

Bad neighbors: how spatially disjunct habitat degradation can cause system-wide population collapse

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Abstract. Movement of individuals links the effects of local variation in habitat quality with growth and persistence of populations at the landscape scale. When the populations themselves are linked by interspecific interactions, such as predation, differential movement between habitats may lead to counterintuitive system-wide dynamics. Understanding the interaction between local drivers and dynamics of widely dispersed species is necessary to predict the impacts of habitat fragmentation and degradation, which may be transmitted across habitat boundaries by species' movements. Here we model predator–prey interactions across unaltered and degraded habitat areas, and we explore the additional effects of adaptive habitat choice by predators on the resilience of prey populations. We show how movement between habitats can produce the “bad neighbor effect,” in which predators' response to localized habitat degradation causes system-wide loss of prey populations. This effect arises because adaptive foraging results in the concentration of predators in the more productive unaltered habitat, even when this habitat can not support the increased prey mortality. The mechanisms underlying this effect are especially sensitive to prey dispersal rate and adaptive predator behavior.

Key words: associational effects; dispersal; evolutionary stable strategy; extinction; model; movement; predation; source–sink; spatial heterogeneity.

INTRODUCTION

Movement of organisms between habitats has led to many ways in which ecologists conceptualize and study interactions in spatially structured populations, e.g., metapopulations, source–sink dynamics, and island biogeography (MacArthur and Wilson 1963, Levins 1969, Pulliam 1988, Polis et al. 1997). The intuitive prediction that dispersal of individuals between habitat patches reduces the risk of system-wide extinction has been formalized in metapopulation theory (reviewed in Hanski 1991). However, connectivity can entail costs as well as benefits, e.g., by spreading diseases (Hess 1996), losing individuals to sink populations (Delibes et al. 2001, Cronin 2007), and increasing population-wide extinction risk by synchronizing temporal dynamics (Earn et al. 1998). With increasing habitat fragmentation and degradation by human activity, we might expect the effects of movement among habitats of different quality to be increasingly pronounced (e.g., Honnay and Jacquemyn 2007, Cheptou et al. 2008, Alfred et al. 2012, Gauffre et al. 2015); therefore it is imperative that we understand the conditions that lead to unintended or unexpected population-level outcomes.

In addition to the within-species effects of dispersal, movement among habitat patches can transmit effects between predators and prey (e.g., White 2008, Orrock et al. 2010, 2013). Indeed, rapidly degraded habitat can

export predators that strongly affect patches of otherwise good quality prey habitat; we dub this the “bad neighbor effect.” The bad neighbor effect is essentially an extension of the concept of associational effects whereby the proximity of other organisms can affect a focal species' vulnerability to predation or parasitism and contribute to net ecological and evolutionary dynamics (Barbosa et al. 2009, Underwood et al. 2014). For example, Lenihan et al. (2001) found that lower trophic levels on North Carolina (USA) oyster reefs in well-mixed shallow water were overwhelmed by mobile predators escaping seasonal hypoxic events on deep-water reefs. Similarly, invasion of the seaweed *Caulerpa taxifolia* in estuaries of southeastern Australia has excluded clams from much of the soft-sediment habitat. Now, predators such as rays and crabs concentrate on the remaining patches of bare sediment, which would otherwise be high-quality clam habitat (Byers et al. 2010).

The examples cited above demonstrate that persistence of populations in high-quality habitat can be tightly linked to the quality of surrounding habitat by the behavioral response of mobile predators. A large body of general theory has been developed to predict the consequences of habitat heterogeneity and individual movement on population dynamics. In single-species density-independent models, dispersal into low-quality habitat patches reduces the overall population growth rate relative to its value in high-quality patches (Doak 1995, Gerber et al. 2005, Teller et al. 2015). The effect of density dependence within patches depends on assumptions regarding dispersal behavior. For example, Holt (1985) assumed that

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individuals have a constant per capita dispersal rate, and showed that increasing dispersal rate could increase equilibrium density by lowering competition in high-quality habitat while subsidizing low-quality habitat. On the other hand, Pulliam (1988) assumed all individuals remain in high-quality source habitat if density there is below carrying capacity, and only individuals in excess of source carrying capacity disperse to sink habitat. With these assumptions, the predicted abundance in source habitat remains at carrying capacity regardless of the amount of sink habitat. More recent models of predator-prey dynamics have examined the consequences of adaptive predator movement on equilibrium stability and the convergence to an evolutionary stable strategy (e.g., Křivan 1997, 2013, Abrams 2007, Abrams et al. 2007, Abrams and Ruokolainen 2011, Ruokolainen et al. 2011). However, little attention has been paid to the effects of adaptive movement behavior on equilibrium abundance over a heterogeneous landscape when the composition of the habitat varies.

We ask how adaptive habitat selection by predators influences prey density as the area of degraded habitat increases, and how the predictions depend on prey movement rate. In order to focus on the effects of adaptive predator behavior, we assume prey move passively and settle in degraded and unaltered habitat in proportion to their areas (consistent with, e.g., wind- or water-dispersed organisms). We then compare the effects of increasing degraded habitat area when predators forage at random vs. predators that move so as to maximize their foraging success. We show that if predators adopt the evolutionary stable strategy (ESS) that maximizes their individual success, the bad neighbor effect reverses the predicted effect of prey movement and exacerbates prey decline in response to increasing habitat degradation.

MODEL

We classify habitat into two states, unaltered and degraded, and we denote the fraction of total area in the degraded state with the parameter a . Prey abundance in unaltered habitat at time t is denoted $N_u(t)$, and prey abundance in degraded habitat is $N_d(t)$. Total predator abundance is $P(t)$, and a fraction c of the total forage in degraded habitat. The fraction of prey killed by predators depends on predator attack rate (α) and density in each habitat. If we scale habitat area by the total area (i.e., total area = 1), then predator densities in unaltered and degraded habitats are $(1 - c)P(t)/(1 - a)$ and $cP(t)/a$, respectively. Fractions of prey killed in the two habitat types are

$$f_u(t) = 1 - e^{-\alpha(1-c)P(t)/(1-a)} \tag{1}$$

$$f_d(t) = 1 - e^{-\alpha cP(t)/a} \tag{2}$$

We use the Beverton-Holt function to model density-dependent prey population dynamics in each habitat type. Density dependence acts on prey that survive predation

$$g_i((1-f_i(t)) N_i(t)) = \frac{r_i (1-f_i(t)) N_i(t)}{1 + b_i (1-f_i(t)) N_i(t)} \tag{3}$$

for habitat $i = u$ or d . The parameter r_i denotes maximum per capita growth of the prey population, and b_i represents the strength of density dependence. We assume b_i is inversely proportional to area of habitat type i : $b_u = B/(1 - a)$ and $b_d = B/a$, where B is the coefficient of proportionality. The key difference between habitat types is in the values of r_u and r_d : we model habitat degradation by lower prey maximum per capita growth ($r_d < r_u$), which represents lower prey productivity in degraded habitat.

The fraction m_u of prey produced in degraded habitat move to unaltered habitat at each time step. Similarly, the fraction m_d of prey produced in unaltered habitat move to degraded habitat. Prey population dynamics in the two habitat types are therefore

$$N_u(t + 1) = g_u((1-f_u(t)) N_u(t)) (1 - m_d) + g_d((1-f_d(t)) N_d(t)) m_u \tag{4}$$

$$N_d(t + 1) = g_d((1-f_d(t)) N_d(t)) (1 - m_u) + g_u((1-f_u(t)) N_u(t)) m_d \tag{5}$$

We assume that the fraction μ of all prey produced enter a “disperser pool,” and settlement of these dispersers into each habitat type is proportional to area; hence, $m_u = \mu(1 - a)$ and $m_d = \mu a$.

The sum of surviving predators and predator offspring in the next time step is proportional to the number of prey killed

$$P(t + 1) = \varepsilon (f_u(t)N_u(t) + f_d(t)N_d(t)) \tag{6}$$

for constant ε that represents the conversion efficiency of prey into predators. Unlike prey, the distribution of predators between the two habitat types does not depend directly on where predator reproduction or survival occurs. This corresponds to relatively rapid predator movement between habitats, with c representing, e.g., the fraction of time each predator spends in degraded habitat.

The model can be simplified somewhat by rescaling the state variables: $n_u(t) = BN_u(t)$, $n_d(t) = BN_d(t)$, and $p(t) = BP(t)/\varepsilon$, and using the parameter combination $\nu = \alpha\varepsilon/B$, which represents prey vulnerability. The scaled model equations are described in Appendix S1, and we list them in Table 1. We used the scaled equations to obtain all of our numerical results with the R 3.2.0 software (R Core Team 2015; see Appendix S2).

We consider two scenarios that differ in the relative speed at which predator and prey populations respond to habitat alteration. First, we model the case in which prey populations respond rapidly to habitat conditions, whereas the predator population remains constant (slow predator dynamics). We simulate this scenario by setting the prey populations to their equilibria (n_u^* , n_d^*) for each value of a . The predator population remains fixed at its

TABLE 1. Scaled model equations: $n_u(t) = BN_u(t)$, $n_d(t) = BN_d(t)$, and $p(t) = BP(t)/\epsilon$, with the parameter combination $v = \alpha\epsilon/B$; the fractions that disperse are $m_u = \mu(1 - a)$ and $m_d = \mu a$.

Description	Equation
Prey population dynamics in unaltered habitat	$n_u(t+1) = g'_u \left((1 - f'_u(t)) n_u(t) \right) (1 - m_d) + g'_d \left((1 - f'_d(t)) n_d(t) \right) m_u$
Prey population dynamics in degraded habitat	$n_d(t+1) = g'_d \left((1 - f'_d(t)) n_d(t) \right) (1 - m_u) + g'_u \left((1 - f'_u(t)) n_u(t) \right) m_d$
Predator population dynamics	$p(t+1) = f'_u(t)n_u(t) + f'_d(t)n_d(t)$
Density-dependent prey population growth in unaltered habitat	$g'_u \left((1 - f'_u(t)) n_u(t) \right) = \frac{r_u(1 - f'_u(t))n_u(t)}{1 + \frac{1}{1-v}(1 - f'_u(t))n_u(t)}$
Density-dependent prey population growth in degraded habitat	$g'_d \left((1 - f'_d(t)) n_d(t) \right) = \frac{r_d(1 - f'_d(t))n_d(t)}{1 + \frac{1}{1-v}(1 - f'_d(t))n_d(t)}$
Fraction of prey killed by predators in unaltered habitat	$f'_u(t) = 1 - e^{-v(1-c)p(t)/(1-a)}$
Fraction of prey killed by predators in degraded habitat	$f'_d(t) = 1 - e^{-vp(t)/a}$

Note: Parameters are defined in *Model* and Appendix S1.

equilibrium (p^*) for $a = 0$ as the fraction of degraded habitat increases. This represents a predator species that has a long generation time relative to the degradation process, or a transient response to rapid habitat degradation (as in Lenihan et al. [2001]). In our second model scenario, the abundance of both predators and prey respond rapidly to habitat alteration (fast predator dynamics). In this scenario, we calculate the simultaneous equilibrium for prey and predator populations for each value of a . In both scenarios, we do not model the habitat degradation process explicitly. Instead, we simply ask how equilibrium prey and predator (in the second scenario) abundances respond to increasing fraction of degraded habitat, a .

In each scenario, we determine the effects of adaptive predator behavior by first finding the equilibrium prey densities when predators forage at random over the two habitat types ($c = a$, i.e., predator density is equal in both habitats). We then suppose predators move between habitat types to maximize prey killed per predator when the prey population is at equilibrium, and thus, predators concentrate where prey density is greater regardless of habitat. We calculate the predator payoffs by dividing the number of prey killed ($f'_u(t)$ and $f'_d(t)$) multiplied by n_u^* and n_d^* , respectively; see Table 1) by the number of predators foraging in unaltered ($(1 - c)p^*$) and degraded (cp^*) habitat. We find the evolutionary stable strategy (ESS) for the predator distribution, $c = \hat{c}$, at which no individual predator can increase its payoff when the predator population is at the ESS. This implies that individual payoffs must be equal in both habitats, otherwise an adaptive predator could increase its payoff by moving from the worse to the better habitat. Furthermore, because individual payoffs are maximized, any deviation from the ESS must be disadvantageous for the individual predator. For example, when the predators are at $c = \hat{c}$, increasing c increases the payoff in unaltered relative to degraded habitat and vice versa.

In the first scenario (slow predator dynamics), predator population size is fixed at its equilibrium for $a = 0$ but prey populations respond to both a and the predator distribution, c . The value $c = \hat{c}$ is an evolutionary stable

strategy equivalent to an ideal free distribution for a fixed number of foragers (Fretwell and Lucas 1969, Cressman and Křivan 2006). In the second scenario (fast predator dynamics), predator population size responds to a via changes in prey population size in each habitat, which in turn depends on both a and consumption by predators. Hence, we find the ESS value \hat{c} such that predator and prey densities are simultaneously at equilibrium.

We present numerical solutions for the population equilibria and ESS over the range of values of fraction degraded habitat ($0 \leq a \leq 1$) and dispersal ($0 \leq \mu \leq 1$). Because analytic solutions are not possible, we use the baseline parameter values in Table 2, which reflect the following broad constraints. We selected the baseline values of r_u and v such that prey and predators can coexist at equilibrium if all habitat is unaltered. For $a = 0$, the predator equilibrium is positive if predators can increase when rare (i.e., $p(t + 1)/p(t) > 1$ for small $p(t)$) and prey are at equilibrium. If $p(t)$ is small, $p(t + 1)/p(t) \approx m_u^*$ with $n_u^* = r_u - 1$ when $a = 0$ (see Table 1 and Appendix S1). The resulting condition is $p^* > 0$ if $p(t + 1)/p(t) > 1$, or $r_u > 1 + 1/v$. As noted above, lower prey productivity in degraded habitat implies $r_d < r_u$. We also assume prey can persist in degraded habitat in the absence of predators ($r_d \geq 1$); however, when predators are at their equilibrium for entirely unaltered habitat and forage at random ($c = a$), the degraded habitat is a sink, i.e., prey can not persist in degraded habitat at equilibrium without immigration from unaltered habitat. This implies $r_d \exp(-vp^*) < 1$, where p^* is the equilibrium for $a = 0$ (see Appendix S1). We demonstrate the general patterns with the baseline parameter values, and we show how the quantitative outcomes are influenced by parameter variation in Appendix S3.

RESULTS

Fixed predator population

We begin with the simpler scenario of slow predator dynamics in which the total number of predators in the system is held at its equilibrium value calculated when the

TABLE 2. Model parameters and baseline values for numerical solutions.

Parameter	Baseline value	Description
v	10	Scaled prey vulnerability
r_u	1.5	Maximum prey per capita growth rate in unaltered habitat
r_d	1.2	Maximum prey per capita growth rate in degraded habitat
a	varied	Fraction of habitat area in degraded state
μ	varied	Fraction of prey that enter disperser pool
c	varied	Fraction of predator population in degraded habitat

habitat is completely unaltered ($a = 0$). Habitat degradation (increasing a) converts area from high to low prey productivity ($r_d < r_u$). Because total abundance of predators does not decrease with deteriorating conditions for prey, the predators can drive prey extinct ($n_u^* = n_d^* = 0$) at high a in this scenario. Regardless of other parameter values, if some prey disperse between habitats ($\mu > 0$), then $n_u(t + 1) = 0$ only if $n_d(t) = 0$, and vice versa. This implies that when $\mu > 0$ the parameter values for which prey go extinct are identical for the two habitats, and we can solve for a single prey extinction boundary in parameter space.

In the absence of adaptive habitat selection by predators (i.e., random foraging), increasing a lowers the equilibrium prey density (Fig. 1a). However, the rate of prey decline with increasing a depends on dispersal. Prey are driven extinct with the least amount of habitat degradation if prey move rapidly between habitat types (high μ). For the maximum value $\mu = 1$ (top edge of Fig. 1a), the value of a at which extinction occurs can be found by linearizing the prey population dynamics around $n_u(t) = n_d(t) = 0$. Extinction occurs when the prey can not grow from low abundance, i.e., when the dominant eigenvalue of the linearized equations is less than 1. The result is the condition $((1 - a)r_u + ar_d)e^{-vp^*} < 1$ for prey extinction at $\mu = 1$ (see Appendix S1). This condition implies that when the prey population is effectively well-mixed (large μ), prey are driven extinct when the area-weighted average productivity $((1 - a)r_u + ar_d)$ becomes insufficient to withstand predation.

At lower prey dispersal, the two habitats act as increasingly isolated prey populations, which allows them to withstand greater habitat degradation (larger threshold a for extinction; Fig. 1a). This occurs because per capita predation rate is constant (with $c = a$, $f_u^*(t) = f_d^*(t)$; see Table 1), whereas lower dispersal causes the prey population to build up in the more productive unaltered habitat. For example, Fig. 2 shows the prey equilibria for a fixed fraction of degraded habitat ($a = 0.3$) over the range of values of prey dispersal (μ). As dispersal decreases,

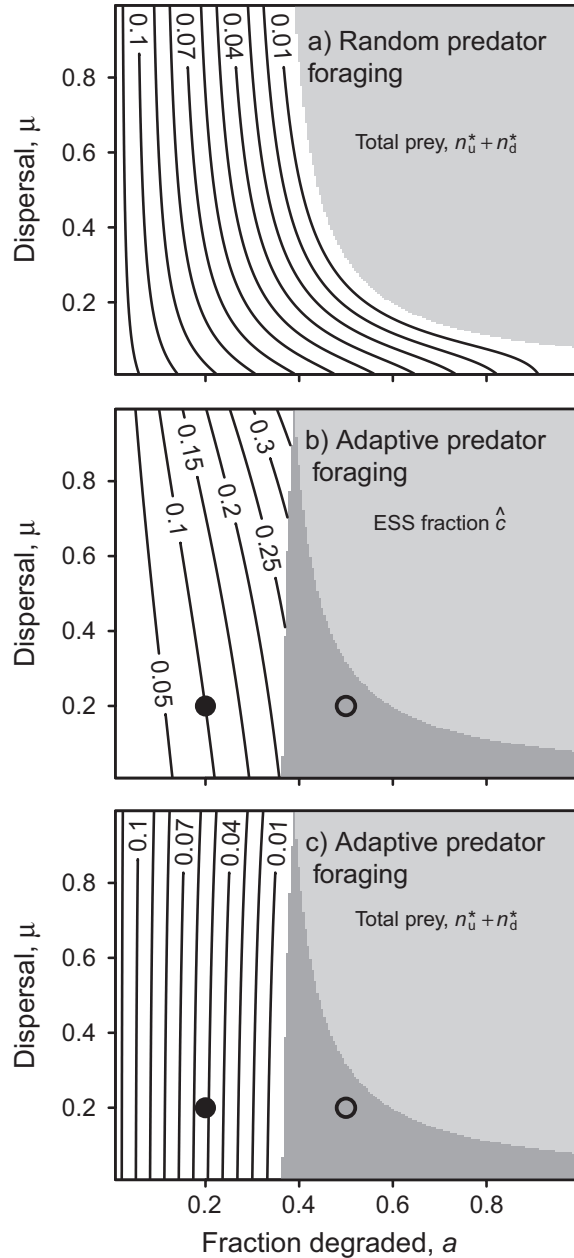


FIG. 1. Predictions of the model with fixed predator density. (a) Total prey equilibrium density at unaltered and degraded sites ($n_u^* + n_d^*$) if predators forage at random ($c = a$). (b) Evolutionary stable strategy (ESS) fraction of predators in degraded habitat (\hat{c}) if predators adopt the ESS distribution. (c) Total prey equilibrium density if predators adopt the ESS distribution. Light gray area indicates parameter space where prey cannot persist ($n_u^* = n_d^* = 0$) if predators forage at random. Dark gray areas (in panels b and c) indicate additional parameter space where prey are driven extinct if predators adopt the ESS. In panels b, c, solid and open circles indicate points for which predator payoffs are plotted in Fig. 3.

prey abundance increases in unaltered habitat. This initially produces a larger total number of dispersers into degraded habitat and, despite lower μ , the equilibrium n_d^*

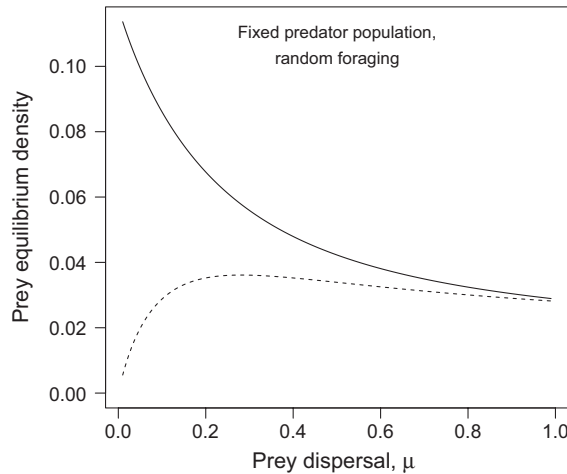


FIG. 2. Prey equilibrium density for the model with fixed predator density when predators forage at random and $a = 0.3$. Solid line indicates prey density in unaltered habitat and dashed line indicates prey density in degraded habitat.

increases slightly as well. For sufficiently low dispersal, n_d^* decreases and approaches zero when all immigration is cut off at $\mu = 0$. However, at low μ the buildup of prey in unaltered habitat buffers the prey population against extinction over a greater range of habitat degradation.

For sufficiently low dispersal, prey can persist for any $a < 1$ (lower edge of Fig. 1a). If μ is small and a is large, the number of immigrants from degraded to unaltered habitat is negligible and the equilibrium in unaltered habitat is approximately $n_u^* \approx (r_u e^{-vp^*}(1 - \mu a) - 1)/e^{-vp^*}$. The equilibrium is therefore positive if

$$\mu < \frac{1}{a} \left(1 - \frac{1}{r_u e^{-vp^*}} \right) \tag{7}$$

with large a (see Appendix S1). The condition that prey can persist with predators when all habitat is unaltered implies $r_u e^{-vp^*} > 1$. Hence, the inequality in Eq. 7 must be true for sufficiently small μ , i.e., there is a threshold value of μ below which prey persist even at large a . (For the baseline parameter values in Table 2, the threshold is $\mu \approx 0.078$ as a approaches 1.) The general prediction is therefore that when predators forage at random, low prey dispersal buffers prey from extinction by stemming losses to dispersal into the degraded (sink) habitat.

Adaptive predator behavior changes the quantitative and qualitative predictions for the effects of prey dispersal on persistence. First, at high prey dispersal rate ($\mu = 1$), the prey population is well-mixed and predators can not increase payoffs by deviating from random foraging. Hence, the ESS value \hat{c} increases in tandem with increasing a and the extinction boundary is identical for adaptive and random predators (upper edge of Fig. 1b). If $\mu < 1$, however, adaptive predator behavior causes prey extinction at a lower fraction of degraded habitat (the extinction boundary shifts to the left in Fig. 1b, c).

Moreover, decreasing prey dispersal results in decreasing the threshold of a for extinction, opposite the prediction when predators forage at random.

The underlying mechanism for the change in predicted effects of decreasing prey dispersal depends on the feedback between prey dynamics and the response of predators. If prey disperse slowly, the buildup of prey in unaltered habitat that occurs if predators forage at random (Fig. 2) implies that individual predators can

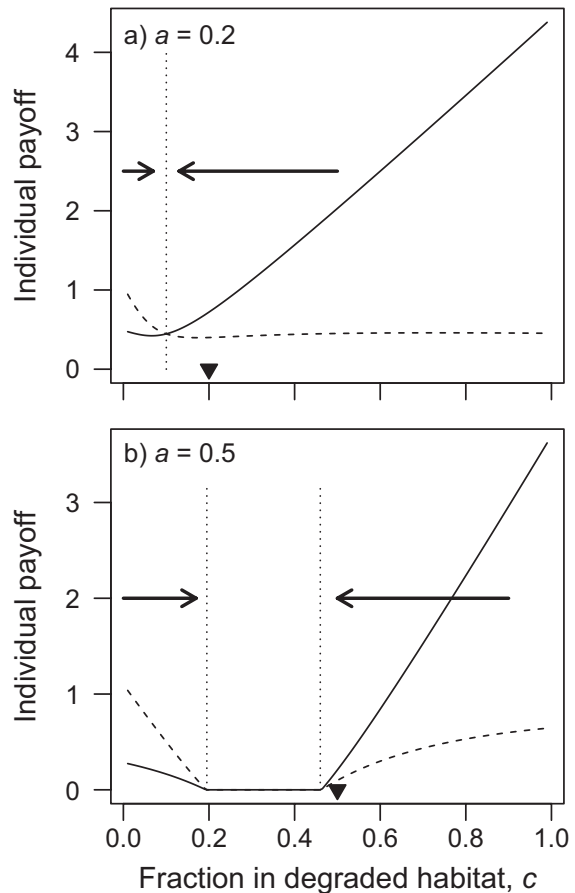


FIG. 3. Individual predator payoffs (prey killed per predator) as functions of the fraction of the total predator population that forages in degraded habitat, c . The payoffs are calculated for the model with fixed total predator abundance and $\mu = 0.2$, where (a) prey persist, $a = 0.2$, and (b) predators drive prey extinct, $a = 0.5$. These points are indicated in Fig. 1b, c by the solid and open circles, respectively. Solid lines represent the payoff to predators foraging in unaltered habitat, and dashed lines represent the payoff to predators in degraded habitat. Arrows show the direction of selection on c , and triangles denote the points where $c = a$. For both values of a , randomly foraging predators ($c = a$) would receive greater payoffs in unaltered habitat than in degraded habitat. For $a = 0.2$, this results in an ESS value $\hat{c} < a$, indicated by the vertical dotted line in panel a. For $a = 0.5$, a predator population with any value of c at which prey can persist is inviable by predators with c closer to the upper and lower threshold values at which prey are driven extinct (indicated by vertical dotted lines in panel b). Here, selection on predator behavior pushes the prey population to extinction, illustrating the bad neighbor effect.

increase their payoffs by foraging more frequently in unaltered habitat. As a consequence, $\hat{c} < a$ and predators forage less in degraded than unaltered habitat over the range of values of a that permit prey persistence (Fig. 1b). In Fig. 3a, we show how the payoff to an individual predator in either unaltered or degraded habitat varies with the fraction of the predator population in degraded habitat, for $a = 0.2$ and $\mu = 0.2$ (corresponding to the solid circle in Fig. 1b). When $c = a$ (random foraging), the payoff to predators in unaltered habitat (solid line) is greater than to predators in degraded habitat (dashed line). Hence, an adaptive predator would switch from degraded to unaltered habitat, decreasing c (as indicated by the arrow). On the other hand, if most predators are in unaltered habitat (c close to 0), competition there reduces the payoff below the payoff in degraded habitat, and an adaptive predator would move to degraded habitat, causing c to increase. At the ESS (indicated by the dotted line), payoffs from both habitats are equal,

and an individual predator that switched habitats would reduce its payoff relative to predators in the habitat that the individual left.

The decrease in the threshold level of degradation for prey extinction implies that there is a range of values of a over which adaptive predators drive prey extinct even though prey could persist if predators foraged at random (dark gray region in Fig. 1b, c). In this region, e.g., at $a = 0.5$ and $\mu = 0.2$ (open circle in Fig. 1b, c), the buildup of prey in unaltered habitat when predators forage at random results in greater payoffs to predators in unaltered habitat (Fig. 3b). However, decreasing c depresses prey populations in unaltered habitat (via increased predation mortality) and in degraded habitat (via reduction in dispersal from unaltered habitat) until prey are driven extinct (right-hand dotted line in Fig. 3b). In the dark gray region of Fig. 1b, c, prey could also persist if predators were extremely concentrated in unaltered habitat (left side of Fig. 3b), but competition for prey would

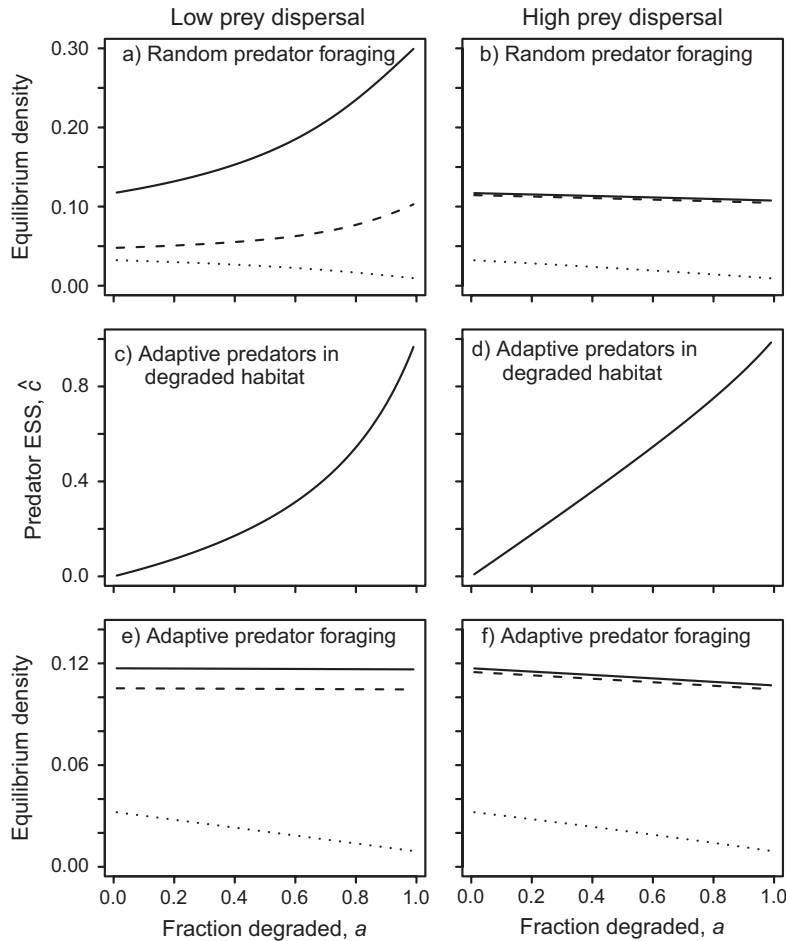


FIG. 4. Predictions of the model in which the predator population equilibrates to prey density (i.e., dynamic predator population), for low and high prey dispersal rate (μ). (a, b) Equilibrium population densities if predators forage at random. (c, d) Fraction of predators foraging in degraded habitat at the ESS (\hat{c}). (e, f) Equilibrium population densities if predators adopt the ESS distribution. In panels a, b, e, and f, dotted lines indicate equilibrium total predator density (n^*), solid lines indicate equilibrium prey density in unaltered habitat (n_u^*), and dashed lines indicate equilibrium prey density in degraded habitat (n_d^*).

cause adaptive predators to move to degraded habitat and the result would again be prey extinction (left-hand dotted line). The overall result is essentially a “tragedy of the commons,” in which habitat selection by individual predators leads to prey extinction across both habitats.

Varying the baseline parameter values causes only quantitative changes in the model predictions, as detailed in Appendix S3. Increasing prey vulnerability (v) lowers the extinction threshold for fraction of degraded habitat, regardless of whether predators forage at random or adaptively. The critical feature of the system is the difference between productivity in unaltered and degraded habitats, e.g., less severe differential effects of degradation (larger r_d) tend to ameliorate the bad neighbor effect (Appendix S3: Fig. S5).

Dynamic predator population

If the predator population responds on the same time scale as prey population dynamics, the value of r_d in Table 2 permits a positive predator equilibrium even when all habitat is degraded ($a = 1$). This follows from our argument in *Model*, i.e., for the predator population to increase when rare, $r_d > 1 + 1/v$. In order to simplify interpretation of the results, we present the equilibria for two values of dispersal (low $\mu = 0.1$, high $\mu = 0.9$), and we provide contour plots for the full range of μ in Appendix S4 for comparison to Fig. 1.

For the case in which predators forage at random, the predator equilibrium declines with increasing habitat degradation regardless of dispersal rate (Fig. 4a, b, dotted lines). Predator population growth depends on average prey productivity across habitats, which declines with increasing a . Although increasing degradation causes a slight decline in average prey density over both habitats

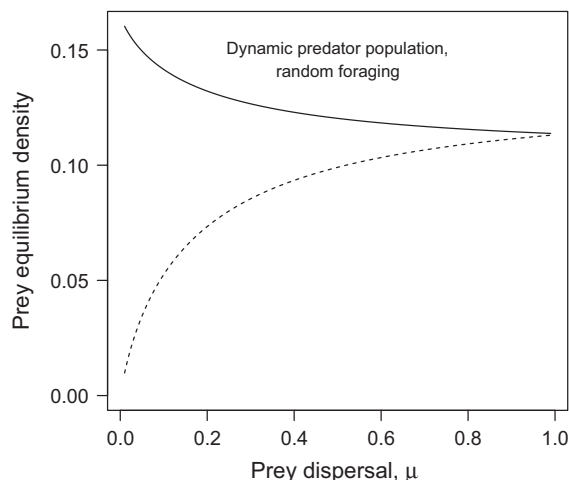


FIG. 5. Prey equilibrium density for the model with dynamic predator population when predators forage at random and $a = 0.8$. Solid line indicates prey density in unaltered habitat and dashed line indicates prey density in degraded habitat.

($ar_u^* + (1-a)n_u^*$, not shown), prey density in each patch increases with a if dispersal is low (Fig. 4a). As in the model with fixed predator abundance, random predator foraging allows the prey population to build up in unaltered habitat as prey dispersal decreases (Fig. 5). Hence, at low dispersal, predators respond to the decrease in average prey density as degradation increases, whereas prey populations are effectively isolated and respond locally to the decrease in predator abundance. This effect on prey is reversed by high dispersal (Fig. 4b), such that both prey populations decrease as habitat degradation increases. The general prediction is therefore that lower dispersal will ameliorate the effect of habitat degradation on prey, as in the model with fixed predator population.

If predators adopt the ESS distribution between unaltered and degraded habitat, we again see the bad-neighbor effect: predators respond to low prey dispersal by disproportionate utilization of unaltered habitat ($\hat{c} < a$, Fig. 4c). This response changes the qualitative effect of habitat degradation when prey dispersal is low, such that prey density in both habitat types decreases with increasing a (the slight decrease in prey density is difficult to see on the scale of Fig. 4e; compare this to Fig. 4a). With adaptive predator behavior, lower prey dispersal no longer allows the prey population to build up in unaltered habitat, as occurs when predators forage at random (Fig. 5). Hence, the effect of increasing degradation on the prey equilibria is essentially the same regardless of prey dispersal rate, similar to the prediction of the fixed predator model.

DISCUSSION

Predator and prey movement couple habitats, and this can transmit negative effects of habitat degradation to populations in unaltered parts of the landscape (Doak 1995). Our model results demonstrate how adaptive habitat selection by predators mediates the effects of prey dispersal rate on prey population density. In the absence of any adaptive response by predators, lower prey dispersal contains the spread of the negative effects stemming from degradation (Figs. 1a, 4a). However, adaptive predator behavior can reverse this outcome, leading to the bad neighbor effect even at low prey dispersal rate (Figs. Fig. 1c, 4e, f).

The consequences of habitat degradation are particularly apparent when the predator population is fixed. For the baseline parameter values, adaptive predator behavior results in prey extinction even at intermediate levels of habitat degradation regardless of dispersal rate (Fig. 1b, c). Without adaptive predator behavior, the threshold value of a resulting in prey extinction for a given dispersal rate depends on average prey productivity, $ar_u + (1-a)r_d$. However, at this threshold an individual predator that can select between habitats would benefit by increasing time spent foraging in unaltered habitat. Hence, with adaptive predator behavior, prey extinction occurs at a value of a at which overall productivity would still be sufficient to support the prey

population if predators forage at random (Fig. 1c, dark gray region). This bad neighbor effect implies that predictions based only on productivity in different habitat types and current mortality due to predators will tend to overestimate the amount of future habitat degradation that a population can withstand.

A similar error in prediction is possible if the predator population dynamics occur on the same time scale as prey. When predator density equilibrates to prey but we ignore the adaptive behavioral response, we predict that the effect of decreasing overall productivity (increasing degradation) is primarily transmitted up to the predator trophic level (Fig. 4a, b). Indeed, if prey dispersal is low, we expect prey in unaltered habitat to benefit from lower predator density (Fig. 4a). If predators adopt the ESS, the positive effect of low prey dispersal is eliminated (Fig. 4e, f).

If predators forage at random with respect to habitat type ($\hat{c} = a$), prey mortality rate is fixed. This assumption is similar to several previous models of density-independent dynamics in spatially heterogeneous habitat (e.g., Doak 1995, Gerber et al. 2005, Teller et al. 2015). Addition of density dependence (Eq. 3) can produce a wide variety of responses to changing habitat and dispersal rate. Early theoretical work showed that low (but >0) dispersal between patches of high- and low-quality habitat could increase total equilibrium density (Holt 1985). Loss of dispersers from high-quality habitat reduces competition and increases per capita growth rate there, and the dispersers support a larger population in low-quality habitat. More recent work demonstrates that the qualitative effect of dispersal depends on the form of density dependence and dispersal (e.g., Franco and Ruiz-Herrera 2015, Křivan and Jana 2015). We predict that adaptive predator behavior can overwhelm the potentially positive effect of low dispersal on equilibrium prey density, and that this bad neighbor effect will exacerbate the consequences of habitat degradation.

Prey dispersal rate is a critical parameter in our model predictions. We adopted the simple assumption that prey disperse passively and settle in proportion to area of each habitat type. Previous theory has shown that spatial heterogeneity in habitat quality makes passive dispersal disadvantageous (Hastings 1983, Holt 1985). Indeed, Cheptou et al. (2008) demonstrated that selection caused a rapid decrease in dispersal rate of plants in an urban population where habitat quality is highly variable. In our model analyses, we varied prey dispersal rate (μ) independently, but we show in Appendix S5 that habitat degradation selects for lower μ even when predators respond adaptively. This implies that as habitat degradation increases, selection will favor lower dispersal rate. In the absence of adaptive predator behavior, we would predict that low dispersal shelters the prey population in unaltered habitat (Fig. 1a). If predators select habitat adaptively, however, decreasing prey dispersal rate pushes the system closer to the prey extinction threshold as degradation increases (e.g., moving down and to the

right in Fig. 1c). Hence, we expect selection on prey dispersal characteristics to exacerbate the bad neighbor effect. However, we note that our model does not include features that potentially favor greater dispersal propensity, such as conditional dispersal and environmental stochasticity (McPeck and Holt 1992, Snyder 2011). Further analysis will be required to understand how these features interact with adaptive predator behavior to influence the outcome of natural selection.

The effects of prey dispersal and adaptive predator behavior ultimately combine to produce the bad neighbor effect. These parameters quantify the degree of interchange among habitats, and greater exchange transmits the negative effects of habitat degradation to prey in unaltered habitat. Our results suggest that adaptive predator behavior can transmit and even amplify this effect when low prey dispersal would otherwise appear to isolate habitat areas. The intertwined fate of disjunct areas is germane to optimal reserve design for threatened and endangered species. The potential advantage of protecting isolated areas, e.g., hedging against spatially localized environmental stochasticity, may be overwhelmed by predators that are able to seek out productive prey populations and draw them down with populations in degraded habitat.

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LITERATURE CITED

- Abrams, P. A. 2007. Habitat choice in predator-prey systems: spatial instability due to interacting adaptive movements. *American Naturalist* 169:581–594.
- Abrams, P. A., and L. Ruokolainen. 2011. How does adaptive consumer movement affect population dynamics in consumer-resource metacommunities with homogeneous patches? *Journal of Theoretical Biology* 277:99–110.
- Abrams, P. A., R. Cressman, and V. Křivan. 2007. The role of behavioral dynamics in determining the patch distributions of interacting species. *American Naturalist* 169:505–518.
- Alfred, R., A. H. Ahmad, J. Payne, C. Williams, L. N. Ambu, P. M. How, and B. Goossens. 2012. Home range and ranging behavior of Bornean elephant (*Elephas maximus borneensis*) females. *PLoS ONE* 7:e31400.
- Barbosa, P., J. Hines, I. Kaplan, H. Martinson, A. Szczepaniak, and Z. Szendrei. 2009. Associational resistance and associational susceptibility: having right or wrong neighbors. *Annual Review of Ecology, Evolution, and Systematics* 40:1–20.
- Byers, J. E., J. T. Wright, and P. E. Gribben. 2010. Variable direct and indirect effects of a habitat modifying invasive species on mortality of native fauna. *Ecology* 91:1787–1798.
- Cheptou, P.-O., O. Carrue, S. Rouifed, and A. Cantarel. 2008. Rapid evolution of seed dispersal in an urban environment in the weed *Crepis sancta*. *Proceedings of the National Academy of Sciences USA* 105:3796–3799.
- Cressman, R., and V. Křivan. 2006. Migration dynamics for the ideal free distribution. *American Naturalist* 168:384–397.
- Cronin, J. T. 2007. From population sources to sieves: the matrix alters host-parasitoid source-sink structure. *Ecology* 88:2966–2976.

- Delibes, M., P. Ferreras, and P. Gaona. 2001. Attractive sinks, or how individual behavioural decisions determine source-sink dynamics. *Ecology Letters* 4:401–403.
- Doak, D. F. 1995. Source-sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly. *Conservation Biology* 9:1370–1379.
- Earn, D. J. D., P. Rohani, and B. T. Grenfell. 1998. Persistence, chaos and synchrony in ecology and epidemiology. *Proceedings of the Royal Society B* 265:7–10.
- Franco, D., and A. Ruiz-Herrera. 2015. To connect or not to connect isolated patches. *Journal of Theoretical Biology* 370:72–80.
- Fretwell, S. D., and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16–36.
- Gaufrre, B., S. Mallez, M.-P. Chapuis, R. Leblois, I. Litrico, S. Delaunay, and I. Badenhausser. 2015. Spatial heterogeneity in landscape structure influences dispersal and genetic structure: empirical evidence from a grasshopper in an agricultural landscape. *Molecular Ecology* 24:1713–1728.
- Gerber, L. R., S. S. Heppell, F. Ballantyne, and E. Sala. 2005. The role of dispersal and demography in determining the efficacy of marine reserves. *Canadian Journal of Fisheries and Aquatic Sciences* 62:863–871.
- Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnean Society* 42:17–38.
- Hastings, A. 1983. Can spatial variation alone lead to selection for dispersal? *Theoretical Population Biology* 24:244–251.
- Hess, G. 1996. Disease in metapopulations models: implications for conservation. *Ecology* 77:1617–1632.
- Holt, R. D. 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theoretical Population Biology* 28:181–208.
- Honnay, O., and H. Jacquemyn. 2007. Susceptibility of common and rare plant species to the genetic consequences of habitat fragmentation. *Conservation Biology* 21:823–831.
- Křivan, V. 1997. Dynamic ideal free distribution: effects of optimal patch choice on predator-prey dynamics. *American Naturalist* 149:164–178.
- Křivan, V. 2013. Behavioral refuges and predator-prey coexistence. *Journal of Theoretical Biology* 339:112–121.
- Křivan, V., and D. Jana. 2015. Effects of animal dispersal on harvesting with protected areas. *Journal of Theoretical Biology* 364:131–138.
- Lenihan, H. S., C. H. Peterson, J. E. Byers, J. H. Grabowski, G. W. Thayer, and D. R. Colby. 2001. Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress. *Ecological Applications* 11:764–782.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15:237–240.
- MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17:373–387.
- McPeck, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. *American Naturalist* 140:1010–1027.
- Orrock, J. L., L. M. Dill, A. Sih, J. H. Grabowski, S. D. Peacor, B. L. Peckarsky, E. L. Preisser, J. R. Vonesh, and E. E. Werner. 2010. Predator effects in predator-free space: the remote effects of predators on prey. *Open Journal of Ecology* 3:22–30.
- Orrock, J. L., E. L. Preisser, J. H. Grabowski, and G. C. Trussell. 2013. The cost of safety: refuges increase the impact of predation risk in aquatic systems. *Ecology* 94:573–579.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28:289–316.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Ruokolainen, L., P. A. Abrams, K. S. McCann, and B. J. Shuter. 2011. The roles of spatial heterogeneity and adaptive movement in stabilizing (or destabilizing) simple metacommunities. *Journal of Theoretical Biology* 291:76–87.
- Snyder, R. E. 2011. Leaving home ain't easy: Non-local seed dispersal is only evolutionarily stable in highly unpredictable environments. *Proceedings of the Royal Society B* 278:739–744.
- Teller, B. J., A. D. Miller, and K. Shea. 2015. Conservation of passively dispersed organisms in the context of habitat degradation and destruction. *Journal of Applied Ecology* 52:514–521.
- Underwood, N., B. D. Inouye, and P. A. Hambäck. 2014. A conceptual framework for associational effects: when do neighbors matter and how would we know. *Quarterly Review of Biology* 89:1–19.
- White, J. W. 2008. Spatially coupled larval supply of marine predators and their prey alters the predictions of metapopulation models. *American Naturalist* 171:E179–E194.

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