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Evolution of Dispersal in a Predator-Prey Metacommunity

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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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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, $c_{R_{\mathrm{P}}}$, 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 $c_{R_{\mathrm{P}}}R_{\mathrm{P}}$ and $c_{R_0}R_0$. Similarly, total predator colonizer production is given by $c_{\mathrm{P}}P$. 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 μ (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, $e_{R_{\mathrm{P}}}$, and the extinction rate when no predator is present ($\mu = e_{R_{\mathrm{P}}} - e_{R_0}$). The differential equations for the occupancy of both the prey resource R and the predator P are given by

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

$$\frac{dP}{dt} = c_{\mathrm{P}}PR_0 - e_{\mathrm{P}}P - (e_{R_0} + \mu)P \text{ (predator)}. \tag{1b}$$

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

$$\tilde{R} = \frac{1}{2}\left[1 - \left(\frac{e_R + \mu}{c_{R_{\mathrm{P}}}}\right) + \Gamma\right] + \frac{1}{2}\sqrt{\left[1 - \left(\frac{e_R + \mu}{c_{R_{\mathrm{P}}}}\right) + \Gamma\right]^2 + 4\left(\frac{\mu - \Delta c_R}{c_{R_{\mathrm{P}}}c_{\mathrm{P}}}\right)(e_{\mathrm{P}} + e_R + \mu)}, \tag{2a}$$

$$\tilde{P} = \tilde{R} - \frac{(e_{\mathrm{P}} + e_R + \mu)}{c_{\mathrm{P}}}. \tag{2b}$$

Here $\Delta c_R = (c_{R_{\mathrm{P}}} - c_{R_0})$, and $\Gamma = [\Delta c_R(e_{\mathrm{P}} + e_R + \mu)/c_{R_{\mathrm{P}}}c_{\mathrm{P}}]$. 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 γ_x and γ_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_P, with frequency of the prey patch becoming extinct, e_{R_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 κ 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 κ 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_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 γ. 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: α 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 $c_{R_{\mathrm{PP}}} = \alpha\gamma_x\tilde{x}_\mathrm{P}$, while β 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 γ_x^*) when it invades a resident wild-type prey metacommunity, with dispersal rate γ_x° 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_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 α 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 γ^* 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_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 ∞, 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 γ^*_x, invading a metacommunity with a resident prey with dispersal rate γ°_x, that is, $W(\gamma^*_x, \gamma^{\circ}_x)$, is then simply the sum of the expected colonizer production from these three scenarios:

$$
\begin{aligned}
W(\gamma^*_x, \gamma^{\circ}_x) = {} & \alpha(1 - \tilde{R})[\gamma^*_x x^*_0 T_{X_0} + \gamma^*_x x^*_\mathrm{P} T_{X_P} \\
& + \langle c_R \tilde{R} \rangle T_{X_0} U + \langle c_R \tilde{R} \rangle T_{X_\mathrm{P}} V] + \alpha \tilde{R}_0 Q + \alpha \tilde{R}_\mathrm{P} Z.
\end{aligned}
$$

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 $\gamma^*_x = \gamma^{\circ}_x$ gives us the selection gradient: $g_x = \partial W_x / \partial \gamma^*_x |_{\gamma^*_x = \gamma^{\circ}_x}$. 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 $\partial^2 W_x / \partial \gamma^{*2}_x |_{\gamma^*_x = \hat{\gamma}_x} < 0$ 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 ($e_{R_\mathrm{P}} - e_{R_0}$) 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

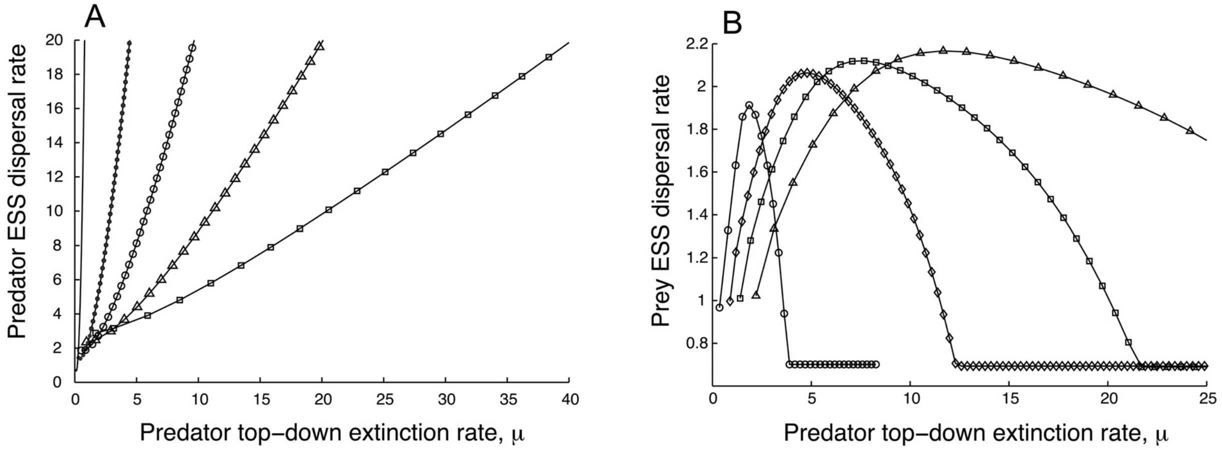

Figure 1: Evolutionarily stable dispersal rates as a response to increasing predator-induced extinction. Values on X-axis represent top-down extinction for a single, locally isolated interacting predator-prey system. Top-down extinctions controlled by increasing predator attack rate are in equation (4a). *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: $r = 10$, $K = 200$, $q = 0.75$, $m = 0.25$, $\gamma_x = 2$, $\alpha = 0.1$, $\beta = 0.1$, $z_y = 0.025$, $(e_R)_\mathrm{min} = 0.01$, $(e_\mathrm{P})_\mathrm{min} = 0.01$, 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: $r = 5$, $K = 200$, $q = 0.45$, m $= 0.3$, $\gamma_y = 20$, $\alpha = 0.01$, $\beta = 0.01$, $z_y = 0.035$, $(e_R)_\mathrm{min} = 0.01$, $(e_\mathrm{P})_\mathrm{min} = 0.01$, 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.

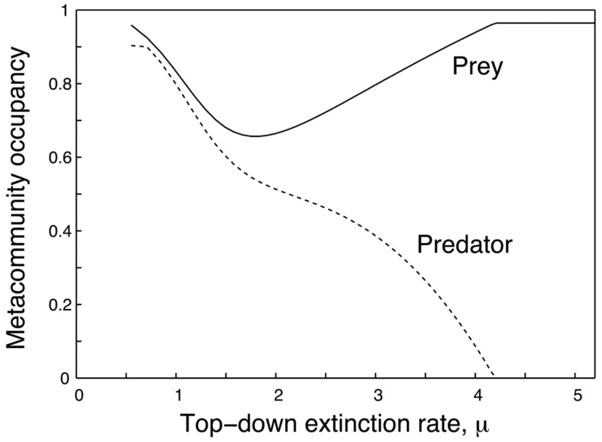

Figure 2: Effect of increasing predator-induced top-down extinction rates on a prey and predator's metacommunity patch occupancy. Increasing extinction-prone interaction has asymmetrical effects on both species as extinction rates increase: at first, both prey and predator decline, with the predator's 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 $(e_{\mathrm{P}})_{\min} = 0.001$.

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 (μ) increases. We can see this illustrated in figure 2 where, for a given predator and prey colonization rate, increasing the predator-induced extinction rate μ 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 μ 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.

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

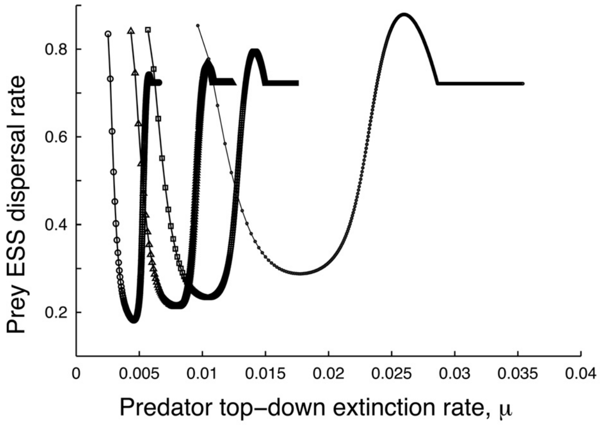

Figure 3: Response of prey evolutionarily stable strategy (ESS) dispersal when strong predator-prey interactions have little or no added effect on prey extinction rates (very low z_x values). Curves show effect of progressively removing the effects of top-down extinction on prey as interaction strength 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 μ 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 μ values, then either decreasing or relatively constant dispersal over a large range of μ 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

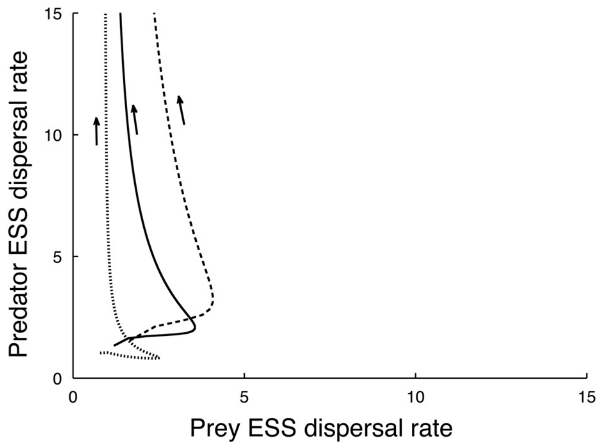

Figure 4: Coevolution of predator and prey dispersal. The joint evolutionarily stable strategy (ESS) dispersal strategies, $(\hat{\gamma}_x, \hat{\gamma}_y)$, for increasing top-down predator effects. Example curves shown for different coevolving predator-prey systems. Arrows give direction of increasing 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 μ are low, increasing μ 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 μ 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.

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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).