, y_H) + (1-h)\bar{V}(x_C, y_C)} \quad (4a)$$

for species X and

$$h_y^* = h \frac{\bar{W}(x_H, y_H)}{h\bar{W}(x_H, y_H) + (1-h)\bar{\Omega}(y_C)} \quad (4b)$$

for Y. Hard selection implies that population sizes are regulated globally (Dempster 1955; Christiansen 1985). In ecological terms, this means there is no local density dependence.

After selection, adults may migrate between hot and cold spots. There are a variety of ways that gene flow could occur, some of which are depicted in figure 1. We denote the probability that an individual in a cold spot migrates to a hot spot by $m_{C \rightarrow H}^X$ for species X and by $m_{C \rightarrow H}^Y$ for species Y. The respective probabilities of migrating from hot to cold spots are $m_{H \rightarrow C}^X$ and $m_{H \rightarrow C}^Y$.

After migration, we assume that random mating and reproduction occurs within each patch. Finally, we assume that postmigration populations are regulated so that newborns within each species occur in proportions h and $1-h$, respectively, in hot and cold spots. Provided mutation and random genetic drift are relatively weak, our assumptions imply that the allele frequencies at the start of the next generation (signified by a prime) are

$$x'_H = \frac{(1 - m_{H \rightarrow C}^X)h_x^*x_H^* + m_{C \rightarrow H}^X(1 - h_x^*)x_C^*}{(1 - m_{H \rightarrow C}^X)h_x^* + m_{C \rightarrow H}^X(1 - h_x^*)}, \quad (5a)$$

$$x'_C = \frac{m_{H \rightarrow C}^X h_x^* x_H^* + (1 - m_{C \rightarrow H}^X)(1 - h_x^*)x_C^*}{m_{H \rightarrow C}^X h_x^* + (1 - m_{C \rightarrow H}^X)(1 - h_x^*)}, \quad (5b)$$

$$y'_H = \frac{(1 - m_{H \rightarrow C}^Y)h_y^*y_H^* + m_{C \rightarrow H}^Y(1 - h_y^*)y_C^*}{(1 - m_{H \rightarrow C}^Y)h_y^* + m_{C \rightarrow H}^Y(1 - h_y^*)}, \quad (5c)$$

$$y'_C = \frac{m_{H \rightarrow C}^Y h_y^* y_H^* + (1 - m_{C \rightarrow H}^Y)(1 - h_y^*)y_C^*}{m_{H \rightarrow C}^Y h_y^* + (1 - m_{C \rightarrow H}^Y)(1 - h_y^*)}. \quad (5d)$$

The postselection frequencies x_i^* and y_i^* and proportions h_x^* and h_y^* are as defined above. Note that the first term in the numerator of each right-hand-side expression is proportional to the total contribution of X_1 or Y_1 alleles that were in hot spots just before migration. Each second term is proportional to the number of the same alleles originally in cold spots. The denominators correspond to the total number of alleles in hot (cold) spots after migration.

The recursions (5) are sufficiently general to include almost any species-specific pattern of gene flow between hot and cold spots (fig. 1). For example, to describe unlimited migration in species X, as in the classical ‘‘Levene model’’ (Levene 1953), one would set $m_{H \rightarrow C}^X = 1 - h$ and $m_{C \rightarrow H}^X = h$ since, by assumption, any individual will migrate (perhaps internally) to hot and cold spots with probabilities h and $1 - h$, respectively. Unidirectional gene flow within a species can be modeled by setting one of that species’ two migration parameters to 0.

The model (5) can easily be extended to diploid species or interacting haploid and diploid species by replacing the local postselection frequencies x_i^* and y_i^* (eqq. [1]) with standard haploid or diploid expressions. One can also

modify the model to describe evolution in a selection mosaic consisting of two coupled hot spots (as in Nuismer et al. 1999) by using frequency-dependent fitnesses in (1d) and allowing the form of frequency dependence to differ between the two hot spots (e.g., a mutualism coupled with an antagonism). These extensions will not be considered here.

For most of our analyses, we focus on one of the simplest possible forms of interspecific frequency-dependent selection, namely, fitnesses that are symmetric and linear functions of frequency (Seger 1988; Gavrillets and Hastings 1998). For species X, we use the following relative fitnesses in hot and cold spots:

$$V_1(y) = 1 + ay, \quad (6a)$$

$$V_2(y) = 1 + a(1 - y), \quad (6b)$$

where y is the local frequency of allele Y_1 . Likewise, the relative fitnesses of species Y in hot spots will be

$$W_1(x_H) = 1 + bx_H, \quad (7a)$$

$$W_2(x_H) = 1 + b(1 - x_H). \quad (7b)$$

(Recall that Y has constant fitnesses Ω_1 and Ω_2 in cold spots.) The parameters a and b determine the sensitivity of an allele's fitness to changes in the frequency of its matching allele in the other species. In particular, the signs of a and b describe the nature of interspecific interactions and their magnitudes reflect (roughly) the strengths of selection. We assume $|a|, |b| < 1$, which ensures that fitnesses are positive for all allele frequencies.

Although mathematically convenient, linear fitnesses arise naturally when individual fitness is determined via random pairwise, between-species interactions (e.g., Hofbauer and Sigmund 1988; Gavrillets 1997), including matching-alleles and gene-for-gene interactions (e.g., Frank 1994). In particular (6) and (7) correspond to average genotypic fitnesses assuming a matching-alleles model in which alleles X_1 and Y_1 are "matched" as are alleles X_2 and Y_2 . To wit, if the fitness payoff to X_1 is $1 + a$ in an interaction with Y_1 but is 1 in an interaction with Y_2 , then (6a) equals the average payoff to X_1 when the frequency of Y_1 is y , assuming random encounters. The remaining fitnesses (6) and (7) may be derived analogously from random pairwise interactions.

Even with simplified fitnesses such as (6) and (7), the general model (5) is complicated enough that a comprehensive mathematical analysis would be impractical. Since our primary aim is to explore the potential impact of gene flow between hot and cold spots on global evolutionary dynamics, we will analyze a representative subset of the migratory schemes shown in figure 1. To explore the qual-

itative features of (5), our strategy will be to first analyze two comparatively "extreme" cases in which gene flow within a species is either completely absent or completely unrestricted (fig. 1E). We then analyze three relatively intermediate cases, two of which address the coevolutionary effects of asymmetric migration (fig. 1A, 1B), while the third considers restricted levels of gene flow (fig. 1F).

Isolated Hot and Cold Spots

We begin with the biologically and mathematically simplest case: a geographic mosaic consisting of mutually isolated coevolutionary hot and cold spots. Imagine, for example, a symbiont that is commensalistic with its host in one closed population but antagonistic or mutualistic in another. Our main purpose in considering this case is to establish a baseline with which to compare subsequent cases.

Consider first the coevolutionary dynamics of X and Y in a closed hot spot. These dynamics are described by (5a) and (5c) with $m_{C \rightarrow H}^X = m_{H \rightarrow C}^X = m_{C \rightarrow H}^Y = m_{H \rightarrow C}^Y = 0$. Given symmetric linear fitnesses (6) and (7), five equilibrium allele frequency pairs (\hat{x}_H, \hat{y}_H) are possible (Seger 1988). Four "corner" equilibria correspond to hot spot monomorphisms, involving either fixed matched alleles, $\hat{x}_H = \hat{y}_H = 0$ and $\hat{x}_H = \hat{y}_H = 1$, or fixed mismatched alleles, $\hat{x}_H = 0, \hat{y}_H = 1$ and $\hat{x}_H = 1, \hat{y}_H = 0$. The fixed matched alleles equilibria are locally stable when the interaction is mutualistic (i.e., when $a > 0$ and $b > 0$; fig. 2A) and are unstable otherwise. Monomorphic equilibria with mismatched alleles are stable whenever the interaction is competitive ($a < 0$ and $b < 0$) and unstable otherwise. At the fifth equilibrium, both species are polymorphic with $\hat{x}_H = \hat{y}_H = 1/2$ (due to symmetry), however, this equilibrium is always unstable.

When all four corner equilibria are unstable, as with exploiter-victim interactions ($a > 0, b < 0$ or $a < 0, b > 0$), the species coevolve arbitrarily closely toward monomorphisms in which one or both species are genetically fixed (Seger 1988; see fig. 2B). Consequently, if population sizes were finite, all genetic variation would ultimately be lost in both species. The particular alleles that become fixed or lost would be unpredictable.

In closed cold spots, the evolutionary dynamics of X depend entirely on those of Y, whereas the evolution of Y is unaffected by X. If allele frequencies in Y are fixed, then fitnesses in X will also be fixed and X, being haploid, will evolve toward a monomorphism that maximizes local fitness.

These results provide two main predictions for isolated hot and cold spots. First, closed hot spots do not support local polymorphisms in either species, and local genetic variation in species X will not be maintained in closed

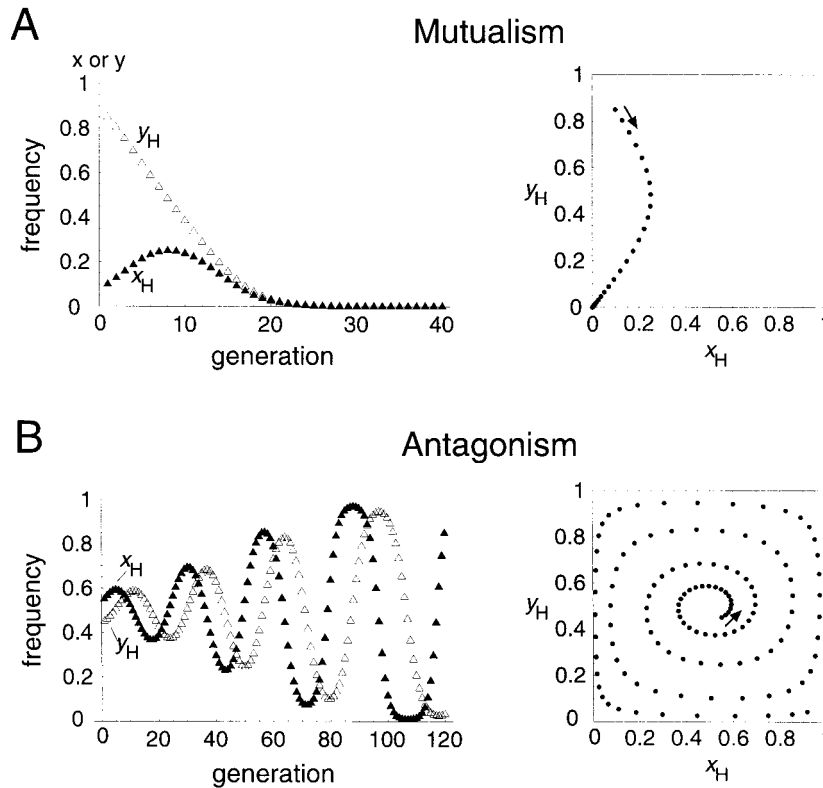


Figure 2: Coevolutionary dynamics in closed hot spots. Left-hand panels show evolutionary trajectories of hot spot allele frequencies x_H and y_H ; right-hand panels display the same dynamics using phase portraits (the arrows indicate directions of coevolution from the initial frequencies). Closely spaced (widely spaced) points in the phase portrait correspond to slow (rapid) coevolution. Simulations are based on equations (5a) and (5c) with $m_{C \rightarrow H}^X = m_{H \rightarrow C}^X = m_{C \rightarrow H}^Y = m_{H \rightarrow C}^Y = 0$ and linear fitnesses (eqq. [6] and [7]). A, Hot spot mutualism: $a = b = 0.5$. B, Hot spot antagonism: $a = -0.5$, $b = 0.5$.

cold spots (“local monomorphisms”). Second, hot and cold spots when mutually isolated can exhibit substantial intraspecific genetic differentiation at a global scale (“geographic differentiation”). Morand et al. (1996) drew a similar conclusion when analyzing a geographically structured model of host-parasite coevolution that assumed no gene flow between separate hot spots. In the cases to follow, we will consider how gene flow between hot and cold spots affects these two “null” predictions.

Unlimited Gene Flow in Both Species

We now examine how gene flow affects coevolution across a geographic mosaic by considering the opposite extreme of the previous section: unlimited gene flow in both species between hot and cold spots (fig. 1E). As an example of this case, recent work on two species of yucca and yucca moths has shown little phylogeographic structure throughout the southwestern United States, potentially indicating extensive gene flow among populations in this interaction

(Leebens-Mack et al. 1998). We assume $m_{H \rightarrow C}^X = m_{H \rightarrow C}^Y = 1 - h$ and $m_{C \rightarrow H}^X = m_{C \rightarrow H}^Y = h$, which implies that allele frequencies within a species are the same in hot and cold spots at the beginning of each generation. Equations (5a) and (5b) are then redundant—as are (5c) and (5d)—so we let $x = x_C = x_H$ and $y = y_C = y_H$ denote the respective (geographically uniform) frequencies of alleles X_1 and Y_1 at the zygote stage. Unlike the case of isolated hot and cold spots, spatial genetic structuring is precluded within species by assumption (at least at the zygote stage). Hence, our main concern in this section lies with the gene flow between hot and cold spots affects the maintenance of monomorphisms and polymorphisms in one or both species.

Hard Selection

If both X and Y are subject to hard selection (4), the general recursions (5) condense to the following pair of equations:

$$x' = x \frac{V_1(y)}{\bar{V}(x, y)}, \tag{8a}$$

$$y' = y \left[\frac{\tilde{W}_1(x)}{y\tilde{W}_1(x) + (1 - y)\tilde{W}_2(x)} \right], \tag{8b}$$

where the mean fitness $\bar{V}(x, y)$ is defined in (2a) and $\tilde{W}_i(x) = hW_i(x) + (1 - h)\Omega_i$ is the average fitness of allele Y_i across hot and cold spots. Recursion (8a) underscores that selection on species X is geographically uniform. In fact, equation (8a) describes hard or soft selection in species X because X must experience exactly the same selection in hot and cold spots.

Assuming fitnesses (6) and (7), the dynamical system (8) has, like an isolated hot spot, four monomorphic corner equilibria with either matched alleles ($\hat{x} = \hat{y} = 0$ and $\hat{x} = \hat{y} = 1$) or mismatched alleles ($\hat{x} = 0, \hat{y} = 1$ and $\hat{x} = 1, \hat{y} = 0$). There is a fifth polymorphic equilibrium at which $\hat{x} = [1 - (1/h - 1)(s/b)]/2$ and $\hat{y} = 1/2$, where $s = \Omega_1 - \Omega_2$ is the coefficient of selection favoring allele Y_1 in cold spots. (Note that b , which is the rate at which the fitness of Y_i changes with x in hot spots, is akin to a selection coefficient.) The polymorphic equilibrium is biologically feasible only for certain combinations of the parameters h, b , and s . Even then, local stability analysis (e.g., Hale and Koçak 1991) reveals that this equilibrium is always unstable. By comparison, the four monomorphic equilibria may be locally stable or unstable. Consider, for example, the matched equilibrium $\hat{x} = \hat{y} = 1$ at which species X is fixed for allele X_1 and Y is fixed for Y_1 . It is not difficult to show that this monomorphism is locally stable if

$$a > 0 \text{ and } b > -s \left(\frac{1}{h} - 1 \right). \tag{9}$$

It is interesting to compare (9) with the stability criterion for the same monomorphism in an isolated hot spot, which is, as discussed above, $a > 0$ and $b > 0$ (i.e., any mutualism). In fact, if $h = 1$, then (9) reduces to the isolated hot spot stability criterion as it should.

If hot spots are not ubiquitous ($h < 1$) and Y_1 is deleterious in cold spots ($s < 0$), a hot spot mutualism might not suffice to stabilize a monomorphism with matched alleles if b is too small. This is because benefits to Y_1 of the mutualism in hot spots fail to compensate for the allele's deleterious effects in cold spots. In this sense, the presence of cold spots restricts the local conditions under which monomorphisms are evolutionarily stable compared to an isolated hot spot. Finally, note that if $s < 0$ and the hot spot mutualism was sufficiently strong to sat-

isfy (9), then species Y would have minimal mean fitness in cold spots at an evolutionarily stable equilibrium.

If, in contrast, Y_1 were favored in cold spots ($s > 0$), then $\hat{x} = \hat{y} = 1$ may be stable when $a > 0$ and $b < 0$. In this situation, species Y is harmed by allelic matches with X in hot spots, but X always benefits from matches with Y. If we think of Y as a host and X as a parasite and equate fitness with resistance and virulence, respectively, then this matched monomorphism would correspond to a stable equilibrium in which the host has minimal resistance in hot spots and the parasite has maximal virulence. Species Y would have minimal fitness in hot (rather than cold) spots at equilibrium. Since fixed matches are always unstable in closed hot spots given antagonistic interactions, (9) indicates that gene flow between hot and cold spots can expand the conditions that stabilize the monomorphism. Similar comments apply to the other three monomorphic equilibria (see table 2).

For certain values of h, s, a , and b , the four corner equilibria may all be unstable. For example, all monomorphic equilibria are unstable if the Y_1 allele is favored in cold spots ($s > 0$) and X and Y have an exploiter-victim interaction in hot spots such that Y is "overexploited": $a > 0$ and $b < -s(1/h - 1)$ (see table 2). However, instability of all monomorphic equilibria does not ensure that a polymorphism will evolve. Indeed, our numerical studies suggest that the species coevolve arbitrarily near one- and two-species monomorphisms, which implies that all genetic variation would ultimately be lost in both species. Recall that this was also the case for an isolated hot spot (fig. 2B). Thus, gene flow between hot and cold spots will not maintain genetic variation in either species, at least not under hard selection.

Soft Selection

In contrast to hard selection, genetic variation can be maintained if species Y is subject to soft selection. With soft selection (eq. [3]), recursion (8b) is replaced by

Table 2: Symmetric fitness parameter values consistent with local stability

Equilibrium	Stability condition
$\hat{x} = 0, \hat{y} = 0$	$a > 0, b > s(1/h - 1)$
$\hat{x} = 1, \hat{y} = 1$	$a > 0, b > -s(1/h - 1)$
$\hat{x} = 0, \hat{y} = 1$	$a < 0, b < s(1/h - 1)$
$\hat{x} = 1, \hat{y} = 0$	$a < 0, b < -s(1/h - 1)$

Note: Values consistent with local stability of the four corner equilibria for unlimited migration in both species (eqq. [8]).

$$y' = y \left[h \frac{W_1(x)}{yW_1(x) + (1-y)W_2(x)} + (1-h) \frac{\Omega_1}{y\Omega_1 + (1-y)\Omega_2} \right]. \quad (8b')$$

By setting $x' = x$ and $y' = y$ in (8a) with (8b'), it is possible to show there is a polymorphic equilibrium with $\hat{y} = 1/2$ and

$$\hat{x} = \frac{1}{2} \left[1 - \left(\frac{1}{h} - 1 \right) \left(\frac{s/\hat{W}}{b/\hat{\Omega}} \right) \right],$$

where $\hat{W} = 1 + b/2$ and $\hat{\Omega} = (\Omega_1 + \Omega_2)/2$ are the local equilibrium mean fitnesses of species Y in hot and cold spots, respectively, and $s = \Omega_1 - \Omega_2$ as above. The expression for \hat{x} is similar to that for hard selection, except that, in this case, the selection coefficients, s and b , are normalized by local mean fitnesses. This normalization traces back to the local density regulation implicit in soft selection. (Indeed, the equilibria for hard and soft selection are identical if mean fitnesses in hot and cold spots are the same: $\hat{W} = \hat{\Omega}$.) It is straightforward to demonstrate that this polymorphic equilibrium can be locally stable under biologically reasonable conditions. In addition, one may prove by applying the Poincaré-Andronov-Hopf bifurcation theorem for maps (e.g., Hale and Koçak 1991, p. 474) that the species can coevolve to stable limit cycles (i.e., permanent, but unstable, polymorphisms) for certain parameter combinations. Thus, polymorphisms are possible in both species given soft selection in Y.

Under soft selection, gene flow between hot and cold spots can support genetic polymorphisms in both species provided that hot spots are sufficiently—but not too—common. Figure 3 shows a series of coevolutionary simulations that assume soft selection in which species X is the victim ($a < 0$) and Y is its exploiter ($b > 0$) in hot spots. The simulations differ only in the hot spot fraction h . All plots assume $\Omega_1 = 1$ and $s = -b < 0$, in which case $\hat{x} = 1/(2h)$ so that allele X_1 will become fixed if $h \leq 0.5$ (fig. 3A). For values of h slightly above 0.5, a stable polymorphism is maintained in both species (fig. 3B, 3C). For values of h above the bifurcation value $h_0 \approx 0.632$ (a value specific to the assumed parameters), cyclical polymorphisms evolve (fig. 3D, 3E). However, when h is large, the coevolutionary cycles pass very close to the boundaries

and so polymorphisms would not be preserved in finite populations (fig. 3F). The same range of qualitative dynamics holds across a broad range of parameter values and initial conditions, although stable polymorphisms occur within smaller ranges of h as selection weakens (simulation results not shown). (Note that genetic variation would be lost for all the parameter sets assumed in fig. 3 given hard selection.)

Our results show that soft selection in species X is neither necessary nor sufficient for the coevolution of polymorphisms. Recall that recursion (8a) is exactly the same for hard and soft selection in species X because selection on X is spatially uniform. Therefore, polymorphisms may be maintained whenever species Y is subject to soft selection—even if X experiences hard selection. Alternatively, if selection is soft for X but hard for Y, both species become monomorphic. Hence, the coevolutionary potential for genetic polymorphisms depends entirely on the ecological dynamics of species Y (local density regulation implied by soft selection versus global regulation implied by hard selection) but not on those of X.

Overall, we found that gene flow can either restrict or expand the conditions under which local monomorphisms are evolutionarily stable compared to isolated hot spots. Gene flow can maintain monomorphic coevolutionary equilibria at which one species is maximally maladapted in part of its range. In contrast to isolated hot and cold spots, local genetic polymorphisms may be maintained with gene flow but only given soft selection in species Y.

Unrestricted Gene Flow in One Species

Species X Philopatric

We now consider the coevolutionary dynamics of our two species when Y moves without limitation between hot and cold spots, while X is philopatric (fig. 1B). This scenario would represent, for example, a highly mobile host that interacts with locally restricted populations of symbionts that affect host fitness in some habitats but not others. This case is identical to the last section except that the migration parameters for X are $m_{H \rightarrow C}^X = m_{C \rightarrow H}^X = 0$, and separate equations are needed to track species X allele frequencies in hot and cold spots. As before, allele frequencies in the mobile species Y are always the same in hot and cold spots at the zygote stage. This again allows us to follow just the shared frequency $y = y_H = y_C$, which eliminates one of the general recursions (5). For hard selection (4b), coevolution is described by the three equations

$$x'_H = x_H \frac{V_1(y)}{\bar{V}(x_H, y)}, \quad (10a)$$

$$x'_C = x_C \frac{V_1(y)}{\bar{V}(x_C, y)}, \quad (10b)$$

$$y' = y \frac{\tilde{W}_1(x_H)}{y\tilde{W}_1(x_H) + (1-y)\tilde{W}_2(x_H)}, \quad (10c)$$

where $\tilde{W}_i(x_H) = hW_i(x_H) + (1-h)\Omega_i$ is again the average fitness of Y_i across hot and cold spots and $\bar{V}(x_i, y)$ is as defined in (2). Notice that the joint evolutionary dynamics of y and x_H (eqq. [10a] and [10c]) are independent of x_C . The coevolutionary dynamics of (10) must therefore be driven completely by the pair of recursions, (10a) and (10c), while x_C evolves solely in response to changes in y (eq. [10b]). (This remark also holds for soft selection.) Moreover, by replacing x_H with x , one can see that the system (10a) and (10c) is mathematically identical to (8). Both coevolutionary systems, thus, share identical dynamical features, including equilibria, stability, and limit cycles. Hence, species Y may minimize its local mean fitness at a stable monomorphic equilibrium. Moreover, polymorphisms will not evolve or be maintained in hot spots if species Y is subject to hard selection, whereas stable and cyclical polymorphisms can be maintained provided soft selection obtains in species Y (see below). Thus, gene flow in just species Y can be sufficient for hot spot polymorphisms to coevolve.

In contrast to the case of completely isolated hot and cold spots, we found in this case that the genetics of an isolated species (X) will not be geographically structured at evolutionary equilibrium. (Y is geographically uniform at the zygote stage, by assumption.) First, consider hard selection in Y . As shown in the last section, the only locally stable equilibria for the system (10a) and (10c) are the hot spot monomorphisms, such as $\hat{x}_H = \hat{y} = 1$ and $\hat{x}_H = 0, \hat{y} = 1$. The only equilibria for X in cold spots are $\hat{x}_C = 0$, and $\hat{x}_C = 1$. Hence, any geographic structuring in X must involve fixed genetic differences between hot and cold spots. Fixed genetic differences between hot and cold spots, however, cannot be maintained in species X given hard selection in Y . That is, equilibria with $\hat{x}_H = 0$, and $\hat{x}_C = 1$ or with $\hat{x}_H = 0$ and $\hat{x}_C = 1$ cannot be evolutionarily stable if Y is subject to hard selection. Indeed, local stability analyses reveal that such fixed differences are always unstable.

When Y is subject to soft selection, local polymorphisms in y and x_H can be maintained. The recursions for soft selection are identical to those of (10) except that (10c) is replaced by

$$y' = y \left[h \frac{W_1(x_H)}{yW_1(x_H) + (1-y)W_2(x_H)} + (1-h) \frac{\Omega_1}{y\Omega_1 + (1-y)\Omega_2} \right]. \quad (10c')$$

This equation is identical to (8b') with x replaced by x_H . Equilibria for species X in cold spots continue to include only the monomorphisms $\hat{x}_C = 0$, and $\hat{x}_C = 1$. At least one of these two local monomorphisms will be stable unless y and x_H coevolve to a limit cycle. Biologically, this means that even with soft selection, a stable equilibrium with both species locally polymorphic in hot and in cold spots is impossible. However, permanent polymorphisms may be maintained in both species within both habitat types if y and x_H coevolve to a limit cycle. In this case, first one and then the other allele in species X will be favored in cold spots as y varies. The fluctuating allele frequencies in X will tend to differ among hot and cold spots at any given time (unless $x_H = x_C$, initially; see fig. 4).

In general, then, complete isolation of both interacting species is not a prerequisite for maintaining spatial variation in allele frequencies. However, unlimited migration in Y apparently precludes the evolution of stable spatial genetic differences in X . In the next section, we consider whether these conclusions hold when Y is the isolated species.

Species Y Philopatric

We now imagine that species X has unlimited access to hot and cold spots, but Y does not migrate (fig. 1A). This scenario might represent, for example, a highly mobile insect herbivore (X) that interacts with a nondispersing plant host (Y). This case is modeled by setting $m_{H \rightarrow C}^X = 1 - h$, $m_{C \rightarrow H}^X = h$, and $m_{H \rightarrow C}^Y = m_{C \rightarrow H}^Y = 0$ in equations (5). At the start of each generation, allele frequencies in X are the same in hot and cold spots, in which case equations (5a) and (5b) are redundant. Let $x = x_H = x_C$ denote the frequency of X_1 among zygotes. Because Y does not disperse, we assume the frequency of Y_1 has already reached a fixed genetic equilibrium in cold spots, $y_C = \psi_C$ (a constant between 0 and 1, inclusive), rather than follow its transient dynamics. Under these conditions, equation (5d) is unnecessary, and the complete coevolutionary dynamics are, thus, described by two equations. The complete coevolutionary dynamics are consequently described by (assuming hard selection in species X)

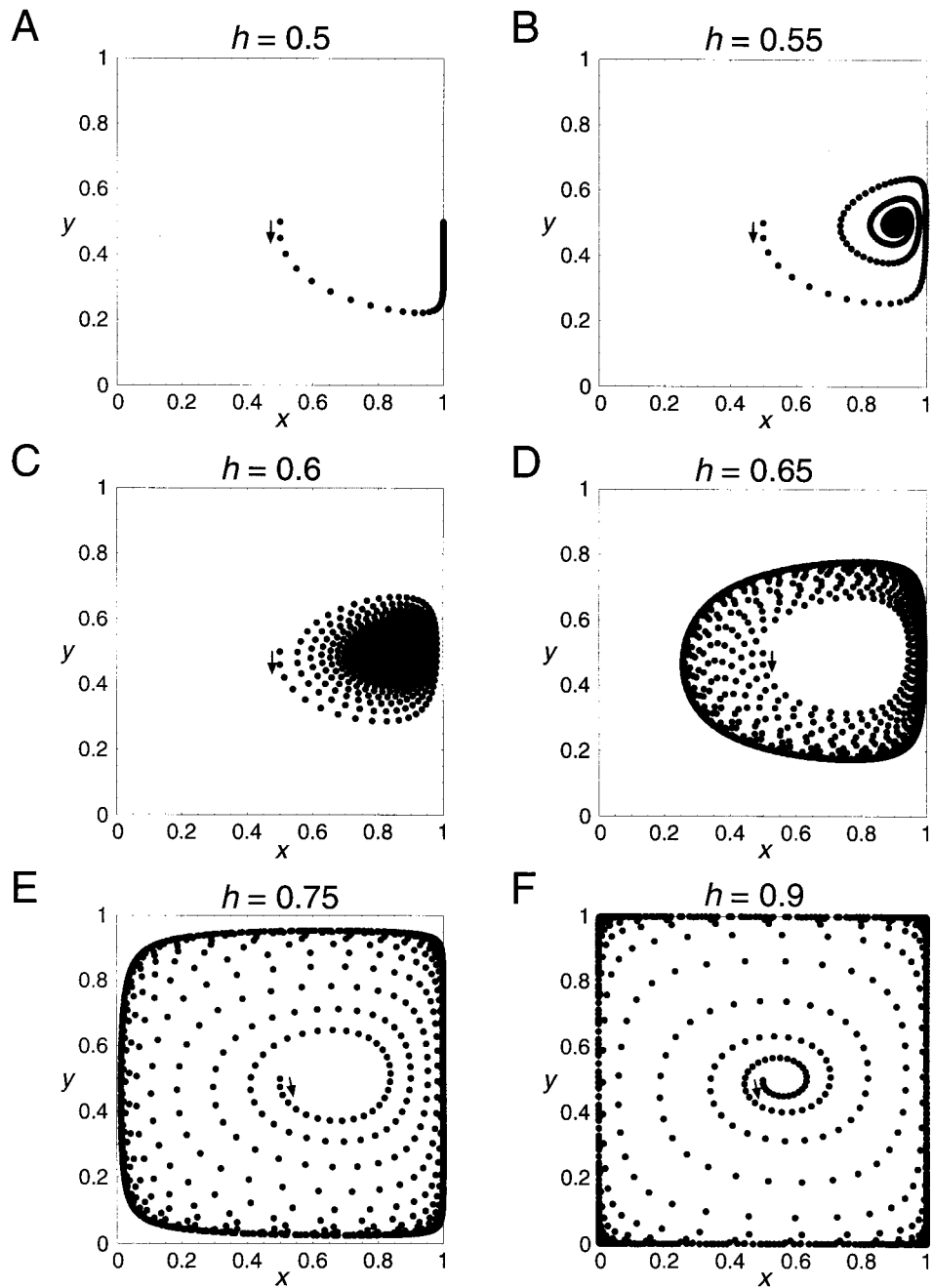


Figure 3: Coevolutionary dynamics for increasing proportions of hot spots (h) assuming unlimited migration and soft selection in both species. Simulation results (displayed as phase portraits for 1,500 generations) are based on (8) and assume fitnesses ([6] and [7]) with $a = -0.5$, $b = 0.5$, $\Omega_1 = 1$, and $\Omega_2 = 1.5$. All cases start from $x_0 = 0.5$, $y_0 = 0.5$. Arrows indicate directions of coevolution from the initial condition.

$$x' = x \frac{\tilde{V}_i(y_H, \psi_C)}{x\tilde{V}_1(y_H, \psi_C) + (1-x)\tilde{V}_2(y_H, \psi_C)}, \quad (11a)$$

$$y'_H = y_H \frac{W_1(x)}{W(x, y_H)}, \quad (11b)$$

where $\tilde{V}_i(y_H, \psi_C) = hV_i(y_H) + (1-h)V_i(\psi_C)$ is the average fitness of allele X_i across hot and cold spots.

Analysis of this case is similar to those of the last two sections. With fitnesses (6) and (7), there are four corner equilibria corresponding to hot spot monomorphisms and

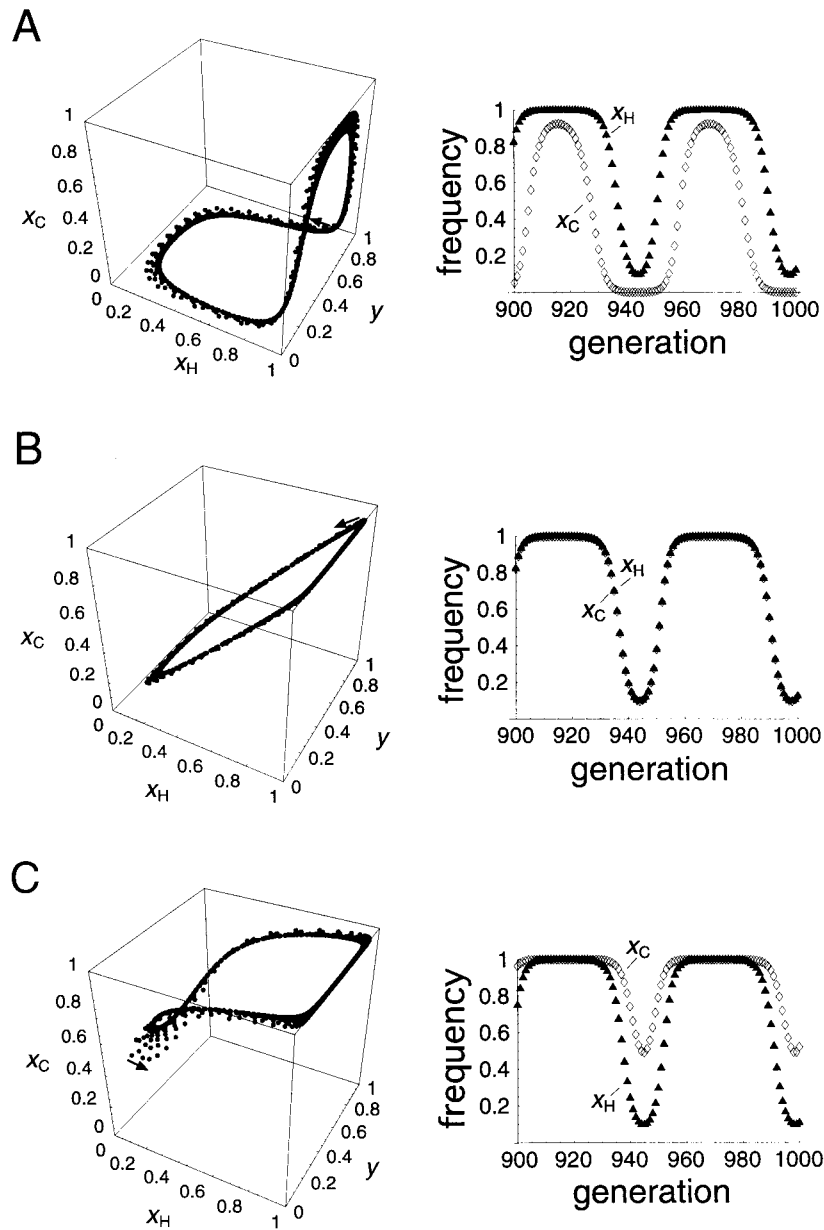


Figure 4: The influence of initial conditions on coevolutionary dynamics, assuming no migration in species X and soft selection in Y. Simulation results are based on equations (10) and (10c') and assume linear fitnesses with $a = -0.5$, $b = 0.5$, $\Omega_1 = 0.7$, $\Omega_2 = 1$, and $h = 0.65$. Left-hand panels: coevolutionary dynamics over 1,000 generations displayed as three-dimensional phase portraits; arrows show directions of coevolution from the initial condition. Right-hand panels: joint evolutionary trajectories of x_H and x_C for generations 900–1,000. A, $x_{H,0} = 0.9$, $x_{C,0} = 0.05$, $y_0 = 0.9$; x_C remains smaller than x_H . B, $x_{H,0} = x_{C,0} = 0.9$, $y_0 = 0.9$; species X allele frequencies in hot and cold spots remain identical. C, $x_{H,0} = 0.1$, $x_{C,0} = 0.5$, $y_0 = 0.1$; x_C tends to be larger than x_H .

an unstable polymorphic equilibrium with $\hat{x} = 1/2$, $\hat{y}_H = \psi_C + (1/2 - \psi_C)/h$, and $\hat{y}_C = \psi_C$. The equilibria with monomorphic hot spots may be locally stable or unstable. For example, the matched equilibrium with $\hat{x} = \hat{y}_H = 0$ is locally stable if either

$$a > 0, \quad b > 0, \quad \text{and} \quad h > 1 - 1/(2\psi_C) \quad (12a)$$

or

$$a < 0, \quad b > 0, \quad \text{and} \quad h < 1 - 1/(2\psi_C). \quad (12b)$$

If either condition held when $\psi_C > 0$, then spatially structured genetic variation could be stably maintained in Y since we would then have $\hat{y}_H = 0 \neq \hat{y}_C = \psi_C$. This result differs from the previous case in which geographically divergent patterns of genetic variation could not evolve under hard selection.

Parallel to the previous two cases, it is possible to show that local polymorphisms cannot be maintained in X under hard selection. One may also prove that genetic variation can be maintained if species X is subject to soft selection. With soft selection (eq. [3]), recursion (11a) is replaced by

$$x' = x \left[h \frac{V_1(y_H)}{xV_1(y_H) + (1-x)V_2(y_H)} + (1-h) \frac{V_1(\psi_C)}{xV_1(\psi_C) + (1-x)V_2(\psi_C)} \right] \quad (11a')$$

Combining (11a') with (11b), it is not difficult to show that there is a polymorphic equilibrium given by $\hat{x} = 1/2$, and $\hat{y}_H = \psi_C + (1/2 - \psi_C)/h$. This equilibrium is the same as for hard selection, except that with soft selection, the polymorphism can be locally stable. It is possible to verify, as in the previous two cases, that the species can coevolve to stable limit cycles for certain parameter combinations. Thus, polymorphisms in both species are possible given soft selection in X. This conclusion is unexpected given the results of the previous cases, which implied that soft selection in Y is necessary for the maintenance of local polymorphisms in hot spots, whereas soft or hard selection in X is irrelevant. Apparently, soft selection in X is relevant to maintaining local polymorphisms but only when Y does not move between hot and cold spots. The underlying reason is that geographic divergence in Y produces spatially variable selection in X, which in turn can maintain polymorphisms in X.

The results of this and the previous section clearly establish that gene flow in just one species can ensure the establishment of local polymorphisms. They also show that gene flow will not necessarily eliminate stable patterns of spatial variation in allele frequencies across hot and cold spots.

Limited Gene Flow in Both Species

We now relax the assumption that gene flow between hot and cold spots is completely unlimited when it occurs and consider restricted migration between hot and cold spots (fig. 1F). The general coevolutionary dynamics in this situation are described by equations (5). Rather than provide a comprehensive analysis, we use results from the previous

four sections to develop an intuition for the qualitative dynamics of this intermediate case.

We consider first how small levels of gene flow alter coevolutionary outcomes from those observed when one or both species is completely isolated in hot and cold spots. One can predict the effects of weak migration using Karlin and McGregor's "small-parameters" argument (Karlin and McGregor 1972a, 1972b). Their argument implies that sufficiently low levels of gene flow will not alter the stability of any polymorphic equilibrium that is present with gene flow absent, although the weak migration may displace the equilibrium slightly. For example, because stable polymorphic equilibria are possible given unlimited migration and soft selection in Y, when species X forms closed populations in hot and cold spots, stable polymorphic equilibria would still exist if a few individuals of X migrated between patches. In addition, the small-parameters argument implies that if both species were completely isolated in hot and cold spots (i.e., our first case) and if both were stably fixed for alternate alleles in the two habitats, then weak coupling would introduce only slight polymorphisms to hot and cold spots. Numerical simulations support the small-parameters reasoning and show further that if stable limit cycles are present without gene flow in one species, they will also occur with weak gene flow present in that species (see below).

Higher, but still restricted, levels of gene flow may significantly modify the overall coevolutionary dynamics. Consider for instance the relatively simple case in which species Y does not migrate while X moves between hot and cold spots, but with some limitation. In particular assume $m_{C \rightarrow H}^Y = m_{H \rightarrow C}^Y = 0$ in (5) and, for simplicity, that gene flow rates in species X are geographically symmetric, that is, $m_{C \rightarrow H}^X = m_{H \rightarrow C}^X = m$. Finally, assume that the frequency of allele Y_1 is held fixed at ψ_C in cold spots, which leaves only x_C , x_H , and y_H as variables. This model is biologically similar to (11) except for the restricted migration in X. As discussed in the last section, stable and cyclical polymorphisms can occur for (11) given soft selection in X. To allow for potentially new stable polymorphisms, assume soft selection holds for the current case, that is, set $h_x^* = h$ in equations (5a) and (5b). These assumptions lead to the following system of recursions:

$$x'_H = \frac{x_H^* h(1-m) + x_C^* (1-h)m}{h(1-m) + (1-h)m}, \quad (13a)$$

$$x'_C = \frac{x_H^* hm + x_C^* (1-h)(1-m)}{hm + (1-h)(1-m)}, \quad (13b)$$

$$y'_H = y_H \frac{W_1(x_H)}{W(x_H, y_H)}, \quad (13c)$$

with postselection frequencies $x_H^* = x_H V_1(y_H) / \bar{V}(x_H, y_H)$ and $x_C^* = x_C V_1(\psi_C) / \bar{V}(x_C, \psi_C)$.

When fitnesses are linear (eqq. [6] and [7]) and selection is antagonistic in hot spots ($a < 0, b > 0$), small values of m lead to the coevolution of monomorphisms, whereas larger values maintain polymorphic limit cycles (fig. 5). Note that $\psi_C = 0$ for all cases shown in figure 5, so X_1 is consistently favored in cold spots because its matching allele (Y_1) is absent. When $m = 0$ (fig. 5A), the species coevolve toward local monomorphisms in both hot and cold spots. With a small amount of migration ($m = .001$, fig. 5B), both species approach monomorphisms in both

locations, confirming the small-parameters argument above. At even higher levels of migration (fig. 5C–5F), cyclical polymorphisms develop in both species. Note that, as m is increased, species X allele frequencies in hot and cold spots become increasingly similar. This is evident in figure 5 where the system dynamics tend increasingly to occur along the 45° plane $x_H = x_C$ for increasing values of m . That is, coevolutionary dynamics amid high (but limited) gene flow resemble those that assume completely “unlimited” dispersal in X since in the latter case, $x_H = x_C = x$ by assumption (see eqq. [11a'] and [11b]).

Nuismer et al. (1999) demonstrated that symmetric mi-

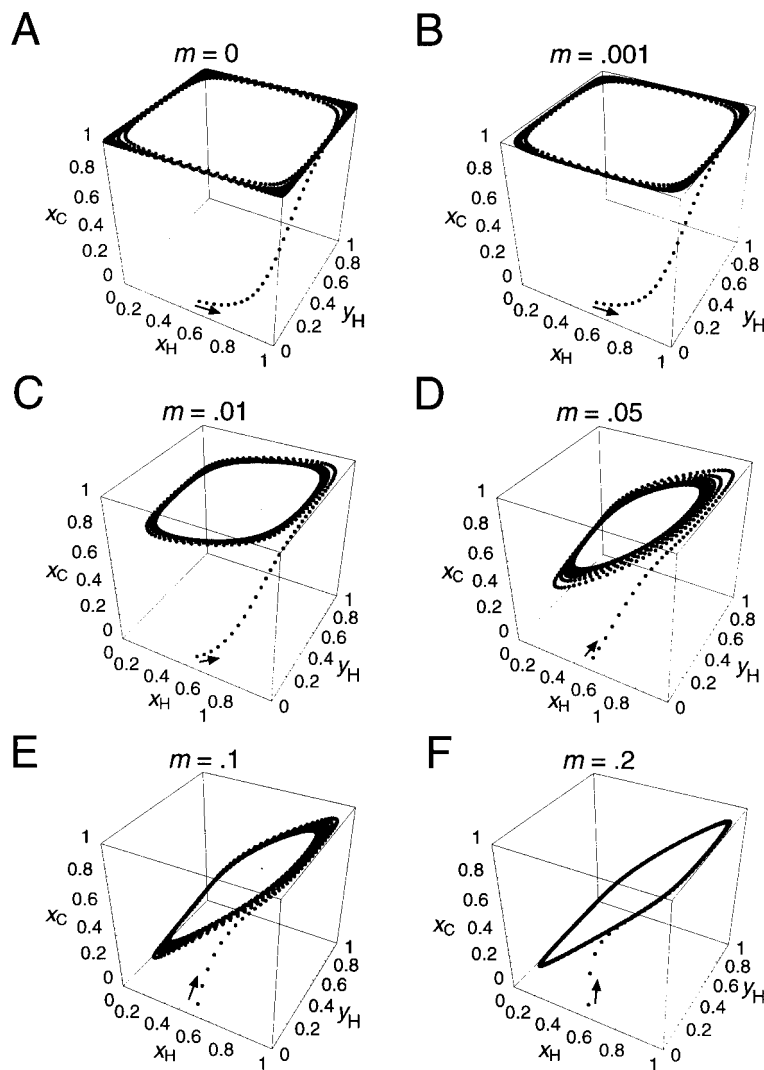


Figure 5: Effect of gene flow (m) on coevolutionary dynamics (displayed as phase portraits for 1,000 generations). Simulation results are based on equations (13) and assume linear fitnesses with $a = -0.2, b = 0.2, h = 0.8$, and $\psi_C = 0$. All simulations start from the initial condition $x_{H,0} = 0.5, x_{C,0} = 0.05, y_0 = 0.05$; arrows indicate directions of coevolution from the initial condition. With increasing m , the long-term coevolutionary dynamics lie increasingly close to the plane $x_C = x_H$.

gration has a homogenizing effect on the dynamics of coupled hot spots that experience different patterns of interspecific selection. In addition, they showed that the form of homogenized dynamics can be predicted from asymmetries in the strengths of local selection: long-term local dynamics in both patches resemble those of an isolated species pair coevolving in the more strongly selected patch. These qualitative properties extend to coupled hot and cold spots. Figure 6 shows an example of the full system (5) in which both species' gene flow parameters are the same and symmetric ($m_{C \rightarrow H}^X = m_{H \rightarrow C}^X = m_{C \rightarrow H}^Y = m_{H \rightarrow C}^Y = m$). In isolation ($m = 0$), allele frequencies eventually alternate between near fixation or near loss in hot spots, whereas in cold spots, allele frequencies approach a definite fixed equilibrium (fig. 6A). If gene flow is moderate ($m = 0.1$) and selection is potentially stronger in hot than cold spots, then local dynamics in both hot and cold spots qualitatively resembles the dynamics of an isolated hot spot (compare both panels of fig. 6B to the left-hand panel of fig. 6A). Alternatively, if selection is stronger in cold than hot spots, the asymptotic (if not the transient) dynamics in both habitat types resembles the asymptotic dynamics of an isolated cold spot in that a definite equilibrium is approached (compare fig. 6C to the right-hand panel of fig. 6A). These examples illustrate how gene flow tends to allow localities with stronger selection to dominate global coevolutionary patterns.

Finally, simulations of the full system (5) with limited gene flow indicate that the effects of intermediate levels of migration on the overall dynamics of both species in hot and cold spots resembles the simpler cases in which gene flow is completely unrestricted or completely absent. This suggests that the simpler cases we analyzed (such as eqq. [8], [10], and [11]) are broadly representative of the qualitative dynamics of more complex systems in which hot and cold spots are only partially coupled by migration. In particular, numerical simulations suggest that polymorphisms are always possible given soft selection in Y, even if X is subject to hard selection at all gene flow rates (as anticipated by our analyses of [8] and [10]). By contrast, soft selection in X allows polymorphisms given hard selection in Y only if gene flow in Y is weak (as expected from analyses of [8] and [11]; see fig. 7). This implies that the potential for polymorphism depends not only on soft selection but also on which species is subject to soft selection.

Discussion

Coevolution at broad geographic scales is influenced by two fundamental features: interacting species tend to be distributed in open populations and fitness interactions between species vary in type and extent across space

(Thompson 1994). Our aim here was to develop and analyze formal models of coevolution between two species that jointly occupy a geographic range over which fitness interactions vary. In part of the range (hot spots), the species have reciprocal impacts on each other's fitness, while in other regions (cold spots), one species is completely unaffected by the other. Our analyses have revealed that, with gene flow, hot spots can significantly affect evolutionary dynamics in cold spots, and vice versa. Hence, patterns of local adaptation, which have been a focus of much recent research on evolving interactions (see Kaltz and Shykoff 1998; Mopper and Strauss 1998 for reviews), can be strongly shaped by the mix of coevolutionary hot and cold spots.

The results here show that the allocation of hot and cold spots affects the evolutionary stability of equilibria at which both species are monomorphic (e.g., see table 2). If the interacting species are mutualists in hot spots, then fixed matched alleles can be maintained, provided the fraction of hot spot habitat is suitably large. Hence a species with maximal fitness in hot spots can be evolutionarily stable even if it has a minimal fitness in cold spots. Our analyses also indicate that matched and mismatched hot spot monomorphisms can be evolutionarily stable under mutualistic or antagonistic conditions (see table 2). It seems likely, however, that some of these genetic equilibria will be demographically unstable if local interactions are antagonistic. However, a species may be demographically sustained when negatively impacted in hot spots if it escapes harmful interspecific effects in cold spots. In this way, sufficiently frequent cold spots could be largely responsible for evolutionary changes in a species.

We found that gene flow allows genetic variation to be maintained in both species under some conditions (see figs. 3–7). In our models, this requires that one migrating species be subject to “soft selection,” which implies that its population size is regulated on a local scale. The potential for polymorphism, however, can depend on which species is subject to soft selection. We found that polymorphisms can result given soft selection in species Y for any pattern of gene flow in X. Alternatively, polymorphisms cannot be sustained given soft selection in X if Y is subject to hard selection, unless gene flow in Y is weak. Since hard and soft selection imply different types of population size regulation (global vs. local), this result highlights the critical and asymmetric role played by population dynamics in maintaining coevolving interactions. It also produces the perhaps surprising prediction that asymmetries in species' intrinsic ecologies may be just as (and at times more) important as asymmetries in gene flow for generating ongoing coevolution.

Our studies also show that coevolutionary trajectories depend separately on the rate of gene flow and strength

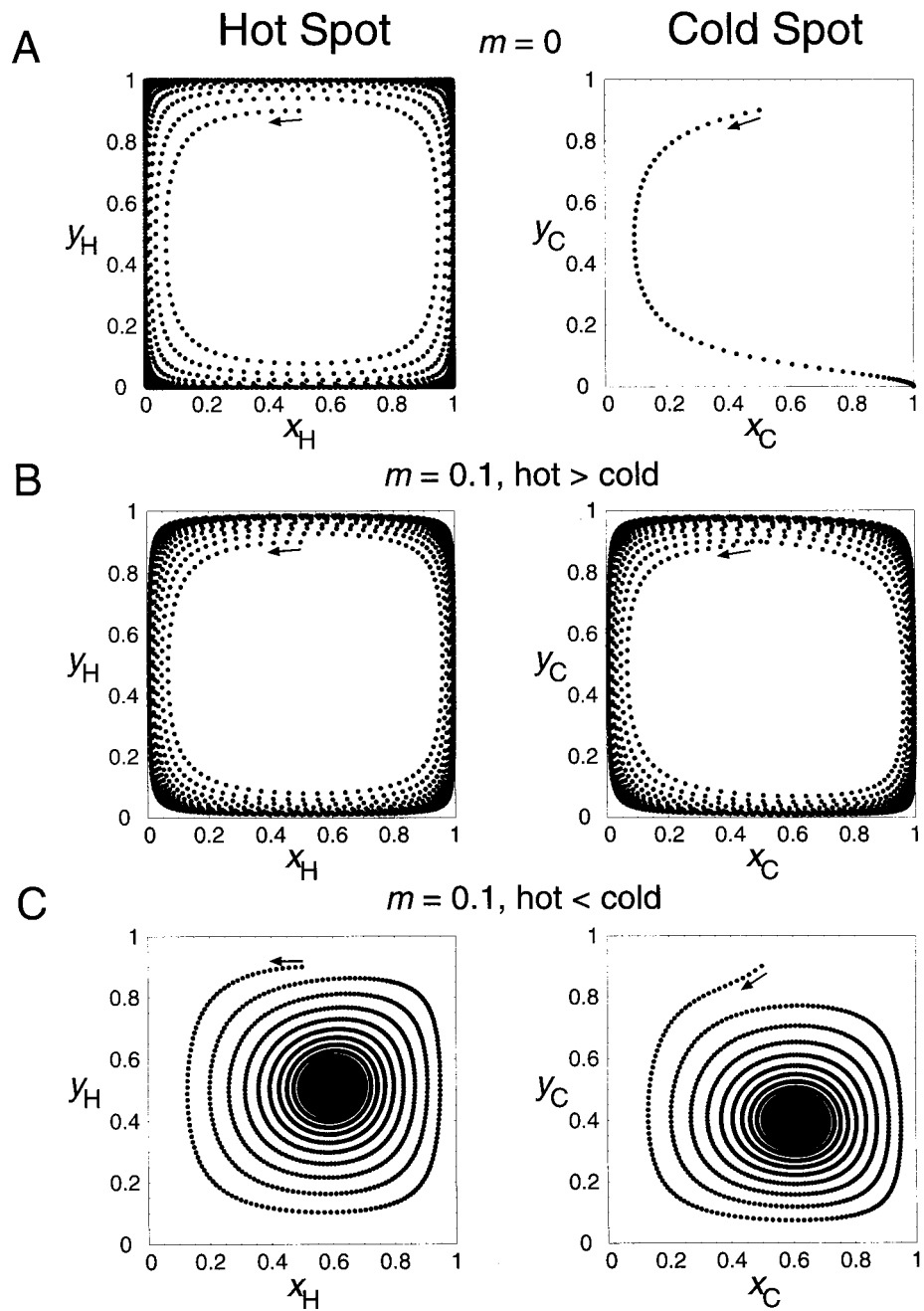


Figure 6: Impact of the strength of local selection on coevolutionary dynamics. Left-hand panels show phase portraits of coevolutionary dynamics in hot spots; right-hand panels show the associated evolutionary dynamics in cold spots. The simulations are based on equations (5) with linear fitnesses assuming $h = 0.8$. All start from the same initial condition ($x_{H,0} = x_{C,0} = 0.5$, $y_{C,0} = 0.9$) and proceed in directions indicated by the arrows. *A*, Dynamics in isolated hot and cold spot habitats for 2,000 generations, assuming $m = 0$, $a = -0.2$, $b = 0.2$, $\Omega_1 = 0.9$, and $\Omega_2 = 1$. *B*, Moderate gene flow with interspecific selection tending to be stronger in hot spots: $m = 0.1$, $a = -0.2$, $b = 0.2$, $\Omega_1 = 0.9$, and $\Omega_2 = 1$ (i.e., $s = -0.1$). Allele frequencies tend toward monomorphisms; 2,000 generations of coevolution are shown. *C*, Moderate gene flow and interspecific selection tending to be weaker in hot spots: $m = 0.1$, $a = -0.1$, $b = 0.1$, $\Omega_1 = 0.8$, and $\Omega_2 = 1$ (i.e., $s = -0.2$). Allele frequencies converge to a polymorphic equilibrium; 4,000 generations of coevolution are shown.

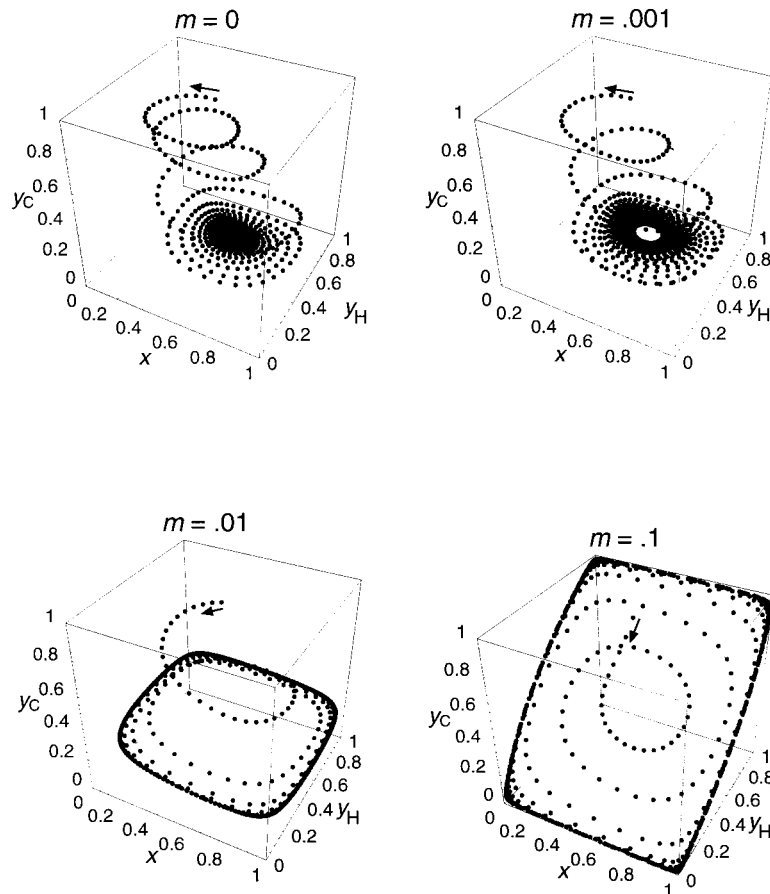


Figure 7: Effect of migration (m) on coevolutionary polymorphisms with interspecific asymmetries in density regulation (i.e., soft vs. hard selection). Simulation results (displayed as three-dimensional phase portraits for 1,000 generations) are based on equations (5) and assume linear fitnesses with $a = -0.5$, $b = 0.5$, $h = 0.7$, $\Omega_1 = 0.94$, and $\Omega_2 = 1$. Species Y has symmetric limited migration ($m_{H \rightarrow C}^Y = m_{C \rightarrow H}^Y = m$) and is subject to hard selection (eq. [4b]). Species X has unlimited gene flow and soft selection so $x_C = x_H = x$; the dynamics of X are described by recursion (11a') with ψ_C replaced by y_C . All simulations are initiated at $x = 0.5$, $y_{H,0} = 0.5$, $y_{C,0} = 0.99$ and proceed as shown by the arrows. With low migration, $y_C \rightarrow 0$, while x and y_H remain polymorphic. As migration increases, y_H and y_C converge as both species coevolve increasingly toward monomorphisms.

of selection. The results are consistent with other theoretical work on geographically structured coevolution (Hochberg and van Baalen 1998; Nuismer et al. 1999). In particular, we found that weak migration does little to alter the coevolutionary dynamics of hot and cold spots from the dynamics that would be attained in isolation. With stronger (but limited) migration, asymmetries in the strength of local selection can drive the global coevolutionary dynamics. That is, the global coevolutionary dynamics tend to resemble the asymptotic dynamics that would occur in the habitat type experiencing the stronger selection (hot or cold spot) if it were closed (fig. 6). Our results demonstrate that local coevolutionary hot spots can strongly influence evolutionary dynamics in neighboring cold spots and vice versa.

Many of our analyses and results were based on models

that assumed linear symmetric fitnesses (eqq. [6] and [7]). However, the same range of qualitative dynamical features described above could potentially occur for any fitnesses that are linear functions of interspecific allele frequencies (R. Gomulkiewicz, unpublished results). As explained previously, linear symmetric fitnesses arise naturally from matching-allele systems of interspecific interactions. Gene-for-gene interactions, which are another important genetic model of interactions for agricultural and other systems, lead to linear “asymmetric” fitnesses. It turns out that polymorphisms will not evolve given gene-for-gene interactions for any of the special cases analyzed above (although polymorphisms can evolve given other types of asymmetric linear fitnesses; R. Gomulkiewicz, unpublished results).

Our conclusions are based on models that assume rel-

atively simple life histories, genetics, interspecific interactions, and geographic structuring. Their main value lies in revealing general features of spatially structured coevolution. We anticipate that similar qualitative features will hold for models based on more complex life-history and genetic assumptions, provided evolutionary forces such as mutation and random genetic drift are weak compared with selection. Of course, we also expect more complicated models to reveal novel coevolutionary features. For example, polymorphisms coevolve more readily in closed hot spots when mutation is significant or when interactions are affected by multiple alleles (Seger 1988). Moreover, simultaneously stable polymorphic equilibria are possible in closed hot spots when the basis of selection is diploid or polygenic (see Gavrillets 1997; Gavrillets and Hastings 1998). Multilocus models of closed populations show an even more tremendous range of coevolutionary dynamics (Seger 1988). It is unlikely that adding geographic structure to these closed-population models would shrink the possible types of coevolutionary outcomes. Indeed, we expect just the opposite (e.g., the dynamics of linkage disequilibrium would be affected not just by selection but by migration as well).

There are several potentially important ecological factors that would doubtless affect our results. For example, the overall influence of hot spots may be modulated considerably by the explicit spatial configuration of selection mosaics (S. L. Nuismer, J. N. Thompson, and R. Gomulkiewicz, unpublished manuscript) or other aspects of spatial structure (Judson 1995; Lively 1999; Parker 1999). Our model assumes that interacting species are distributed among hot and cold spots in the same proportions. However, differences in how each species is explicitly spread among habitats could alter the coevolutionary patterns we found. Finally, some of the long-term coevolutionary outcomes that are possible in our models (such as stable antagonistic interactions; e.g., table 2) may be overridden by density effects (Holt et al. 1999) or extinction (Gandon et al. 1996). In fact, the transient dynamics of the coevolutionary process (such as shifting degrees of matching and mismatching of traits) may themselves have important influences on the short-term ecological dynamics of interacting species (Thompson 1998, 1999). These issues warrant further investigation.

In a broader sense, we have extended single-species genetic models of spatially variable selection (reviewed in Felsenstein 1976; Hedrick et al. 1976; Hedrick 1986) to pairs of interacting species. Our results show that many major features of spatially variable selection ascertained from one-species models also hold for geographically variable species interactions, such as the well-known principle that genetic polymorphisms occur under a wider range of conditions for soft selection than for hard selection (Chris-

tiansen 1975). A second shared attribute is that the evolutionary potential for polymorphisms increases with the strength of local selection (Hedrick 1986).

With the basic components of the geographic mosaic theory formally established, we close by revisiting the "practical" questions posed in the introduction to this article concerning how ongoing coevolution contributes to biodiversity. First, we have shown that hot spots need not be ubiquitous to have a global influence on coevolution, although rare hot spots will not have a disproportionate impact unless selection in hot spots is relatively intense. Second, we found that asymmetries in gene flow can influence local adaptation by, for example, stabilizing evolutionary equilibria at which a species experiences minimal fitness in hot spots and maximal fitness in cold spots. However, asymmetries in gene flow seem no more or less important than asymmetries in population regulation for determining the evolutionary potential for polymorphisms. Finally, we found that allele frequency differences between hot and cold spots within species will evolve under some (but by no means all) circumstances. That is, selection mosaics are indeed capable of producing spatially variable coevolutionary outcomes across the landscapes over which species interact.

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Literature Cited

- Althoff, D. M., and J. N. Thompson. 1999. Comparative geographic structures of two parasitoid-host interactions. *Evolution* 53:818–825.
- Benkman, C. W. 1999. The selection mosaic and diversifying coevolution between crossbills and lodgepole pines. *American Naturalist* 153:S75–S91.
- Berenbaum, M., and A. Zangerl. 1998. Chemical phenotype matching between a plant and its insect herbivore. *Proceedings of the National Academy of Sciences of the USA* 95:13743–13748.
- Brodie, E. D., and E. D. Brodie. 1991. Evolutionary response of predators to dangerous prey—reduction of

- toxicity of newts and resistance of garter snakes in island populations. *Evolution* 45:221–224.
- . 1999. Costs of exploiting poisonous prey: evolutionary trade-offs in a predator-prey arms race. *Evolution* 53:626–631.
- Burdon, J. J., and P. H. Thrall. 1999. Spatial and temporal patterns of coevolving plant and pathogen associations. *American Naturalist* 153:S15–S33.
- Carroll, S. P., H. Dingle, and S. P. Klassen. 1997. Genetic differentiation of fitness-associated traits among rapidly evolving populations of the soapberry bug. *Evolution* 51:1182–1188.
- Christiansen, F. B. 1975. Hard and soft selection in a subdivided population. *American Naturalist* 109:11–16.
- . 1985. Selection and population regulation with habitat variation. *American Naturalist* 126:418–429.
- Dempster, E. R. 1955. Maintenance of genetic heterogeneity. *Cold Spring Harbor Symposium on Quantitative Biology* 20:25–32.
- Dybdahl, M. F., and C. M. Lively. 1996. The geography of coevolution: comparative population structures for a snail and its trematode parasite. *Evolution* 50:2264–2275.
- Felsenstein, J. 1976. The theoretical population genetics of variable selection and migration. *Annual Review of Genetics* 10:253–280.
- Frank, S. A. 1994. Recognition and polymorphism in host-parasite genetics. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 346:283–293.
- Gandon, S., Y. Capowiez, Y. Dubois, Y. Michalakis, and I. Olivieri. 1996. Local adaptation and gene-for-gene coevolution in a metapopulation model. *Proceedings of the Royal Society of London B, Biological Sciences* 263:1003–1009.
- Gavrilets, S. 1997. Coevolutionary chase in exploiter-victim systems with polygenic characters. *Journal of Theoretical Biology* 186:527–534.
- Gavrilets, S., and A. H. Hastings. 1998. Coevolutionary chase in two-species systems with applications to mimicry. *Journal of Theoretical Biology* 191:415–427.
- Hale, J. K., and H. Koçak. 1991. *Dynamics and bifurcations*. Springer, Berlin.
- Hedrick, P. W. 1986. Genetic polymorphism in heterogeneous environments. *Annual Review of Ecology and Systematics* 17:535–566.
- Hedrick, P. W., M. E. Ginevan, and E. P. Ewing. 1976. Genetic polymorphism in heterogeneous environments. *Annual Review of Ecology and Systematics* 7:1–32.
- Hochberg, M. E., and M. van Baalen. 1998. Antagonistic coevolution over productivity gradients. *American Naturalist* 152:620–634.
- Hofbauer, J., and K. Sigmund. 1988. *The theory of evolution and dynamical systems*. Cambridge University Press, Cambridge.
- Holt, R. D., M. E. Hochberg, and M. Barfield. 1999. Population dynamics and the evolutionary stability of biological control. Pages 219–230 in B. A. Hawkins and H. V. Cornell, eds. *The theory of biological control*. Cambridge University Press, Cambridge.
- Judson, O. P. 1995. Preserving genes: a model of the maintenance of genetic variation in a metapopulation under frequency-dependent selection. *Genetical Research* 65:175–191.
- Kaltz, O., and J. A. Shykoff. 1998. Local adaptation in host-parasite systems. *Heredity* 81:361–370.
- Karlin, S., and J. McGregor. 1972a. Application of the method of small parameters to multi-niche population genetics models. *Theoretical Population Biology* 3:186–209.
- . 1972b. Polymorphisms for genetic and ecological systems with weak coupling. *Theoretical Population Biology* 3:210–238.
- Kraaijeveld, A. R., and H. C. J. Godfray. 1999. Geographic patterns in the evolution of resistance and virulence in *Drosophila* and its parasitoids. *American Naturalist* 153:S61–S74.
- Leebens-Mack, J., O. Pellmyr, and M. Brock. 1998. Host specificity and the genetic structure of two yucca moth species in a yucca hybrid zone. *Evolution* 52:1376–1382.
- Levene, H. 1953. Genetic equilibrium when more than one ecological niche is available. *American Naturalist* 87:331–333.
- Lively, C. M. 1999. Migration, virulence, and the geographic mosaic of adaptation by parasites. *American Naturalist* 153:S34–S47.
- Michalakis, Y., A. W. Sheppard, V. Noel, and I. Olivieri. 1993. Population structure of a herbivorous insect and its host plant on a microgeographic scale. *Evolution* 47:1611–1616.
- Mopper, S., and S. Y. Strauss, ed. 1998. *Genetic structure and local adaptation in natural insect populations: effects of ecology, life history, and behavior*. Chapman & Hall, New York.
- Morand, S., S. D. Manning, and M. E. J. Woolhouse. 1996. Parasite-host coevolution and geographic patterns of parasite infectivity and host susceptibility. *Proceedings of the Royal Society of London B, Biological Sciences* 263:119–128.
- Nagylaki, T. 1992. *Introduction to theoretical population genetics*. Springer, Berlin.
- Nuismer, S. L., J. N. Thompson, and R. Gomulkiewicz. 1999. Gene flow and geographically structured coevolution. *Proceedings of the Royal Society of London B, Biological Sciences* 266:605–609.

- Parker, M. A. 1999. Mutualism in metapopulations of legumes and rhizobia. *American Naturalist* 153:S48–S60.
- Parker, M. A., and J. M. Spoerke. 1998. Geographic structure of lineage associations in a plant-bacterial mutualism. *Journal of Evolutionary Biology* 11:549–562.
- Radtkey, R. R., S. M. Fallon, and T. J. Case. 1997. Character displacement in some *Cnemidophorus* lizards revisited: a phylogenetic analysis. *Proceedings of the National Academy of Sciences of the USA* 94:9740–9745.
- Ritland, D. B. 1995. Comparative unpalatability of mimetic viceroy butterflies (*Limenitis archippus*) from four south-eastern United States populations. *Oecologia (Berlin)* 103:327–336.
- Seger, J. 1988. Dynamics of some simple host-parasite models with more than two genotypes in each species. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 319:541–555.
- Thompson, J. N. 1994. *The coevolutionary process*. University of Chicago Press, Chicago.
- . 1997. Evaluating the dynamics of coevolution among geographically structured populations. *Ecology* 78:1619–1623.
- . 1998. Rapid evolution as an ecological process. *Trends in Ecology & Evolution* 13:329–332.
- . 1999. The evolution of species interactions. *Science (Washington, D.C.)* 284:2116–2118.
- Thrall, P. H., and J. J. Burdon. 1997. Host-pathogen dynamics in a metapopulation context: the ecological and evolutionary consequences of being spatial. *Journal of Ecology* 85:743–753.
- Travis, J. 1996. The significance of geographic variation in species interactions. *American Naturalist* 148:S1–S8.

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