VOL. 179, NO. 2 THE AMERICAN NATURALIST FEBRUARY 2012

# Evolution of Dispersal in a Predator-Prey Metacommunity

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*Submitted February 7, 2011; Accepted September 23, 2011; Electronically published December 21, 2011*

*Online enhancement:* appendix.

ABSTRACT: Dispersal is crucial to allowing species inhabiting patchy or spatially subdivided habitats to persist globally despite the possibility of frequent local extinctions. Theoretical studies have repeatedly demonstrated that species that exhibit a regional metapopulation structure and are subject to increasing rates of local patch extinctions should experience strong selective pressures to disperse more rapidly despite the costs such increased dispersal would entail in terms of decreased local fitness. We extend these studies to consider how extinctions arising from predator-prey interactions affect the evolution of dispersal for species inhabiting a metacommunity. Specifically, we investigate how increasing a strong extinction-prone interaction between a predator and prey within local patches affects the evolution of each species' dispersal. We found that for the predator, as expected, evolutionarily stable strategy (ESS) dispersal rates increased monotonically in response to increasing local extinctions induced by strong predator top-down effects. Unexpectedly for the prey, however, ESS dispersal rates displayed a nonmonotonic response to increasing predator-induced extinction rates—actually decreasing for a significant range of values. These counterintuitive results arise from how extinctions resulting from trophic interactions play out at different spatial scales: interactions that increase extinction rates of both species locally can, at the same time, decrease the frequency of interaction between the prey and predator at the metacommunity scale.

*Keywords:* dispersal evolution, predator-prey, metacommunity, adaptive dynamics, patch-dynamic models.

## Introduction

For locally isolated populations, extinction in the long run can be thought of as a near certainty. The dispersal ability of a species is thus an important factor in explaining how it can regionally persist despite potentially frequent extinctions of its local subpopulations. The perceived role of dispersal in allowing species spatial refuge from local extinctions (Taylor 1990) has motivated numerous theoretical studies of dispersal evolution as a response to increasing rates of stochastic extinction arising from unstable local dynamics or high rates of patch disturbance. However, an important source of local extinction that has not been explored in such studies is that arising from strong interspecific interactions—in particular, extinctions arising from the unstable dynamics inherent to predator-prey interactions. If dispersal is, as has often been assumed, crucial in allowing both predators and prey to escape the extinction-prone effects of strong trophic interactions (Taylor 1990, 1991), then the possible role played by such interspecific interactions in driving dispersal evolution must also be taken into account.

Although the benefits of dispersal for spatially subdivided species may appear obvious, the evolution of increasing dispersal ability requires that the benefits of escaping locally detrimental conditions must more than compensate for the costs entailed by dispersing. For example, dispersing migrants may potentially experience high mortality in transit or they may face barriers to successfully establishing themselves in new patches, both of which are expected to drive down evolutionary dispersal rates (Hamilton and May 1977; Levin et al. 1984). As well, too much emigration can lead to low densities in local populations and, hence, an increased chance of local extinction and lower overall metapopulation abundance (Hanski and Zhang 1993; Rousset and Ronce 2004). An additional cost of dispersal arises from the fact that when species are already sorted according to habitat quality, passive diffusion or movement of migrants will more likely lead them toward habitats whose quality is poorer instead of better (Hastings 1983; Holt 1985), implying that spatial variability in habitat quality alone is not enough to confer an adaptive advantage for increased dispersal and in fact may actually select against it unless it is also accompanied by temporal variability in local population dynamics, including variability brought on by stochastic extinctions (Levin et al. 1984).

A more fundamental cost to dispersal arises from the potential trade-off between increased dispersal ability between habitat sites and lower fitness within sites. Such a trade-off can arise from how resources are allocated to

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Am. Nat. 2012. Vol. 179, pp. 204–216.
0003-0147/2012/17902-52798$15.00.
DOI: 10.1086/663674

different life-history strategies or to different morphological structures, as has been extensively observed in plant species (Ehrlen and van Groenendael 1998) and insects (Wagner and Liebherr 1992). It can also simply arise from the fact that different strategies with the same reproductive output, but differing in the proportion of offspring that are dispersed away from a site, will have different local equilibrium densities; as a result, strategies that lead to higher dispersal will likely have a lower within-patch fitness compared to more philopatric strategies. This gives rise to potential antagonisms between selective forces operating at local and regional levels (Van Valen 1971).

There have been numerous theoretical studies that have shown how dispersal can still evolve in the face of such costs. One potential advantage of dispersal is that it may offer a means of avoiding kin competition (Hamilton and May 1977; Comins et al. 1980; Frank 1986). By reducing competition between close relatives, dispersal can be seen as a form of altruistic behavior that can be adaptive even when no reproductive or ecological benefits accrue directly to the dispersing individual. Dispersal may also be advantageous if it arises as a consequence of bet hedging, whereby individuals in a population can switch phenotypic strategies to maximize fitness in a temporally varying environment (Cohen 1966; Slatkin 1974; Philippi and Seger 1989).

Stochastic extinction of local populations can also provide an adaptive advantage favoring dispersal between habitat sites despite the fitness disadvantage within sites. Not surprisingly, several theoretical studies have demonstrated how evolutionarily stable dispersal rates will increase monotonically as a response to increasing rates of stochastic extinction (Van Valen 1971; Comins et al. 1980; Levin et al. 1984; Olivieri et al. 1995). These studies were based on models that assumed a basic metapopulation framework where dynamics within local sites occurred at a much faster timescale than the colonization-extinction dynamics occurring between sites at the regional level. In particular, these models assumed that successful colonization of a new site by a migrant would result in a local population instantaneously achieving carrying capacity. An important exception to this basic pattern was demonstrated by Ronce et al. (2000), when they showed how evolutionary dispersal rates could potentially exhibit a nonmonotonic response to increasing extinction rates if the metapopulation assumption regarding separation of time scales were relaxed.

In almost all models that investigate dispersal evolution as a response to increasing extinction rates, local extinction is assumed to be caused by some form of demographic stochasticity, patch disturbance, or successional dynamics. Yet the role of extinctions arising from interspecific interactions—in particular, predator-prey interactions—in driving dispersal evolution has not been as thoroughly investigated. Experimental (Holyoak and Lawler 1996*a*, 1996*b*; Bonsall et al. 2002) and theoretical evidence (Vandermeer 1973; Sabelis and Diekmann 1988; Sabelis et al. 1991) has long suggested that, due to the highly unstable and extinction prone nature of the predator-prey interaction, the ability of both interacting species to disperse at sufficiently high rates is critical for persistence of the interaction at large spatial scales (for a review, see Taylor 1990). In a classic experiment, Huffaker (1958) demonstrated how the opportunity to disperse to new habitat patches allowed a predator and prey mite species to regionally persist despite the frequent local extinctions of both species. As dispersal offers the possibility of a spatial refuge for a prey escaping an unstable interaction with its predator, it would be expected that increasing the predator-induced top-down extinction rate on the prey would drive the evolutionary dispersal rates of both the prey and predator upward.

In this study we investigate the evolution of dispersal in a predator-prey metacommunity, using a deterministic model based on a classic Levins-type metapopulation. The evolutionarily stable dispersal rates for both predator and prey are calculated for increasing levels of predator-induced top-down extinction rates. As would be expected, and in agreement with previous studies of dispersal evolution in a metapopulation, we show that the evolutionarily stable strategy (ESS) dispersal rate of the predator is a monotonically increasing function of the predator-induced extinction rate. Surprisingly, however, the prey's ESS dispersal rate is shown to respond nonmonotonically to increasing predator-induced extinction rates; the prey's ESS dispersal rate actually decreases for certain ranges of top-down extinction. We also show that this basic pattern is also observed when dispersal rates of both predator and prey coevolve in response to increasing predator-induced extinction rates: the predator exhibits a consistent monotonic increase in its ESS dispersal rate while the prey tends to show an increase, then a decrease in ESS dispersal rate before remaining relatively constant over increasing extinction rates. We discuss how antagonistic selection operating at different spatial scales and how extinction arising from the effects of species interactions can give rise to such counterintuitive results.

## The Model

The model we use here considers dynamics at both the local and metacommunity scales for a pair of asexual predator and prey organisms that are each capable of dispersing individual migrants from occupied habitat sites and colonizing empty patches. Within habitat sites we assume that prey dynamics are described by a logistic growth function and that predator growth results from a type I functional response. For metacommunity-scale dynamics, the model we use is based on Levins's (1969) formulation of a patch-dynamic metapopulation that has been extended to account for trophic interactions (Pillai et al. 2010). The model tracks the changing patch occupancy of various species and interactions and assumes an infinite number of homogeneous habitat patches. At the metacommunity scale, dynamics involve colonization of new patches and extinction of local subpopulations within occupied sites; local within-patch dynamics are assumed to occur at much faster rate than the colonization-extinction dynamics occurring at the metacommunity scale. This means that local populations are assumed to be either present at equilibrium or absent from local sites and that successful colonization of patches by migrants results in local populations instantly reaching equilibrium. As per classic metapopulation assumptions, it will also be assumed that migration of dispersers is rare enough so as to not affect the local dynamics of already occupied patches receiving colonizers. Although they operate at different time scales, metacommunity and local dynamics are linked by the fact that metacommunity scale rates of colonization and extinction for both predator and prey are dependent on the average local densities of predators and prey within patches.

Our method of investigating evolutionary dynamics within this metacommunity is an extension of Jansen and Vitalis's (2007) approach to studying the evolution of dispersal in a single species metapopulation. It defines the fitness of a mutant strategy by measuring its ability to invade a metacommunity (similar to the $R_m$ measure in Metz and Gyllenberg 2001). At the metacommunity scale this involves calculating the average number of dispersers that will be produced by a site colonized by a single mutant invasive colonizer. At the local level this involves tracking the dynamics and changes in local population sizes that occur when mutant and resident strategies compete within patches.

## The Predator-Prey Metacommunity Model

Our predator-prey metacommunity model is a mean-field infinite patch model where the proportion of occupied predator patches $P$ and total proportion of prey resource patches $R$ are tracked and where dispersal between patches occurs in a well-mixed manner. Prey are capable of colonizing any habitat patch not already occupied by another prey population, while predators require their prey to be present in a patch before colonization and are thus restricted to colonizing only prey patches where a predator is not already present. We assume that prey colonization rates depends on whether a predator is present, $c_{R_P}$, or absent, $c_{R_0}$. If $R_P$ is the proportion of prey patches with a predator and $R_0$ is the proportion prey-only patches, then the total prey colonizer production will be given by the sum of $c_{R_P}R_P$ and $c_{R_0}R_0$. Similarly, total predator colonizer production is given by $c_P P$. Local predator populations can also becoming extinct at a rate $e_P$. The presence of its required prey in a patch means that a local predator population cannot survive in a patch once its prey becomes locally extinct. Local prey populations in the absence of predators will become extinct at a rate $e_{R_0}$. Because of a predator's top-down effects on local prey population size, local prey populations in the presence of a predator will experience an added top-down extinction rate given by $\mu$ (Bascompte and Sole 1998; Pillai et al. 2010), which can be understood as the difference between the prey's extinction rate in the presence of a predator, $e_{R_P}$, and the extinction rate when no predator is present ($\mu = e_{R_P} - e_{R_0}$). The differential equations for the occupancy of both the prey resource $R$ and the predator $P$ are given by

$$\frac{dR}{dt} = (c_{R_P}R_P + c_{R_0}R_0)(1 - R) - e_{R_0}R - \mu P \text{ (prey)}, \quad (1a)$$

$$\frac{dP}{dt} = c_P PR_0 - e_P P - (e_{R_0} + \mu)P \text{ (predator)}. \quad (1b)$$

Solving for the equilibrium patch occupancy of both the prey and predator ($\tilde{R}$, $\tilde{P}$) when $\tilde{P} > 0$ gives

$$\tilde{R} = \frac{1}{2}\left[1 - \left(\frac{e_R + \mu}{c_{R_P}}\right) + \Gamma\right] + \frac{1}{2}\sqrt{\left[1 - \left(\frac{e_R + \mu}{c_{R_P}}\right) + \Gamma\right]^2 + 4\left(\frac{\mu - \Delta c_R}{c_{R_P}c_P}\right)(e_P + e_R + \mu)}, \quad (2a)$$

$$\tilde{P} = \tilde{R} - \frac{(e_P + e_R + \mu)}{c_P}. \quad (2b)$$

Here $\Delta c_R = (c_{R_P} - c_{R_0})$, and $\Gamma = [\Delta c_R(e_P + e_R + \mu)/c_{R_P}c_P]$. If $P = 0$, then $\tilde{R} = 1 - (e_R/c_{R_0})$.

## Local (Within-Patch) Predator-Prey Dynamics

We follow local prey size $x$ using a simple continuous logistic growth function with intrinsic growth rate $r$ and carrying capacity $K$. Although the local prey size is a discrete and not continuous variable, we assume variation in demographic parameters (birth and death) can lead to variation in local size; this allows us to approximate local population abundances using the mean ensemble of local population sizes and thus to track local population size as a continuous variable using a deterministic logistic equation (Parvinen et al. 2003; Jansen and Vitalis 2007). We also assume that growth in predator population size $y$ arises from a linear predator functional response: $f(x) = aqx$, where $a$ represents the attack rate and $q$ the predator conversion efficiency. Predators suffer mortality $m$, while prey suffer an additional loss due to feeding by predators. In addition, a density-independent fraction of both the prey and predator disperse from local populations at rates $\gamma_x$ and $\gamma_y$, respectively. The equations for this system are then given by

$$\dot{x} = rx\left(1 - \frac{x}{K}\right) - \gamma_x x - axy \text{ (prey)}, \tag{3a}$$

$$\dot{y} = aqxy - \gamma_y y - my \text{ (predator)}. \tag{3b}$$

At equilibrium the population size of the predator, $\tilde{y}$; of the prey population when no predator is present, $\tilde{x}_0$; and of the prey population when the predator is present, $\tilde{x}_\mathrm{P}$, are given by

$$\tilde{x}_0 = K\left(1 - \frac{\gamma_x}{r}\right), \tag{4a}$$

$$\tilde{x}_\mathrm{P} = \frac{(m + \gamma_y)}{aq}, \tag{4b}$$

$$\tilde{y} = \frac{r}{a}\left(1 - \frac{m + \gamma_y}{aqK}\right) - \frac{\gamma_x}{a}. \tag{4c}$$

This system represents a top-down predator-prey system where any gains in prey productivity in the presence of a predator will be immediately siphoned off to the predator's population size. Since the dynamics represented by equations (3) are assumed to occur at a much faster rate than metacommunity level colonization-extinction dynamics, resident populations of predator and prey, when present, are assumed to be at the equilibrium values represented by equations (4). Also, as stated above, migration and successful colonization of dispersers is rare enough such that colonizers arriving into already occupied patches are not expected to affect local dynamics appreciably.

## Linking Local and Metacommunity Dynamics

### *Extinction Rates*

Extinction and colonization rates at the metacommunity scale are dependent on the equilibrium population sizes of predators and prey within local patches. To capture the increase in prey extinction due to top-down predator effects we need to relate how decreases in prey abundances will translate into an increased chance of local patch extinction. Since this is a deterministic model we need a simple functional relation between local population size and metacommunity-scale patch extinction rate that will at the same time allow us to test the robustness of our parameter assumption. As such, we can relate local population size of a prey population in the presence of a predator, $x_\mathrm{P}$, with frequency of the prey patch becoming extinct, $e_{R_\mathrm{P}}$, by the function

$$e_{R_\mathrm{P}} = \kappa_R \tilde{x}_\mathrm{P}^{-z_x}. \tag{5}$$

Here $z_x$ represents a power scaling parameter, while $\kappa$ is a constant for scaling the patch extinction rate of the prey according to its local patch abundance. For the purposes of our model we will define $\kappa$ by the product $\kappa = (e_R)_\mathrm{min} K^{z_x}$, where $(e_R)_\mathrm{min}$ is a constant representing the baseline extinction rate of a prey population when $x$ is at carrying capacity $K$. Without making any special assumptions about how local extinction rates will vary with local population sizes we can test the qualitative robustness of our results by varying the scaling parameter $z_x$. Very low $z_x$ values ($z_x \ll 1$), for example, indicate that extinction increases very little with drops in local population size, while $z_x > 1$ would represent a highly elastic response where even small decreases in population size will result in large increases in local extinction rates. Similarly, for the extinction rate of the predator, $e_\mathrm{P}$, we have $e_\mathrm{P} = \kappa_\mathrm{P} \tilde{y}^{-z_y}$, where $\kappa_\mathrm{P} = (e_\mathrm{P})_\mathrm{min} y_\mathrm{max}^{z_y}$; and for the extinction rate of the prey when the predator is absent we have $e_{R_0} = \kappa_R \tilde{x}_0^{-z_x}$. (For convenience we can define $y_\mathrm{max} = K$ so the scaling parameters $z_x$ and $z_y$ are comparable.)

### *Colonization Rates*

Clearly, the rate of disperser production from a site is the product of local population size and the dispersal rate $\gamma$. The metacommunity colonization rate, however, results from the total number of dispersers that both survive migration and successfully colonize a new site. We will for convenience subsume these two factors under a single parameter value for each species: $\alpha$ represents the probability of a prey disperser surviving migration and successfully establishing itself in a new habitat site, giving us $c_{R_0} = \alpha\gamma_x\tilde{x}_0$ and $c_{R_{\mathrm{P}P}} = \alpha\gamma_x\tilde{x}_\mathrm{P}$, while $\beta$ is the probability of successful migration and establishment of a predator disperser, giving us $c_\mathrm{P} = \beta\gamma_y\tilde{y}$.

Below we outline how we use the model described above to calculate the ESS dispersal rate of the prey, $\hat{\gamma}_x$, by first finding expressions for the prey's metacommunity fitness and gradient of selection. We then use the approach developed for calculating ESS dispersal rates to study how the evolution of dispersal is affected by increasing extinction prone predator-prey interactions. In the appendix, available online, we demonstrate in more mathematical detail the derivation of the ESS dispersal rates for both the prey and the predator.

## Calculating the Evolutionarily Stable Dispersal Strategy of the Prey

### *Fitness Equation of the Prey*

We study the evolutionary dispersal response of a prey to increasing predator-induced extinction rates by first developing an expression for the metacommunity fitness of a rare mutant prey colonizer (with a dispersal strategy $\gamma_x^*$) when it invades a resident wild-type prey metacommunity, with dispersal rate $\gamma_x^\circ$ that at equilibrium is described by equation (2a). The focal mutant colonizer's ability to invade the metacommunity will be determined by the equilibrium patch occupancy of the resident prey; we will at the same time assume, however, that the invasive mutant is rare enough that it will not affect the equilibrium metacommunity abundance of the resident prey. The fitness of the mutant invasive trait will be defined by the average number of dispersers that will be produced during the lifetime of a local subpopulation founded by a single mutant colonizer. Thus, our metacommunity fitness approach utilizes the metapopulation fitness measure $R_\mathrm{m}$ (Metz and Gyllenberg 2001; Massol and Calcagno 2009), which is the metapopulation equivalent of the measure $R_0$, the lifetime reproductive output of a single individual. Since the specific approach we use to measure fitness is an extension of Jansen and Vitalis's (2007) model of dispersal evolution in a single-species metapopulation, we follow their mathematical formulation in describing our model.

There are three possible fates of a single focal mutant colonizer invading a resident prey metacommunity: it can either land (i) in an empty patch, (ii) in a resident prey patch, or (iii) in a patch occupied by both a resident prey and predator. The probability of the focal invasive landing in each of these patch types, multiplied both by the probability of the colonizer successfully establishing a local subpopulation and by the total number of dispersers that will be subsequently produced by the local population before it becomes extinct will give the expected reproductive output for each of the above scenarios. Summing the expected reproductive outputs across all three scenarios will give the total expected disperser production of the focal mutant colonizer and, hence, its metacommunity fitness $W$. If $W > 1$, then the mutant invasive can successfully invade and replace the resident; if $W < 1$, then the invasive will be excluded from the metacommunity. If the fitness of the resident prey strategy and the invasive strategy are identical, then $W = 1$. If we derive the fitness equation while assuming that the dispersal strategy of the mutant invasive is larger than that of the resident, then we can use this fitness equation to determine how the sign of fitness changes along a continuous dispersal trait gradient, which will then, as we will show below, allow us to determine the invasibility of a mutant strategy whether its dispersal rate is a higher or lower than that of the resident (see "Selection Gradient and the Evolutionarily Stable Strategy" below). We can now consider in detail the three possible fates of the focal mutant prey invading the resident prey metacommunity.

i) Since $\alpha$ represents the probability of the focal mutant successfully establishing itself in an empty patch, the frequency of the focal colonizer landing and successfully founding a local population in an empty patch is simply $\alpha(1 - \tilde{R})$. Once the population is established, before becoming extinct or being reinvaded by a resident strategy colonizer, it will continuously produce new colonizers at a rate determined both by the invasive strategy's dispersal rate $\gamma^*$ and by the local population size of the invasive prey population. However, before extinction or reinvasion the local invasive strategy patch will switch between being occupied and not occupied by a predator. The rate of colonizer production from a patch with and without a predator will be $\gamma_x^*\tilde{x}_\mathrm{P}^*$ and $\gamma_x^*\tilde{x}_0^*$, respectively. The total number of dispersers produced will then be determined by the time spent in each of these two states. If we represent the total time the invasive patch will spend in each of these two states before becoming extinct or being reinvaded by a resident colonizer by $T_{X_\mathrm{P}}$ and $T_{X_0}$, then the total number of colonizers produced before extinction or reinvasion will be $\gamma_x^*\tilde{x}_0^*T_{X_0} + \gamma_x^*\tilde{x}_\mathrm{P}^*T_{X_\mathrm{P}}$.

As mentioned, the local population will continue to produce dispersers until it either becomes extinct or it is reinvaded. Reinvasion of a focal patch occurs at a rate of $c_{R_\mathrm{P}}\tilde{R}_\mathrm{P} + c_{R_0}\tilde{R}_0$, which we will represent by the expression $\langle c_R\tilde{R}\rangle$. Thus, the probability at which a focal invasive patch will become reinvaded while either in a prey-only or predator-prey state is given by $\langle c_R\tilde{R}\rangle T_{X_0}$ and $\langle c_R\tilde{R}\rangle T_{X_\mathrm{P}}$, respectively. Once a resident prey colonizes an invasive prey patch, the production of dispersers by the local invasive strategy will be determined by the competitive dynamics between both strategies in a mixed patch. If we let $\tilde{s}_x(t)$ represent the total population size of both the invasive and resident prey in a mixed-strategy patch at any given time $t$, and $f(t)$ the fraction of invasives in the mixed prey population, then $\tilde{s}_x(t)f(t)$ will give the number of invasives in a mixed-strategy patch at time $t$. This expression allows us to track the number of invasive individuals in a local population over time. If the invasive strategy has a higher dispersal rate than the resident then we would expect that the resident in a mixed-strategy patch to eventually exclude the invasive strategy locally, or alternatively, the invasive to competitively exclude the resident if it has a lower dispersal rate.

Tracking the number of invasive individuals in a local population allows one to measure the number of mutant dispersers produced over time as the invasive (or resident strategy) is being competitively excluded. As a result, the invasive disperser production at time $t$ from a mixed-strategy patch is $\gamma_x^* \tilde{s}_x(t) f(t)$. Assuming the invasive strategy has a larger dispersal rate, integrating this expression with respect to $t$ from $t = 0$ to $\infty$, while also taking into account the frequency at which the mixed-strategy patch is occupied by a predator, allows one to measure disperser production as the population size of the invasive strategy decays to 0 after invasion of the focal patch by a resident. Thus, the expected number of dispersers produced by the focal patch that is reinvaded when in a prey-only state is $\langle c_R \tilde{R} \rangle T_{X_0} U$, with $U$ representing the total number of invasive dispersers produced after reinvasion of a prey-only patch by a resident wild-type strategy; while the number of dispersers produced when the focal patch is reinvaded while in a predator-prey state is $\langle c_R \tilde{R} \rangle T_{X_\mathrm{P}} V$, where $V$ represents the total number of invasive dispersers produced after reinvasion of the predator-prey patch by a resident strategy. Note that for mathematical tractability we assume once an invasive prey patch has been reinvaded by a resident colonizer, no further invasions by residents occur before one of the two strategies is excluded from the patch. This requires for consistency in the fitness equation that we restrict in our model the maximum number of colonizers that any given prey subpopulation will have received over its lifetime to two. This is a justified model simplification since we adhere to the classic metapopulation assumption that colonization between patches is rare enough relative to local population dynamics, such that recurrent colonization is unlikely to affect local dynamics. The competitive exclusion of the invasive strategy within a local patch should be fast enough relative to the colonization dynamics at the regional or metacommunity scale that we can reasonably ignore further resident reinvasions. Jansen and Vitalis (2007) used this approach under the same assumptions for a single species metapopulation model and demonstrated that more than two invasions did not qualitatively affect the results for their evolutionary model. The total number of invasive colonizers produced by the focal invasive landing in an empty patch will thus be $\alpha(1 - \tilde{R})[\gamma_x^* x_0^* T_{X_0} + \gamma_x^* x_P^* T_{X_\mathrm{P}} + \langle c_R \tilde{R} \rangle T_{X_0} U + \langle c_R \tilde{R} \rangle T_{X_\mathrm{P}} V]$.

ii) The second possible fate of the focal invasive colonizer is to land in an already occupied resident prey-only patch. This will happen with frequency $\alpha \tilde{R}_0$. On being reinvaded, the mixed-strategy prey patch will continue to produce invasive colonizers as one of the strategies is excluded. If the total invasive colonizer production after landing on a resident prey-only patch is $Q$, then the total expected number of invasive colonizers produced by this scenario is $\alpha \tilde{R}_0 Q$.

iii) The final possible outcome for the focal invasive colonizer is to land on a predator-occupied resident prey patch with frequency $\alpha \tilde{R}_\mathrm{P}$ and then to produce $Z$ number of invasive colonizers from the mixed-strategy patch before extinction, giving a total expected invasive colonizer output of $\alpha \tilde{R}_\mathrm{P} Z$.

The total metacommunity fitness of the focal mutant invasive prey with dispersal rate $\gamma_x^*$, invading a metacommunity with a resident prey with dispersal rate $\mathring{\gamma}_x$, that is, $W(\gamma_x^*, \mathring{\gamma}_x)$, is then simply the sum of the expected colonizer production from these three scenarios:

$$W(\gamma_x^*, \mathring{\gamma}_x) = \alpha(1 - \tilde{R})[\gamma_x^* x_0^* T_{X_0} + \gamma_x^* x_\mathrm{P}^* T_{X_P} + \langle c_R \tilde{R} \rangle T_{X_0} U + \langle c_R \tilde{R} \rangle T_{X_\mathrm{P}} V] + \alpha \tilde{R}_0 Q + \alpha \tilde{R}_\mathrm{P} Z.$$

We give explicit expressions and derivations for all the terms in the fitness equation in the appendix.

### *Selection Gradient and the Evolutionarily Stable Strategy*

Once we define an expression for fitness and assume that the trait under selection—that is, dispersal rate—varies along a continuous gradient, we can then use the tools of adaptive dynamics, or continuous evolutionary game theory (Brown and Vincent 1987; Metz et al. 1992; Geritz et al. 1998; Doebeli and Dieckmann 2000), to study the evolutionary dynamics of the metacommunity. Taking the derivative of the fitness equation with respect to the invasive's dispersal rate, and setting $\gamma_x^* = \mathring{\gamma}_x$ gives us the selection gradient: $g_x = \partial W_x / \partial \gamma_x^* |_{\gamma_x^* = \mathring{\gamma}_x}$. The sign of the selection gradient tells us the direction in which the invasive's fitness is increasing relative to the resident when the invasive's strategy is arbitrarily close to the resident. Thus, for example, $g_x > 0$ tells us that an invasive with a slightly higher (lower) dispersal rate than the resident will also have a higher (lower) metacommunity fitness than the resident strategy and will therefore be successful (unsuccessful) in invading and eventually excluding the resident from the metacommunity.

Of particular interest are those points in trait space where $g_x = 0$; it is at these critical points—also known as "evolutionarily singular" trait values (Metz et al. 1996; Geritz et al. 1998; Doebeli and Dieckmann 2000)—that the change in fitness is 0, indicating that such trait values may represent potential evolutionary attractors and end points in evolution. In order for a singular value to represent an evolutionary attaractor—or the point toward which evolution drives the strategy—the condition $dg_x / d\gamma_x |_{\gamma_x = \hat{\gamma}_x} < 0$ must hold. On the other hand, for a singular trait value to represent an evolutionary end point in trait space where evolution stops and the strategy is incapable of being invaded further by neighboring phenotypes, the condition $\partial^2 W_x / \partial \gamma_x^{*2} |_{\gamma_x^* = \hat{\gamma}_x} < 0$ must hold. Such singular points where evolution comes to a halt represent evolutionarily stable strategies.

By defining expressions for the gradient of selection of both the prey and predator (appendix) we can track how both the prey and predator's ESS will change with increasing predator-induced extinction rates. We give detailed derivations and expressions for the selection gradients in the appendix.

## Results and Analysis

Figure 1 shows how the ESS dispersal rate for predator and prey changes with increasing rates of added prey extinction caused by top-down predator effects. These results were obtained by increasing the strength of the predator-prey interaction through the predator's attack rate, $a$, on the prey (eq. [4b]). The resulting reduction in local prey abundance (eq. [4b]) causes an increase in the extinction rate of the prey (eq. [5]), and consequently that of the local predator population. Thus, predator top-down effects are destabilizing for both prey and predator. (Interaction strength was explored above the minimum value needed to ensure a positive within-patch population size for the predator; see eq. [4c].) The $X$-axis in figure 1 gives the added rate of prey extinction (eq. [1]) that would be experienced due to predation $(e_{R_P} - e_{R_0})$ in a single patch-system (i.e., when $\gamma_x = \gamma_y = 0$). In figure 1*A*, the evolutionary response of the predator is as expected, with the predator's ESS dispersal rates showing a monotonically increasing response to increasing prey extinction rates. This corresponds to the results obtained in previous studies where single-species metapopulations showed a monotonic response to increasing patch extinction rates (Van Valen 1971; Comins et al. 1980; Levin et al. 1984; Olivieri et al. 1995). Surprisingly however, ESS dispersal rates for the prey show a nonmonotonic response to increasing predator-induced extinction rates (fig. 1*B*): prey ESS dispersal increases up to a maximum and then declines as extinction rates continue to rise.

We also see that ESS responses are qualitatively the same regardless of the assumption we make regarding how frequency of extinction is related to local population size. Both predator and prey show qualitatively robust ESS response patterns to changing $z_x$ parameter values. The quantitative difference in ESS responses arises from the fact that large $z_x$ values cause small drops in local prey abundances to translate in large increases in the local extinction rate. As a result, increasing the value of $z_x$ used will quantitatively shift the curves of both predator and prey rightward, as species experience increased predator-induced extinction rates for a given top-down predator attack rate.

As mentioned, the predator's response pattern arises for the same reason that was observed in previous studies of single-species metapopulations—because of the predator

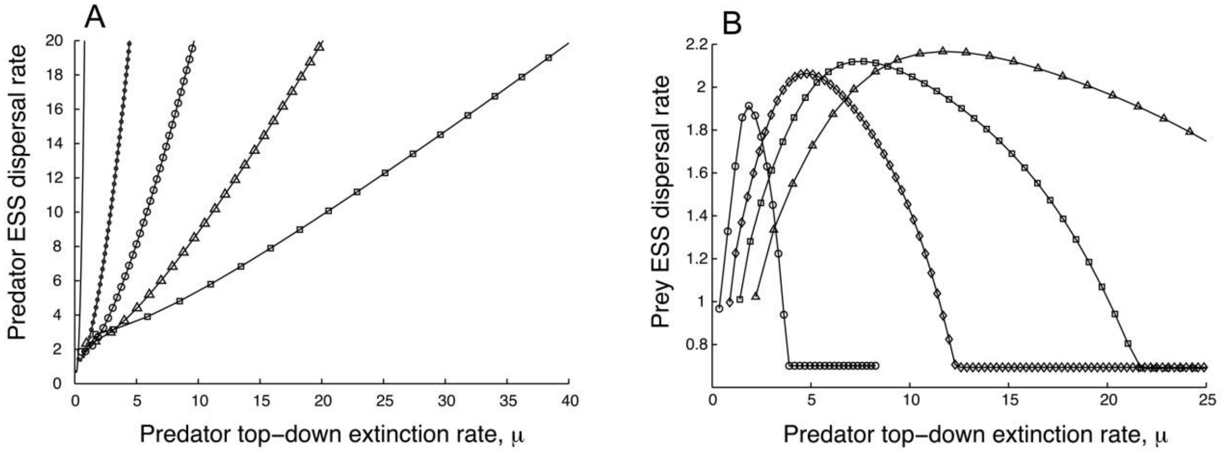

**Figure 1:** Evolutionarily stable dispersal rates as a response to increasing predator-induced extinction. Values on $X$-axis represent top-down extinction for a single, locally isolated interacting predator-prey system. Top-down extinctions controlled by increasing predator attack rate are in equation (4a). *A*, Predator evolutionarily stable strategy (ESS) dispersal rates as a response to increasing predator-induced extinctions. Curves show different values of $z_x$: 0.4 (line), 0.6 (dots), 0.7 (circles), 0.8 (triangles), 0.9 (squares). All other parameters: $r = 10$, $K = 200$, $q = 0.75$, $m = 0.25$, $\gamma_x = 2$, $\alpha = 0.1$, $\beta = 0.1$, $z_y = 0.025$, $(e_R)_{\min} = 0.01$, $(e_P)_{\min} = 0.01$, and range of $a$ values used: 0.5 to 100. *B*, Prey ESS dispersal rates as a response to predator-induced extinction rates. Prey ESS responses show a nonmonotonic response to increasing predator-induced extinction rates. After the predator goes extinct at the metacommunity scale, prey dispersal rates level off and remain constant at the prey-only ESS. Values for $z_x$ are 0.8 (circles), 1.0 (diamonds), 1.1 (squares), and 1.2 (triangles). All other parameters: $r = 5$, $K = 200$, $q = 0.45$, $\mathrm{m} = 0.3$, $\gamma_y = 20$, $\alpha = 0.01$, $\beta = 0.01$, $z_y = 0.035$, $(e_R)_{\min} = 0.01$, $(e_P)_{\min} = 0.01$, and range of $a$ values used: 0.3 to 15.

needing to escape higher frequencies of local patch extinction. As with single-species metapopulations, increasing patch extinction rates in our model offsets the cost of lower local fitness caused by increasing dispersal.

However, the prey's response is more complicated, as it is determined by how the predator-prey interaction, playing out at both local and regional scales, affects the balance between antagonistic forces of selection that both favor and select against increased dispersal (Van Valen 1971). When predator-induced prey extinctions are relatively weak, increasing the strength of the extinction-prone predator-prey interaction results in prey dispersal being favored by the need to escape local extinction, even at the cost of lower local fitness. This changes significantly, however, when the predator-induced extinction rate of the prey passes a point where the cost of decreased fitness within patches exceeds the benefit from increased dispersal between patches. This shift occurs due to the fact that, although the effects of strong extinction-prone interactions are the same for both predators and prey locally within patches, the effect of extinction-prone interactions is strongly asymmetric at the metacommunity scale. Because predators can only settle and persist in patches that are already occupied by prey, predators are always associated with their prey in local patches, and as a result, increasing the destabilizing nature of the predator-prey interaction increases the extinction frequency of all predator subpopulations uniformly, leading to reduced predator viability at the metacommunity scale. On the other hand, only a fraction of prey are associated with the predators in local patches. As local predator-induced extinction rates increase, both prey and predators become extinct equally within patches, but at the metacommunity level predators are more affected by the interaction than prey, being driven to lower patch occupancy levels at much faster rate. At high predator-induced extinction rates, the number of patches where predators and prey interact with each other begins to rapidly decline, allowing prey patches to actually increase in metacommunity abundance as top-down extinctions ($\mu$) increases. We can see this illustrated in figure 2 where, for a given predator and prey colonization rate, increasing the predator-induced extinction rate $\mu$ affects predator (dashed lines) and prey (solid lines) differently. For low extinctions, prey are more strongly associated with predators and are more strongly affected by increases in their extinction-prone interactions with predators; at higher $\mu$ values the rapid decrease in patch occupancy of the predator decreases the association of prey with predators within patches; at this point the prey can actually start to recover occupancy of the metacommunity, while predators are rapidly driven out of the metacommunity. At the point where top-down extinction rates drive the predator extinct at the metacommunity scale the prey's dispersal rate returns to the prey-only ESS, and remains constant in the absence of the predator.

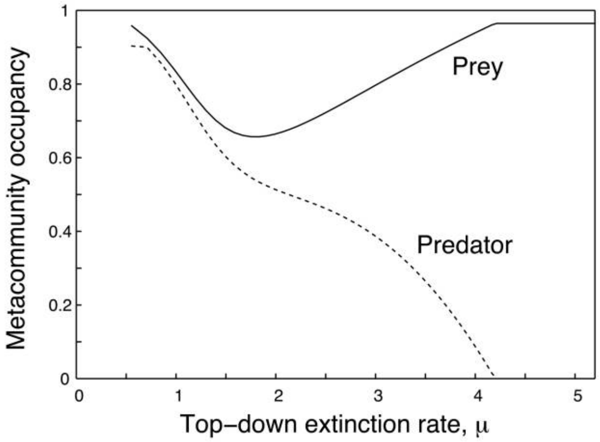

**Figure 2:** Effect of increasing predator-induced top-down extinction rates on a prey and predator's metacommunity patch occupancy. Increasing extinction-prone interaction has asymmetrical effects on both species as extinction rates increase: at first, both prey and predator decline, with the predator's decline being more drastic; with further extinction increases, the predator is rapidly driven out of the metacommunity as the prey recovers in metacommunity abundance. Parameter values used here: $r = 5$, $K = 200$, $q = 0.45$, $m = 0.3$, $\gamma_x = 2$, $\gamma_y = 10$, $\alpha = 0.008$, $\beta = 0.1$, $z_x = 0.6$, $z_y = 0.035$, $(e_R)_{\min} = 0.05$, and $(e_\mathrm{P})_{\min} = 0.001$.

It is important to note that by decreasing local prey abundances (eq. [4b]), increases in the strength of the predator-prey interaction will actually have two potential consequences for the prey's ESS dispersal rates. First, by increasing the rate of local extinctions (eq. [5]) it can affect the dispersal rate as described above. It also, however, can drive ESS dispersal rates solely through its effect on local fitness when top-down extinctions are minimal. This second mechanism appears to predominate if the prey's extinction rates are not significantly affected by the local prey population size, as described by equation (5). In other words, if $z_x$ is relatively low and as a result increases in predator interactions have little effect on the prey's extinction rate, then the prey's ESS dispersal rate will be primarily driven by the effects of decreasing local fitness. Figure 3 demonstrate the ESS response for very low $z_x$ values: the observed initial drop in ESS dispersal rates are actually responses to the decrease in local fitness that happens to be correlated with the small increases in extinction shown on the $X$-axis. For the increasing interaction strengths that correspond to these small extinction scales, decreases in local population size make it easier for the resident strategy to more quickly displace mutant invasives with higher dispersal rates. This makes dispersal too costly

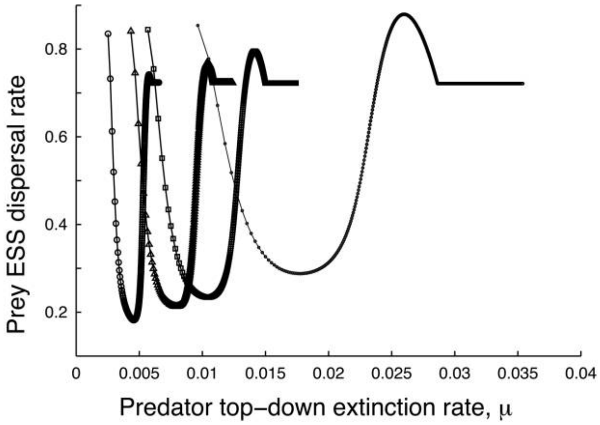

**Figure 3:** Response of prey evolutionarily stable strategy (ESS) dispersal when strong predator-prey interactions have little or no added effect on prey extinction rates (very low $z_x$ values). Curves show effect of progressively removing the effects of top-down extinction on prey as interaction strength increased. Curves shown for $z_x = 0.01$ (circles), 0.08 (triangles), 0.1 (squares), 0.15 (dots). When $z_x$ is very low such that prey extinction is not significantly affected by decreases in local prey size arising from predation, the effects of local fitness determines ESS dispersal rate. The effects of extinction only take effect as $\mu$ increases to sufficiently high levels (as can be seen by the hump-shaped portion of curve). After the predator becomes extinct at the metacommunity scale, prey dispersal rates level off and remain constant at the prey-only ESS. As $z_x$ determines how local population sizes affect extinctions, higher values of $z_x$ cause the prey's ESS dispersal to respond more to the effects of top-down extinctions and less to the decease in local fitness as the strength of trophic interactions increase. All other parameters same as in figure 1*B*.

because of the decreased local fitness it entails and therefore leads to the observed rapid drop in ESS dispersal rates. As the prey's dispersal rate drops, its metacommunity abundance drastically declines, which drives the predator toward lower metacommunity abundances and eventual extinction, at which point the prey's ESS dispersal rate can begin to recover upward to its prey-only ESS. Notice for the response curves in figure 3, that continuously increasing the extinction rate eventually allows the effects of predator-induced extinction, as described in the previous paragraph, to begin to take effect near the end and overwhelm the effects of local fitness declines due to low population size. This leads to the curve, just before the dispersal rate returns to its prey-only ESS value, displaying a small hump shape similar to that observed in figure 1*B*.

The results presented above demonstrate how dispersal rates of a predator or prey evolve when the dispersal strategy of the other species is assumed to remain constant. If, however, both predator and prey dispersal strategies could coevolve together, how would the joint ESS strategy, $(\tilde{\gamma}_x, \tilde{\gamma}_y)$, respond to increasing predator-induced extinction rates? Solving the equations for each species' selection gradient (appendix) simultaneously as a system of nonlinear equations for different top-down extinction rates gives us the joint ESS strategies shown in figure 4 (which are also convergently stable strategies when mutational processes are assumed to have an identical and constant affect on the speed of evolution for each species; see Marrow et al. 1996; Doebeli and Dieckmann 2000; Leimar 2009). From this figure it can be seen that for increasing extinction-prone interactions coevolution still leads to a consistent increase in predator dispersal rates, while the prey's dispersal strategy shows a nonmonotonic response: a small dispersal increases for low $\mu$ values, then either decreasing or relatively constant dispersal over a large range of $\mu$ values. Note that most of the trait evolution in this coevolving system occurs largely along the direction of the *Y*-axis representing the predator's dispersal gradient, as opposed to the *X*-axis representing the prey.

## Discussion

Most theoretical studies on the evolution of dispersal in a metapopulation have demonstrated how evolutionarily stable dispersal rates rise with increasing patch extinction rates (Van Valen 1971; Comins et al. 1980; Levin et al. 1984; Olivieri et al. 1995). These results were all obtained

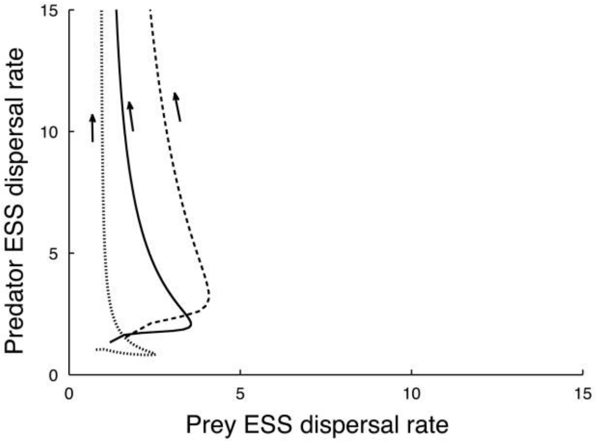

**Figure 4:** Coevolution of predator and prey dispersal. The joint evolutionarily stable strategy (ESS) dispersal strategies, $(\hat{\gamma}_x, \hat{\gamma}_y)$, for increasing top-down predator effects. Example curves shown for different coevolving predator-prey systems. Arrows give direction of increasing predator-induced extinction rates. Note how most evolutionary change occurs along the predator's trait gradient. Parameter values: hashed line, $z_x = 0.4$; solid line, $z_x = 0.8$; dashed line, $z_x = 1.2$. All other parameter values: $r = 10$, $K = 200$, $q = 0.45$, $m = 0.3$, $\alpha = 0.001$, $\beta = 0.01$, $z_y = 0.025$, $(e_R)_{\min} = 0.01$, $(e_P)_{\min} = 0.001$, and range of $a$ values used: 0.05 to 20.

using single-species models that adhered to classic metapopulation assumptions; specifically, they assumed that local within-patch population dynamics were relatively fast compared to metapopulation scale processes such as colonization and extinction and that local populations were saturated; that is, they were either present at carrying capacity or absent from a given patch altogether. By relaxing the assumption of site saturation, Olivieri et al. (1995), using a succession model, showed how decreased fecundity could give rise to lower ESS dispersal rates. The implications of this result were investigated by Ronce et al. (2000), who studied a model without site saturation and where carrying capacity was not achieved instantaneously within sites. They demonstrated a nonmonotonic response of ESS dispersal to increasing patch extinction rates, where at small extinction rates, ESS dispersal increased with extinction (as expected) but then declined with extinction when rates were relatively high. This result arose because at high extinction rates local sites were not likely to be saturated, and as a result, individuals experienced less competitive pressure within sites and thus less of a fitness advantage to dispersing.

The counterintuitive, nonmonotonic response of prey ESS dispersal rates observed in this study arose from a very different mechanism: the effects of species interactions playing out at two different spatial scales. In this study we kept to classic metapopulation assumptions regarding local site saturation and local dynamics occurring much more rapidly than regional-scale processes. Because of these assumptions we do not track local population dynamics and do not account for competition between individual conspecifics. The result is that in our model individuals are not driven to disperse to avoid competition, and increasing dispersal rates do not alleviate the local competitive pressure on philopatric individuals as would be expected in natural systems (Olivieri et al. 1995; Ronce et al. 2000). Our study was focused on how dispersal evolves as a response to demographic stochasticity in the form of local extinctions. However, unlike in previous studies, our model involved a metacommunity with interacting predator-prey species. Here extinction arose from both patch extinctions, as in previous models, but also as a result of strong interspecific interactions between a specialist predator and prey. These strong extinction-prone interactions have two different effects at local and metacommunity scales. Locally, strong interactions lead to symmetrical effects on both predator and prey in the form of increased local extinction frequencies, while at the metacommunity scale, increasing interaction strength affects the degree to which prey are associated with their predators in local patches and, as result, have a strongly asymmetric effect on patch occupancies of both species. This gives rise to antagonistic effects on the evolution of dispersal. When top-down extinction rates $\mu$ are low, increasing $\mu$ has a negative metacommunity-scale effect on prey occupancy due to high rates of local extinctions arising from a strong association between prey and predators. This gives a fitness advantage to dispersing more rapidly. On the other hand, when top-down extinction rates are relatively high, far fewer prey patches are occupied by predators, and increasing $\mu$ rapidly decreases this association even further, driving the predator out of the metacommunity while allowing the prey to recover or increase in patch occupancy—all of which decreases the fitness advantage arising from dispersal in the face of strong extinction-prone interactions.

The basic modeling framework assumed here was motivated by the widespread assumption that dispersal and some form of metapopulation spatial structure are critical in allowing the persistence of potentially unstable or extinction-prone predator-prey interactions. We would argue that this is a justifiable assumption as the possible role of dispersal in maintaining populations of interacting predators and prey at large spatial scales in the face of high-frequency extinctions has been repeatedly demonstrated in laboratory and greenhouse experiments going back to the work of Huffaker (1958) and Pimental et al. (1963; although see Taylor 1990) and more recently Nachman (1991), Holyoak and Lawler (1996*a*), and Ellner et al. (2001). However, in field studies, the evidence for the role of dispersal and metacommunity dynamics appears to be lacking, due to the difficulty of detecting local extinctions in the field and in distinguishing between movement or foraging within populations on one hand and true colonization between patches on the other (for a review see Taylor 1990, 1991). Nevertheless, some field evidence is strongly suggestive of a critical role for dispersal in allowing prey refuge from extinction-prone interactions with predators, as is illustrated in the case of pea aphids producing winged dispersal morphs in response to the presence of predator ladybugs (Sloggett and Weisser 2002). Intuitively, one would expect then that an increase in the destabilizing nature of the interaction, and thus the likelihood of extinction, would select for higher dispersal rates. Our analysis demonstrates that this may not be so, as one needs to also consider also how species interactions play out larger spatial scales.

The model studied here also assumed a trade-off between dispersal ability and local fitness. An important issue would be whether such a trade-off corresponds to the way life-history traits are actually structured in natural predator-prey systems. Although the trade-off in our model is not physiologically based but instead simply arises as a direct demographic consequence of increased dispersal leading to lower local competitive ability within patches, the results obtained here should still be relevant to cases where increased dispersal trades off with local fitness due to physiological constraints. Strong evidence exists, particularly among wing-dimorphic insects, that dispersal ability does, in fact, trade off with local fitness and competitive ability. Roff (1986) in an intraspecific comparison of 22 wing-polymorphic insect species found that brachypterous (flightless) morphs had higher fecundity and earlier reproduction than macropterous (migratory) morphs (see also Roff 1984; Aukema 1991). Furthermore, evidence that extinction frequency could select for different dispersal abilities was demonstrated in a study of dimorphic planthopper species where selection was found to have favored high levels of dispersal (measured as percent macroptery) in species occupying temporary habitats, while insects in persistent habitats showed a significant decline in macroptery (Denno et al. 1991; Denno 1994).

An important model simplification made in our study involved assuming that once a mixed-strategy patch was established through reinvasion, no further invasions by resident colonizers would occur until one of the strategies was competitively displaced from the patch (see eq. [A11a], [A11b] in the appendix). This model simplification, made in order to facilitate the calculation of the ESS, also required, in order to ensure consistency in the fitness equation, that we also restrict the total number of colonizers that can arrive during any local subpopulation's lifetime to a maximum of two (including the founder colonizer; see "Fitness and Selection Gradient of a Rare Mutant Prey Invasive" in app. A). We found that relaxing this latter restriction limiting reinvasion events to two during a subpopulation's lifetime does not appear to have an appreciable qualitative effect on the results observed here.

As for us not accounting for the effect of subsequent invasions of resident colonizers into a mixed-strategy patch, we believe our model simplification will not have a significant qualitative effect on the results obtained here but will likely lead to a simple quantitative shift in the response curves shown in figure 1. This is because allowing a marginal increase in the number of residents colonizers that can arrive into a mixed-strategy patch will simply speed up the rate at which the mutant is being competitively displaced from the mixed patch (and thus decrease its overall reproductive output), which, in the case of the prey, will cause the costs of dispersing more rapidly to offset the fitness benefits sooner, leading to an earlier downturn in ESS dispersal rates, particularly as the resident prey's metacommunity abundance begins to recover; thus, a similar nonmonotonic ESS response to increasing extinction rates should obtain. The slight increase in the cost of dispersal would be expected to shift the predator's ESS responses to an even lesser degree, since increasing top-down extinction rates rapidly lead to low metacommunity abundances for the resident predator, making invasions of resident colonizers into mixed-strategy patches even more infrequent.

There are a couple of other model simplifications that were necessitated by the modeling approach assumed here that deserve to be noted. For one, our investigation of dispersal evolution was based on the use of a mean-field model that assumed well-mixed dynamics and that did not account for how the scale of dispersal or the spatial structure of habitat patches would affect selective pressures on dispersal. Since many interacting predator and prey species migrate at different spatial scales, spatially explicit simulations would provide a useful extension of this study, allowing us to explore the effects of realistic, spatially correlated migration on the evolution of dispersal. Another important model simplification was the fact that we restricted ourselves to a constant per capita, or density-independent, dispersal. Dispersal can often be conditional on the presence of a predator (e.g., Sloggett and Weisser 2002), and it can be intra- or interspecific density dependent (Hauzy et al. 2007; Hauzy et al. 2010), depending on the densities of either the prey or predator.

Regardless of these model simplifications, the study presented here highlights the important fact that the source of patch extinction can profoundly affect the evolution of dispersal. Previous investigations of dispersal evolution as a response to patch extinctions underappreciated an important point: extinctions often arise because of the way a species interacts with its environment, including the way it interacts with other species. Interspecific interactions, in particular trophic interactions, can add an additional layer of complexity, whereby the interaction itself can give rise to emergent processes that can feed back and change the context in which selection is operating. Here we showed how increasing predator-induced extinction rates, capable of driving both predator and prey extinct locally, could also give rise to dynamics at the metacommunity scale that negated the selective pressure that extinction could have on the prey species. Acknowledging and incorporating such spatially emergent complexity into our theoretical and empirical investigations is a vital step in developing a research program that can more properly account for the evolution of life-history processes structuring natural communities.

## Acknowledgments

We would like to thank C. de Mazancourt and F. Guichard for useful comments. A. Gonzalez and M. Loreau were supported by the Canada Research Chair program, Natural Sciences and Engineering Research Council Discovery grants, and an FQRNT (Fonds québécois de la recherche sur la nature et les technologies) team grant.

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Associate Editor: Vlastimil Křivan
Editor: Mark A. McPeek

Pronghorn antelope in October, immediately after shedding the horns. "When the horn drops off, the horn-core is found covered with a thick skin, and coated with hair, the same as the face of the animal, with a small portion of the tip having already begun to harden; this acting as a wedge, forces the horn off." From "The Prong-Horn Antelope," by W. J. Hays (*American Naturalist*, 1868, 2:131–133).

# Appendix from P. Pillai et al., “Evolution of Dispersal in a Predator-Prey Metacommunity”

(Am. Nat., vol. 179, no. 2, p. 204)

## Evolutionary Dynamics of a Prey and Predator

In this appendix we demonstrate how to calculate the evolutionarily stable strategy (ESS) dispersal rates for both the prey and the predator based on the predator-prey metacommunity model outlined in “The Model” section of the main article.

### Competitive Dynamics between Resident and Invasive Prey Strategies within Local Mixed-Strategy Patches

Our measure of metacommunity fitness requires us to follow the average number of dispersers that will be produced by a local population founded by a single focal mutant invasive with a dispersal rate $\gamma^*$ after it invades a resident metacommunity with a wild-type dispersal strategy of $\gamma^{\circ}$ that is at equilibrium. Since the number of dispersers produced is the product of the local population size of the invasive prey and the invasive strategy dispersal rate, we need a means to calculate the number of invasive individuals in a local prey population. For an invasive population in a patch without any resident individuals, this is simply calculated using either equation (4a) or (4b) in the main article, depending on whether a predator is absent or present. However, the focal mutant invasive may end up settling in a resident-occupied patch, or alternatively, an empty patch that may, over time, become reinvaded by a resident strategy colonizer. For such mixed-strategy patches containing both resident and invasive strategies, determining the number of local invasive individuals becomes much more complicated. To make such a determination we will need to account for possible competitive interactions between an invasive strategy and a resident strategy in a local habitat patch. We will assume here that a mutant invasive strategy differs only from the wild-type resident strategy in its dispersal rate $\gamma_x$. The method described below is based on and follows the formalism of Jansen and Vitalis (2007).

*Local Prey Dynamics due to Competition between Resident and Mutant Strains*

Competitive Dynamics between a Resident and Invasive Prey Strategy within a Patch in the Presence of a Predator

We define a resident strategy’s dispersal rate and its average local abundance in the presence of a predator by $\gamma_x^{o}$ and $x_{\mathrm{P}}^{o}$, respectively, and a mutant invasive’s dispersal strategy and abundance in the presence of a predator by $\gamma_x^{*}$ and $x_{\mathrm{P}}^{*}$. With both resident and invasive strategies occupying the same habitat patch the total size of a local prey population with a predator present is represented by the sum $s_{x_{\mathrm{P}}} = x_{\mathrm{P}}^{o} + x_{\mathrm{P}}^{*}$. In a mixed population with both prey strategies we have the following dynamic equations:

$$\dot{x}^{\circ}{}_{\mathrm{P}} = rx^{\circ}{}_{\mathrm{P}}\left(1 - \frac{x^{\circ}{}_{\mathrm{P}} + x^{*}_{\mathrm{P}}}{K}\right) - \gamma^{\circ}_{x}x^{\circ}{}_{\mathrm{P}} - ax^{\circ}{}_{\mathrm{P}}y \text{ (resident),}$$

$$\dot{x}^{*}_{\mathrm{P}} = rx^{*}_{\mathrm{P}}\left(1 - \frac{x^{\circ}{}_{\mathrm{P}} + x^{*}_{\mathrm{P}}}{K}\right) - \gamma^{*}_{x}x^{*}_{\mathrm{P}} - ax^{*}_{\mathrm{P}}y \text{ (invasive).}$$

Since the predator cannot distinguish between different prey strains, it responds to total prey size, and its dynamics are given by

$$\dot{y} = aq(x^{\circ}{}_{\mathrm{P}} + x^{*}_{\mathrm{P}})y - \gamma_y y - my \text{ (predator).} \tag{A1}$$

If the invasive strategy has a higher dispersal rate ($\gamma^{*}_{x} > \gamma^{\circ}_{x}$), we would expect the number of invasive strategy individuals competing with residents in a mixed-strategy patch to eventually decay to 0 over time. If we let $f$ be the fraction of the total prey population that is made up of the mutant strategy, that is, $f = x^{*}_{\mathrm{P}}/s_{x_{\mathrm{P}}}$, then the total prey population dynamic equation becomes

$$\begin{aligned}\dot{s}_{x_{\mathrm{P}}} &= rs_{x_{\mathrm{P}}}\left(1 - \frac{s_{x_{\mathrm{P}}}}{K}\right) - \gamma^{\circ}_{x}x^{\circ}{}_{\mathrm{P}} - \gamma^{*}_{x}x^{*}_{\mathrm{P}} - ays_{x_{\mathrm{P}}}\\ &= s_{x_{\mathrm{P}}}\left[r\left(1 - \frac{s_{x_{\mathrm{P}}}}{K}\right) - \gamma^{\circ}_{x}(1-f) - \gamma^{*}_{x}f - ay\right].\end{aligned} \tag{A2}$$

Using the above expression we can derive the rate of change in the frequency of mutants in the population $\dot{f}$:

$$\begin{aligned}\dot{f} &= \frac{d}{dt}\left(\frac{x^{*}_{\mathrm{P}}}{s_{x_P}}\right),\\ &= \frac{\dot{x}^{*}_{\mathrm{P}}s_{x_{\mathrm{P}}} - x^{*}_{\mathrm{P}}\dot{s}_{x_{\mathrm{P}}}}{s^{2}_{x_{\mathrm{P}}}},\\ &= f\left[r\left(1 - \frac{s_{x_{\mathrm{P}}}}{K}\right) - \gamma^{*}_{x} - ay\right] - f\left[r\left(1 - \frac{s_{x_{\mathrm{P}}}}{K}\right) - \gamma^{\circ}_{x}(1-f) - \gamma^{*}_{x}f - ay\right],\end{aligned}$$

which simplifies down to

$$\dot{f} = (\gamma^{\circ}_{x} - \gamma^{*}_{x})f(1-f). \tag{A3}$$

A closed form solution of equation (A3) can be easily obtained to give us an expression for the fraction of mutants in the population as a function of time:

$$f(t) = \frac{\phi}{\phi + (1-\phi)\exp\left[(\gamma^{*}_{x} - \gamma^{\circ}_{x})t\right]} \tag{A4}$$

Here we used Jansen and Vitalis's (2007) formulation where the initial fraction of the invasive within the local population at time $t = 0$ is represented by $\phi$ (i.e., $\phi = f(0)$). As can be seen from equation (A3), if the mutant invasive has a higher dispersal strategy than the resident, then the fraction of mutants in the local population will decay to 0, or alternatively, the resident will decay to 0 if the invasive dispersal strategy is less than the resident dispersal strategy.

Using expressions (A2) and (A4) we can track the deterministic outcome of competitive interactions in a mixed-strategy patch. Mixed-strategy patches arise when a local patch composed solely of either resident-strategy or invasive-strategy individuals subsequently becomes reinvaded by an individual colonizer with the alternate strategy. In order to distinguish between these two scenarios—that is, when a resident patch is reinvaded by an individual mutant and when an invasive mutant patch is reinvaded by an individual resident—we will use a subscript in the symbol for the initial invasive fraction $\phi$ to indicate the original dispersal strategy of the local prey patch and whether a predator was present or absent before the subsequent reinvasion by the alternate strategy colonizer. For example, the initial fraction of invasive mutants in a resident patch with a predator at the time of reinvasion by a single mutant colonizer is given by $\phi_{\tilde{x}^{\circ}{}_{\mathrm{P}}}$, while the initial fraction of invasives in a invasive patch, with a predator, at the time of reinvasion by a single resident colonizer is $\phi_{\tilde{x}^{*}_{\mathrm{P}}}$. The initial invasive fraction in an invasive patch with a predator at the time of colonization by a single resident individual, $\phi_{\tilde{x}^{*}_{\mathrm{P}}}$, can be calculated by

$$\phi_{\tilde{x}^{*}_{\mathrm{P}}} = \frac{\tilde{x}^{*}_{\mathrm{P}}}{\tilde{x}^{*}_{\mathrm{P}} + 1}.$$

Similarly, the initial invasive fraction when a resident patch with a predator is invaded by a single mutant invasive is $\phi_{\tilde{x}^{\circ}_{\mathrm{P}}} = 1/\tilde{x}^{\circ}_{\mathrm{P}} + 1$. Similar equations can be written for when no predator is present in a resident patch at the time of recolonization, $\phi_{\tilde{x}^{\circ}_0} = \tilde{x}^{*}_0/\tilde{x}^{*}_0 + 1$, and for when no predator is present in an invasive patch at the time of recolonization, $\phi_{\tilde{x}^{\circ}_0} = 1/\tilde{x}^{\circ}_0 + 1$. Since we can calculate the initial state ($\phi = f(0)$) of a patch at the time of reinvasion, we can now determine the fraction $f(t)$ of the local prey population that are invasive individuals at any subsequent time $t$ in a local mixed-strategy population. When using $f(t)$ to represent the fraction of mutant invasives in a patch at time $t$, we will also use a superscript to indicate what the initial invasive fraction $\phi$ was. Thus, we can represent the fraction of mutant invasives at time $t$, given an initial mutant invasive fraction of $\phi$, by $f^{\phi}(t)$.

We make assumptions typical of most metapopulation models, specifically that local within-patch dynamics occur at a much faster rate than colonization-extinction dynamics between patches. When equation (A1) is set to 0, we can derive a quasi steady state expression for the total prey abundance in a patch at each point in time $t$, $\tilde{s}_{x\mathrm{P}}$. Note that because of the top-down effect of the predator, total prey number $\tilde{s}_{x\mathrm{P}}$ stays constant at a value of $\tilde{x}_P$ and is not dependent on the fraction of residents or invasives in the population. Assuming the total prey and predator populations reaches a quasi steady state when $\dot{s}_{x\mathrm{P}} = 0$ and $\dot{y} = 0$, from equation (A1) we get

$$\tilde{s}_{x\mathrm{P}}(t) = \frac{m + \gamma_y}{aq} = \tilde{x}_{\mathrm{P}}. \tag{A5}$$

## Competitive Dynamics between Resident and Invasive Prey Strategies within a Patch in the Absence of a Predator

The case of a local prey population in patches without a predator is similar to the case studied by Jansen and Vitalis (2007) for a single-species metapopulation. Following the same method as above for a predator-occupied patch, we can derive the population sizes of the resident and invasive strategies, the total population size of both strategies, and the invasive fraction of the total population, respectively, as

$$\dot{x}^{\circ}_0 = r x^{\circ}_0\left(1 - \frac{x^{\circ}_0 + x^{*}_0}{K}\right) - \gamma^{\circ}_x x^{\circ}_0, \tag{A6a}$$

$$\dot{x}^{*}_0 = r x^{*}_0\left(1 - \frac{x^{\circ}_0 + x^{*}_0}{K}\right) - \gamma^{*}_x x^{*}_0, \tag{A6b}$$

$$\begin{aligned} \dot{s}_{x0} &= r s_{x0}\left(1 - \frac{s_{x0}}{K}\right) - \gamma^{\circ}_x x^{\circ}_0 - \gamma^{*}_x x^{*}_0, \\ &= s_{x0}\left[r\left(1 - \frac{s_{x0}}{K}\right) - \gamma^{\circ}_x (1-f) - \gamma^{*}_x f\right], \end{aligned} \tag{A7}$$

$$f^{\phi_{\tilde{x}_0}}(t) = \frac{\phi}{\phi + (1-\phi)\exp[(\gamma^{*}_x - \gamma^{\circ}_x)t]}. \tag{A8}$$

Again, when $\dot{s}_{x_0} = 0$, $\tilde{s}_{x_0}$ quickly reaches a quasi steady state at time $t$, which can be derived from equation (A7):

$$\begin{aligned} \tilde{s}_{x_0}(t) &= K\left\{1 - \frac{\gamma^{\circ}_x[1 - f(t)]}{r} - \frac{\gamma^{*}_x f(t)}{r}\right\}, \\ &= \tilde{x}^{\circ}_0 + f(t)(\tilde{x}^{*}_0 - \tilde{x}^{\circ}_0). \end{aligned} \tag{A9}$$

Note how in a prey-only patch the total population size of the prey will increase over time as the resident strategy slowly displaces the invasive; as a result, $\tilde{s}_{x_0}(t)$ will depend on the proportions of the invasive and resident strategies in the local population.

## Local Population Size of the Invasive Prey Population in a Mixed-Strategy Patch

If $\tilde{s}_{x_\bullet}(t)$ is the total local population size of both prey strategies at time $t$ (here the solid dot represents $P$ or 0, depending on whether the predator is present or absent at time $t$), and if $f^{\phi_{\tilde{x}_0}}(t)$ and $f^{\phi_{\tilde{x}_P}}(t)$ give the fraction of invasives in local populations for both the cases where the predator was initially absent and present at the time of invasion, then the products $\tilde{s}_{x_\bullet}(t) \times f^{\phi_{\tilde{x}_0}}(t)$ and $\tilde{s}_{x_\bullet}(t) \times f^{\phi_{\tilde{x}_P}}(t)$ respectively give the number of mutant prey individuals in a given prey patch at any time $t$ for both the case where the predator was initially absent at the time of invasion and when it was initially present. In other words, we can count the total number of invasive prey individuals in a mixed-strategy population at any given moment before it is driven from the patch.

## Various States of a Prey-Occupied Patch

The local population sizes of invasive populations within patches will be affected by the presence or absence of predators, and as a result, the colonizer production of such populations will also be affected. In order to determine the number of colonizers produced during the lifetime of an invasive patch we will also need to know the time an invasive population will have spent with a predator and without a predator before becoming extinct.

### *Total Time Mutant Patch Spends in Various States before Colonization by a Resident*

A local mutant invasive disperser after settling in an empty patch will give rise to a local invasive prey population. Before the local invasive population becomes extinct or is reinvaded by a resident colonizer, it will produce a certain number of migrant dispersers. The number of dispersers produced depends on the time the mutant population spends in one of two states: a prey-only patch and a predator-prey patch. If we are interested in the total number of dispersers such a prey patch will produce before being colonized by a resident strategy migrant we will need to determine the total time a local prey population will be in each state. We can use figure A1 to see the various states and transitions of a mutant invasive population. Here $X_0$ represents the number of invasive mutant patches in a prey-only state, and $X_P$ represents the number of invasive patches in a predator-prey state.

In order to calculate the total time spent in both states we will follow the fate of a single prey patch founded by our focal invasive prey landing on an empty patch; the prey patch will move between both predator-prey and prey-only states, and will be lost A local mutant invasive patch will become extinct with frequency $e^*_{R_0}$ in a prey-only patch, and $e^*_{R_P}$ in a predator-prey patch. Alternatively it can be reinvaded by a wild-type resident strategy with frequency $c_{R_P}\tilde{R}_P + c_{R_0}\tilde{R}_0$ (see "The Predator-Prey Metacommunity Model" in the main text). This is essentially the weighted mean number of prey colonizers produced by the resident prey metapopulation, and it will be represented henceforth by $\langle c_R\tilde{R}\rangle$ (fig. A1*A*). Before either of these two events occur, the invasive prey population will move back and forth between a prey-only and predator-prey state with frequency$e_P$ and $c_P\tilde{P}$, respectively. The state diagram in figure A1*A* can be represented by the following differential equation system:

$$\dot{X}_0 = -(e^*_{R_0} + c_P\tilde{P} + \langle c_R R\rangle)X_0 + e_P X_P,$$

$$\dot{X}_P = (c_P\tilde{P})X_0 - (e_P + e^*_{R_P} + \langle c_R R\rangle)X_P.$$

Alternatively, it can be represented by a single linear second-order differential equation:

$$0 = X_0'' - (A + D)X_0' + (AD - BC)X_0,$$

where $A = -(e^*_{R_0} + c_P\tilde{P} + \langle c_R R\rangle)$, $C = c_P\tilde{P}$, $B = e_P$, and $D = -(e_P + e^*_{R_P} + \langle c_R R\rangle)$. The solution to the ordinary differential equation (ODE) system is

$$X_0(t) = \frac{1}{(\lambda_1 - \lambda_2)}[(A - \lambda_2)e^{\lambda_1 t} - (A - \lambda_1)e^{\lambda_2 t}]$$

$$X_P(t) = \left(\frac{C}{\lambda_1 - \lambda_2}\right)(e^{\lambda_1 t} - e^{\lambda_2 t}).$$

The eigenvalues of the solution to this system are given by $\lambda_1 = (1/2)(A + D) + (1/2)[(A - D)^2 + 4BC]^{1/2}$, and $\lambda_2 = (1/2)(A + D) - (1/2)[(A - D)^2 + 4BC]^{1/2}$.

*Total time spent in two different states*. Since we are following the fate of a single average patch, summing or integrating the frequencies of the patch being in a given state from the time the individual patch is established

($t = 0$) to infinity gives the total time it is in a given state. We can calculate the total time spent without a predator, $T_{X_0}$, and with a predator, $T_{X_\mathrm{P}}$, as $T_{X_0} = \int_0^\infty X_0(t)dt$ and $T_{X_\mathrm{P}} = \int_0^\infty X_\mathrm{P}(t)dt$. Since it can be demonstrated that for all eigenvalues, $\lambda_i < 0$ for $i \in \{1, 2\}$, we can express the times in the two different states explicitly as

$$T_{X_0} = \int_0^\infty X_0(t)dt = \frac{A - \lambda_1 - \lambda_2}{\lambda_1 \lambda_2}, \tag{A10a}$$

$$T_{X_\mathrm{P}} = \int_0^\infty X_\mathrm{P}(t)dt = \frac{C}{\lambda_1 \lambda_2}. \tag{A10b}$$

### *Total Time Mutant Patch Spends in Various States after Colonization by Resident*

If the invasive prey patch has not already become extinct, it will, on being recolonized by a resident strategy migrant, be driven to competitive exclusion over a period of time. However, the invasive strategy can still produce a diminishing number of migrant dispersers as its population size decays to 0 that will still contribute to its overall measure of fitness. To determine how many dispersers the invasive strategy will produce on its way to extinction we need to determine the frequency at which the invasive strategy is in one of its two states (fig. A1*B*).

The state transition diagram in figure A1*B* is identical to figure A1*A*, except for the fact that the invasive-occupied patch cannot be recolonized again by a resident. This means that we have restricted the number of recolonizations after an initial colonization to one, or in other words, there is a maximum of two colonization events in total during the lifetime of a local population before patch extinction. This is a justified model simplification since we adhere to the classic metapopulation assumption that recurrent colonization is rare enough as to not affect local dynamics. The competitive exclusion of the invasive strategy within a local patch should be fast enough relative to the colonization dynamics at the regional or metacommunity scale that we can reasonably ignore further resident reinvasions. Jansen and Vitalis (2007) used this approach under the same assumptions and further demonstrated that more than two invasions did not qualitatively affect the results for a similar metapopulation model.

In figure A1*B* we now represent the frequency at which the local invasive population is with a predator as $\chi_\mathrm{P}$ and without a predator as $\chi_0$. The differential equation representing this transition diagram is similar to the one above for figure A1*A*, such that the ODE becomes

$$\dot{\chi}_0 = -(e_{R_0} + c_\mathrm{P} P)\chi_0 + (e_\mathrm{P})\chi_\mathrm{P}, \tag{A11a}$$

$$\dot{\chi}_\mathrm{P} = (c_\mathrm{P} P)\chi_0 - (e_\mathrm{P} + e_{R_\mathrm{P}})\chi_\mathrm{P}. \tag{A11b}$$

Note that $e_{R_0}$ and $e_{R_\mathrm{P}}$ in expressions (A11a) and (A11b) are now based on the total population size of the prey, as given by $s_{x_0}$ and $s_{x_\mathrm{P}}$, and not $x_0$ or $x_\mathrm{P}$, as per equation (5).

Since at the time of recolonization of the invasive patch by a resident strategy migrant the invasive strategy population can be found either with or without a predator, there are now two initial conditions with which to solve the above differential equation. We will represent the solution to this differential equation for both the prey-only and predator-prey patches when the initial condition involves no predator at the time of recolonization as $\chi_0(t)$ and $\chi_\mathrm{P}(t)$, respectively, and the solution when a predator is initially present at the time of recolonization will be indicated with a check mark: $\check{\chi}_0(t)$ and $\check{\chi}_\mathrm{P}(t)$.

#### Initial Condition: No Predator Present

If we represent the terms in equations (A11a), (A11b) as $A_2 = -(e^*_{R_0} + c_{\mathrm{P}}\tilde{P})$, $C = c_{\mathrm{P}}\tilde{P}$, $B = e_{\mathrm{P}}$, and $D_2 = -(e_{\mathrm{P}} + e^*_{R_{\mathrm{P}}})$, then the solution to the system when no predator is present at $t = 0$ is

$$\chi_0(t) = \frac{1}{(\nu_1 - \nu_2)}[(A_2 - \nu_2)e^{\upsilon_1 t} - (A_2 - \nu_1)e^{\upsilon_2 t}], \tag{A12a}$$

$$\chi_{\mathrm{P}}(t) = \left(\frac{C}{\nu_1 - \nu_2}\right)(e^{\upsilon_1 t} - e^{\upsilon_2 t}), \tag{A12b}$$

with the eigenvalues defined by $\nu_1 = (1/2)(A_2 + D_2) + (1/2)[(A_2 - D_2)^2 + 4BC]^{1/2}$ and $\nu_2 = (1/2)(A_2 + D_2) - (1/2)[(A_2 - D_2)^2 + 4BC]^{1/2}$.

Initial Condition: Predator Is Present

The solution for the ODE system given by equations (A12a) and (A12b) for when the predator is present at $t = 0$ is

$$\breve{\chi}_0(t) = \frac{B}{(\nu_1 - \nu_2)}(e^{\nu_1 t} - e^{\nu_2 t}), \tag{A13a}$$

$$\breve{\chi}_P(t) = \left(\frac{1}{\nu_1 - \nu_2}\right)[(D - \nu_2)e^{\nu_1 t} - (D - \nu_1)e^{\nu_2 t}]. \tag{A13b}$$

The eigenvalues $\nu_1$ and $\nu_2$ are defined as above.

## Fitness and Selection Gradient of a Rare Mutant Prey Invasive

We will use an adaptive dynamics approach based on continuous evolutionary game theory (Brown and Vincent 1987; Metz et al. 1992; Geritz et al. 1998; Doebeli and Dieckmann 2000) in order to study the evolution of both prey and predator dispersal along a continuous trait gradient. An adaptive dynamics approach requires that we can determine the conditions under which a rare mutant can invade a system in which a wild-type resident is at equilibrium. Invasibility becomes possible when the fitness of the mutant invasive $W$ is greater than 1. Measuring fitness in a metacommunity requires that we follow the fate of a focal mutant individual with dispersal rate $\gamma^*_x$ invading a metacommunity where the wild-type resident, with dispersal rate $\gamma^{\circ}_x$, is at equilibrium patch occupancy, and then calculating the average number of dispersers that will be produced by the local population founded by that single invasive colonizer before the population goes extinct. This approach corresponds to Metz and Gyllenberg's (2001) metric$R_{\mathrm{m}}$ for measuring fitness in a metapopulation and is the approach taken by Jansen and Vitalis (2007).

A mutant invasive entering a metacommunity can fall on one of three patch types: an empty patch, a resident prey-only patch, or a resident prey patch with a predator. We will consider the total migrant colonizer output resulting from all of these outcomes.

*Empty patch*. The chance of the invasive colonizer landing in an empty patch is $(1 - \tilde{R})$, and the frequency of it successfully establishing itself is $\alpha$, which gives the total frequency of an invasive colonizer successfully establishing itself in an empty patch as $\alpha(1 - \tilde{R})$. Once established this invasive migrant, with a dispersal rate $\gamma^*_x$, will instantly reach its equilibrium population size $\tilde{x}^*_0$. Before becoming or being recolonized by a resident migrant it will continuously produce dispersers while in one of two states: with a predator or without. Knowing the time spent in each of these two states, $T_{X_0}$ and $T_{X_{\mathrm{P}}}$ (see eqq. [A10], [A10b]), we can calculate the average total number of dispersers produced before extinction or recolonization as $\gamma^*_x x^*_0 T_{X_0} + \gamma^*_x x^*_{\mathrm{P}} T_{X_{\mathrm{P}}}$.

Recolonization by a resident while the local invasive prey population is without a predator occurs with a probability of $\langle c_R R\rangle T_{X_0}$. When this happens, the local invasive prey population will decay to extinction while still producing diminishing numbers of dispersers. We will let $U$ represent the average total disperser production after a local invasive prey-only population is recolonized by a resident migrant. At some time $t$ after recolonization by a resident, the number of dispersers produced will depend on the probability of the patch being without a predator $\chi_0(t)$ at time $t$, multiplied by the local invasive population size $\tilde{s}_{x_0}(t)f^{\phi_{\tilde{x}^*_0}}(t)$ and the probability of being with a predator $\chi_{\mathrm{P}}(t)$ at time $t$, multiplied by the local invasive population size $\tilde{s}_{x_{\mathrm{P}}}(t)f^{\phi_{\tilde{x}_0^*}}(t)$. The total number of dispersers produced, $U$, by an invasive prey population after colonization by a resident prey migrant is

$$U = \gamma_x^* \int_0^\infty \tilde{s}_{x_0}(t)f^{\phi_{\tilde{x}_0^*}}(t)\chi_0(t)dt + \gamma_x^* \int_0^\infty \tilde{s}_{x_{\mathrm{P}}}(t)f^{\phi_{\tilde{x}_0^*}}(t)\chi_{\mathrm{P}}(t)dt. \tag{A14}$$

Similarly, if recolonization by a resident occurs in an invasive prey patch containing a predator, with frequency $\langle c_R R\rangle T_{X_{\mathrm{P}}}$, then the average total disperser production will be $V$. As before, the number of dispersers produced at time $t$ will depend on the product of the local invasive population size and the probability of the patch being without a predator at time $t$, $\tilde{s}_{x_0}(t)f^{\phi_{\tilde{x}_{\mathrm{P}}^*}}(t)\breve{\chi}_0(t)$, added to the product of the local invasive population size and the probability of the patch being with a predator at time $t$, $\tilde{s}_{x_{\mathrm{P}}}(t)f^{\phi_{\tilde{x}_{\mathrm{P}}^*}}(t)\breve{\chi}_{\mathrm{P}}(t)$. Thus, the total disperser production, $V$ becomes

$$V = \gamma_x^* \int_0^\infty \tilde{s}_{x_0}(t)f^{\phi_{\tilde{x}_{\mathrm{P}}^*}}(t)\breve{\chi}_0(t)dt + \gamma_x^* \int_0^\infty \tilde{s}_{x_{\mathrm{P}}}(t)f^{\phi_{\tilde{x}_{\mathrm{P}}^*}}(t)\breve{\chi}_{\mathrm{P}}(t)dt. \tag{A15}$$

The total number of dispersers produced by an empty site that has been recolonized by a resident thus becomes $\langle c_R R\rangle T_{X_0}U + \langle c_R R\rangle T_{X_{\mathrm{P}}}V$.

*Resident prey-only patch*. The proportion of prey-only resident patches is $\tilde{R}_0$. However, this proportion cannot represent the probability of the focal invasive migrant landing on a prey-only occupied patch. Recall that we assumed that once a mixed-strategy patch has been established, there will be no further resident invasions. This implies that a local invasive prey population will have received, at most, a total of two colonizers before its local extinction. In order to ensure symmetry between the conditions experienced by the invasive mutant and wild-type resident strategies and consistency in the fitness equation, we have restricted the maximum number of recolonizations in all local prey populations to two. As a result, we can only consider the focal migrant landing on a prey-occupied patch that has only yet received one colonizer.

If we define $i\tilde{R}_0$ as the proportion of resident prey-only patches that have received $i$ colonizers, then total proportion of prey-only patches can be expressed as $\tilde{R}_0 = \sum_{i=1}^{ni} \tilde{R}_0$, where $n$ is the maximum possible number of recolonizations in a patch (Jansen and Vitalis 2007). Since the focal invasive can only land on a prey-only patches that has received one colonizer, the frequency of the focal invasive migrant colonizing a prey-only patch is actually $\alpha(1\tilde{R}_0)$ (see eq. [A20a]) below for the expression for $1\tilde{R}_0$). If $Q$ is the total number of dispersers produced after the focal invasive lands on a resident prey-only patch, then

$$Q = \gamma_x^* \int_0^\infty \tilde{s}_{x_0}(t)f^{\phi_{\tilde{x}^{\circ}_0}}(t)\chi_0(t)dt + \gamma_x^* \int_0^\infty \tilde{s}_{x_P}(t)f^{\phi_{\tilde{x}^{\circ}_0}}(t)\chi_{\mathrm{P}}(t)dt. \tag{A16}$$

*Resident predator-prey patch*. The frequency with which the focal migrant invasive will land in a resident prey patch containing a predator is $\alpha(1\tilde{R}_{\mathrm{P}})$ (see eq. [A20b] below for the expression for $1\tilde{R}_{\mathrm{P}}$). The total number of dispersers produced from such a mixed-strategy patch, $Z$, will be

$$Z = \gamma_x^* \int_0^\infty \tilde{s}_{x_0}(t)f^{\phi_{\tilde{x}^{\circ}_{\mathrm{P}}}}(t)\breve{\chi}_0(t)dt + \gamma_x^* \int_0^\infty \tilde{s}_{x_{\mathrm{P}}}(t)f^{\phi_{\tilde{x}^{\circ}_{\mathrm{P}}}}(t)\breve{\chi}_{\mathrm{P}}(t)dt. \tag{A17}$$

The total fitness of a single mutant prey invasive with dispersal strategy $\gamma_x^*$ invading a predator-prey metacommunity at equilibrium, where the resident prey dispersal strategy is $\mathring{\gamma}_x$, is represented by $W_x(\gamma_x^*, \mathring{\gamma}_x)$, which gives the sum of all the dispersers produced by the different patch types before extinction or competitive exclusion by a resident as defined in equations (A14)–(A17):

$$W_x(\gamma_x^*, \mathring{\gamma}_x) = \alpha(1-\tilde{R})[\gamma^* x_0^* T_{X_0} + \gamma^* x_{\mathrm{P}}^* T_{X_{\mathrm{P}}} + \langle c_R R\rangle T_{X_0}U + \langle c_R R\rangle T_{X_{\mathrm{P}}}V] + \alpha(1\tilde{R}_0)Q + \alpha(1\tilde{R}_{\mathrm{P}})Z. \tag{A18}$$

When the fitness of the mutant invasive is greater than 1, the mutant strategy can successfully invade; if fitness is less than 1, the mutant strategy will be excluded from the metacommunity. When fitness is equal to 1 the invasive strategy is identical to the resident strategy at equilibrium. Studying the evolutionary dynamics of this system requires us to know how invasive fitness changes with increases in dispersal rate when the invasive dispersal strategy is arbitrarily close to the resident strategy. The gradient of selection, which indicates the direction of fitness change at each point along a continuous trait gradient, can be defined for the prey by taking the derivative of equation (A18) with respect to the invasive dispersal rate $\gamma_x^*$ and solving at $\gamma_x^* = \gamma^\circ_x$. By setting the selection gradient $g_x$ equal to 0,

$$g_x = \frac{\partial W_x}{\partial \gamma_x^*}\Big|_{\gamma_x^* = \gamma^\circ{}_x} = 0, \tag{A19}$$

and solving for $\gamma_x$, we get the critical points along the dispersal gradient where the change in fitness is 0: $\hat{\gamma}_x$ (see eq. [A21] below for an expression for $g_x$). These points, known as "evolutionarily singular strategies" (Metz et al. 1996; Geritz et al. 1998; Doebeli and Dieckmann 2000), are interesting because they represent potential evolutionary attractors and endpoints in evolution. Singular strategy dispersal rates are evolutionary attractors (convergent stable strategies) if the condition $(dg_x/d\gamma_x)|_{\gamma_x=\hat{\gamma}_x} < 0$ holds, and are points in trait space where evolution stops and the strategy cannot be invaded further (evolutionarily stable strategy, or ESS) if $(\partial^2 W_x/\partial \gamma_x^{*2})|_{\gamma_x^*=\hat{\gamma}_x} < 0$. Due to the complex nature of the expression in equation (A19) we solved $g_x = 0$ numerically and found all evolutionarily singular strategies studied to be both convergently stable and an ESS stable.

## Prey Patches Receiving Different Numbers of Migrant Colonizers

For our structured metacommunity we need to be able to calculate the population size of prey patches that have received different numbers of colonizers. For this model we restrict the maximum number of colonizers that a local population can receive before extinction to two. We will indicate the number of migrant colonizers that a prey patch has received by a left-hand superscript. Thus the total metacommunity patch occupancy of the prey without a predator can be given by $R_0 = \sum_{i=1}^{2} {}^{i}R_0 = ({}^{1}R_0 + {}^{2}R_0)$, and the occupancy for a prey with a predator can be given by $R_\mathrm{P} = \sum_{i=1}^{2} {}^{i}R_\mathrm{P} = ({}^{1}R_\mathrm{P} + {}^{2}R_\mathrm{P})$. In order to determine the expressions for ${}^{1}\tilde{R}_0$ and ${}^{1}\tilde{R}_\mathrm{P}$ we first write the equations describing the metacommunity dynamics of prey patches that have received only one migrant colonizer:

$${}^{1}\dot{R}_0 = \langle c_R R\rangle(1 - R) - e_{R_0} - \langle c_R R\rangle({}^{1}R_0) - [c_\mathrm{P} P({}^{1}R_0) - e_\mathrm{P}({}^{1}R_\mathrm{P})], \tag{A20a}$$

$${}^{1}\dot{R}_\mathrm{P} = c_\mathrm{P} P({}^{1}R_0) - e_{R_P}({}^{1}R_\mathrm{P}) - \langle c_R R\rangle({}^{1}R_\mathrm{P}). \tag{A20b}$$

Solving these equations for ${}^{1}\dot{R}_0 = 0$ and ${}^{1}\dot{R}_P = 0$ gives the desired equilibrium expressions

$${}^{1}\tilde{R}_0 = \frac{(e_{R_\mathrm{P}} + e_\mathrm{P} + \langle c_R R\rangle)(1 - \tilde{R})}{(e_{R_\mathrm{P}} + e_\mathrm{P} + \langle c_R R\rangle)(e_{R_0} + \langle c_R R\rangle) + c_\mathrm{P} P(e_{R_\mathrm{P}} + \langle c_R R\rangle)},$$

$${}^{1}\tilde{R}_\mathrm{P} = \frac{c_\mathrm{P} P\langle c_R R\rangle(1 - \tilde{R})}{(e_{R_\mathrm{P}} + e_\mathrm{P} + \langle c_R R\rangle)(e_{R_0} + \langle c_R R\rangle) + c_\mathrm{P} P(e_{R_\mathrm{P}} + \langle c_R R\rangle)}.$$

## Prey Selection Gradient Equation

The equation for the prey selection gradient $g_x = (\partial W_x/\partial \gamma_x^*)|_{\gamma_x^*=\gamma^\circ{}_x}$ is given by

$$\begin{aligned} g_x = {} & \frac{(W)_{\gamma_x^*=\gamma^\circ{}_x}}{\gamma_x} + \gamma\alpha(1 - \tilde{R})\{T'_{X_0}[x_0^* + \langle c_R R\rangle(U)] + T_{X_0}[(x_0^*) + \langle c_R R\rangle(U)'] \\ & + T'_{X_\mathrm{P}}[x_P^* + \langle c_R R\rangle(V)] + T_{X_\mathrm{P}}[(x_\mathrm{P}^*) + \langle c_R R\rangle(V)']\}_{\gamma_x^*=\gamma^\circ{}_x} \\ & + \gamma\alpha(1\tilde{R}_0)(Q')_{\gamma_x^*=\gamma^\circ{}_x} + \gamma\alpha(1\tilde{R}_\mathrm{P})(Z')_{\gamma_x^*=\gamma^\circ{}_x}. \end{aligned} \tag{A21}$$

Explicit expressions for $(U)_{\gamma^*=\gamma^\circ}$, $(V)_{\gamma^*=\gamma^\circ}$, $(Q)_{\gamma^*=\gamma^\circ}$, $(Z)_{\gamma^*=\gamma^\circ}$, and derivatives $(U')_{\gamma^*=\gamma^\circ}$, $(V')_{\gamma^*=\gamma^\circ}$, $(Q')_{\gamma^*=\gamma^\circ}$, and

$(Z')_{\gamma^*=\gamma^{\circ}}$ can be found. Setting this equation to 0 and then numerically solving for $\gamma_x$ gives the evolutionarily singular strategy for the prey, $\hat{\gamma}_x$.

## Deriving the Predator Fitness and Selection Gradient Equation

### *Competitive Dynamics between a Resident and Invasive Predator Strategy*

Again, as with the prey, we consider a single patch with a prey population and its predator. The predator population consists of two possible strategies, a resident wild-type strategy with resident dispersal strategy $\gamma^{\circ}_y$ and a mutant invasive strategy with a dispersal strategy $\gamma^*_y$. Let $y^{\circ}$ local population size of resident predator strategy, $y^*$ the local population size of mutant predator strategy, and $y^{\circ} + y^* = s_y$ as the total predator population size in local patch, then in a mixed population with both predator strategies we have the following predator equations:

$$\dot{y}^{\circ} = aqxy^{\circ} - \gamma^{\circ}_y y^{\circ} - my^{\circ} \text{ (resident)},$$

$$\dot{y}^{*} = aqxy^{*} - \gamma^{*}_y y^{*} - my^{*} \text{ (mutant)}.$$

The mutant dispersal strategy is considered to be higher than the resident dispersal strategy. As a result the resident dispersal strategy is expected to displace the mutant dispersal strategy over time.

If we let $f = y^*/s_y$ be the fraction of the total predator population that is made up of the mutant strategy, then as with the prey, we can derive expressions for $f$ as a function of time,

$$f(t) = \frac{\phi}{\phi + (1-\phi)\exp\left[(\gamma^*_x - \gamma^{\circ}_x)t\right]},$$

and the total predator population, $\tilde{s}_y(t)$,

$$\begin{aligned}\tilde{s}_y(t) &= \frac{r}{a}\left\{1 - \frac{m + \gamma^{\circ}_y[1-f(t)] + \gamma^*_y f(t)}{aqK}\right\} - \frac{\gamma_x}{a},\\ &= \tilde{y}^{\circ} + f(t)(\tilde{y}^* - \tilde{y}^{\circ}).\end{aligned}$$

### *Total Colonizer Production of a Focal Invasive Predator Patch*

#### Colonizer Production before Recolonization by Resident Strategy

If we follow the fate of an invasive predator migrant landing on an empty prey patch, the persistence of any population it founds will follow the simple decay dynamics represented by

$$\dot{Y} = -(c_{\mathrm{P}}\tilde{P} + e_{\mathrm{P}} + e_{R_{\mathrm{P}}})Y.$$

If the initial value of $Y$ at time $t = 0$ is 1, the solution to this equation gives us the probability that the population still exists (has not become extinct or been invaded by a resident strategy colonizer) at time $t$:

$$Y(t) = \exp\left[-(c_{\mathrm{P}}\tilde{P} + e_{\mathrm{P}} + e_{R_{\mathrm{P}}})t\right].$$

The total lifetime of this mutant predator patch before extinction or recolonization by a predator resident is

$$T_Y = \int_0^{\infty} Y dt = \int_0^{\infty} e^{-(c_{\mathrm{P}}\tilde{P} + e_{\mathrm{P}} + e_{R_{\mathrm{P}}})t} dt = \frac{1}{(c_{\mathrm{P}}\tilde{P} + e_{\mathrm{P}} + e_{R_{\mathrm{P}}})}.$$

The average total number of colonizers produced by this population before extinction or recolonization by a predator resident is

$$\gamma^*_y \tilde{y}^* T_Y = \gamma^*_y \tilde{y}^* \left(\frac{1}{c_{\mathrm{P}}\tilde{P} + e_{\mathrm{P}} + e_{R_{\mathrm{P}}}}\right).$$

Average Total Colonizer Production after Recolonization by a Resident Strategy

The patch will be reinvaded with frequency $cPT_Y$. The number of dispersers produced by such a patch is

$$c_{\mathrm{P}}\tilde{P}T_Y\{\gamma_y^* \int_0^\infty \tilde{s}_y f^{\phi}(t) \exp[-(e_{\mathrm{P}} + e_{R_{\mathrm{P}}})t]dt\} = \frac{c_{\mathrm{P}}\tilde{P}}{c_{\mathrm{P}}\tilde{P} + e_{\mathrm{P}} + e_{R_{\mathrm{P}}}}\{\gamma_y^* \int_0^\infty \tilde{s}_y f^{\phi_{\tilde{y}^*}}(t) \exp[-(e_{\mathrm{P}} + e_{R_{\mathrm{P}}} + \mu)t]dt\},$$

where $\exp[-(e_{\mathrm{P}} + e_{R_{\mathrm{P}}})t]$ is the probability that a patch has not gone extinct $t$ time units after reinvasion by a resident. Notice that $\exp[-(e_{\mathrm{P}} + e_{R_{\mathrm{P}}})t]$ is identical to $Y$ without the effects of loss due to $c_{\mathrm{P}}\tilde{P}$; that is, the recolonization of the patch by a resident predator (assumed to be relatively rare enough to ignore after the first recolonization event by a resident).

### *Predator Selection Gradient*

If we also consider the colonizer production of an invasive landing on a resident-occupied patch, as described by $\int_0^\infty \tilde{s}_y f_y^{\phi_{\tilde{y}^\circ}}(t) \exp[-(e_{\mathrm{P}} + e_{R_{\mathrm{P}}})t]dt$, and define $\beta$ as the probability of a predator colonizer successfully establishing itself, we get the total fitness equation described in equations A13:

$$W_y(\gamma_y^*, \mathring{\gamma}_y) = \frac{\gamma_y^* \beta \tilde{R}_0}{c_{\mathrm{P}}\tilde{P} + e_{\mathrm{P}} + e_R + \mu}\left\{\tilde{y}^* + c_{\mathrm{P}}\tilde{P}\int_0^\infty \tilde{s}_y f^{\phi_{\tilde{y}^*}}(t) \exp[-(e_{\mathrm{P}} + e_{R_{\mathrm{P}}})t]dt\right\}$$
$$+ \beta({}^1\tilde{P})\gamma_y^* \int_0^\infty \tilde{s}_y f^{\phi_{\tilde{y}^\circ}}(t) \exp[-(e_{\mathrm{P}} + e_{R_{\mathrm{P}}})t]dt. \tag{A22}$$

If $M = \int_0^\infty \tilde{s}_y f_y^{\phi_{\tilde{y}^*}}(t) \exp[-(e_{\mathrm{P}} + e_{R_{\mathrm{P}}})t]dt$, and $N = \int_0^\infty \tilde{s}_y f_y^{\phi_{\tilde{y}^\circ}}(t) \exp[-(e_{\mathrm{P}} + e_{R_{\mathrm{P}}})t]dt$, then the gradient of selection for the predator, $\gamma_y^* = \mathring{\gamma}_y$, is given by

$$G_y = \frac{(W)_{\gamma_y^* = \gamma^\circ_y}}{\gamma_y^*} - \gamma_y^* \beta \tilde{R}_0 \left(\frac{(e_{\mathrm{P}})' + (e_{R_{\mathrm{P}}})'}{(c_{\mathrm{P}}\tilde{P} + e_{\mathrm{P}} + e_{R_{\mathrm{P}}})^2}\right)[\tilde{y}^* + c_{\mathrm{P}}\tilde{P}M]$$
$$+ \gamma_y^* \beta \tilde{R}_0 \left(\frac{1}{c_{\mathrm{P}}\tilde{P} + e_{\mathrm{P}} + e_{R_{\mathrm{P}}}}\right)[(\tilde{y}^*)' + c_{\mathrm{P}}\tilde{P}M'] + \gamma_y^* \beta({}^1\tilde{P})N'.$$

All evolutionarily singular strategies studied for the predator were found to be both ESS and convergent stable.

## Metacommunity Abundance of Predator Patches with Only One Colonizer

The equilibrium metacommunity abundance of predator patches that received only one colonizer, ${}^1P$, can be found by solving the differential equation

$${}^1\dot{P} = c_{\mathrm{P}}PR_0 - (e_{\mathrm{P}} + e_{R_{\mathrm{P}}})({}^1P) - c_{\mathrm{P}}P({}^1P),$$

when ${}^1\dot{P} = 0$ to get

$${}^1\tilde{P} = \frac{c_{\mathrm{P}}\tilde{P}\tilde{R}_0}{(e_{R_{\mathrm{P}}} + e_{\mathrm{P}}) + c_{\mathrm{P}}\tilde{P}}.$$

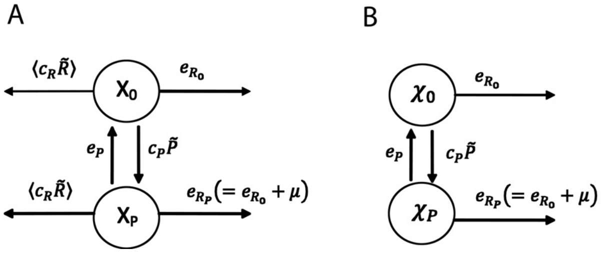

**Figure A1:** State transition diagrams of a mutant invasive prey patch. *A*, State transition diagram for an invasive patch before recolonization by a resident prey. The invasive prey patch exists in one of two states over time: in a patch without a predator ($X_0$) or in a predator-occupied patch ($X_P$). It moves between these two states through extinction of local predators in a predator-occupied patch (at frequency $e_P$), or by colonization of a prey-only patch by predator colonizers (at frequency $c\tilde{P}$). It ceases to be a strictly mutant invasive patch through either patch extinction (with frequencies $e_{R_0}$ or $e_{R_P}$) or by conversion to a mixed-strategy patch through recolonization by resident strategy colonizers (with frequency $\langle c_R\tilde{R}\rangle$). *B*, State transition diagram for an invasive patch after recolonization by a resident prey. After recolonization by a resident prey, the patch will once again exist in one of two states: a mixed-strategy patch without a predator ($\chi_0$), or a mixed-strategy patch with a predator ($\chi_P$). Transitions are similar to those described in *A*; see text for details.