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Antagonistic Coevolution over Productivity Gradients

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ABSTRACT: This study addresses the question of how spatial heterogeneity in prey productivity and migration act to determine geographic patterns in antagonistic coevolution with a predator. We develop and analyze a quantitative coevolutionary model for a predator-prey interaction. If the model is modified appropriately, the results could broadly apply to multispecies communities and to herbivore-plant, parasite-host, and parasitoid-host associations. Model populations are distributed over a gradient in prey birth rate (as a measure of productivity). Each population, in each patch, is made up of a suite of strains. Each strain of the predator has a certain ability to successfully attack each strain of the prey. We consider scenarios of isolated patches, global migration, and stepping-stone (i.e., local) migration over a linear string of patches. The most pervasive patterns are the following: investments in predator offense and prey defense are both maximal in the patches of highest prey productivity; when there are no constraints on maximal investment, mean predation evolves to highest levels in the most productive patches; similarly, the predator has a greater impact (measured as the percentage reduction in prey density) on the prey population in high productivity patches as compared with low productivity ones—in spite (even after evolution) of prey abundance being highest in the most productive patches; and migration has the net effect of shunting relatively offensive and defensive strains from productive patches to nonproductive ones, potentially resulting in the elimination of otherwise rare, low-investment clones. A modification of the model to gene-for-gene type interactions predicts that generalist strains (in terms of the range of strains the predator can exploit or the prey can fend off) dominate in productive areas of the prey, whereas specialists prevail in marginal habitats. Assuming a wide range of productivities over the prey's geographical distribution, the greatest strain diversity should be found in habitats of intermediate productivity. We discuss the implications of our study for adaptation and conservation. Empirical studies are in broad accord with our findings.

Keywords: coevolution, predator-prey interactions, geographic range, productivity gradient, spatial models, adaptation, conservation.

It is an empirical fact that plant and animal populations vary spatially in local abundance, and it is often the case that they are most abundant toward the centers of their geographical ranges (Lawton 1996). A widely accepted reason is that a species' population size tends to follow underlying distributions in the suitabilities of environmental factors (i.e., the abundance and quality of a species' own resources: Lawton 1993; Holt et al. 1997; the impact of predators and competitors: Oksanen et al. 1981). Less well established than population abundance, but equally likely, is that species survival and reproduction (i.e., demography) vary in predictable ways with environmental suitability.

Given that species abundance and demography are influenced to some extent by local resources, interactions with predators and competitors should vary along resource gradients, since these types of interspecific interactions are tempered by local density and demography (Hochberg 1996; Leibold 1996). For instance, in specialist predator-prey interactions, the predator may be most influential on its prey's population dynamics toward the center of the latter's geographical range where the prey is most abundant and productive and of less consequence toward the edges. Despite considerable knowledge on how resource levels and productivity may affect exploiter/victim interactions (Rosenzweig 1973; Oksanen et al. 1981; DeAngelis 1992; McLaughlin and Roughgarden 1992; Leibold 1996; Clarke et al. 1997), this subject remains little explored for systems with explicit geographical gradients in these variables; what studies do exist to our knowledge involve single species (e.g., García-Ramos and Kirkpatrick 1997; Kawecki et al. 1997).

If a predator's influence differs spatially over its prey's geographical range, then this can lead to spatially varying selection pressures for the evolution of prey defenses and predator countermeasures to these defenses. Recent years have seen an explosion in theoretical developments on the coevolution of exploiter-victim associations (e.g., Abrams 1986; Seger 1992; Frank 1993*a*, 1994; Dieckmann et al. 1995; Hochberg and Holt 1995; Abrams and Matsuda 1997; Hochberg 1997; van Baalen 1997), but only a small number of models have dealt with coevolution in spatial systems (van Baalen and Sabelis 1993; Gandon et

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al. 1996; Morand et al. 1996), and no studies to date have considered antagonistic coevolution over geographical ranges. Thompson (1994) has argued that geographical patterns in species interactions, fueled or impeded by migration and environmental heterogeneity, may be the product of coevolutionary interactions.

We find Thompson's geographic mosaic theory of coevolution compelling, and as a first step toward a quantitative understanding of its predictions, we develop a quantitative theory of a tightly coupled, predator-prey interaction. To this end, we employ two mathematical models, each combining population and adaptive dynamics. Our main purpose is to predict where along a gradient in prey productivity one should expect antagonistic coevolution to be most pronounced. Other questions addressed in this study include, How do low levels of passive migration affect patterns? How should the phenotypic diversity of predators and their prey vary along productivity gradients? How should specialist and generalist offensive/defensive strategies be distributed over productivity gradients?

Model Development

Definitions

"Productivity" is used to mean the maximum growth rate of the prey population in the absence of the predator. Use of terms such as *productive patches* or *productive habitats* refers to areas in which the prey population has high potential growth rates. We employ "patch" to mean the largest area over which it is reasonable to assume spatial homogeneity in predation. "Migration" refers to unconditional (i.e., passive) movement from patch to patch. "Global migration" means that one or both species migrate from patch to patch, but there is no explicit spatial arrangement to the patches themselves. "Local migration" refers to a linear string of patches over which one or both species migrate by a stepping-stone process. "Investment" refers to the offensiveness (predator) or defensiveness (prey) of the mean phenotype. "Sink" refers to habitats in which the intrinsic growth rate of a species is <0. "Marginal habitat" is that in which the intrinsic rate of increase of a species is just >0.

The Ecological Model

The population model is of an interaction between exploiters and victims, broadly used to mean predators and their prey but also applicable, if appropriately modified, to herbivores, parasites, pathogens, or parasitoids and their hosts. The model is not intended to mimic the dynamics of any particular biological system, but rather intended to see what patterns are predicted in spatial coevolution for a set of plausible, but simple, assumptions. The mathematical framework includes a number of realistic extensions of the classic Lotka-Volterra predator-prey model, and although the assumptions are quite basic, the final model is mathematically complex.

We assume that both species exhibit continuous, overlapping generations (as would many tropical and some temperate predator-prey systems) and that the predator is specialized on the single species of prey considered in the model (as would particularly be the case for many insect parasitoids). The two species are distributed over a total of n patches, with prey and predators at densities $N_{\mathrm{k},t}$ and $P_{\mathrm{k},t}$, respectively, at patch k, at time t.

In the most general model, all vital rates are patch specific, and the differential equations for patch k take the form

$$dN_{\mathrm{k}}/dt = (a_{\mathrm{k}} - b_{\mathrm{k}})N_{\mathrm{k}} - \alpha_{\mathrm{k}}N_{\mathrm{k}}^2 - \beta_{\mathrm{k}}P_{\mathrm{k}}N_{\mathrm{k}} - E_{N,\mathrm{k}} + I_{N,\mathrm{k}} \quad (1)$$

and

$$dP_{\mathrm{k}}/dt = -d_{\mathrm{k}}P_{\mathrm{k}} + \gamma_{\mathrm{k}}\beta_{\mathrm{k}}P_{\mathrm{k}}N_{\mathrm{k}} - E_{P,\mathrm{k}} + I_{P,\mathrm{k}}, \quad (2)$$

where a_{k} and b_{k} are the birth rate and natural death rate of the prey, and d_{k} is the natural mortality rate of the predator.

The prey is subject to two different forms of density dependent limitation. First, we assume logistic-type limitation at a per capita rate of $\alpha_{\mathrm{k}}N_{\mathrm{k}}$, resulting in a standing crop of $(a_{\mathrm{k}} - b_{\mathrm{k}})/\alpha_{\mathrm{k}}$ prey in patch k (in the absence of the predator and of patch-to-patch movement). The parameter α, therefore, is a measure of density dependent factors limiting the productivity of the prey population (e.g., natural enemies other than the predator and/or intraspecific competition). Second, the prey is subject to a per capita predation rate $\beta_{\mathrm{k}}P_{\mathrm{k}}$, with a conversion rate from prey eaten to predators produced of γ_{k} (hereafter assumed for simplicity to equal unity). Oksanen and colleagues (1981) have considered how other per capita predation rates may affect dynamics along a productivity gradient.

The patch-to-patch emigration rates are $E_{N,\mathrm{k}}$ and $E_{P,\mathrm{k}}$; $I_{N,\mathrm{k}}$ and $I_{P,\mathrm{k}}$ are the corresponding immigration rates of prey and predator, respectively. Patch-to-patch movement can be modeled in a variety of ways (Murray 1989). For simplicity, we assume that per capita movement rates are independent of density.

Three spatial submodels, each employing different sets of E and I, will be considered below. In the first, neither predator nor prey are assumed to migrate. This would hold in situations where populations were isolated by distance, barriers, and/or simply negligible dispersal rates. In the second submodel, predators and/or prey migrate equally among all patches, implying that the global migrant pool is well mixed and that migrants distribute themselves uniformly over the patches. This may apply to species with very restricted geographical ranges and/or extreme mobility. Finally, in the third submodel, migration is a directional, step-by-step process along a string of patches. Species with very limited mobility over widespread geographical systems is one plausible scenario for such local dispersal.

Let constant per capita rates $\epsilon_{N,\mathrm{k}}$ and $\epsilon_{P,\mathrm{k}}$ of prey and predators disperse from any patch k. In the model with no migration, evidently $E_{N,\mathrm{k}} = 0$ and $I_{N,\mathrm{k}} = 0$. For the prey (or for the predator, with appropriate modifications to subscripts and densities), $E_{N,\mathrm{k}} = \epsilon_N N_\mathrm{k}$ and $I_{N,\mathrm{k}} = (\sum_j \epsilon_N N_j)/n$ in the global migration model. Finally, $E_{N,\mathrm{k}} = \epsilon_{N,\mathrm{k}} N_\mathrm{k}$ and $I_{N,\mathrm{k}} = (\epsilon_{N,\mathrm{k}-1} N_{\mathrm{k}-1} + \epsilon_{N,\mathrm{k}+1} N_{\mathrm{k}+1})/2$ for the prey in the local migration model. It is further assumed in the local migration model that half of the dispersers in patches at the two edges of the distribution are absorbed into the boundaries and perish. Relaxing this assumption has little quantitative effect as long as dispersal is not too pronounced (i.e., $\epsilon \ll 1$), the number of sites is not too small (i.e., $n \gg 1$), and the leaky edge patches are not the most productive.

The Productivity Gradient

Vital rates of predator and prey may spatially vary in diverse and complex ways. Along an environmental gradient, prey productivity will vary if the qualities of the prey's own resources were to vary predictably over the gradient or if there were a gradient in temperature (e.g., for arthropods), such that development rates (and hence prey productivity) were maximal at an intermediate temperature. To keep the model as simple as possible, with the exception of the parameter a, we assume all other constants to be invariant (and the subscript notation is therefore dropped). Numerical studies, not presented, of systems in which prey density dependence (α) varies spatially produce results broadly similar to those presented below.

In local migration systems, the most favorable conditions are assumed to be at the center of the prey's geographic range. However, other spatioenvironmental scenarios are possible, such as a monotonic increase in favorability from one end of the range to the other (as would be the case for certain latitudinal species' distributions), or the inverse of our model, that is, conditions being best toward the edges of the range (e.g., for coastal species). We leave these other possibilities for future investigation.

The gradient in prey productivity is modeled as variation in prey birth rates and is assumed to follow a modified Gaussian distribution (for discussion of population density, see Brown 1984; see also Holt et al. 1997), such that

$$a_\mathrm{k} = a_0 \exp\{-[(n+1)/2 - \mathrm{k}]^2/2\sigma^2\}, \tag{3}$$

where a_0 is the theoretical maximum prey birth rate and σ^2 is a measure of the spatial variance in birth rate. Often this distribution in maximal birth rate will lead to parallel spatial variation in abundance, particularly if direct density dependence is constant.

Predator-Prey Trade-offs

Conventionally, ecological models are employed to explore how levels of a single parameter (or more rarely two) influence the spatiotemporal dynamics and persistence of populations. This protocol neglects the fact that different parameters may be interdependent within a population; it also overlooks how fundamental biological, chemical, and physical constraints may link various parameters when making comparisons across species or higher taxonomic units. To explore the coevolution of predator and prey over space, we assume that there are explicit metabolic costs to predator offense and prey defense.

The trade-offs are between predation rate and intrinsic survival for the predator and between escaping predation and intrinsic survival for the prey. Each predator strain has a costly offensive strategy j, and each prey a costly defensive strategy i (see below). The effects of these strategies on population changes can be represented in a variety of ways, and following Frank (1994), we make the following assumptions (fig. 1).

First, predators of strain j can only attack prey of strains $i = 1, \ldots, j-1, j$, and therefore, prey of strains $i = j+1, \ldots, m_i$ evade predation at the hands of this same predator strain. We assume for simplicity that both species have the same number of strains m, or $m = m_i = m_j$. As the difference between strains j and i grows, so too does the predation constant β (but see the gene-for-gene model below). This assumption is valid if the phenotypic characters in predator and prey are each under quantitative genetic control (i.e., multiple genes, multiple loci; Frank 1994). Examples of characters that may be under quantitative control for the predator (prey) are predator visual acuity (prey camouflage), predator (prey) running speeds, and predator subjugation of prey (prey escape) (Hochberg 1997; Endler 1991).

Second, the predation constant β is a linear function of the difference between predator strain j and prey strain i, such that

$$\beta_{i,j} = \beta_0(j - i + 1)/m, \tag{4}$$

where β_0 is the maximum predation constant (i.e., when

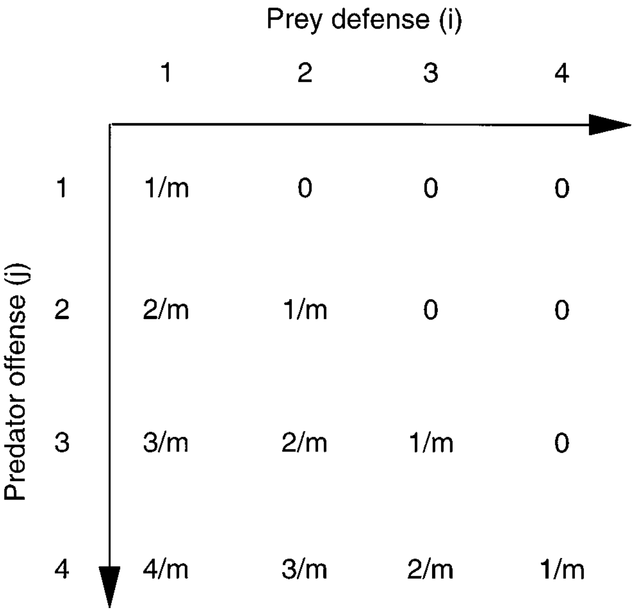

Figure 1: Interaction contingencies $[(j - 1 + 1)/m]$ between predator and prey in a system with m strains of each. Only the four least investing strains of each species are shown.

the most effective predator is faced with the most susceptible prey).

Third, costs of phenotypic characters are deducted from the natural survival constants of each species. Thus, the natural mortality rate of strain j of the predator is

$$d_j = d_0 + d_1(j/m)^{\rho_P} \tag{5}$$

and for strain i of the prey is

$$b_i = b_0 + b_1(i/m)^{\rho_P}, \tag{6}$$

where d_0, d_1, b_0, and b_1 are constants, such that the mortality rate for the most offensive predator strain is $d_0 + d_1$ and, for the most defensive prey strain, is $b_0 + b_1$. The constants ρ_P and ρ_N control nonlinearities in the trade-offs (Frank 1994). When $\rho < 1$, unit increases in strain effectiveness are accompanied by saturating increases in mortality rate, whereas when $\rho > 1$, the trade-off is accelerating. Often a selected phenotypic character will entail accelerating increases in associated metabolic costs. However, arguments could be made for saturating increases, such as when several mutations are required for the character to become effective. In this study both ρ_P and ρ_N are assumed greater than unity.

The Coevolutionary Model

The population dynamic model is now modified to incorporate adaptive evolution, represented as differential growth rates among a set of asexual strains each for the predator and prey. Transitions from strain to strain are assumed to occur in a manner analogous to patch-to-patch migration in structured systems—that is, by mutation to the next higher investment class and by back mutation to the next lower class. For example, prey in strain class i are transferred at a per capita rate μ_N to the two adjacent strain classes, $i - 1$ and $i + 1$ (with 50% going into each class). It is further assumed that half of the mutants produced by each "edge-strain" class ($i = 1$ and m_i for the prey and $j = 1$ and m_j for the predator) perish. This final assumption should have little effect on the results since mutation and back mutation are assumed to occur at low rates (i.e., 10^{-4}) compared to other model processes. (It is important to note that many of the results presented below are extendable to multispecies communities of predators and their prey. In extrapolating to such scenarios, it would be important to modify the mutation process to emigration/immigration of species between the patches and the extrinsic landscape/biogeographical region.)

The final equations for prey strain i and predator strain j in patch k are

$$\begin{aligned} dN_{i,\mathrm{k}}/dt = {} & (a_{\mathrm{k}} - b_i)N_{i,\mathrm{k}} - \alpha N_{i,\mathrm{k}}\Sigma_i N_{i,\mathrm{k}} - N_{i,\mathrm{k}}\Sigma_j\beta_{i,j}P_{j,\mathrm{k}} \\ & - E_{N,\mathrm{k}} + I_{N,\mathrm{k}} + \mu_N(N_{i-1,\mathrm{k}} + N_{i+1,\mathrm{k}})/2 \\ & - \mu_N N_{i,\mathrm{k}} \end{aligned} \tag{7}$$

and

$$\begin{aligned} dP_{j,\mathrm{k}}/dt = {} & -d_j P_{j,\mathrm{k}} + \gamma P_{j,\mathrm{k}}\Sigma_i\beta_{i,j}N_{i,\mathrm{k}} - E_{P,\mathrm{k}} \\ & + I_{P,\mathrm{k}} + \mu_P(P_{j-1,\mathrm{k}} + P_{j+1,\mathrm{k}})/2 - \mu_P P_{j,\mathrm{k}}. \end{aligned} \tag{8}$$

Note again that these equations function under the compatibility constraints described above (i.e., predator strain j can only attack prey strain i if $j \geq i$.

Analytical Results

The analytical results we report involve nonmigratory systems (i.e., $E_{\mathrm{k}} = I_{\mathrm{k}} = 0$). Assuming the number of possible strains of each species approaches infinity, we obtain two continuous coevolutionarily stable strategy (CSS) sets: both the prey defense strategy (now denoted x, corresponding to i/m) and predator strategy (y, corresponding to j/m) can have any value between 0 and 1. Let there be one resident strain on each trophic level: the resident prey population with strategy x^* and density N^*, and the resident predator population with strategy y^* and density P^*. The approach we employ is a straightforward extension of standard evolutionarily stable strategy (ESS) analysis: we are looking for that combination of strategies, x^* and y^*, that, when adopted by the resident populations of prey and predator, respectively, resist invasion of mutants (x and y). This implies that $x = x^*$ and $y = y^*$ should both be local optima (Vincent and Brown 1989; van Baalen and Sabelis 1993).

The per capita fitness of a rare mutant prey strain with strategy x is

$$\mathrm{f}_N\{x, N^*, P^*, x^*, y^*\} = dN/Ndt|^* = a - b(x) - \alpha N^* - \beta(y^* - x)P^*, \tag{9}$$

where $|^*$ denotes evaluated at $N = N^*$ and $P = P^*$. If $\mathrm{f}_N\{x, N^*, P^*, x^*, y^*\}$ is positive, then the strain with strategy x can invade; in other words, if the per capita fitness is negative for all strategies x except $x = x^*$, then all possible mutant strains will go extinct. Such an ESS strategy x^* can be found in two steps: first, work out the optimum strategy x^{o} for a rare mutant in a system dominated by the resident population x^* and, second, find that resident strategy x^* that is the optimum. (To find a pair of CSSs, the same procedure must be followed for y^*).

The optimum strategy x^{o} should satisfy

$$d\mathrm{f}_N\{x, N^*, P^*, x^*, y^*\}/dx = 0, \tag{10}$$

which leads to

$$b'(x^{\mathrm{o}}) = \beta P^*, \tag{11}$$

where $b'(x) = db/dx$. Note that the optimum x^{o} depends on the shape of the cost function and on predator density (see fig. 2 for a graphical indication of the optimum), but it does not depend directly on the resident attack strategy y^*. It is only through the equilibrium density P^* that x^{o} depends on x^* and y^*. This indirect dependence arises because the net attack rate depends linearly on the strategies of prey and predators. As a consequence, the marginal value of the predation term is independent of either x or y^*, and costs must increase in an accelerating manner in order to have an optimum (Frank 1993*a*).

Evolutionary stability implies that the resident strategy is the optimum strategy itself, so with $b(x) = b_0 + b_1 x^{\rho_N}$, the first condition for the CSS pair (x^*, y^*) is

$$b_1 \rho_N x^{*\rho_{N-1}} = \beta P^*, \tag{12}$$

the solution of which requires equilibrium predator density P^* to be solved simultaneously.

Per capita fitness of a mutant predator is given by

$$\mathrm{f}_P\{y, N^*, P^*, x^*, y^*\} = \beta(y - x^*)N^* - d(y), \tag{13}$$

from which the optimum predator strategy y^{o} is given by

$$\beta N^* = d'(y^{\mathrm{o}}), \tag{14}$$

or, with $d(y) = d_0 + d_1 y^{\rho_P}$,

$$d_1 \rho_P y^{*\rho_{P-1}} = \beta N^*. \tag{15}$$

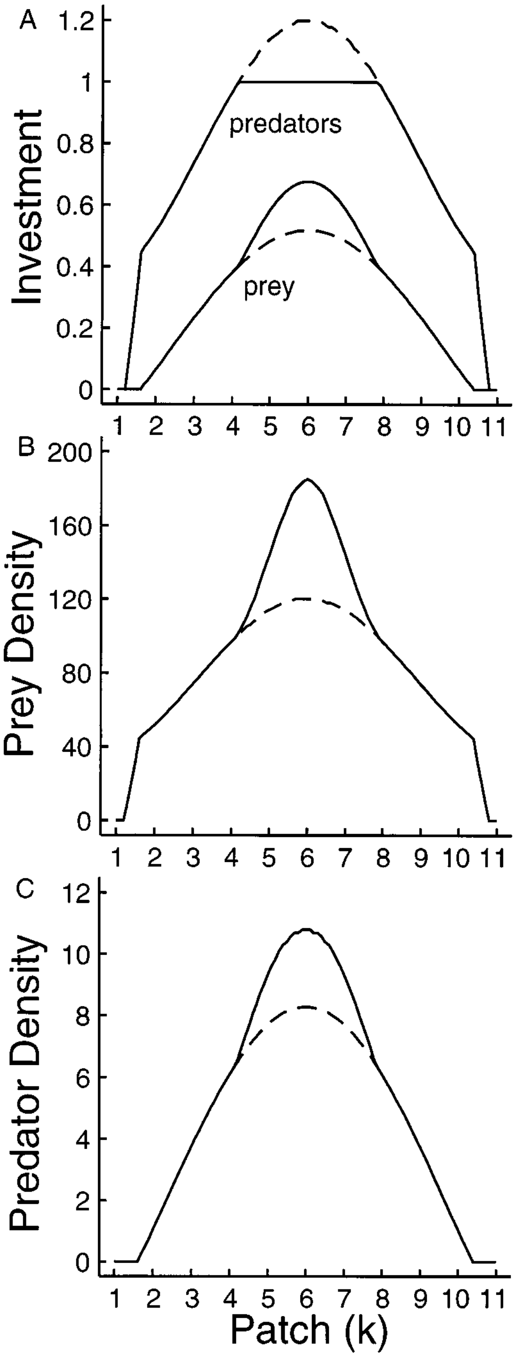

Figure 2: Numerical solutions to analytical model with no migration (eqq. [12] and [15]). CSS investment in offense and defense (*A*) and corresponding equilibrium densities of (*B*) prey and (*C*) predators. *Solid lines* = actual CSSs. *Dashed lines* = CSSs for $y > 1$. Parameters: $\beta = 0.1$, $b_0 = 0.1$, $b_1 = 0.8$, $d_0 = 1$, $d_1 = 5$, $\rho_N = 2$, $\rho_P = 2$, $a_0 = 1$, $\sigma = 5$, $\alpha = 10^{-3}$, and $n = 11$. Numbers next to lines refer to the investment class (i in the case of prey and j in the case of predators); see figure 1. Note that patches 1 and 11 are sinks for the prey (i.e., $a - b < 0$).

Note that if $y^* = 1$ is the ESS, then (15) becomes the boundary condition $d_1\rho_P < \beta N^*$.

The two conditions (12) and (15) have to be evaluated at the equilibrium densities of resident prey and predator. These are given by

$$N^* = d(y^*)/[\beta(y^* - x^*)] \tag{16}$$

and

$$P^* = 1/[\beta(y^* - x^*)]\{a - b(x^*) - \alpha d(y^*)/[\beta(y^* - x^*)]\}, \tag{17}$$

provided

$$[a - b(x^*)]/\alpha > d(y^*)/[\beta(y^* - x^*)] \tag{18}$$

(otherwise the resident predators cannot maintain themselves).

Simultaneous analytical solutions for x^* and y^* from (12) and (15) (using [16] and [17]) do not exist. Numerical solutions for the environmental gradient corresponding to that used below in numerical simulations are shown in figure 2. Notice that the numerical solutions assume no migration along the gradient: at every point along the axes, the local populations of prey and predators are assumed to have reached a coevolutionary equilibrium.

It is clear that the coevolutionary interaction is most intense (i.e., strains most offensive and defensive) in patches where prey productivity or carrying capacity is maximal (fig. 2*A*). In the most productive patch, prey invest maximally in defense, and predators invest maximally in offense. Investment levels decrease toward less productive patches (i.e., as $a \rightarrow b$) and toward patches with increasingly intense prey density dependence (i.e., α becomes large). It may seem counterintuitive that predators cannot invade at the margin (assuming that the patches are spatially Gaussian distributed), even though prey are undefended, but this is simply because these prey are not dense or productive enough to locally sustain a predator population.

Note also that in sufficiently productive patches, predator investment can hit the ceiling (i.e., $y^* = 1$; *solid line* between patches 4 and 8 of fig. 2*A*). This has the paradoxical consequence that higher levels of prey defense are favored than would have been the case with no upper constraint on y^* (see also Hochberg and Holt 1995). This effect becomes clear if one considers the CSSs as they would be in the absence of the $y^* = 1$ ceiling, indicated by the dashed lines in figure 2*A*. The intuitive explanation is as follows: the constraint $y^* = 1$ basically implies that the predators cannot attain the optimum attack strategy. Less efficient predators lead to increased prey densities (fig. 2*B*), and the increased prey densities support, in turn, higher numbers of (inefficient) predators (fig. 2*C*). Since it is both the density of the predators and their attack strategy that determines the optimum defense strategy for the prey, increased prey defense is favored.

Numerical Results

To explore spatioadaptive models with migration, we conducted numerical simulations (see legend of fig. 3 for more details). We restrict the presentation of results to spatial variation in prey productivity (eq. [3]); however, analytical results and simulations of gradients in density dependence (α) and carrying capacity $\{[a - (b_0 + b_1)]/\alpha\}$ produce many of the patterns outlined below. Representative results based on $m = 7$ strains of prey and predators, and $n = 11$ patches are presented; simulations of smaller (simulated down to $n = 3$) or larger (simulated up to $n = 30$) numbers of patches gave the same qualitative results as those presented below. Finally, we have limited the greater part of our exploration to systems with low levels of migration (<10% per time step) and accelerating costs to predator offense and prey defense (i.e., $\rho > 1$); further studies will be necessary to elucidate the effects of other migration rates and saturating costs.

Nonmigratory Systems

Numerical simulations of nonmigratory systems with a small number of prey and predator strains produce the same general pattern as the analytical treatment for an infinite number of strains: per capita investment is maximal for both species in maximally productive patches. Note that the numerical simulations predict a slightly lower mean investment in predator offense than the analytical finding (cf. fig. 2*A* with fig. 3*A*). This numerical result is a consequence of the subdivision of the strategy set in a number of discrete strains. If the number of strains (m) is increased, mean investment approximates that predicted by the CSS analysis (not shown). Notice too that more than one strain may be present at any given (isolated) site (fig. 3*B*, *C*), whereas in the analytical treatment (i.e., when $m \rightarrow \infty$), only a single strain of each prey and predator persists per site at equilibrium. This is because, as m becomes small, single strains are increasingly less likely to approximate the CSS value—rather, two strains sandwich it, permitting a persistent polymorphism.

Global Migratory Systems

Migration spatially averages mean investments (fig. 4). The example of figure 4 shows that even modest amounts of migration can expunge the patterns produced in nonmigratory (cf. fig. 3) and local migratory (see below) systems. Moreover, the shunting of strains among sites permits one or both species to persist in what would otherwise be sink habitats for either species. It is interesting to note, for instance, that when the predator migrates but the prey does not, the mean predator strain is more offensive in prey sinks than in predator sinks with both predators and prey present (fig. 4*D*). This is because the predator adapts locally to prey only in source habitats (i.e., in patches 2–10 of fig. 4*D*) and because relatively inoffensive predators are found in patches of low productivity (patches 2, 3, 9, and 10). In contrast, more offensive, numerically abundant predators migrating from productive sites dominate in the most marginal habitats (patches 2 and 10) and in sink habitats (patches 1 and 11), where local adaptation is impeded (see also Holt 1996). The net result is that predators are on average the least offensive in marginal (and not sink) habitats.

Spatial turnover in strain diversity is sensitive to a species' own migration but also to the migration of the other species (fig. 4*B, C, E, F, H, I*). Given that the system attains an equilibrium in local strain densities, it is not surprising that there tends to be less overall diversity, and less spatial turnover in the identities of strains, in global migratory systems as compared with their nonmigratory analogues (cf. fig. 4*B, C, E, F, H, I* with fig. 3*B, C*).

Local Migratory Systems

Like the global migratory systems, passive local migration tends to shunt strains of prey and predator from highly

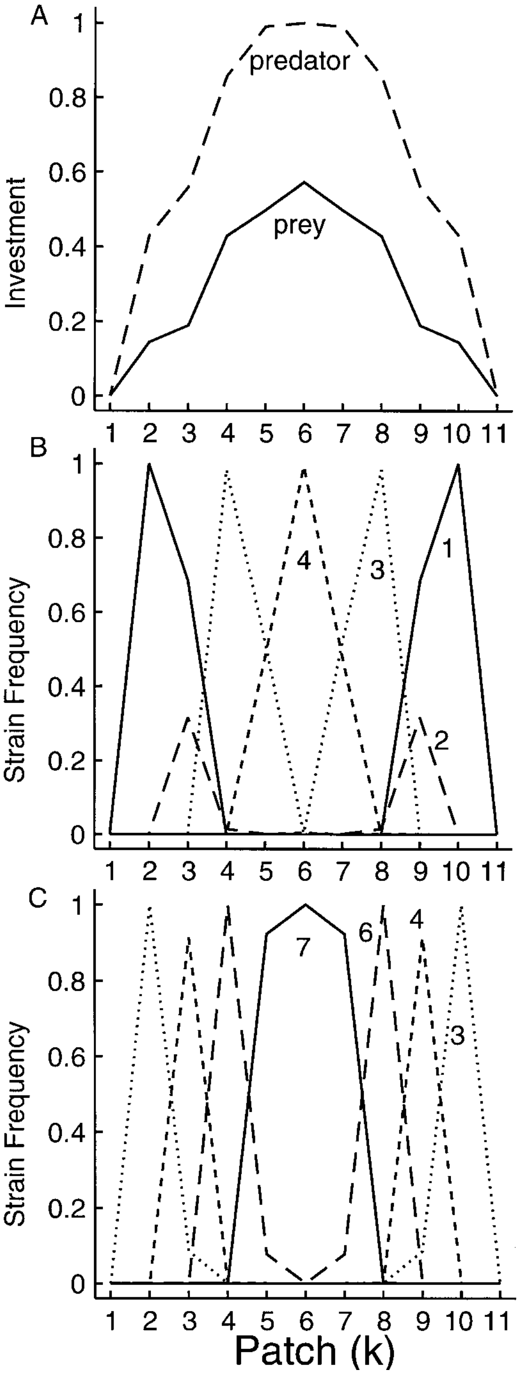

Figure 3: Numerical results of nonmigratory systems. Distribution of (*A*) mean investments of each species, (*B*) frequencies of prey strains, and (*C*) frequencies of predator strains. Mean investment is calculated as $iN_{i,\mathrm{k}}/m\sum N_{\mathrm{k}}$ for strain i of the prey in patch k. *B, C,* Numbers refer to strain defense (i) for the prey and offense (j) for the predator, respectively. Parameters as in figure 2; $m = 7$ and $\mu_N = \mu_P = 10^{-4}$. The differential equations were integrated using the adaptive time-step Runge-Kutta integration algorithm (Press et al. 1989). Each simulation was run for 10,000 time steps with a density error level of 10^{-5}. The least defensive prey strain was introduced at low densities and allowed to equilibrate to its carrying capacity along the spatial gradient (since it excludes all other strains in the absence of mutation). Due to nonzero mutation employed in the simulations, other strains were present at low densities at the end of this equilibration period. All predator strains were then introduced at a density of 0.001 in all patches with the prey present, and the model was run for 100 time steps. During this period, 0.0001 predators and/or 0.0001 prey of any strain were injected into patches in which they fell below this level at any given time step. At time 101, this condition was relaxed, and populations were allowed to vary freely. Measures were recorded at generation 10,000 once populations had settled to a repetitive pattern (either unvarying or oscillating). Although we cannot exclude the possibility of parameter combinations and initial densities giving rise to sustained nonequilibrium trajectories in strain frequencies, in no cases were they observed (for how cycles can occur in spatial systems, see Jansen 1995 and Ruxton and Doebeli 1996).

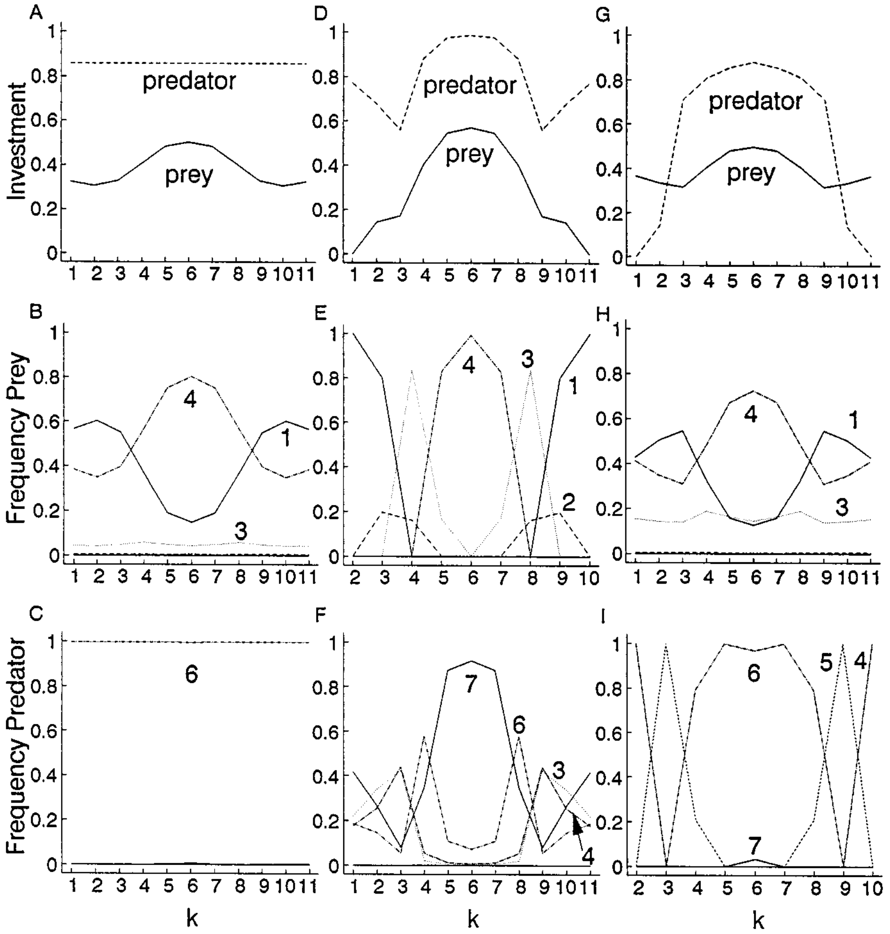

Figure 4: Global migratory systems. Distribution of mean investments (*A*, *D*, and *G*) for each species, and strain frequencies of prey (*B*, *E*, *H*) and predators (*C*, *F*, *I*). *A–C*, $\epsilon_N = 0.1$, $\epsilon_P = 0.1$. *D–F*, $\epsilon_N = 0$, $\epsilon_P = 0.1$. *G–I*, $\epsilon_N = 0.1$, $\epsilon_P = 0$. Other parameters and indices as in figures 2 and 3. For either species, only patches in which densities were $>10^{-3}$ are reported. Note that, although prey migrate into the sinks (patches 1 and 11), their populations are too small to consider them as persisting in panels *G* and *I*.

productive sites to more marginal sites in which they are otherwise maladapted. But in contrast to the global migratory scenarios, these centrally abundant strains are gradually lost (due to their maladaptiveness and the time it takes to migrate from centrally productive patches to the boundaries) as they proceed across the productivity gradient. As a consequence, coevolution often results in more spatial turnover in local migratory systems (fig. 5) than in their global counterparts (fig. 4).

A second qualitative difference between migration in global and local migratory systems is that a greater global diversity of strains is generally maintained in the latter scenario (cf. panels *B*, *C*, *E*, *F*, *H*, *I* of fig. 4 with corresponding ones in fig. 5; see Holt 1984 for this result in an ecological setting). Numerical simulations suggest this effect to be sensitive to prey as compared to predator migration. Moreover, although local mean investments differ little between local and global migratory scenarios (cf. panels *A*, *D*, *G* of fig. 4 with fig. 5), there is a tendency for the more offensive and defensive strains to dominate in productive areas and less offensive and defensive strains to dominate in nonproductive areas in local as compared with global migratory systems (cf. panels *B*, *C*, *E*, *F*, *H*, *I* of fig. 4 with fig. 5).

Migration can have other effects on local migratory systems. For instance, because migration of one species tends to lessen its investment at productive sites and to increase it at nonproductive ones, a nonmigrating antagonist tends to follow suit by lessening investment in productive areas and by increasing it in nonproductive areas (cf. fig. 3 with fig. 5*D–I*). Furthermore, when prey sinks are present on the edges of the system, sufficiently low

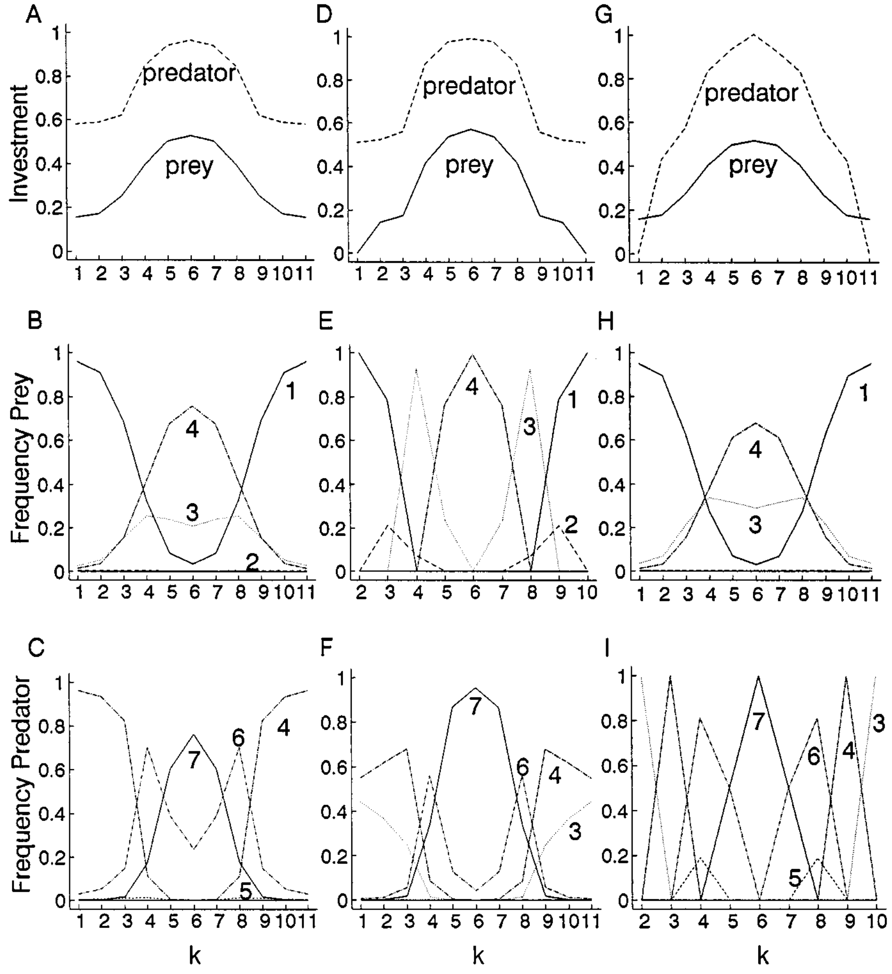

Figure 5: Local migratory systems; details as in figures 3 and 4

levels of migration of one species will mean that that species persists there but that the antagonist does not (fig. 5*E, F, H, I*). This is obvious in the case where the predator migrates but the prey does not; in the reverse scenario, the predator does not persist because population levels of the prey, maintained by low migration, are insufficient to support the predator (although high enough migration rates can support a locally persistent predator population).

Gene-for-Gene Interactions

Our model envisaged a single type of offensive/defensive interaction between exploiter and victim, with quantitative strain-to-strain differences. Antagonistic coevolution in many systems, however, is better approximated by an all-or-nothing interaction, such that single (or small numbers of) genes are involved in determining if the interaction is compatible or not. Frank (1993*a*) has contrasted quantitative and qualitative mechanisms with regard to the evolution of parasite virulence. We modified the model to a gene-for-gene scenario (e.g., Frank 1993*b*) to see whether our quantitative predictions held for another major category of genetic interactions between antagonists.

In the gene-for-gene model, we assume a cost (via eqq. [5] and [6]) for each predator offensive and prey defensive factor expressed (i.e., there are metabolic costs to being a generalist) at a fixed number of loci. The predator attacks the prey if the former has an offensive factor (1) at every locus where the prey has a defensive factor (1), or, in the limiting case where neither predator or prey have costly factors at any loci (i.e., all 0). Take, for example, a system with three loci. Assume the prey has a defense sequence (001) and the predator an offense sequence (100). Because the predator does not match the third locus of the prey, the latter successfully defends itself against the former (eq. [4] becomes $\beta_{i,j} = 0$). Now imagine a different predator strain with sequence (101). It can attack this same prey strain, with $\beta_{i,j} = \beta_0$. Note that both aforementioned predator strains pay an extra cost for unnecessary offense with regard to high frequencies of the particular prey strain: the third locus for the first predator and the first locus for the second predator serve no purpose but entail metabolic costs to the predator. Thus, the number of alleles permitting offense (predator) or defense (prey) is an indication of that strain's level of costly generalism in the interaction.

As for numerical results, the strains in the gene-for-gene model tend to yield more dynamic population trajectories than for the analogous case in the quantitative model (not shown); however, strain densities and frequencies were always observed to eventually settle down to an equilibrium (with differing parameter values and/or with differing initial densities). Clear patterns emerge with regards spatial patterns in coevolution.

Generalist phenotypes (i.e., with many or most factors being 1) tend to dominate in productive areas, whereas specialists prevail in more marginal habitats. If the range of productivities is sufficiently large, then the lowest diversity of strains occurs at each of the habitat extremes. This is because there are more combinations (strains) expressing any given intermediate level of investment at intermediate productivities than at either very high or very low productivities. However, since the predator generally invests more than the prey at any given site, this will mean predator diversity tends be minimal at the most productive sites (a complete generalist), whereas the prey is least diverse at the least productive sites (a complete specialist).

Discussion

We predict predator-prey coevolution should be most intense in areas of high prey productivity. Although not the main focus of our analysis, the same finding applies to areas with low prey density dependence (α) and high prey carrying capacity $\{[a - (b_0 + b_1)]/\alpha\}$. These conditions should be increasingly obtained when the abiotic environment is most favorable for prey metabolism, the prey's resources are of high quality/abundance, and natural enemies (other than the predator) and competitors are of little importance to prey population levels.

Our investigation focused on CSSs (analytical model) and approximations of CSSs (numerical models). These approaches are most appropriate in situations where the patches are of large enough size such that demographic stochasticity has little importance for population and adaptive dynamics. Had we accounted for demographic stochasticity in our models, it could have had two major effects. First, if abundances were small throughout the system, then local strain extinctions could have induced more complex dynamics than observed in our model. Second, small patch sizes (i.e., low strain abundances) would differentially affect areas of marginal productivity, where relatively low investment/specialized strains of predator and prey would be particularly vulnerable to extinction.

Experimentally detecting the spatial differences in antagonistic investment predicted by our model evidently requires that there be sufficient spatial variation in prey demography. This is most likely to occur for geographically (especially, latitudinally) widely distributed species, for relatively sessile species, and between patches at the productivity extremes (e.g., patches 1 and 6 of figs. 2–5). Below we discuss the relevance of our results to geographic patterns in antagonistic coevolution.

The Importance of Population Density

Employing multispecies population models, Vance (1974) has shown that resistant prey species should differentially inhabit high-productivity areas because they can support higher populations of predators (see also Holt 1977), whereas competitive species should be found in low-productivity spots due to the comparatively high cost of resistance. Our treatment shows a similar effect when both enemy and victim coevolve and there are no differences in intrinsic competitive ability. A nonspatial coevolutionary model of a host-parasitoid interaction also shows how investments in offense and defense should increase with prey productivity and prey carrying capacity (Hochberg and Holt 1995). Along with the present work, these studies indicate that models omitting population dynamics will miss salient features of exploiter-victim coevolution (Abrams 1990).

Coevolutionary Mosaics

One of the tenets of Thompson's geographic mosaic theory of coevolution is that the causes and dynamics of coevolution may often require a geographical perspective (Thompson 1994, 1997). The two models examined here concord in their basic predictions regarding geographical patterns in coevolution, with some notable contrasts.

The model with quantitative inheritance predicts that local differences in prey productivity and low migration rates are sufficient to produce a geographic mosaic of coevolutionary hot spots and cold spots (Thompson 1997). Though the gene-for-gene interactions yield the same results, they lend themselves somewhat more readily to interpretations concerning specialization and biodiversity over geographical ranges. Two predictions emerge. First, the most generalized offensive and defensive strains (or species, if we were to draw analogies with multispecies systems) should characterize hot spots and most specialized strains (or species) cold spots. Second, given a sufficiently large range of prey productivities, the highest genetic diversity of predators should be found in regions of low to intermediate prey productivity (and lowest diversity at the highest prey productivities), and highest prey diversity in areas of intermediate to high productivity (with lowest diversities at the lowest productivities).

Interactions between Coevolution and Adaptive Habitat Selection

We have been principally concerned with coevolution over geographic ranges, but our results can also be interpreted at small spatial scales. Assume that the interaction occurs at a single patch with local differences in resource quantity or quality for the prey. In exploiting a range of local habitat types, the prey in a sense has two antipredator strategies: an explicit one in which it evolves resistance to the predator and an implicit one where it can escape predation by inhabiting areas of low resource quantity or quality—even habitat sinks (Holt 1997). Assuming that habitat preference by the prey is labile to evolution, it stands to reason that such preference can be influenced by the action of a coevolving natural enemy. As long as strong selection pressure is maintained in productive microhabitats, prey can be selected to differentially occupy marginal areas; this should be all the more so if prey are of little nutritive value in marginal habitats. An alternative way to view this effect is that the propensity of prey to defend themselves should decrease as the frequency of marginal habitats increases.

Migration

A number of authors have suggested that migration over spatial networks of patches is of considerable importance to spatial variation in adaptation (e.g., Burdon et al. 1989; Frank 1992; Antonovics et al. 1994; Gandon et al 1996). These studies involve strong frequency dependence and account for genetic drift but do not include spatial gradients in environmental suitability.

Our study includes costs other than implicit ones associated with frequency dependence and does not allow for the local extinction of strains. The results indicate that, without spatial gradients in productivity, there should be little or no spatial pattern in adaptation, whereas when such a gradient exists, passive migration should lead to increasing maladaptation (as compared to the same system with no migration) as one goes from productive to nonproductive environments (see also García-Ramos and Kirkpatrick 1997).

Furthermore, although low migration rates in our model are of little consequence to mean investments in offense and defense over the whole system, we did find it to be of substantial importance to the spatial turnover in strain identities (see Burdon and Jarosz 1992). In migratory systems, relatively offensive predator strains and defensive prey strains are differentially shunted from patches of high prey productivity toward those of low productivity. These strains tend to numerically dominate the back dispersal of inoffensive predator and permissive prey strains. The major effects of migration are to increase the spatial ranges of the strains otherwise dominant in the most productive patches (thus, decreasing the spatial turnover in diversity) and to decrease overall diversity (because highly offensive and defensive strains potentially eliminate otherwise locally superior edge strains; see also García-Ramos and Kirkpatrick 1997). These effects are expected to be most pronounced when there are relatively few patches, when the range of prey productivities is large, when the habitat gradient is steep, and/or when patches of substantially differing productivities are found in proximity to one another.

Conservation

Our results indicate that the conservation of genetic diversity in prey-predator associations depends upon the preservation of both productive and marginal habitats for the prey. This runs counter to intuition for two reasons. First, one often associates conservation goals with the amelioration of habitat conditions. Bettering the quality or quantity of resources in otherwise marginal habitat will mean the exclusion of locally adapted prey and predator genotypes (i.e., low investment specialists). Second, when choices have to be made given various constraints, marginal habitat for a conserved species is likely to be sacrificed first (i.e., priorities are directed toward abundant, productive populations). Again, such policy is more apt to erode genetic diversity than one in which equivalent areas of productive habitat are relinquished. We suggest that conservationists should aim to preserve a range of habitat types (perhaps even predator and prey sinks), especially when migration rates are very low.

Evidence

There is scant data on geographical gradients of exploiter-victim coevolution. Burdon et al. (1983) showed a north-south gradient in resistance of wild oats (*Avena*) to their rust pathogen *Puccinia coronata* in New South Wales, Australia. As predicted by our model, they found that northern populations in more favorable mesic conditions were more resistant to the pathogen than populations in southern, arid environments. They hypothesized that this difference may be due to temperature-driven geographical differences in pathogen development. Indeed, if our model is modified such that only predator growth varies in space, then investment patterns for the predator are qualitatively the same as we observed. In a companion study, Oates et al. (1983) showed a trend for increasing pathogen virulence from south to north latitudes. They also found a greater racial diversity of the pathogen in the mesic north, supported by our scenario of local migratory systems with prey migration and intermediate levels of prey productivity in the northern populations. Burdon and colleagues (1989) review this and other cases of spatial structure in the evolution of pathogen-plant interactions.

Another notable case is work on *Drosophila melanogaster* and its insect parasitoid *Asobara tabida* (Mollema 1988; Kraaijeveld and van Alphen 1994, 1995). These studies showed, first, that the encapsulation ability of *D. melanogaster* has parasitoid species-specific components, second, that highest parasitoid virulence tends to occur in southernmost latitudes, and, third, that highest encapsulation abilities occur toward the center of the host's range. (The third finding is based on fewer points than the second, and it is conceivable that, had additional points in southern latitudes existed, the second pattern would have held for the third.) Kraaijeveld and van Alphen's (1994, 1995) results, in particular, suggest a regional association between parasitoid virulence and host resistance, which is consistent with our findings. Assuming that both virulence and resistance are found to be most intense in the center of the geographic distribution, it would be interesting to know if this is linked to *Drosophila* productivity or some combination of spatial structure and host productivity. Most recently, Kraaijeveld and Godfray (1997) have shown that encapsulation ability comes at a cost (in competitive ability), suggestive of the assumptions underlying our quantitative and gene-for-gene models (see also Carton and David 1983). Our model can explain Kraaijeveld and Godfray's finding if competition is lowest in the center of the fly's geographical range (i.e., cost associated with the third finding). Why *D. melanogaster* does not exhibit a geographical pattern in encapsulation to another parasitoid (*Leptopilina boulardi*) remains unexplained.

Limitations and Future Directions

In addition to the need to account for demographic stochasticity noted above, there are several factors that may attenuate or even qualitatively change the basic results of our study.

Ecological Stability. The version of the Lotka-Volterra model we studied produced asymptotically constant densities. However, it is important to stress that predator-prey systems can be characterized by variable long-term dynamics. For example, our model could have produced limit cycles if the predators had a saturating functional response (May 1974). It is very likely that cycles would have evolutionary consequences in the spatial settings we considered. This is because cycles will mean selection pressures varying in time and in space (e.g., Holt 1997), and this will increase the pertinence of genetic drift (and therefore migration and mutation) and local population extinctions on the patterns generated.

Prey Quality. Our model could be modified to account for spatial variation in the nutritive quality of prey individuals by assuming the number of predator progeny produced per attack, γ_k, is proportional to prey productivity, a_k, and/or inversely proportional to prey density dependence, α_k. Examination of the quantitative model (eqq. [1] and [2]) suggests that both predators and prey should invest increasingly less (in marginal habitats) as the conversion efficiency from prey to predator decreases.

Environmental Determinants of Offense and Defense. A possibility not considered in our models is that predator attack and prey defense will, in part, be determined by the local environment (and not entirely be under genetic control, as assumed here). It is reasonable to assume that relatively sedentary prey found in marginal habitats will be differentially more susceptible to predation than the same prey strain living in productive habitats. The same argument goes for predators. Whether coevolution is influenced by environmental effects is likely to depend on how the two species are differentially affected at each patch over the geographical range and on relative rates of migration.

Saturating Costs. We considered cases of accelerating costs as a function of strain investment. For a somewhat different ecological model, Frank (1993*a*) has shown that saturating costs (i.e., $\rho < 1$) have the effect of promoting greater polymorphism in host-parasite associations.

Predator Functional Response. We assumed a linear functional response of the predator to its prey density. Had the response been a saturating one, then predation pressure would have been more limited in areas of high productivity. This would mean less patch-to-patch variation in predator investment than observed.

Predator Phagy. The predator was assumed to be a specialist of the prey species. Had the predator been a polyphage, the coevolutionary trajectories may have differed considerably from those observed. Our results suggest that coevolution in polyphagous systems will depend to some extent on the spatial covariation in productivities among alternative prey. Studies of this problem merit urgent attention.

Coevolution of Migration. In our model, migration is assumed to be passive (i.e., independent of patch condition and prey and predator densities) and evolutionarily static. A considerable theoretical base now exists relaxing one or both of these two constraints (e.g., McPeek and Holt 1992), and we do not know how more complex ecological and evolutionary models of migration would affect our findings.

Inducible Defenses. It is interesting that when the cost of defense for the victim species is paid at each encounter with the natural enemy (i.e., it is inducible), maximum victim investments may occur in patches of intermediate productivity (M. van Baalen, unpublished simulations). This is because the pressure the exploiter inflicts on its victim is expected to positively correlate with productivity, and the evolution of victim resistance in such systems should be maximal at intermediate levels of pressure by the exploiter (van Baalen 1997). In the context of predator-prey interactions, this could occur if the prey is somehow either injured or prevented from reproducing when it evades the predator. The major finding of our study may not hold if the expected costs of injury reduce prey fitness to levels approaching the expectation if the prey were to have no defenses, and the prey has no other more cost-effective form of defense at its disposal.

In Conclusion. We have shown that spatial variation in prey productivity, what is undoubtedly a feature of many species over their geographical ranges, can drive spatial patterns in coevolution with a predatory species. Numerous predictions of this theory outlined in this article should readily lend themselves to verification.

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Literature Cited

Abrams, P. A. 1986. Adaptive responses of predators to prey and prey to predators: the failure of the arms race analogy. Evolution 40:1229–1247.

———. 1990. The evolution of anti-predator traits in prey in response to evolutionary change in predators. Oikos 59:147–156.

Abrams, P. A., and H. Matsuda. 1997. Fitness minimization and dynamic instability as a consequence of predator-prey coevolution. Evolutionary Ecology 11: 1–20.

Antonovics, J., P. Thrall, A. M. Jarosz, and D. Stratton. 1994. Ecological genetics of metapopulations: the *Silene-Ustilago* plant-pathogen system. Pages 146–170 *in* L. A. Real, ed. Ecological genetics. Princeton University Press, Princeton, N.J.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. American Naturalist 124:255–279.

Burdon, J. J., and A. M. Jarosz. 1992. Temporal variation in the racial structure of flax rust (*Melampsora lini*) populations growing on natural stands of wild flax (*Linum marginale*)—local versus metapopulation dynamics. Plant Pathology (Oxford) 41:165–179.

Burdon, J. J., J. D. Oates, and D. R. Marshall. 1983. Interactions between *Avena* and *Puccinia* species. I. The wild hosts: *Avena barbata* Pott ex link, *A. fatua* L., *A. ludoviciana* Durieu. Journal of Applied Ecology 20: 571–584.

Burdon, J. J., A. M. Jarosz, and G. C. Kirby. 1989. Pattern and patchiness in plant-pathogen interactions—causes and consequences. Annual Review of Ecology and Systematics 20:119–136.

Carton, Y., and J. R. David. 1983. Reduction of fitness in *Drosophila* adults surviving parasitization by a cynipid wasp. Experientia (Basel) 39:231–233.

Clarke, R. T., J. A. Thomas, G. W. Elmes, and M. E. Hochberg. 1997. The effects of spatial patterns in habitat quality on community dynamics within a site. Proceedings of the Royal Society of London B, Biological Sciences 264:347–354.

DeAngelis, D. L. 1992. Dynamics of nutrient cycling and food webs. Chapman & Hall, London.

Dieckmann, U., P. Marrow, and R. Law. 1995. Evolutionary cycling in predator-prey interactions: population dynamics and the red queen. Journal of Theoretical Biology 178:91–102.

Endler, J. A. 1991. Interactions between predators and prey. Pages 169–201 *in* J. R. Krebs and N. B. Davies, eds. Behavioural ecology. 3d ed. Blackwell, Oxford.

Frank, S. A. 1992. Models of plant-pathogen coevolution. Trends in Genetics 8:213–219.

———. 1993*a*. Evolution of host-parasite diversity. Evolution 47:1721–1732.

———. 1993*b*. Specificity versus detectable polymorphism in host-parasite genetics. Proceedings of the Royal Society of London B, Biological Sciences 254: 191–197.

———. 1994. Coevolutionary genetics of hosts and parasites with quantitative inheritance. Evolutionary Ecology 8:74–94.

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.

García-Ramos, G., and M. Kirkpatrick. 1997. Genetic models of adaptation and gene flow in peripheral populations. Evolution 51:21–28.

Hochberg, M. E. 1996. An integrative paradigm for the dynamics of monophagous parasitoid-host interactions. Oikos 77:556–560.

———. 1997. Hide or fight? the competitive evolution of camouflage and encapsulation in host-parasitoid interactions. Oikos 80:342–352.

Hochberg, M. E., and R. D. Holt. 1995. Refuge evolution and the population dynamics of coupled host-parasitoid associations. Evolutionary Ecology 9:633–661.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:197–229.

———. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. American Naturalist 124:377–406.

———. 1996. Demographic constraints in evolution: towards unifying the evolutionary theories of senescence and niche conservatism. Evolutionary Ecology 10:1–11.

———. 1997. On the evolutionary stability of sink populations. Evolutionary Ecology 11:723–731.

Holt, R. D., J. H. Lawton, K. J. Gaston, and T. M. Blackburn. 1997. On the relationship between range-size and local abundance: back to basics. Oikos 78:183–190.

Jansen, V. A. A. 1995. Regulation of predator-prey systems through spatial interactions: a possible solution to the paradox of enrichment. Oikos 74:384–390.

Kawecki, T. J., N. H. Barton, and J. D. Fry. 1997. Mutational collapse of fitness in marginal habitats and the evolution of ecological specialisation. Journal of Evolutionary Biology 10:407–429.

Kraaijeveld, A. R., and H. C. J. Godfray. 1997. Trade-off between parasitoid resistance and larval competitive ability in *Drosophila melanogaster*. Nature (London) 389:278–280.

Kraaijeveld, A. R., and J. J. M. van Alphen. 1994. Geographical variation in resistance of the parasitoid *Asobara tabida* against encapsulation by *Drosophila melanogaster* larvae: the mechanism explored. Physiological Entomology 19:9–14.

———. 1995. Geographical variation in encapsulation ability of *Drosophila melanogaster* larvae and evidence for parasitoid-specific components. Evolutionary Ecology 9:10–17.

Lawton, J. H. 1993. Range, population abundance and conservation. Trends in Ecology & Evolution 8:409–413.

———. 1996. Population abundances, geographic ranges and conservation: 1994 Witherby Lecture. Bird Study 43:3–19.

Leibold, M. A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. American Naturalist 147:784–812.

May, R. M. 1974. Stability and complexity in model ecosystems. Princeton University Press, Princeton, N.J.

McLaughlin, J. F., and J. Roughgarden. 1992. Predation across spatial scales in heterogeneous environments. Theoretical Population Biology 41:277–299.

McPeek, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. American Naturalist 140:1010–1027.

Mollema, C. 1988. Cellular immune response of *Drosophila melanogaster* against *Asobara tabida*. Ph.D. diss., University of Leiden, Leiden.

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.

Murray, J. D. 1989. Mathematical biology. Springer, Berlin.

Oates, J. D., J. J. Burdon, and J. B. Brouwer. 1983. Interactions between *Avena* and *Puccinia* species. II. The pathogens: *Puccinia coronata* CDA and *P. graminis* Pers. F. sp. *avenae* Eriks. and Henn. Journal of Applied Ecology 20:585–596.

Oksanen, L., S. Fretwell, J. Arruda, and P. Niemala. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118:240–261.

Press, W. H., B. P. Flannery, S. A. Teukolsky, and W. T. Vetterling. 1989. Numerical recipes in Pascal. Cambridge University Press, Cambridge.

Rosenzweig, M. L. 1973. Exploitation in three trophic levels. American Naturalist 107:275–294.

Ruxton, G. D., and M. Doebeli. 1996. Spatial self-organisation and persistence of transients in a metapopulation model. Proceedings of the Royal Society of London B, Biological Sciences 263:1153–1158.

Seger, J. 1992. Evolution of exploiter-victim relationships. Pages 3–25 *in* M. J. Crawley, ed. Natural enemies: the population biology of predators, parasites and diseases. Blackwell, Oxford.

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.

van Baalen, M. 1997. Coevolution in recovery ability and virulence. Proceedings of the Royal Society of London B, Biological Sciences 265:317–325.

van Baalen, M., and M. W. Sabelis. 1993. Coevolution of patch selection strategies of predator and prey and the consequences for ecological stability. American Naturalist 142:646–670.

Vance, R. R. 1974. Predation and resource partitioning in one predator-two prey model communities. American Naturalist 112:797–813.

Vincent, T. L., and J. S. Brown. 1989. The evolutionary response of systems to a changing environment. Applied Mathematics and Computation 32:185–206.

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