Ⓔ

Evolution of Predator and Prey Movement into Sink Habitats

Sebastian J. Schreiber[1,*] and Evan Saltzman[2]

1. Department of Evolution and Ecology and Center for Population Biology, University of California, Davis, California 95616;
2. School of Industrial and Systems Engineering, Georgia Institute of Technology, Atlanta, Georgia 30332

ABSTRACT: Mathematical models of predator-prey interactions in a patchy landscape are used to explore the evolution of dispersal into sink habitats. When evolution proceeds at a single trophic level (i.e., either prey or predator disperses), three evolutionary outcomes are observed. If predator-prey dynamics are stable in source habitats, then there is an evolutionarily stable strategy (ESS) corresponding to sedentary phenotypes residing in source habitats. If predator-prey dynamics are sufficiently unstable, then either an ESS corresponding to dispersive phenotypes or an evolutionarily stable coalition (ESC) between dispersive and sedentary phenotypes emerges. Dispersive phenotypes playing an ESS persist despite exhibiting, on average, a negative per capita growth rate in all habitats. ESCs occur if dispersal into sink habitats can stabilize the predator-prey interactions. When evolution proceeds at both trophic levels, any combination of monomorphic or dimorphic phenotypes at one or both trophic levels is observed. Coevolution is largely top-down driven. At low predator mortality rates in sink habitats, evolution of predator movement into sink habitats forestalls evolution of prey movement into sink habitats. Only at intermediate mortality rates is there selection for predator and prey movement. Our results also illustrate an evolutionary paradox of enrichment, in which enriching source habitats can reduce phenotypic diversity.

Keywords: dispersal evolution, predator-prey interactions, source-sink dynamics.

Introduction

Some habitats are better places to live than other habitats. Populations constrained to source habitats are, by definition, able to persist (Pulliam 1988, 1996). In contrast, populations constrained to sink habitats are deterministically driven to extinction. Nonetheless, there is growing evidence that populations occupy sink habitats (Dias 1996; Vierling 2000; Keagy et al. 2005), which raises the question, How and why do sink populations exist? The how is easy: sink populations are maintained by an influx of immigrants. The why, on the other hand, is more challenging

* Corresponding author; e-mail: sschreiber@ucdavis.edu.

from an evolutionary perspective. After all, why should individuals disperse from habitats with a higher mean fitness to habitats with a lower mean fitness? Indeed, if there is no variation of fitness within either habitat, such movements are maladaptive (Holt 1985). Maladaptive behavior may arise if individuals have not evolved appropriate responses to environmental changes (Remeš 2000; Delibes et al. 2001) or have perceptual constraints (Abrams 1986). When there is within-patch variation of fitness, however, sink populations can evolve. This within-patch variation may arise from individual or temporal variation in fitness. For instance, if a source habitat has more individuals than breeding sites, then individuals with breeding sites may have higher fitness than individuals without breeding sites (Pulliam 1988). In this case, individuals without breeding sites may increase their fitness by acquiring a breeding site in a sink habitat. On the other hand, temporal variation of fitness within a source habitat may result in moments when the fitness in the sink exceeds the fitness in the source. At such moments, it can be advantageous for individuals to disperse from source habitats to sink habitats (Holt 1997; van Baalen and Sabelis 1999; Schreiber et al. 2006).

There is widespread theoretical evidence that temporal variation in spatially heterogeneous environments can promote the evolution of dispersal from "higher-quality" habitats (e.g., sources) to "lower-quality" habitats (e.g., sinks). For instance, numerical simulations of two-patch models have shown that dispersal can evolve, provided that the fitness in one patch oscillates above and below the fitness in the other patch (McPeek and Holt 1992; Holt and McPeek 1996; Harrison et al. 2001). These oscillations in fitness can promote the evolution of sink populations (Holt 1997) as well as the evolution of dispersal dimorphisms (McPeek and Holt 1992; Doebeli and Ruxton 1997; Mathias et al. 2001; Kisdi 2002). These dimorphisms coexist by spatial niche partitioning: low-dispersal phenotypes residing primarily in higher-quality habitat and high-dispersal phenotypes spreading individual risk across all habitat types. In these studies, within-patch temporal variation is driven by exogenous forcing of the system

(McPeek and Holt 1992; Mathias et al. 2001; Kisdi 2002) or by overcompensating density dependence (Holt and McPeek 1996; Doebeli and Ruxton 1997).

A potent source of temporal variation is species interactions. Most notably, theoretical studies have shown that antagonistic interactions between predators and their prey can generate oscillatory dynamics (Rosenzweig 1971; Chesson 1978; Hastings and Powell 1991), which have been observed in laboratory experiments (Huffaker 1958; Luckinbill 1973; Fussman et al. 2000) and field studies (Elton and Nicholson 1942; Hanski et al. 1993). In predator-prey systems, source-sink dynamics can arise in a variety of ways (Holt 1993). Predators have a negative per capita growth rate without their prey. Hence, a sink habitat for the prey is always a sink habitat for the predator-prey interaction; that is, both species become locally extinct when neither species immigrates into the habitat. However, sink habitats for the prey may serve as source habitats for predators (i.e., sustain predators without immigration by predators) if immigration by the prey sustains sufficiently high prey densities. Conversely, source habitats for the prey may act as sink habitats for predators if these habitats sustain only low prey densities. Using two-patch models, Holt (1985, 1993) found that that diffusive movement of predators into prey-free habitats or diffusive movement of prey into sink habitats for the prey can stabilize predator-prey interactions, a prediction supported by microcosm studies (Amezcua and Holyoak 2000). While predator-prey populations exhibiting ideal free dynamics are known to form transient sink populations (van Baalen and Sabelis 1999; Schreiber et al. 2006), it remains to be understood when evolution favors continual movement into sink habitats.

Because dispersal into sink habitats can stabilize predator-prey interactions and temporal variability in fitness influences the evolution of dispersal, there are likely to be strong ecological and evolutionary feedbacks for predator-prey populations dispersing into sink habitats. To understand these feedbacks, we use predator-prey models with two types of habitat: source habitat, which can sustain predator-prey interactions without immigration, and sink habitat, which cannot sustain the prey without immigration. Using these models, we examine three evolutionary scenarios. The first two scenarios assume that the dispersal rate evolves for only one of the species. For these scenarios, we find three evolutionary outcomes, determined by the severity of predator-prey oscillations in source habitats. If the predator-prey interactions are sufficiently stable, then there is selection against dispersal. If the predator-prey interactions are sufficiently unstable, then either dispersal into sink habitats is evolutionarily stable or there are evolutionarily stable coalitions with sedentary phenotypes that reside in source habitats. In our final scenario, we allow

dispersal to evolve for both species. We find that dispersal between source and sink habitats evolves at both trophic levels only if the predator has some (but not too much) fitness advantage (e.g., lower mortality rate) in the sink habitats for the prey. Collectively, these scenarios allow us to understand when dispersal into sink habitats evolves and when dispersal polymorphisms evolve at one or multiple trophic levels.

Models and Methods

Our models consider interacting predator-prey populations that occupy a landscape with two habitat types: source habitat and sink habitat for the prey. In source habitats, the intrinsic per capita birth rate b_1 of the prey exceeds its intrinsic per capita death rate d_1. Let K_1 denote the total number of available source sites. By contrast, the intrinsic per capita death rate d_2 exceeds the intrinsic per capita birth rate b_2 in sink habitats. Hence, prey constrained to this habitat always have a negative per capita growth and are deterministically driven to extinction. We assume that the prey and predator disperse diffusively between the two habitats. This assumption is consistent with earlier studies of evolution of dispersal for a single species (Hastings 1983; McPeek and Holt 1992; Doebeli and Ruxton 1997; Mathias et al. 2001; Kisdi 2002) and allows us to contrast our results with those of previous studies that have considered ideal free movement of prey or predators (van Baalen and Sabelis 1999; Schreiber et al. 2006). These contrasts are useful because most organisms' modes of dispersal lie between these extremes. Let m be the per capita dispersal rate of the prey between the two habitats and μ be the per capita dispersal rate of the predator between the two habitats. We assume that the predators exhibit a Type II functional response $aN_i/(1 + ahN_i)$, where N_i is the prey abundance in habitat type i, a is the predator's attack rate, and h is the predator's handling time (equivalently, $1/h$ is the maximal uptake rate of the predator). Predators convert consumed prey with conversion efficiency θ. For simplicity, we have assumed that the predator's attack rates, handling times, and conversion efficiencies are not patch specific (i.e., a, h, and θ are unsubscripted). Let δ_i be the predator per capita death rate in habitat type i. If P_i denotes the predator abundance in habitat type i, then the predator-prey dynamics are given by

$$\frac{dN_1}{dt} = b_1 N_1 \left(1 - \frac{N_1}{K_1}\right) - d_1 N_1 - \frac{aP_1}{1 + haN_1} N_1$$
$$+ m(N_2 - N_1),$$

$$\frac{dN_2}{dt} = r_2 N_2 - \frac{aP_2}{1 + haN_2} N_2 + m(N_1 - N_2), \quad (1)$$

$$\frac{dP_1}{dt} = \frac{\theta a N_1}{1 + haN_1} P_1 - \delta_1 P_1 + \mu(P_2 - P_1),$$

$$\frac{dP_2}{dt} = \frac{\theta a N_2}{1 + haN_2} P_2 - \delta_2 P_2 + \mu(P_1 - P_2),$$

where $r_2 = b_2 - d_2 < 0$ is the prey per capita growth rate in sink habitats. For several cases of special interest, it is possible to find explicit expressions for the equilibria and conditions for ecological stability. These expressions and conditions are presented in appendix A in the online edition of the *American Naturalist* and used to contrast evolutionary outcomes with the underlying ecological dynamics.

We investigate the evolutionary dynamics from two perspectives: invasion exponents and simulations of the ecological and evolutionary dynamics. To define the prey and predator invasion exponents, consider a prey-predator population with abundances (N_1, N_2, P_1, P_2) that has been playing the dispersal strategy (m, μ) sufficiently long for the ecological dynamics to settle on an asymptotic state (e.g., an equilibrium or a periodic orbit). The invasion exponent $\mathcal{I}_{\text{prey}}(m, \tilde{m})$, which is defined formally in appendix B in the online edition of the *American Naturalist*, corresponds roughly to the average per capita growth rate of prey with dispersal rate $\tilde{m}$ (and otherwise is identical to the resident population) when introduced at low abundances to the resident population. When the invasion exponent is positive, the invasion of the "mutant" strategy $\tilde{m}$ succeeds; otherwise, it fails. The predator invasion exponent $\mathcal{I}_{\text{pred}}(\mu, \tilde{\mu})$ is defined similarly.

Using invasion exponents, we can identify evolutionarily stable strategies (ESSs) and create pairwise invasibility plots (PIPs) that play a fundamental role in the study of adaptive dynamics (Geritz et al. 1997). PIPs are two-dimensional contour plots in which the resident strategy varies on the horizontal axis and the mutant strategy varies on the vertical axis. In these plots, the zero contour of the invasion exponent separates regions of the phenotype space where the mutant can invade the resident population from regions where the mutant cannot invade. These diagrams convey qualitative insight into requirements for coexistence, exclusion, and bistability of competing phenotypes as well as information about the evolutionary dynamics.

In addition to employing invasion exponents, we simulate the ecological and evolutionary dynamics by assuming that there is a continuum of prey and predator phenotypes, differing only in their dispersal rates. Let $N_i = N_i(t, m)$ and $P_i = P_i(t, \mu)$ denote the abundance of the prey and predator populations, respectively, with dispersal rates m and μ at time t in habitat i. If the variances of the mutation process of the prey and predator are given by s^2 and σ^2, respectively and if we follow the approach of Kimura (1965), the evolution dynamics are given by the integrodifferential equations

$$\frac{\partial N_1}{\partial t} = \left(1 + \frac{s^2}{2}\frac{\partial^2}{\partial m^2}\right) b_1 N_1 \left(1 - \frac{\tilde{N}_1}{K_1}\right) - d_1 N_1$$
$$- \frac{aP_1}{1 + ha\tilde{N}_1} N_1 + m(N_2 - N_1),$$

$$\frac{\partial N_2}{\partial t} = \left(1 + \frac{s^2}{2}\frac{\partial^2}{\partial m^2}\right) b_2 N_2 - d_2 N_2$$
$$- \frac{aP_2}{1 + ha\tilde{N}_2} N_2 + m(N_1 - N_2), \quad (2)$$

$$\frac{\partial P_1}{\partial t} = \left(1 + \frac{\sigma^2}{2}\frac{\partial^2}{\partial \mu^2}\right) \frac{\theta a \tilde{N}_1}{1 + ha\tilde{N}_1} P_1 - \delta_1 P_1$$
$$+ \mu(P_2 - P_1),$$

$$\frac{\partial P_2}{\partial t} = \left(1 + \frac{\sigma^2}{2}\frac{\partial^2}{\partial \mu^2}\right) \frac{\theta a \tilde{N}_2}{1 + ha\tilde{N}_2} P_2 - \delta_2 P_2$$
$$+ \mu(P_1 - P_2),$$

where

$$\tilde{N}_i(t) = \int_0^\infty N_i(t, m) dm$$

is the total abundance of prey in habitat i; $\tilde{N}_i$ appears in the prey per capita birth rate and in the predator functional responses because both of these quantities depend on the total abundance of prey. To complete the model, we assume that there are reflecting boundary conditions at $m = 0$ and $\mu = 0$ (i.e., $(\partial N_1/\partial m)|_{m=0} = (\partial P_1/\partial m)|_{m=0} = 0$).

Results

In our analysis and numerical simulations, we investigate three scenarios: evolution of prey movement into enemy-

free sinks, evolution of predator movement into victimless sinks, and coevolution of predator and prey movement into sink habitats.

Evolution of Prey Movement into Enemy-Free Sinks

Initially, we focus on prey movement between the two habitats and assume that the predator cannot occupy sink habitats (i.e., $\mu = 0$, $\sigma = 0$, and $P_2 = 0$). Therefore, we call this sink an "enemy-free sink," which acts as a refuge for the prey. Prey dispersing in this environment must weigh the benefits of resource availability and predation intensity. In the field, there are many examples of this type of predator-prey system (Schreiber et al. 2006). For instance, hypoxic environments are lethal to yellow perch but not to their prey, fathead minnows (Robb and Abrahams 2002). Hence, fathead minnows can disperse in and out of hypoxic patches, while yellow perch avoid these patches.

When the resident predator-prey dynamics are governed by a stable equilibrium, we show in appendix B that mutants dispersing at a lower rate can invade the resident population. Alternatively, resident populations with stable ecological dynamics resist invasion attempts from faster-dispersing populations. Hence, if a resident community without dispersing prey persists at a stable equilibrium, then the nondispersing prey are playing an ESS. These conclusions closely mirror earlier work on the evolution of dispersal of a single species (Hastings 1983; McPeek and Holt 1992; Doebeli and Ruxton 1997; Dockery et al. 1998; Kirkland et al. 2006). More generally, numerical simulations suggest that if the prey per capita growth rate exhibits insufficient variation in the source habitat, then evolution selects for slower dispersers and culminates in the prey specializing on the source habitat.

Conversely, when the ecological dynamics in the source are sufficiently oscillatory, the rank ordering of patch quality for the prey varies in time. Specifically, the per capita growth rate of the prey is greater in the sink when the predator is abundant in the source habitat. When predator abundance wanes, the prey's per capita growth rate in the source exceeds its per capita growth rate in the sink. As observed in single-species models (McPeek and Holt 1992; Holt and McPeek 1996; Doebeli and Ruxton 1997; Mathias et al. 2001), temporal variation in the rank ordering of the patch quality can result in higher-dispersing phenotypes displacing lower-dispersing phenotypes. These higher-dispersing phenotypes use both habitats and may be regarded as a generalist strategy that is spreading its risk across space. Because increasing dispersal rates initially stabilizes predator-prey dynamics, selection for faster dispersers reduces the variation in the prey's per capita growth rates, thereby decreasing the intensity of selection

for increased dispersal rates. As selection pressures wane, the prey dispersal strategy approaches a value at which the fitness gradient $(\partial \mathcal{I}_{\text{prey}}/\partial \tilde{m})(m, m)$ is 0 (fig. 1). This singular strategy can correspond either to an ESS or to an evolutionary branching point (Metz et al. 1996; Geritz et al. 1997).

When there is sufficiently strong variation in the prey per capita growth rates at the singular strategy, the singular strategy is an ESS, resisting invasion attempts by faster- or slower-dispersing phenotypes (fig. 1*A*, 1*B*; fig. 3*A*, with $h > 0.07$). For this evolutionary end state, the temporal average of the prey per capita growth rate in the source habitats is negative (fig. 3*B*, with $h > 0.07$). Indeed, if the per capita growth rate were positive in the source habitats, sedentary prey could invade, and the resident prey would not be playing an ESS. Thus, despite this evolutionary end state resulting in the average per capita growth rate being negative in all habitats, the prey population persists by spreading risk across space.

When there is weaker temporal variation in the prey per capita growth rate at the singular strategy, the singular strategy is evolutionarily unstable. Coalitions of faster- and slower-dispersing prey can displace the resident population and coexist with one another. Consequently, after a period of stasis near the singular strategy, the phenotypic dynamics undergo evolutionary branching. Faster phenotypes continue to experience selection for higher dispersal rates, while slower phenotypes experience selection for lower dispersal rates. Evolution ultimately culminates in an evolutionarily stable coalition (ESC), consisting of a sedentary phenotype and a dispersing phenotype (fig. 1*C*, 1*D*). In contrast to a monomorphic end state, persistence of the sedentary prey forces the prey's per capita growth rate in the source to be 0 rather than negative (see fig. 3, with $h < 0.07$). When low-dispersal and high-dispersal phenotypes coexist, their relative frequencies may oscillate in response to the underlying ecological dynamics. As shown in figure 2, low temporal variation in the rank ordering of the source and sink habitats can result in oscillatory dynamics in the phenotypic distribution. More specifically, low variation in the prey per capita growth rate initially selects against dispersal. However, as the abundance of high-dispersal phenotypes decreases, the ecological dynamics become more oscillatory and strengthen selection pressures for dispersal. As the abundance of the high-dispersal phenotypes increases in response to the shift in selection pressures, these phenotypes stabilize the ecological dynamics, and the cycle of evolutionary and ecological feedbacks repeats.

To understand how environmental conditions and life-history traits influence evolutionary outcomes (i.e., selection only for a sedentary phenotype, selection only for a high-dispersal phenotype, and selection for a coalition of
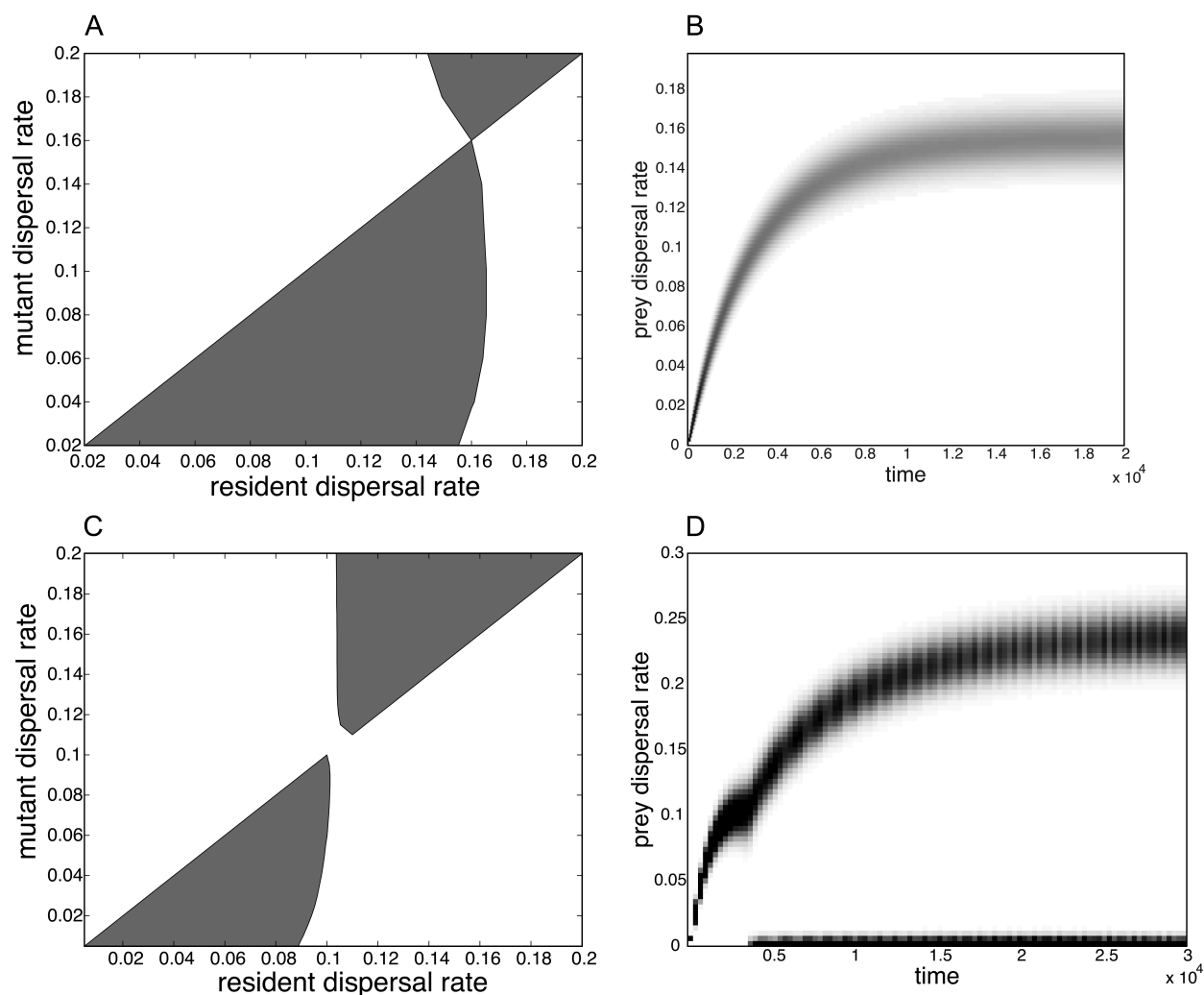
Figure 1: Evolution of monomorphic and dimorphic dispersal phenotypes. *A*, *C*, Pairwise invasibility plot (PIP) showing how the invasion rate of a mutant phenotype depends on the phenotype of the resident population. The shaded region indicates where the invasion rate is negative. *B*, *D*, Distribution of phenotypes plotted vertically against time. Darker shading corresponds to phenotypes with higher densities. Parameter values common to all figures are $b_1 = 4$, $b_2 = 0.4$, $d_1 = 0.5$, $K_1 = 5,000$, $h = 0.05$, $a = 0.1$, $c = 0.3$, $\delta_1 = 0.1$, and $s = 10^{-4}$. In *A* and *B*, $d_2 = 0.75$. In *C* and *D*, $d_2 = 0.5$.

low- and high-dispersal phenotypes), we created evolutionary bifurcation diagrams with respect to different species parameter values (figs. 3, 4). These figures illustrate two trends observed in our extensive numerical simulations. First, evolutionary branching typically occurs when high-dispersal phenotypes can stabilize the predator-prey interaction but sedentary prey are unable to do so. For example, figure 3*A*, with $0.005 < h < 0.065$, and figure 4*A*, with $d_2 < 3$, illustrate that when branching occurs, the dispersal rate of the dispersive phenotype lies in or close to the region of stability for the ecological model. As discussed earlier, slower-dispersing phenotypes are able to invade a community supporting these higher-dispersal

phenotypes. Alternatively, the high-dispersal phenotypes can invade when the ecological dynamics are sufficiently oscillatory. This mutual invasibility argument provides an intuitive explanation of why coalitions of low- and high-dispersal phenotypes can coexist after an evolutionary branching event. The second trend observed in these simulations is that evolution selects only for high-dispersal phenotypes when higher-dispersal phenotypes cannot stabilize the ecological dynamics (fig. 3, with $h > 0.065$, or fig. 4, with $3 < d_2 < 5$).

As a result of these observed trends, life-history traits of the prey (e.g., per capita birth rate in the source) or the predator (e.g., handling time) promoting ecological
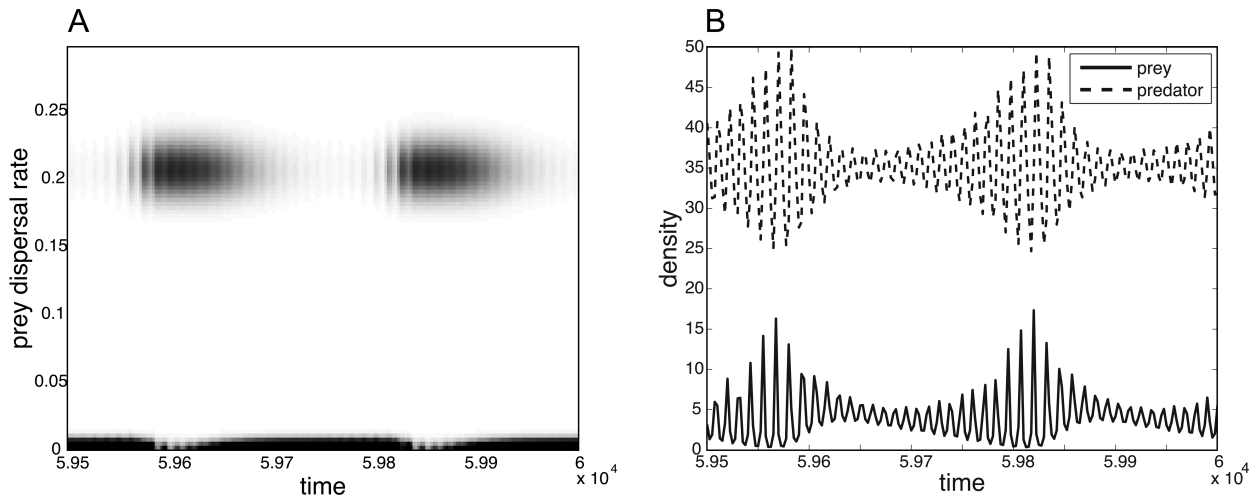
Figure 2: Oscillatory phenotype and population dynamics following a branching event. *A,* Plot of evolutionary dynamics of the prey phenotype. *B,* Total prey and predator abundances plotted against time. Parameter values are $b_1 = 4$, $b_2 = 0.4$, $d_1 = d_2 = 0.5$, $a = 0.1$, $h = 0.03$, $\delta_1 = 0.1$, $\theta = 0.3$, $K_1 = 5,000$, and $s = 10^{-4}$.

instability enhance selection for dispersal into sink habitats. For instance, predators with short handling times stabilize predator-prey dynamics, resulting in the evolution of sedentary prey (fig. 3). Predators with intermediate handling times destabilize the ecological dynamics and lead to an ESC of sedentary and dispersive phenotypes. Predators with long handling times generate sufficiently unstable dynamics to result in selection for only a high-dispersive phenotype. Surprisingly, when the prey per capita birth rate in source habitats is sufficiently high, increasing the per capita death rate in sink habitats can destabilize the ecological dynamics (fig. 4*A*). Hence, under these circumstances, increasing prey mortality in the sink can select for only high-dispersal phenotypes and thereby reduces phenotypic diversity (fig. 4*B*).

We also examined the evolution of prey dispersal when the predator disperses into the sink habitat. In general, predator dispersal into sink habitats inhibited the evolution of prey dispersal. For instance, we examined this inhibitory effect when the prey exhibited an ESC in the absence of predator dispersal (fig. C1 in the online edition of the *American Naturalist*). Low predator dispersal rates decreased the dispersal rate of the dispersive prey in the ESC. High predator dispersal rates prevented evolutionary branching and resulted in an ESS of sedentary prey. Consistent with our other results, an ESS of sedentary prey occurred when predator movement into sink habitats stabilized predator-prey interactions.

Evolution of Predator Movement into Victimless Sinks

Complementing the evolution of enemy-free sinks, we investigate the evolution of dispersive movement into hab-

itats without prey (i.e., $m = s = N_2 = 0$ in the models). Victimless sinks occur when there is a trade-off between resource availability in the source and lower mortality risk in the sink (Schreiber et al. 2006). For example, consumers may go to habitats with low resource availability to reduce predation risk. Alternatively, victimless sinks may correspond to a behavioral or physiological state (Beers 1925).

The evolutionary dynamics of victimless sinks mirror the enemy-free sink model in several ways. First, if sedentary predators can stabilize ecological dynamics, then evolution selects for sedentary predators. Second, if dispersing predators can stabilize the ecological dynamics but sedentary predators cannot, then evolutionary branching occurs. Finally, if dispersal into sink habits cannot stabilize the ecological dynamics, then the evolutionary end state consists of only high-dispersal phenotypes. These similarities can be seen by comparing figures 3*A* and 5*B*, in which the effect of increasing predator handling time on evolutionary outcomes is qualitatively similar in the two models, transitioning from a sedentary evolutionary end state to a dimorphic end state to a high-dispersal end state.

Despite these similarities, notable differences exist between the evolution of prey movement into enemy-free sinks and predator movement into victimless sinks. For instance, per capita death rates in the sink have different impacts on the evolutionary end states for the two models. Figure 5 illustrates a sharp transition from a dimorphic end state to a sedentary monomorphic end state by increasing predator mortality rates in the sink. In contrast, increasing prey sink mortality in the enemy-free sink model leads to a transition from a dimorphic end state to a monomorphic high-dispersal end state. A possible ex-
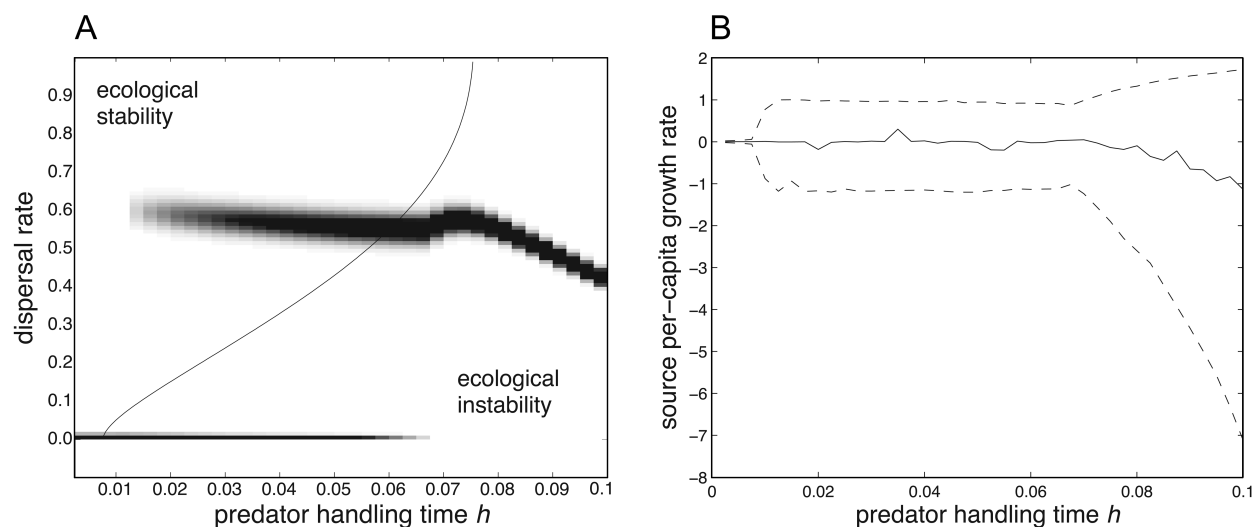
Figure 3: Effects of predator handling time on the evolution of enemy-free sinks. For each parameter value, evolutionary dynamics were simulated for 25,000 time steps. *A*, Plot of temporal average of the distribution of dispersal phenotypes in the last 2,500 time steps. The thin line delineates the region of parameter space corresponding to ecological stability for a community consisting of one prey and one predator phenotype. *B*, Plot of minimum, average, and maximum per capita growth of the prey in the last 2,500 time steps. Parameter values are $b_1 = 5$, $b_2 = 0.4$, $d_1 = d_2 = 0.5$, $K_1 = 1500$, $a = 0.1$, $\theta = 0.3$, $\delta_1 = 0.5$, and $s = 10^{-4}$.

planation for this difference is that for evolution of enemy-free sinks, the variation of the prey's per capita growth rate in the source continually increases with mortality rates in sink habitats. Conversely, for the evolution of victimless sinks, the variation in the predator's per capita growth rate in the source saturates as its mortality rate in sink habitats increases. Thus, for predators, staying in sink habitats becomes more costly than staying in source habitats.

Coevolution of Predator and Prey Movement into Sink Habitats

Our analysis concludes by looking at how predator and prey sink populations coevolve. In our extensive numerical simulations, we observed nine different outcomes, in which each trophic level could exhibit only sedentary phenotypes, only high-dispersal phenotypes, or dispersal dimorphisms (figs. 6, 7). The numerical simulations reveal two consistent trends.

First, coevolution at both trophic levels can generate evolutionary end states that differ substantially from when only one trophic level evolves. For instance, the evolution of predator dispersal can disrupt or inhibit the evolution of prey dispersal. This phenomenon is illustrated in figure 6*A*. Because of highly oscillatory dynamics in the source, evolution initially favors prey dispersal. As more prey move into the sink, there is selection for predator dispersal. The increased presence of predators causes the prey phenotypes to undergo evolutionary branching, but with the contin-

ued selection for predator dispersal, the prey dispersing into sink habitats experience strong negative selection and are ultimately lost. This predatory disruption of the evolution of prey dispersal occurs when the predator per capita mortality rate in sink habitats is significantly lower than its mortality rate in source habitats.

Second, the greatest phenotypic diversity occurs at intermediate levels of productivity in source habitats (i.e., intermediate per capita birth rates for the prey). Low productivity in source habitats encourages ecologically stable dynamics, allowing only two phenotypes (sedentary prey and predators) to evolve. In contrast, high productivity in source habitats generates sufficiently oscillatory dynamics to inhibit evolutionary branching, allowing each trophic level to support only one phenotype. For instance, figure 7*A* illustrates that if the predator mortality rates in sink habitats are sufficiently low, then high-dispersal monomorphisms evolve at both trophic levels. When predator mortality rates in sink habitats are too high, predators specialize on the source habitat while prey use both habitats. At intermediate levels of source productivity, evolutionary end states can support higher levels of phenotypic diversity, with at least one trophic level supporting a dispersal dimorphism. For instance, figure 7*A* illustrates that if the predator mortality rates in the sink are sufficiently low, then the higher trophic level can exhibit greater phenotypic diversity than the lower trophic level. When predator mortality rates are sufficiently high in sink habitats, this pattern is reversed: the lower trophic level can
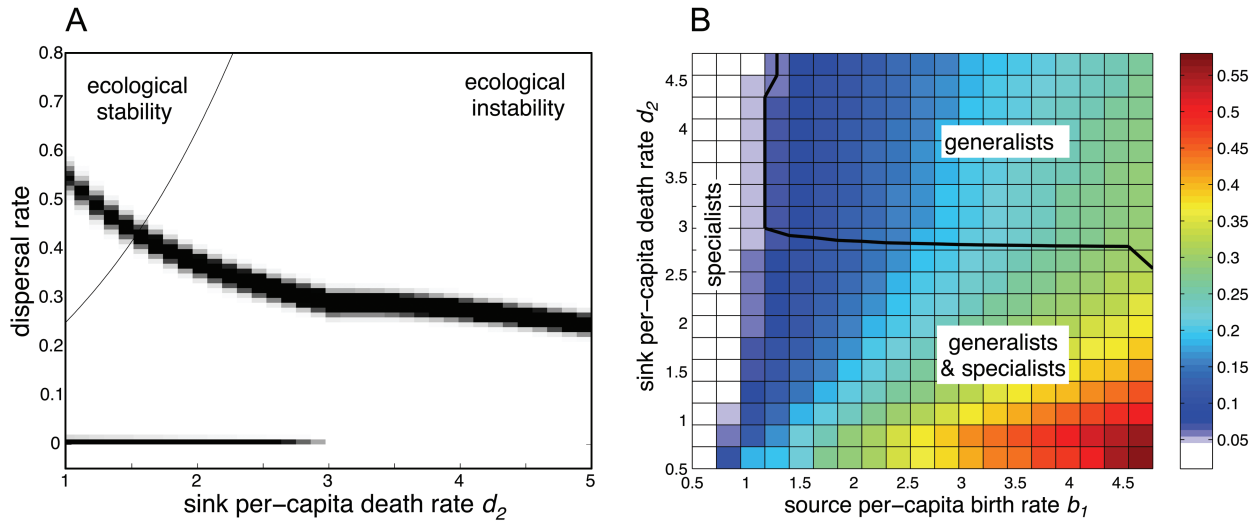
Figure 4: Effects of prey life-history traits on the evolution of prey movement into enemy-free sinks. *A*, Evolutionary end state (as a distribution of phenotypes) plotted against the per capita death rate of the prey. The thin line separates regions where the ecological dynamics with a single phenotype are stable. *B*, Dispersal rate of the fastest phenotype plotted as a function of the per capita death rate in the sink and the per capita birth rate in the source. Warmer colors correspond to faster phenotypes. Regions corresponding to three possible evolutionary outcomes (sedentary phenotypes, i.e. "specialists"; high-dispersal phenotypes, i.e., "generalists"; and coalitions of low- and higher-dispersal phenotypes) are delineated. Parameter values are $b_2 = 0.4$, $K_1 = 5,000$, $d_1 = 0.5$, $c = 0.3$, $h = 0.01$, $a = 0.1$, $\delta_1 = 0.5$, and $s = 10^{-4}$. In *A*, $b_1 = 5$.

exhibit greater phenotypic diversity than the higher trophic level. Interestingly, maximal phenotypic diversity (i.e., dimorphisms at both trophic levels) occurs only under a narrow range of conditions. For instance, figure 7*B* illustrates that maximal phenotypic diversity occurs for $0.225 \leq \delta_2 \leq 0.3$.

Discussion

Sink populations are maintained by immigration of individuals from other locations. These persisting sink populations can occur at the borders of species ranges (Hoffmann and Blows 1994; Holt and Gomulkiewicz 1997; Holt et al. 2003*a*), inflate metapopulation abundance (Holt 1985; Pulliam 1988; Holt et al. 2003*b*), stabilize predator-prey interactions (Holt 1985, 1993; Ylönen et al. 2003; Schreiber et al. 2006), and alter competitive outcomes (Schmidt et al. 2000; Schreiber and Kelton 2005). Given the obvious cost of dispersing into sink habitats, one is confronted with the question of what factors promote the evolution of dispersal into sink habitats. Previous research has shown that dispersal into sink habitats can be advantageous when there are asymmetric competitive interactions (e.g., dominance relations among individuals; Pulliam 1988) or when environmental fluctuations reduce individual fitness in other habitats below the fitness within sink habitats (Holt 1997; van Baalen and Sabelis 1999). In this article, we focused on how oscillations generated by

predator-prey interactions favor the evolution of dispersal between source habitats, in which the prey and the predator can coexist, and sink habitats, in which neither the predator nor the prey could persist. Per capita dispersal rates were allowed to evolve at one or both trophic levels.

We found that evolution at a single trophic level resulted in three possible evolutionary outcomes determined by the stability of the predator-prey interaction. If the predator-prey interaction in the source habitat is stable, then sedentary populations are playing an ESS and there is no selection for sink populations. Intuitively, when the sedentary populations are at equilibrium, their per capita growth rates in source habitats are constantly zero. Consequently, because individuals dispersing into sink habitats would lower their per capita growth rate, evolution selects against dispersal. This finding is consistent with many previous findings on the evolution of dispersal for a single species in a spatially heterogeneous environment (Hastings 1983; Holt 1985; McPeek and Holt 1992; Doebeli and Ruxton 1997; Dockery et al. 1998; Kirkland et al. 2006). However, the argument presented in appendix B extends prior work by applying to models with any number of species, habitat types, and arbitrary dispersal patterns. Our simulations suggest that the sedentary ESS persists when the predator-prey interactions are unstable but not sufficiently unstable to cause the per capita growth rate in the source habitats to fall substantially in duration or in magnitude below the per capita growth rate in the sink habitats.
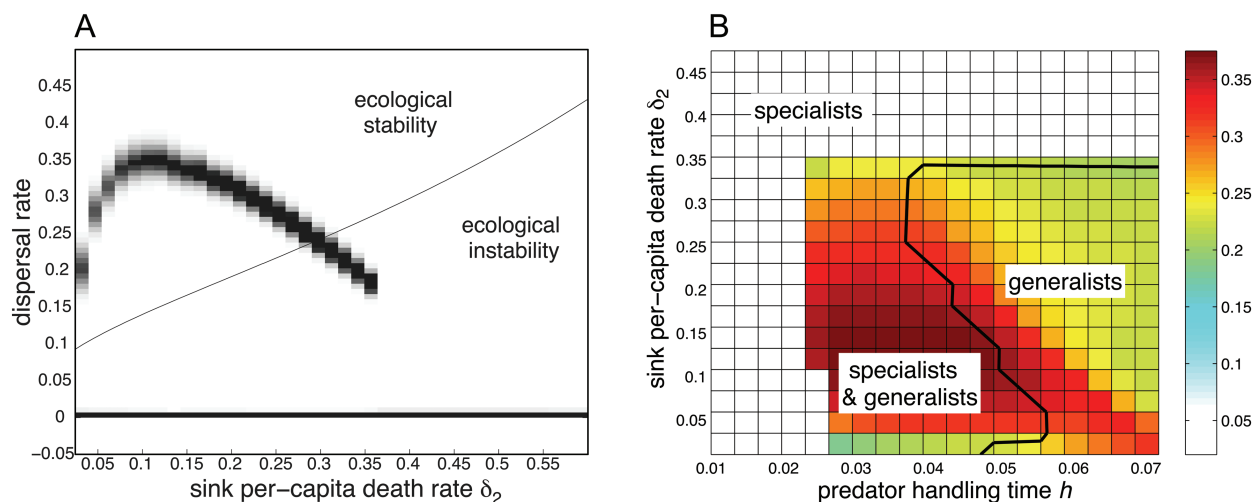
Figure 5: Evolution of predator movement into victimless sinks. *A,* Evolutionary bifurcation diagram showing how the distribution of predator phenotypes in the evolutionary end state varies as a function of the predator's per capita mortality rate in the sink. For each per capita mortality level, simulations were run for 10,000 time units. For the last 500 time units, the temporal average of the predator's distribution of dispersal rates is plotted. *B,* Dispersal rate of the fastest predator phenotype plotted as a function of its per capita death rate in the sink and its handling time. Warmer colors correspond to faster phenotypes. Regions corresponding to three possible evolutionary outcomes (sedentary phenotypes, i.e., "specialists"; high-dispersal phenotypes, i.e., "generalists"; and coalitions of low- and higher-dispersal phenotypes) are delineated. Parameter values for both figures are $b_1 = 3$, $d_1 = 0.5$, $K_1 = 2,000$, $a_1 = 0.1$, $\theta_1 = 0.3$, $\delta_1 = 0.5$, and $\sigma = 10^{-4}$. In *A,* $h = 0.03$.

This prediction differs from prior work on discrete-time single-species models where all patches are sources (Cohen and Levin 1991; Mathias et al. 2001; C. K. Li and S. J. Schreiber, unpublished data). In these models, there is no sedentary ESS whenever there is spatial and temporal heterogeneity in the species' carrying capacities. The discrepancy between these predictions stems from the observation that the temporal average of the per capita growth rates must be zero in source patches occupied by sedentary populations. Consequently, if all patches are sources and occupied by sedentary populations, then spatial asynchrony in the fluctuations of the per capita growth rates provides fitness gains to individuals that disperse (Cohen and Levin 1991; C. K. Li and S. J. Schreiber, unpublished data). In contrast, if some patches are sinks, then the negative per capita growth rate in the sinks can outweigh any benefits of dispersal. Including costs of dispersal in the single-species models can also result in a sedentary ESS despite spatially varying temporal fluctuations (Doebeli and Ruxton 1997).

When the predator-prey interactions are sufficiently unstable to cause the per capita growth rate in source habitats to fall substantially below the per capita growth rate in sink habitats, there is selection for dispersal into sink habitats, resulting in two additional possible evolutionary outcomes. First, if dispersal into the sink habitats is unable to stabilize the ecological dynamics, then there is an ESS for which all individuals (within the appropriate trophic

level) passively disperse between the sink habitats and the source habitats. One can view individuals playing this ESS as generalists using sink habitats to hedge their bets against moments of low fitness in source habitats (e.g., as a result of high predation rates or low prey availability). A high-dispersal ESS has been observed in single-species models when there are costs for dispersal (Doebeli and Ruxton 1997) or large differences in habitat quality (Kisdi 2002). For populations playing this ESS, the temporal averages of the per capita growth rates in source and sink habitats are negative despite the population persisting. This counterintuitive effect follows from spatial averaging of asynchronous per capita growth rates yielding a higher metapopulation growth rate than within-patch growth rates. This effect is similar to Jansen and Yoshimura's (1998) work on persistence of coupled sink populations. However, unlike Jansen and Yoshimura's example, where both habitats are required for persistence, our results indicate that only the loss of the source habitat results in the extinction of both species. In the terminology of Watkinson and Sutherland (1995), the high-dispersal ESS produces "pseudo-sink" populations in source habitats.

Second, sufficiently unstable predator-prey interactions in source habitats can lead populations to undergo evolutionary branching if dispersal into sinks habitats can stabilize these interactions. This branching culminates in an ESC of sedentary and dispersive individuals that resists invasion attempts from all other phenotypes. One can view
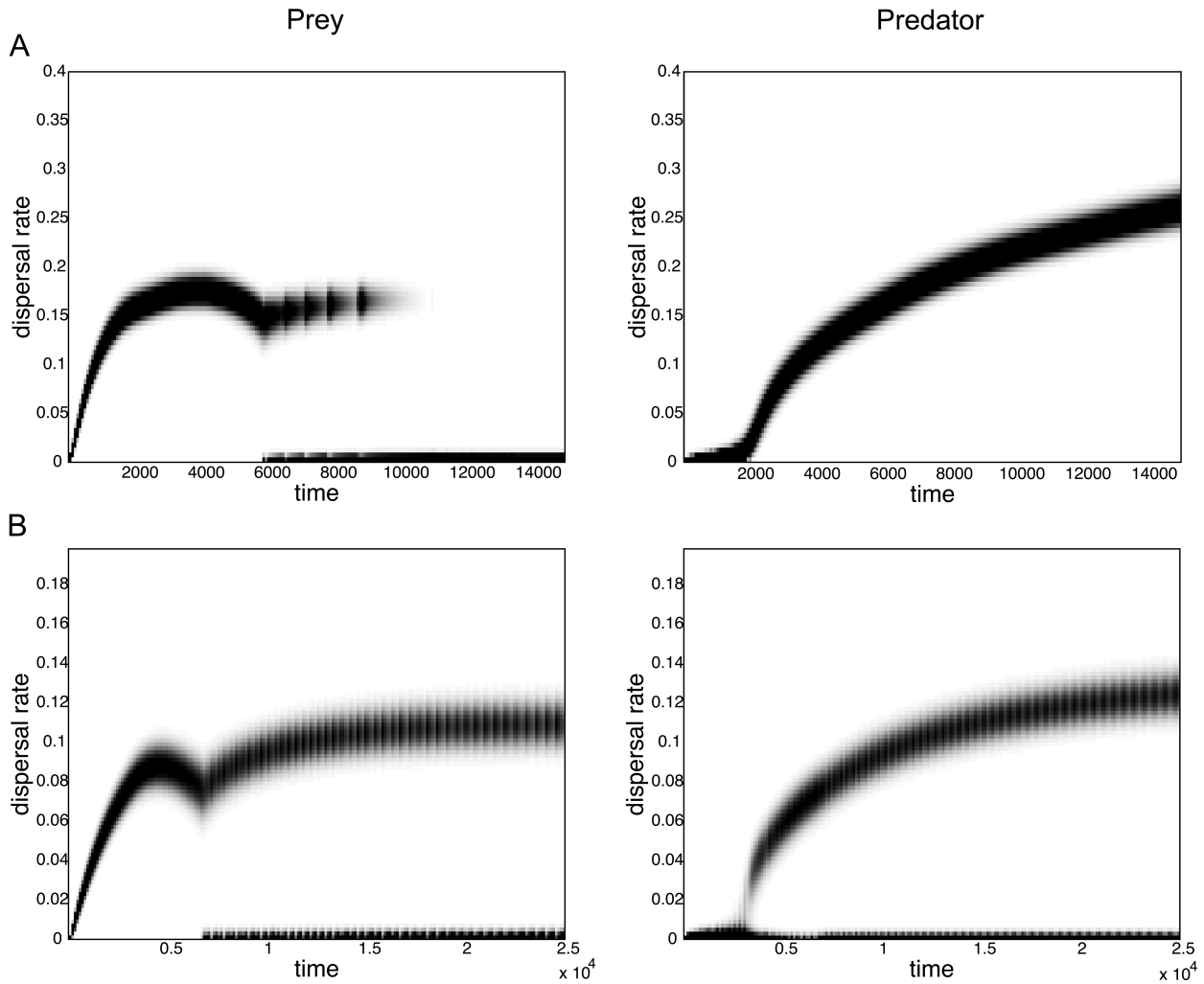
Prey

Predator

A

B

Figure 6: Coevolution of predator and prey sink populations. Prey and predator distributions are plotted against evolutionary time. *A*, Evolution of the predator disrupts evolutionary branching of the prey. *B*, Both predator and prey exhibit evolutionary branching. Parameter values common to *A* and *B* are $h = 0.05$, $a = 0.05$, $b_2 = 0.4$, $d_1 = d_2 = \delta_1 = 0.5$, $K_1 = 2,500$, and $s = \sigma = 10^{-4}$. In *A*, $c = 0.3$, $\delta_2 = 0.1$, and $b_1 = 3$. In *B*, $c = 0.1$, $\delta_2 = 0.25$, and $b_1 = 1.2$.

this ESC as coexistence between phenotypes that specialize on source habitats and generalist phenotypes that use both habitat types. Evolutionary branching of this sort has been extensively studied in single-species models (Doebeli and Ruxton 1997; Mathias et al. 2001; Kisdi 2002). In these models, the spatial-temporal fluctuations are driven either by overcompensating density dependence (Doebeli and Ruxton 1997) or by stochastic forcing (Mathias et al. 2001; Kisdi 2002). Unlike the high-dispersal ESS, this ESC has, on average, a negative per capita growth rate only in sink habitats, and, consequently, the ESC produces no pseudosink populations. While the mean dispersal rates of the two phenotypes supported by this ESC do not vary significantly over time, the fraction of high- versus low-

dispersal individuals can oscillate substantially due to feedbacks between the ecological dynamics and the evolutionary dynamics. Increasing frequencies of high-dispersal phenotypes stabilize the ecological dynamics and thereby increase selective pressures for specialists. Conversely, increasing frequencies of low-dispersal phenotypes destabilize the ecological dynamics and increase selective pressures for high-dispersal phenotypes. Doebeli and Ruxton (1997) observed similar feedbacks between ecological and evolutionary dynamics in single-species models with overcompensating density dependence. In their case, cyclic branching could be observed because of demographic stochasticity: generalist phenotypes would be lost as their densities waned, and evolutionary branching would reoc-
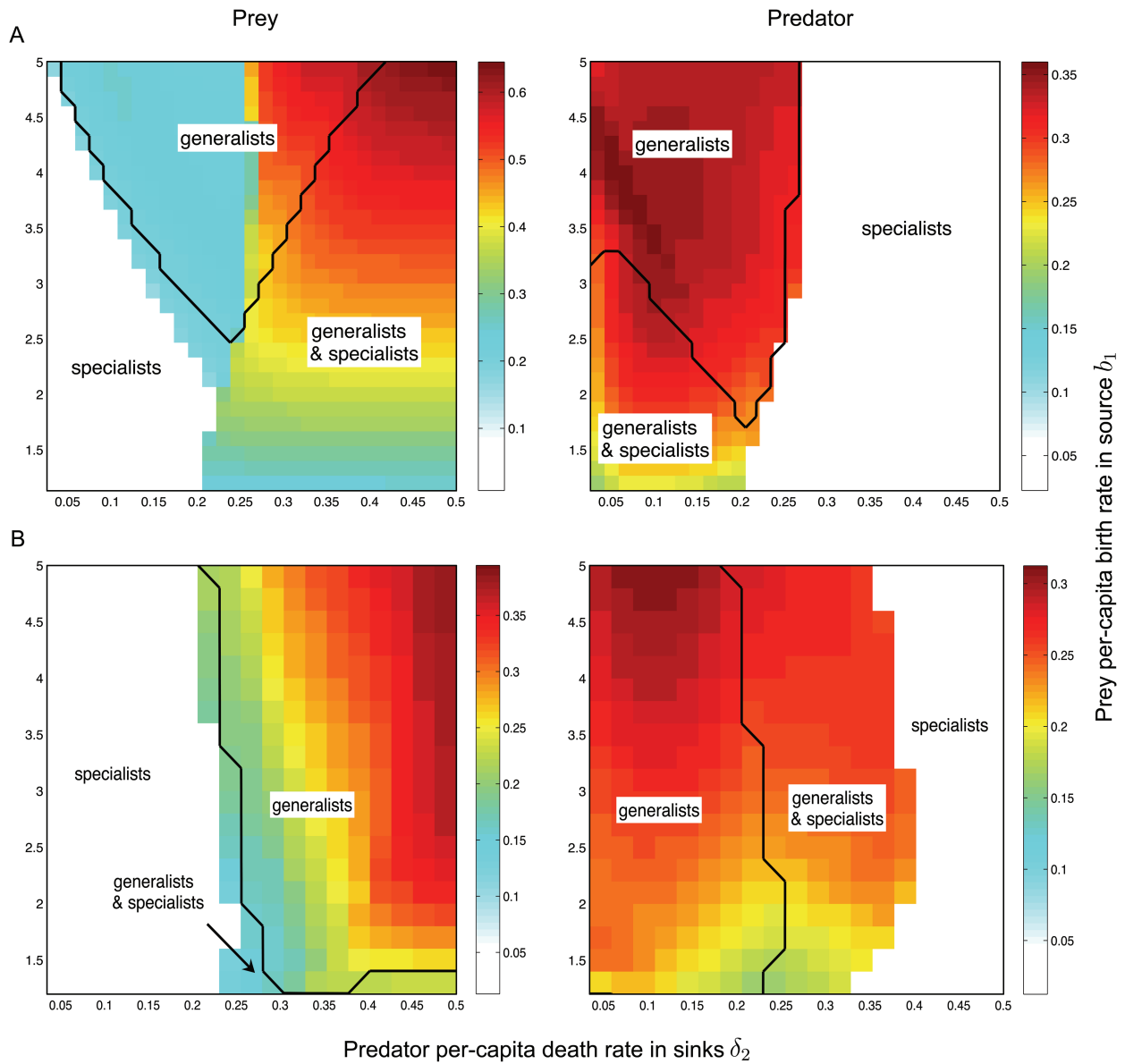
Figure 7: Coevolution of predator and prey sink populations. Warmer colors correspond to faster phenotypes. Regions corresponding to the three possible evolutionary outcomes within a trophic level are delineated. Parameter values common to all figures are $h = 0.05$, $a = 0.05$, $c = 0.3$, $d_1 = d_2 = \delta_1 = 0.5$, $K_1 = 2,500$, and $s = \sigma = 10^{-4}$. In *A*, $c = 0.3$. In *B*, $c = 0.1$.

cur. Similar phenomena could be observed in our simulations if thresholding is included to account for a minimal population density.

Our results highlight how different ecological factors can influence the evolution of dispersal within a trophic level. For ecological factors that tend to destabilize predator-prey interactions, maximal phenotypic diversity occurs at intermediate values of these factors. These destabilizing factors include predator handling times, predator

searching and conversion efficiencies, prey per capita birth rates in source habitats, and the number of available source sites. For instance, consider the effect of enriching source habitats by increasing the prey per capita birth rate in sources. At low levels of enrichment, the predator-prey interaction is stable, and, consequently, the evolutionary end state is a sedentary ESS. At high levels of enrichment, dispersal of either species to sink habitats is unable to stabilize the predator-prey interaction, and, consequently,

the evolutionary end state is a high-dispersal ESS. At intermediate levels of enrichment, the predator-prey interaction in the source habitat is unstable, but dispersal into the sink habitat can stabilize the interaction, and there is an ESC of low- and high-dispersal phenotypes. Hence, there is an evolutionary paradox of enrichment: enriching the source habitat too much can result in a loss of phenotypic diversity. One ecological factor, the per capita death rate in sinks, has a counterintuitive effect on the evolutionary and ecological dynamics. When there is dispersal into sink habitats, increasing the sink per capita death rate can destabilize the predator-prey interactions. Consequently, increasing mortality rates in the sink can favor an ESS of a high-dispersal phenotype despite ESCs being favored at lower mortality rates. We note that many of these conclusions also hold when the predator does not evolve but is allowed to disperse into sink habitats. In these circumstances, predator movement into the sink inhibits prey dispersal into sink habitats.

When the dispersal rates coevolve at both trophic levels, nine evolutionary outcomes corresponding to any combination of dispersal monomorphisms or dimorphisms at one or both trophic levels were observed. Coevolution is largely top-down driven in that the per capita death rate of the predator in sink habitats plays an important role in constraining the possible evolutionary outcomes. If this death rate is sufficiently low, then there is enough selection pressure for predator movement into sink habitats to forestall the evolution of prey sink populations. Alternatively, if the predator mortality rate in sinks is too high, the predators ultimately play a sedentary ESS and the evolution of the prey proceeds as if only the prey are evolving. At intermediate predator mortality rates, there is selection for predator and prey movement into sink habitats. Under these circumstances, the prey typically exhibit a high-dispersal ESS while the predators exhibit either a high-dispersal ESS or an ESC of low- and high-dispersal phenotypes. ESCs at both trophic levels, which yield the greatest phenotypic diversity, occur only under very restricted circumstances.

The diversity of evolutionary outcomes we observed is in stark contrast to what occurs when predators exhibit greater phenotypic plasticity (van Baalen and Sabelis 1999; Schreiber et al. 2006). For instance, van Baalen and Sabelis (1999) consider discrete-time models of predator-prey interactions in which both the predator and the prey can freely distribute their progeny between generations in response to population densities and environmental conditions. Under these conditions, there is a single ESS corresponding to an ideal free distribution: individuals are distributed such that their per capita fitness is equal in all occupied patches and lower in unoccupied patches (Fretwell and Lucas 1970). Persistent populations playing this density-dependent strategy exhibit chaotic dynamics. Consequently, while all individuals within a trophic level distribute their progeny across space in the same manner at any point in time, this distribution changes in time. In particular, van Baalen and Sabelis (1999) found that the populations move into sink habitats only during periods of low fitness in the source habitats. Consequently, in contrast to our findings, this high level of plasticity prevents the evolution of permanent sink populations and a diversity of phenotypes.

At species borders, sink habitats may be only marginally lower quality than neighboring habitats. Thus, our results suggest that the instability of predator-prey interactions may foster speciation near species borders. More precisely, evolutionary branching is likely whenever the per capita growth rate in the sinks is barely negative and the predator-prey interaction is unstable in source habitats. While we considered evolutionary branching only in a clonal model, evolutionary branching also occurs in diploid populations, provided that it co-occurs with the evolution of assortative mating within the phenotypic branches (Dieckmann and Doebeli 1999; Kisdi and Geritz 1999). The partial spatial segregation of the phenotypes following evolutionary branching in our models (i.e., one phenotype remains in source habitats while the other spends a fraction of its time outside of source habitats) is likely to reduce the number of recombination events and thereby facilitate the establishment of assortative mating (Mathias et al. 2001). Moreover, individuals dispersing into the sink habitat are likely to experience selective pressures to adapt to conditions in the sink habitats and thereby provide additional selective forces promoting speciation.

In conclusion, our study has examined the role of predator-prey interactions, a source of temporal variation, in the evolution of sink populations. In answering why sink populations evolve, we observed the significance of sufficiently unstable predator-prey interactions in source habitats in fostering movement into sink habitats. If such movement has a stabilizing effect on the predator-prey interactions, an ESC of sedentary and dispersive individuals can emerge at one or even both trophic levels. Hence, our simulations indicate that phenotypic diversity is one consequence of the evolution of sink populations, agreeing with the results of previous evolutionary studies (McPeek and Holt 1992; Doebeli and Ruxton 1997; Mathias et al. 2001; Kisdi 2002). The feedback mechanisms between ecological and environmental dynamics that we have detailed and quantified in our analysis play an important role in determining the degree of phenotypic diversity. Further examination of these mechanisms will help in understanding why sink populations evolve and why dispersal polymorphisms can persist in ecological communities.

Acknowledgments

Literature Cited

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

Amezcua, A. B., and M. Holyoak. 2000. Empirical evidence for predator-prey source-sink dynamics. Ecology 81:3087–3098.

Beers, C. D. 1925. Encystment and the life cycle in the ciliate *Didinium nasutum.* Proceedings of the National Academy of Sciences of the USA 11:523–528.

Chesson, P. L. 1978. Predator-prey theory and variability. Annual Review of Ecology and Systematics 9:323–347.

Cohen, D., and S. A. Levin. 1991. Dispersal in patchy environments: the effects of temporal and spatial structure. Theoretical Population Biology 39:63–99.

Delibes, M., P. Gaona, and P. Ferreras. 2001. Effects of an attractive sink leading into maladaptive habitat selection. American Naturalist 158:277–285.

Dias, P. C. 1996. Sources and sinks in population biology. Trends in Ecology & Evolution 11:326–330.

Dieckmann, U., and M. Doebeli. 1999. On the origin of species by sympatric speciation. Nature 400:354–357.

Dockery, J., V. Hutson, K. Mischaikow, and M. Pernarowski. 1998. The evolution of slow dispersal rates: a reaction diffusion model. Journal of Mathematical Biology 37:61–83.

Doebeli, M., and G. D. Ruxton. 1997. Evolution of dispersal rates in metapopulation models: branching and cyclic dynamics in phenotype space. Evolution 51:1730–1741.

Elton, C., and M. Nicholson. 1942. The ten-year cycle in numbers of the lynx in Canada. Journal of Animal Ecology 11:215–244.

Fretwell, S. D., and H. L. Lucas Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36.

Fussmann, G. F., S. P. Ellner, K. W. Shertzer, and N. G. Hairston Jr. 2000. Crossing the Hopf bifurcation in a live predator-prey system. Science 290:1358–1360.

Geritz, S. A. H., J. A. J. Metz, E. Kisdi, and G. Meszéna. 1997. Dynamics of adaptation and evolutionary branching. Physical Review Letters 78:2024–2027.

Hanski, I., P. Turchin, E. Korpimäk, and H. Henttonen. 1993. Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. Nature 364:232–235.

Harrison, M. A., Y. C. Lai, and R. D. Holt. 2001. Dynamical mechanism for coexistence of dispersing species. Journal of Theoretical Biology 213:53–72.

Hastings, A. 1983. Can spatial variation alone lead to selection for dispersal? Theoretical Population Biology 24:244–251.

Hastings, A., and T. Powell. 1991. Chaos in a three-species food chain. Ecology 72:896–903.

Hoffmann, A. A., and M. W. Blows. 1994. Species borders: ecological and evolutionary perspectives. Trends in Ecology & Evolution 9: 223–227.

Holt, R. D. 1985. Patch dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. Theoretical Population Biology 28:181–208.

———. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. Pages 77–88 *in* R. E. Ricklefs and D. Schluter, eds. Species diversity in ecological communities. University of Chicago Press, Chicago.

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

Holt, R. D., and R. Gomulkiewicz. 1997. How does immigration influence local adaptation? a reexamination of a familiar paradigm. American Naturalist 149:563–572.

Holt, R. D., and M. A. McPeek. 1996. Chaotic population dynamics favors the evolution of dispersal. American Naturalist 148:709–718.

Holt, R. D., M. Barfield, and A. Gonzalez. 2003a. Impacts of environmental variability in open populations and communities: "inflation" in sink environments. Theoretical Population Biology 64: 315–330.

Holt, R. D., R. Gomulkiewicz, and M. Barfield. 2003b. The phenomenology of niche evolution via quantitative traits in a "black-hole" sink. Proceedings of the Royal Society B: Biological Sciences 270: 215–224.

Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. Hilgardia 27:343–383.

Jansen, V. A. A., and J. Yoshimura. 1998. Populations can persist in an environment consisting of sink habitats only. Proceedings of the National Academy of Sciences of the USA 95:3696–3698.

Keagy, J., S. J. Schreiber, and D. A. Cristol. 2005. Replacing sources with sinks: when do populations go down the drain? Restoration Ecology 13:529–535.

Kimura, M. 1965. A stochastic model concerning the maintenance of genetic variability in quantitative characters. Proceedings of the National Academy of Sciences of the USA 54:731–736.

Kirkland, S., C. K. Li, and S. J. Schreiber. 2006. On the evolution of dispersal in patchy landscapes. SIAM Journal of Applied Mathematics 66:1366–1382.

Kisdi, E. 2002. Dispersal: risk spreading versus local adaptation. American Naturalist 159:579–596.

Kisdi, E., and S. A. H. Geritz. 1999. Adaptive dynamics in allele space: evolution of genetic polymorphism by small mutations in a heterogeneous environment. Evolution 53:993–1008.

Luckinbill, L. S. 1973. Coexistence in laboratory populations of *Paramecium aurelia* and its predator *Didinium nasutum.* Ecology 54: 1320–1327.

Mathias, A., E. Kisdi, and I. Olivieri. 2001. Divergent evolution of dispersal in a heterogeneous landscape. Evolution 55:246–259.

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

Metz, J. A. J., S. A. H. Geritz, G. Meszéna, F. J. A. Jacobs, and J. S. van Heerwaarden. 1996. Adaptive dynamics: a geometrical study of the consequences of nearly faithful reproduction. Pages 183–231 *in* S. J. van Strien and S. M. Verduyn-Lunel, eds. Stochastic and spatial structures of dynamical systems and their applications. Elsevier/North-Holland, Amsterdam.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

———. 1996. Sources and sinks: empirical evidence and population consequences. Pages 45–69 *in* O. E. Rhodes Jr., R. K. Chesser, and

M. H. Smith, eds. Population dynamics in ecological space and time. University of Chicago Press, Chicago.

Remeš, V. 2000. How can maladaptive habitat choice generate source-sink population dynamics? Oikos 91:579–582.

Robb, T., and M. V. Abrahams. 2002. The influence of hypoxia on risk of predation and habitat choice by the fathead minnow, *Pimephales promelas*. Behavioral Ecology and Sociobiology 52:25–30.

Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. Science 171:385–387.

Schmidt, K. A., J. M. Earnhardt, J. S. Brown, and R. D. Holt. 2000. Habitat selection under temporal heterogeneity: exorcizing the ghost of competition past. Ecology 81:2622–2630.

Schreiber, S. J., and M. Kelton. 2005. Sink habitats can alter ecological outcomes for competing species. Journal of Animal Ecology 74: 995–1004.

Schreiber, S. J., R. Lipcius, R. Seitz, and C. Long. 2006. Dancing between the devil and the deep blue sea: the stabilizing effect of enemy-free sinks and victimless sinks. Oikos 113:67–81.

van Baalen, M., and M. W. Sabelis. 1999. Nonequilibrium population dynamics of ideal and free prey and predators. American Naturalist 154:69–88.

Vierling, K. T. 2000. Source and sink habitats of red-winged blackbirds in a rural/suburban landscape. Ecological Applications 10: 1211–1218.

Watkinson, A. R., and W. J. Sutherland. 1995. Sources, sinks and pseudo-sinks. Journal of Animal Ecology 64:126–130.

Ylönen, H., R. Pech, and S. Davis. 2003. Heterogeneous landscapes and the role of refuge on the population dynamics of a specialist predator and its prey. Evolutionary Ecology 17:349–369.

Appendix A from S. J. Schreiber and E. Saltzman, "Evolution of Predator and Prey Movement into Sink Habitats"

(Am. Nat., vol. 174, no. 1, p. 68)

Equilibria and Stability

In this appendix, we derive the equilibria and stability conditions for the enemy-free sink and victimless sink models. These results are used to create the stability diagrams in the figures.

Ecological Stability of Enemy-Free Sinks

For ease of exposition, we consider the more general model,

$$\frac{dN_1}{dt} = N_1 f(N_1) - P_1 g(N_1) + m(N_2 - N_1),$$

$$\frac{dN_2}{dt} = r_2 N_2 + m(N_1 - N_2),$$

$$\frac{dP_1}{dt} = P_1 h(N_1),$$

where $f(N_1)$ is a decreasing function with $f(0) > 0$ and $f(N_1) < 0$ for N_1 sufficiently large and $g(N_1)$ and $h(N_1)$ are increasing functions with $g(0) = 0$, $h(0) < 0$.

At an equilibrium (N_1^*, N_2^*, P_1^*) supporting both species, we get

$$N_1^* = h^{-1}(0),$$

$$N_2^* = \frac{m}{m - r_2} N_1^* = \frac{m}{m - r_2} h^{-1}(0),$$

$$P_1^* = \frac{N_1^* f(N_1^*) + m(N_2^* - N_1^*)}{g(N_1^*)} = \frac{h^{-1}(0)\{f(N_1^*) + [r_2/(m - r_2)]\}}{g(N_1^*)}.$$

Because we assume that $r_2 < 0$, it follows that $N_2^* > 0$.

Linearizing about this equilibrium yields the Jacobian matrix

$$\mathbf{J} = \begin{bmatrix} \alpha & m & -g(N_1^*) \\ m & -\beta & 0 \\ P_1^* h'(N_1^*) & 0 & 0 \end{bmatrix},$$

where $\alpha = N_1^* f'(N_1^*) + f(N_1^*) - P_1^* g'(N_1^*) - m$ and $\beta = m - r_2$. According to the Routh-Hurwitz criteria, this equilibrium is linearly stable if the characteristic equation $\lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3 = 0$ satisfies the following conditions: $a_1 > 0$, $a_1 a_2 - a_3 > 0$, and $a_3 > 0$. The coefficients a_1 and a_3 are given by the negative of the trace and the negative of the determinant, respectively. Furthermore, a_2 is the sum of the determinants of three minors, as shown below:

1

$$a_1 = \beta - \alpha,$$

$$a_2 = \begin{vmatrix} \alpha & m \\ m & -\beta \end{vmatrix} + \begin{vmatrix} -\beta & 0 \\ 0 & 0 \end{vmatrix} + \begin{vmatrix} \alpha & -g(N_1^*) \\ P_1^* h'(N_1^*) & 0 \end{vmatrix}$$

$$= -\alpha\beta - m^2 + P_{1\delta}^* g(N_1^*) h'(N_1^*),$$

$$a_3 = \beta P_{1\delta}^* g(N_1^*) h'(N_1^*).$$

Because β is always positive and α is negative by assumption, the first Routh-Hurwitz condition is given by $a_1 = \beta - \alpha > 0$. Furthermore, the second condition is given by

$$a_1 a_2 - a_3 > 0 \Leftrightarrow -\alpha\beta^2 - \beta m^2 + \beta P_{1\delta}^* g(N_1^*) h'(N_1^*) + \alpha^2\beta + \alpha m^2$$

$$- \alpha P_{1\delta}^* g(N_1^*) h'(N_1^*) - \beta P_{1\delta}^* g(N_1^*) h'(N_1^*) > 0$$

$$\Leftrightarrow (\beta - \alpha)(\alpha\beta + m^2) < -\alpha P_{1\delta}^* g(N_1^*) h'(N_1^*).$$

Finally, the third Routh-Hurwitz condition is always true because $a_3 = \beta P_{1\delta}^* g(N_1^*) h'(N_1^*) > 0$.

Ecological Stability of Victimless Sinks

Here, we consider the more general model,

$$\frac{dN_1}{dt} = N_1 f(N_1) - P_1 g(N_1),$$

$$\frac{dP_1}{dt} = P_1 h(N_1) + \mu(P_2 - P_1),$$

$$\frac{dP_2}{dt} = -\delta_2 P_2 + \mu(P_1 - P_2),$$

where $f(N_1)$ is a decreasing function with $f(0) > 0$ and $f(N_1) < 0$ for N_1 sufficiently large and $g(N_1)$ and $h(N_1)$ are increasing functions with $g(0) = 0$, $h(0) < 0$. It can be shown that the equilibria supporting both species are given by

$$N_1^* = h^{-1}\left(\frac{\delta_2 \mu}{\delta_2 + \mu}\right),$$

$$P_1^* = \frac{N_1^* f(N_1^*)}{g(N_1^*)},$$

$$P_2^* = \frac{\mu}{\delta_2 + \mu} \frac{N_1^* f(N_1^*)}{g(N_1^*)}.$$

One can also write the Routh-Hurwitz conditions for this model. However, because they do not simplify substantially, we refrain from doing so.

Appendix B from S. J. Schreiber and E. Saltzman, "Evolution of Predator and Prey Movement into Sink Habitats"
(Am. Nat., vol. 174, no. 1, p. 68)

Invasion Exponents and Selection for Slower Dispersers

Invasion Exponents

To define the prey and predator invasion exponents, consider a prey-predator population, with abundances (N_1, N_2, P_1, P_2), that has been playing the dispersal strategy (m, μ) sufficiently long for the ecological dynamics to settle on its asymptotic state (e.g., an equilibrium or a periodic orbit). In the initial phase of their invasion, the dynamics of the mutant population are well approximated by the linear system of differential equations

$$
\begin{bmatrix} \dfrac{d\tilde{N}_1}{dt} \\[2mm] \dfrac{d\tilde{N}_2}{dt} \end{bmatrix} = \mathbf{A}_{\text{prey}}(t) \begin{bmatrix} \tilde{N}_1 \\[1mm] \tilde{N}_2 \end{bmatrix},
$$

where

$$
\mathbf{A}_{\text{prey}}(t) = \begin{bmatrix} b_1\left(1 - \dfrac{N_1(t)}{K_1}\right) - d_1 - \dfrac{aP_1(t)}{1 + haN_1(t)} - \tilde{m} & \tilde{m} \\[4mm] \tilde{m} & r_2 - \dfrac{aP_2(t)}{1 + haN_2(t)} - \tilde{m} \end{bmatrix}
$$

and ($N_1(t)$, $N_2(t)$, $P_1(t)$, $P_2(t)$) corresponds to the resident system. Let $\mathbf{\Phi}_{\text{prey}}(t)$ be a time-varying matrix such that $\mathbf{\Phi}_{\text{prey}}(0)$ is the identity matrix and $(d/dt)\mathbf{\Phi}_{\text{prey}} = \mathbf{A}_{\text{prey}}(t)\mathbf{\Phi}_{\text{prey}}$. Whenever the limit exists, we define the invasion exponent of the mutant prey as

$$
\mathcal{I}_{\text{prey}}(m, \tilde{m}) = \lim_{t \to \infty} \frac{1}{t} \ln \| \mathbf{\Phi}_{\text{prey}}(t) \| ,
$$

where $\| \mathbf{A}(t) \|$ denotes the operator norm of the fundamental matrix $\mathbf{\Phi}_{\text{prey}}(t)$. If the invasion exponent $\mathcal{I}_{\text{prey}}$ is positive (respectively, negative), then the mutant prey can (respectively, cannot) invade the resident population. If the resident population is at an equilibrium, then $\mathbf{A}(t)$ does not vary in time, and the invasion exponent is given by the stability modulus $\rho(\mathbf{A})$ of $\mathbf{A}$: the largest real part of the eigenvalues of $\mathbf{A}$ (see, e.g., Smith 1995).

We can define the predator invasion exponent in a similar manner. Namely, if a rare mutant population of predators the dispersal strategy $\tilde{\mu}$ appears in the resident population, then we define the predator invasion exponent as

$$
\mathcal{I}_{\text{pred}}(\mu, \tilde{\mu}) = \lim_{t \to \infty} \frac{1}{t} \ln \| \mathbf{\Phi}_{\text{pred}}(t) \| ,
$$

where $\mathbf{\Phi}_{\text{pred}}(0)$ is the identity matrix, $(d/dt)\mathbf{\Phi}_{\text{pred}} = \mathbf{A}_{\text{pred}}(t)\mathbf{\Phi}_{\text{pred}}$, and

$$\mathbf{A}_{\mathrm{pred}}(t) = \begin{bmatrix} \dfrac{\theta a N_1(t)}{1 + ha N_1(t)} - \delta_1 - \tilde{\mu} & \tilde{\mu} \\[2ex] \tilde{\mu} & \dfrac{\theta a N_2(t)}{1 + ha N_2(t)} - \delta_2 - \tilde{\mu} \end{bmatrix}.$$

Selection against Dispersal

Here, we provide a general argument for the evolution of slower dispersers in temporally homogenous environments with n patches. Consider a one-parameter family of matrices

$$\mathbf{B}(\tilde{m}) = \mathbf{D} + \tilde{m}\mathbf{M},$$

where $\mathbf{D}$ is a nonscalar $n \times n$ diagonal matrix and $\mathbf{M}$ is an irreducible matrix with zero column sums and nonnegative off-diagonal elements. One should think of the diagonal entries of $\mathbf{D}$ corresponding to the per capita growth rates in the different patches. The off-diagonal entries of $\mathbf{M}$ correspond to normalized per capita immigration rates, and the diagonal entries of $\mathbf{M}$ correspond to normalized per capita emigration rates.

For example, the invasion exponent for the prey is determined by the matrix

$$\mathbf{A} = \begin{bmatrix} b_1\left(1 - \dfrac{N_1}{K_1}\right) - d_1 - \dfrac{aP_1}{1 + ha N_1} - \tilde{m} & \tilde{m} \\[2ex] \tilde{m} & r_2 - \dfrac{aP_2}{1 + ha N_2} - \tilde{m} \end{bmatrix},$$

and this matrix can be rewritten as

$$\mathbf{A} = \underbrace{\begin{bmatrix} b_1\left(1 - \dfrac{N_1}{K_1}\right) - d_1 - \dfrac{aP_1}{1 + ha N_1} & 0 \\[2ex] 0 & r_2 - \dfrac{aP_2}{1 + ha N_2} \end{bmatrix}}_{\mathbf{D}} + \tilde{m}\underbrace{\begin{bmatrix} -1 & 1 \\ 1 & -1 \end{bmatrix}}_{\mathbf{M}}.$$

Under equilibrium conditions for the resident population, the per capita growth rates are positive in patch type 1 and negative in patch type 2. Hence, $\mathbf{D}$ is not a scalar matrix.

We will show that the stability modulus $\rho(\mathbf{B}(\tilde{m}))$ of $\mathbf{B}(\tilde{m})$ is a strictly decreasing function of m. In the case of our models, this fact implies that the invasion exponent $\mathcal{I}_{\mathrm{prey}}(m, \tilde{m})$ is a decreasing function of $\tilde{m}$ whenever the resident population playing strategy m is at equilibrium. Because $\mathcal{I}_{\mathrm{prey}}(m, m) = 0$, it follows that $\mathcal{I}_{\mathrm{prey}}(m, \tilde{m}) < 0$ whenever $\tilde{m} > m$ and $\mathcal{I}_{\mathrm{prey}}(m, \tilde{m}) > 0$ whenever $\tilde{m} < m$. In other words, the faster dispersers cannot invade the equilibrium determined by the slower dispersers, while slower dispersers can invade the equilibrium determined by faster dispersers. This implication is biologically meaningful only when the equilibrium determined by the resident populations is stable. A similar argument applies to the predator invasion rates.

Let $f(\tilde{m}) = \rho(\mathbf{B}(\tilde{m}))$. We will show that $f'(\tilde{m}) < 0$. Given any $\tilde{m} = x > 0$, choose $a > 0$ such that $ax\mathbf{I} \ge \min\{D, 0\} + x\min\{M, 0\}$, where $\mathbf{I}$ is the $n \times n$ identity matrix. Define

$$\boldsymbol{\Lambda} = \frac{1}{x}\mathbf{D} + a\mathbf{I},$$

$$g(t) = \rho(\boldsymbol{\Lambda} + t\mathbf{M}).$$

Our choice of a and our assumption that $\mathbf{M}$ is irreducible imply that $\mathbf{M} + \boldsymbol{\Lambda}$ is a nonnegative irreducible matrix. Moreover, because the column sums of $\mathbf{M}$ are 0, the column sums of $\mathbf{M} + \boldsymbol{\Lambda}$ equal the diagonal entries of $\boldsymbol{\Lambda}$. The following Lemma from Kirkland et al. (2006), applied to $\boldsymbol{\Lambda} + t\mathbf{M} = (1 - t)\boldsymbol{\Lambda} + t(\mathbf{M} + \boldsymbol{\Lambda})$, implies that $g'(1) < 0$.

Lemma. Suppose that $\mathbf{A}$ is an irreducible nonnegative matrix, and let $\mathbf{D_A}$ be the diagonal matrix of column sums of $\mathbf{A}$. Let $\mathbf{\Lambda}$ be a diagonal matrix such that $\mathbf{\Lambda} \geq \mathbf{D_A}$. For $0 \leq t \leq 1$, let $h(t) = \lambda[(1 - t)\mathbf{\Lambda} + t\mathbf{A}]$. Then $h'(1) < 0$.

Because

$$
\begin{aligned}
g(t) &= \frac{\rho(x\mathbf{\Lambda} + tx\mathbf{M})}{x} \\[2mm]
&= \frac{\rho(\mathbf{D} + ax\mathbf{I} + tx\mathbf{M})}{x} \\[2mm]
&= \frac{\rho(\mathbf{D} + tx\mathbf{M})}{x} + a \\[2mm]
&= \frac{f(xt)}{x} + a,
\end{aligned}
$$

it follows that $g'(1) = f'(x) < 0$. Because $x = \tilde{m} > 0$ was arbitrary, $f(\tilde{m})$ is a decreasing function of $\tilde{m} > 0$ as claimed.

Literature Cited Only in Appendix B

Smith, H. L. 1995. Monotone dynamical systems: an introduction to the theory of competitive and cooperative systems. Mathematical Surveys and Monographs. Vol. 41. American Mathematical Society, Providence, RI.

Appendix C from S. J. Schreiber and E. Saltzman, "Evolution of Predator and Prey Movement into Sink Habitats"

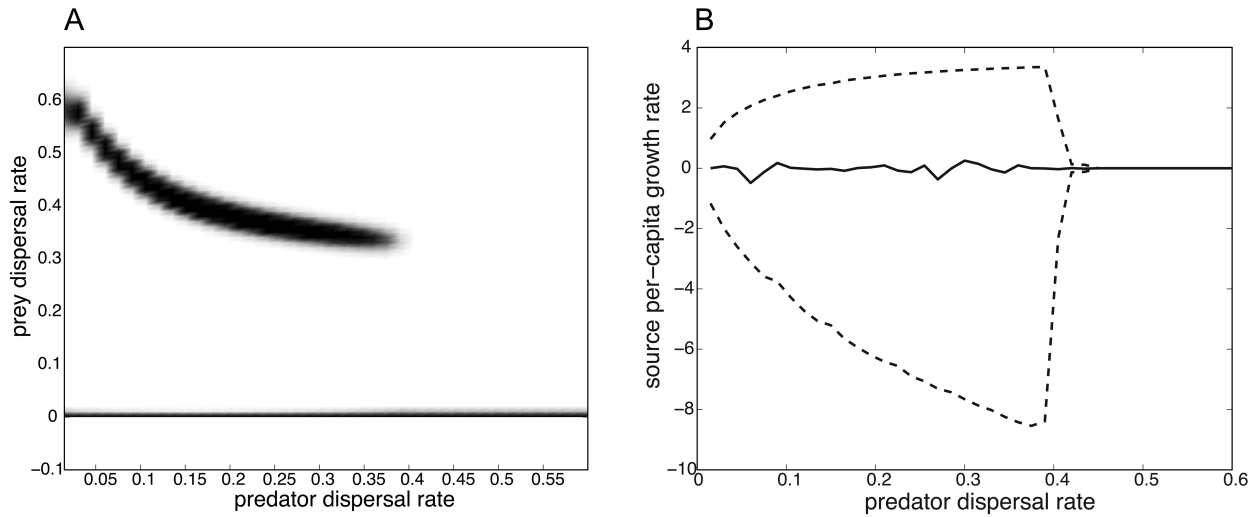## Predator Movement and Prey Evolution

Figure C1: Effects of predator movement on the evolution of prey movement into sinks. For each parameter value, evolutionary dynamics were simulated for 25,000 time steps. *A*, Plot of temporal average of the distribution of dispersal phenotypes in the last 2,500 time steps. *B*, Plot of minimum, average, and maximum per capita growth of the prey in the last 2,500 time steps. Parameter values are $b_1 = 5$, $b_2 = 0.4$, $d_1 = d_2 = 0.5$, $K_1 = 1,500$, $h = 0.02$, $a = 0.1$, $\theta = 0.3$, $\delta_1 = 0.5$, and $s = 10^{-4}$.