

# Maladapted Prey Subsidize Predators and Facilitate Range Expansion\*

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Submitted January 18, 2019; Accepted May 23, 2019; Electronically published August 21, 2019

Online enhancements: appendix, supplemental figures, source code. Dryad data: <https://doi.org/10.5061/dryad.13gv04f>.

**ABSTRACT:** Dispersal of prey from predator-free patches frequently supplies a trophic subsidy to predators by providing more prey than are produced locally. Prey arriving from predator-free patches might also have evolved weaker defenses against predators and thus enhance trophic subsidies by providing easily captured prey. Using local models assuming a linear or accelerating trade-off between defense and population growth rate, we demonstrate that immigration of undefended prey increased predator abundances and decreased defended prey through eco-evolutionary apparent competition. In individual-based models with spatial structure, explicit genetics, and gene flow along an environmental gradient, prey became maladapted to predators at the predator's range edge, and greater gene flow enhanced this maladaptation. The predator gained a subsidy from these easily captured prey, which enhanced its abundance, facilitated its persistence in marginal habitats, extended its range extent, and enhanced range shifts during environmental changes, such as climate change. Once the predator expanded, prey adapted to it and the advantage disappeared, resulting in an elastic predator range margin driven by eco-evolutionary dynamics. Overall, the results indicate a need to consider gene flow–induced maladaptation and species interactions as mutual forces that frequently determine ecological and evolutionary dynamics and patterns in nature.

**Keywords:** eco-evolution, predator-prey interactions, local adaptation, gene flow, climate change.

## Introduction

Few concepts integrate ecology and evolutionary biology more than a species' geographic range. In ecology, the species' range

is a central concept that links niches, abundances, distributions, and diversity (Darwin 1859; Grinnell 1917; MacArthur 1972; Gaston 2003; Holt 2003; Sexton et al. 2009). In evolution, location within a range can determine adaptive dynamics, and the separation of ranges affects the probability of speciation (Kirkpatrick and Barton 1997; Case and Taper 2000; Schluter 2000; Bridle and Vines 2007). In conservation biology, climate change, invasive species, and other disturbances increasingly compel a deeper understanding of range boundaries, constraints, and the capacity to expand under altered conditions (Angert et al. 2011; Chen et al. 2011; Hill et al. 2011; Urban 2015). Still, debates simmer about the causes of range limits and their dynamic responses to environmental change (Pulliam 2000; Bridle and Vines 2006; Sexton et al. 2009; Kubisch et al. 2014; Urban et al. 2016).

Ultimately, species' range borders are constrained by a failure to disperse or adapt. Some range edges have not yet reached an equilibrium from past disturbances or introductions because species simply have not reached the edge of their possible range (Phillips et al. 2008). For example, researchers calculated that the European beech (*Fagus sylvatica*) requires another 7,000 years of natural dispersal before it reaches its northern range boundary in Great Britain (Davis and Shaw 2001; Svenning and Skov 2007). Successful transplants beyond the current range of the focal species and invasive species often provide evidence for this dispersal limitation (Hargreaves et al. 2013). In one study, 41% of populations of the perennial forest herb *Hyacinthoides non-scripta* survived beyond their natural range after 45 years (Van der Veken et al. 2007).

Yet most transplant experiments indicate that range boundaries correspond to niche limits (Hargreaves et al. 2013; Lee-Yaw et al. 2016), determined by the set of environmental factors that reduce fitness below replacement (Holt 2003). These factors include both abiotic and biotic factors, which can vary in their importance across a species' range. Ultimately, each of these niche-based range boundaries represents a failure of range-edge populations to adapt to conditions

\* The Special Feature on Maladaptation is a product of a working group that convened in December 2015 and 2016 at McGill University's Gault Preserve and of a symposium held at the 2018 meeting of the American Society of Naturalists in Asilomar, California, inspired by the working group.

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DOI: 10.1086/704780

outside the range. One explanation for this failure is that genes adapted to conditions in the dense range center disperse into and overcome adaptive evolution in the smaller populations near the range edge (Kirkpatrick and Barton 1997). However, this prediction breaks down depending on the particular assumptions about the environmental gradient and genetic architecture (Case and Taper 2000; Bridle and Vines 2007). In particular, dynamic genetic variation can overcome this constraint (Barton 2001).

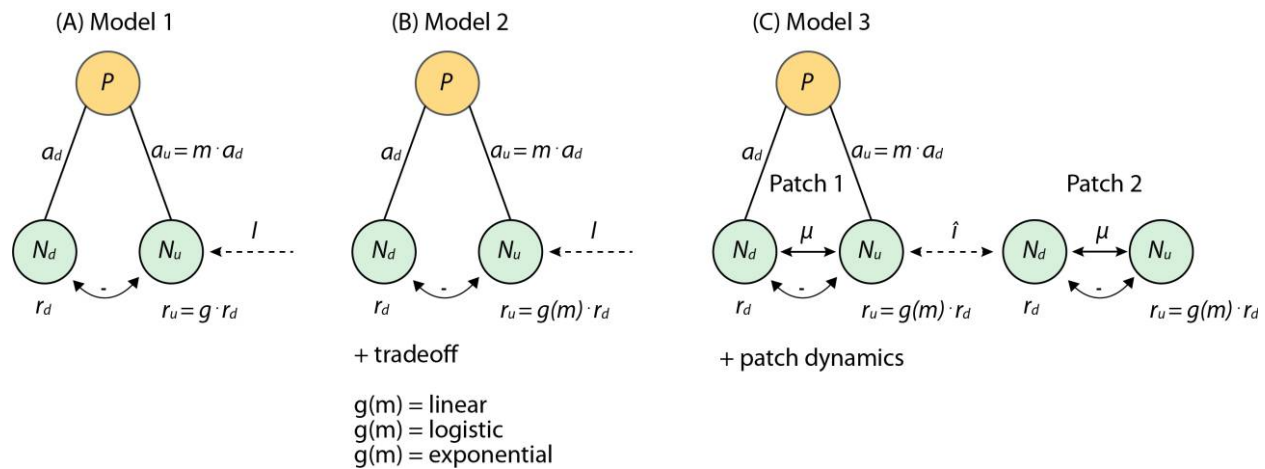
Whereas much research has focused on ecological or evolutionary reasons for range edges, less attention has focused on the interplay between evolutionary and community dynamics that might often characterize a range edge. In this framework of evolving metacommunities, range edges might be more dynamic than a purely ecological or evolutionary perspective alone can convey (Urban and Skelly 2006; Urban et al. 2008; Holt et al. 2011; Bocedi et al. 2013; De Meester et al. 2016; Osmond et al. 2017). For example, competition between two species can lead to the evolution of character displacement where they occur in sympatry and generate a stable range boundary (Case and Taper 2000). Although these explorations have focused on competition, enemy-victim interactions also might create dynamic eco-evolutionary range dynamics (Case et al. 2005). For example, Hochberg and van Baalen (1998) analyzed a predator-prey coevolutionary model along a resource gradient and found that low resources reduced prey densities, which in turn reduced the predator's range size. Less appreciated has been the role that prey maladaptation might play in altering range boundaries and dynamics. In general, the burgeoning field of eco-evolutionary dynamics has focused on how local adaptation affects ecological dynamics while neglecting the potentially equally important effects of maladaptation (Farkas et al. 2015, 2016). For instance, maladaptive gene flow could alter evolutionary dynamics, change trait means, and increase phenotypic variances, all of which could affect ecological properties at multiple scales (Urban 2006; Urban et al. 2008; Farkas et al. 2013). However, such insights have mainly been relegated to conceptual arguments rather than rigorously constructed theory with explicit assumptions.

Prey maladapted to predators could play an important role in setting predator range boundaries. Usually, investment in predator defenses trades off against investments in other fitness components, such as competitive ability, growth, or reproduction (Lively 1986; Skelly and Werner 1990; Yoshida et al. 2003; Relyea and Auld 2004; Fischer et al. 2014). Therefore, as predator densities and subsequent selection for defense decline toward the edge of a predator's range, prey populations are likely to become increasingly maladapted to rarer and rarer predation risk (Billerbeck et al. 2000; Laurila et al. 2008). Victims from naïve populations that live just outside the predator range can immigrate into and subsidize recipient populations by providing easily

captured or infected resources. This effect provides a spatial genetic subsidy (Urban and Skelly 2006) that is a special form of an ecological spatial subsidy, defined as the movement of energy or resources between habitats (Polis et al. 1997). Spatial genetic subsidies could enhance predator-prey coexistence by preventing the extinction of specialist predators after prey evolve effective defenses against them (Holt 2005; Urban and Skelly 2006). Spatial genetic subsidies from evolving prey might also affect predator abundances, range boundaries, and eco-evolutionary dynamics. In particular, such dynamics might be especially relevant during environmental changes such as climate change, where predators colonize newly suitable habitats (Gilman et al. 2010) and encounter an easily exploitable resource in the form of naïve, undefended victims. These undefended victims might facilitate more rapid or extensive range expansions than expected if prey defenses do not evolve (Cudmore et al. 2010; Urban et al. 2012). Such spatial genetic subsidies have rarely been addressed.

To address this gap, we develop a body of theory that addresses how the evolution of prey defense affects a predator's local abundance and range boundary and dynamics. Here we extend a strong tradition in understanding how maladaptive gene flow can swamp local adaptation (Haldane 1930; Wright 1931; Kirkpatrick and Barton 1997; Lenormand 2002) to how maladaptive gene flow can generate suboptimal defenses against predators, which can then subsidize predator abundances, persistence, and range distribution and dynamics. Although we use the specific terms "predator" and "prey" throughout, slightly different parameterizations make the model generally applicable to any victim-enemy interaction. Hereafter, we use the term "maladapted defenses" to indicate suboptimal defenses against predators. We reserve the term "local population maladaptation" for populations with suboptimal fitness in a particular environment (e.g., predator or no predator) after accounting for any potential fitness trade-offs.

We first develop a series of analytical models to understand how the immigration of undefended prey affects a local predator population (fig. 1). After developing insights with simple one- and two-patch models, we relax assumptions and explore an individual-based model with defense modeled both as a polymorphic trait and as a quantitative trait underlain by explicit multilocus genetics implemented across a landscape containing multiple patches. We assume a prey population that survives across the entire landscape and a predator that faces a unimodal fitness gradient across an environmental gradient (e.g., climate). We compare models with and without the evolution of prey defense and in the context of increasing levels of prey dispersal, which should increase a predator's abundance and range by enhancing spatial genetic subsidies. We also evaluate how prey evolution affects the predator's range dynamics during environmental change.



**Figure 1:** Local predator-prey models: a predator ( $P$ ) attacks ( $a$ ) prey that are either defended ( $N_d$ ) or undefended ( $N_u$ ) due to having, respectively, adapted and maladapted defenses against the predator. In baseline model 1 (A), the prey with maladapted defenses arrive through immigration ( $I$ ) and compete with prey (two-way arrow with negative sign). Prey with maladapted defenses ( $m > 1$ ) to the predator suffer a higher attack rate by the predator defined by the ratio  $m = a_u/a_d$ . In model 2 (B), defense against predators trades off against population growth rate ( $g = r_u/r_d$ ) through linear, logistic, and exponential functions. In model 3, we explicitly include the predator-prey dynamics in patch 2, symmetric and proportional dispersal between patches ( $\hat{I}$ ), and mutation between prey types at rate  $\mu$ .

### Model 1: Local Predator-Prey Dynamics

To build understanding, we begin by analyzing local eco-evolutionary dynamics before exploring more complex simulations of explicit spatial eco-evolutionary dynamics. In model 1 (fig. 1A), we envision a predator population ( $P$ ) that consumes two prey types: a defended prey type ( $N_d$ ) that has evolved defenses against the predator and an undefended prey type ( $N_u$ ) that is maladapted to predators and instead adapted to the predator-free environment. The undefended prey type immigrates at a constant rate ( $I$ ) into the population. Initially, we do not assume emigration and instead assume a fixed inflow of maladapted immigrants from a non-predator patch where the undefended genotype is optimal, but we allow joint immigration and emigration of both prey types in model 3. We assume that the two prey types represent distinct genetic polymorphisms and that mutation between them is negligible, but we later relax these assumptions. The two prey types compete with each other directly with a competition coefficient equal to one, assuming equivalent competition both among and within types. Prey types grow logistically with a maximum growth rate ( $r_d$  and  $r_u$ ) and carrying capacity ( $K$ ):

$$\frac{dN_d}{dt} = N_d \left( r_d - r_d \frac{N_d + N_u}{K} - a_d P \right), \quad (1)$$

$$\frac{dN_u}{dt} = N_u \left( r_u - r_u \frac{N_d + N_u}{K} - a_u P \right) + I. \quad (2)$$

The predator population grows in relation to its attack rate on each prey type ( $a_d$  and  $a_u$ ), modulated by a variable converting prey eaten into predator offspring ( $\beta$ ) and a constant death rate ( $d$ ):

$$\frac{dP}{dt} = \beta P (a_d N_d + a_u N_u) - dP. \quad (3)$$

We initially assume no trade-off between prey maximum reproductive rate and defense (i.e., predator attack rate). We defined prey maladaptation to the predator as the ratio of attack rates on the maladapted versus adapted defenses ( $m = a_u/a_d$ ), which we evaluate from one (equally defended prey) to higher levels of suboptimal defenses in the immigrant prey. We also define  $g$  as the ratio of the reproductive rates of undefended to defended prey ( $g = r_u/r_d$ ). In this modeling framework, an ecological spatial subsidy to predators is defined by  $\partial P^*/\partial I > 0$ . A genetic spatial subsidy also requires that  $\partial P^*/\partial m > 0$ , such that maladapted immigrants increase equilibrium predator abundances.

We solved this system of equations  $\{dN_u/dt = 0; dN_d/dt = 0; dP/dt = 0\}$  for joint equilibria and define  $\gamma = K - d/\beta a_d$  and  $\delta = IK/r_d$ . When predator and both prey types coexist and  $\gamma > 0$ , an analytical solution exists (see the appendix, available online). Both  $P^*$  and  $N_d^*$  are always positive for  $m \geq 1$  and  $m > g$ ; however,  $N_d^*$  can become negative when  $m$  is small and  $I$  is large (see explicit conditions in the appendix). We adopt values of  $I$  and  $m$  that ensure positive  $N_d^*$  for all plots. The equilibrium abundances are

$$N_d^* = \frac{d}{\beta a_d} - mN_u^*, \tag{4a}$$

$$N_u^* = \frac{-\gamma + \sqrt{\gamma^2 + 4\delta((m-1)/(m-g))}}{2(m-1)}, \tag{4b}$$

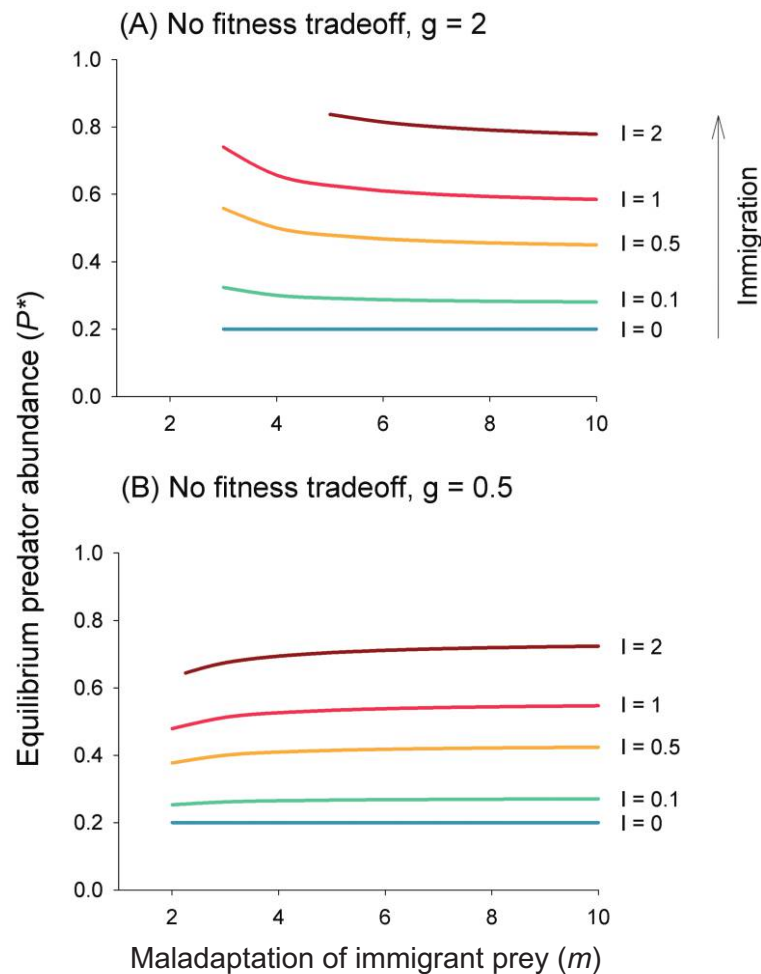
$$P^* = \frac{r_d}{Ka_d}(\gamma + (m-1)N_u^*) \tag{4c}$$

$$= \frac{r_d}{2Ka_d} \left( \gamma + \sqrt{\gamma^2 + 4\delta \frac{m-1}{m-g}} \right). \tag{4d}$$

We demonstrate that these equilibria are stable in the appendix. Equation (4a) indicates that defended prey decrease when

undefended prey increase (an effect of apparent competition) but increase with larger maladaptation ratios,  $m$ , between prey types (for explicit conditions, see the appendix).

The change in predator abundances with respect to dispersal ( $\partial P^*/\partial I > 0$ ) is positive when  $m > 1$  and  $m > g$ . Hence, the dispersal of undefended prey subsidizes predator abundances, constituting the familiar ecological trophic subsidy, as illustrated with numerical solutions in figure 2. We solved for the derivative of predator abundances with respect to defense maladaptation after considering  $g$  as a function of  $m$ , where  $g'(m) = \partial g/\partial m$ . We obtain the following conditions for predators to increase with the maladaptation ratio (see the appendix):



**Figure 2:** Equilibrium predator abundances without a fitness trade-off in relation to increasingly maladapted defenses and immigration of prey. The blue line indicates no immigration ( $I = 0$ ). In both models, predator abundances increase with higher immigration of prey (an ecological trophic subsidy), as indicated with colored lines from green to dark red. When  $g > 1$  (A), maladapted defenses decrease predator abundances. When  $g < 1$  (B), maladapted defenses increase predator abundances (a spatial genetic subsidy). Parameter values for A:  $r_d = 0.1, r_u = 0.2, K = 50, a_d = 0.1, d = 0.4, \beta = 0.1$ . Parameter values for B: same as for A except that  $r_u = 0.05$ . Values are shown only for feasible conditions, including where  $m > g$ .



$$(m - g) > (1 - g')(m - 1), \tag{5}$$

with the caveat that  $m > g$ . Without a trade-off between  $g$  and  $m$ ,  $g' = 0$ . The derivative ( $\partial P^*/\partial m > 0$ ) is positive when  $g < 1$ , zero when  $g = 1$ , and negative when  $g > 1$  (fig. 2). Thus, spatial genetic subsidies exist when the undefended prey have a lower population growth rate than defended prey, which somewhat unrealistically requires maintenance of a low-fitness prey genotype that grows slowly and encounters high attack rates. However, these outcomes assume that investment in defense entails no fitness cost.

**Model 2: Local Model with Fitness Trade-Off**

We next include the fitness trade-off that usually characterizes local adaptation to predator and predator-free environments. One way that this trade-off might be expressed is between prey investments in maximum growth rate and in defenses against the predator that decrease attack rates ( $a$ ). We explore three functions for this trade-off that characterize a linear, accelerating, and decelerating effect of increasing attack rates (declining defenses) on population growth rate. For the linear case, we assume that growth rates are proportional to attack rates, such that  $g = cm$ , where  $c$  determines the slope of that relationship. Setting  $g' = \partial g/\partial m = c$  and substituting into equation (5) gives

$$c < 1, \tag{6}$$

which is always true under the initial constraint that  $m > g$ . Hence, predator abundances increase with more maladapted defenses for all feasible values with a linear trade-off (i.e.,  $m > g$ ,  $c < 1$ ; fig. 3A). We might also add the extra constraint that  $c > 1/m$  to ensure that  $g > 1$  and the undefended prey type has a larger population growth rate than the defended prey type. When population growth rate exponentially accelerates with maladapted defenses, predator abundances increase even faster (fig. 3B), assuming conditions in which  $m > g$  and  $N_d^*$  is nonnegative (see the appendix). However, when population growth rate decelerates logistically with maladapted defenses, predator abundances decrease (fig. 3C; see the appendix). As in model 1, the derivative of  $\partial P^*/\partial I$  was positive for all trade-off models, indicating a general ecological subsidy from immigrating prey.

**Model 3: Two Patches and Evolution**

Thus far, we assumed a constant flow of undefended immigrants from a predator-free patch and no evolution. We now relax these assumptions and develop numerical solutions for two patches linked by dispersal (fig. 1C). Predators inhabit patch 1 but not patch 2, simulating two patches on the edge of a predator's range. The prey in the two patches are linked by dispersal rate ( $\hat{I}$ ), where dispersal is now indicated by the frac-

tional dispersal rate of prey types (i.e.,  $I_{2 \rightarrow 1} = \hat{I} \cdot N_2$ , where  $N_2$  was undefined previously) and assumes no costs to dispersal. We model a symmetric mutation rate ( $\mu$ ) between prey morph types within a patch, assuming a discrete and simple genetic polymorphism. Predator equation (3) stays the same. Assuming the linear trade-off from model 2, the two-patch system of equations for prey is

$$\begin{aligned} \frac{dN_{d1}}{dt} = & N_{d1} \left( r_d - r_d \frac{N_{d1} + N_{u1}}{K} - a_d P \right) - \hat{I} N_{d1} \\ & + \hat{I} N_{d2} + \mu N_{u1} - \mu N_{d1}, \end{aligned} \tag{7a}$$

$$\begin{aligned} \frac{dN_{u1}}{dt} = & N_{u1} m \left( cr_d - cr_d \frac{N_{d1} + N_{u1}}{K} - a_u P \right) - \hat{I} N_{u1} \\ & + \hat{I} N_{u2} + \mu N_{d1} - \mu N_{u1}, \end{aligned} \tag{7b}$$

$$\begin{aligned} \frac{dN_{d2}}{dt} = & N_{d2} \left( r_d - r_d \frac{N_{d2} + N_{u2}}{K} \right) - \hat{I} N_{d2} + \hat{I} N_{d1} \\ & + \mu N_{u2} - \mu N_{d2}, \end{aligned} \tag{7c}$$

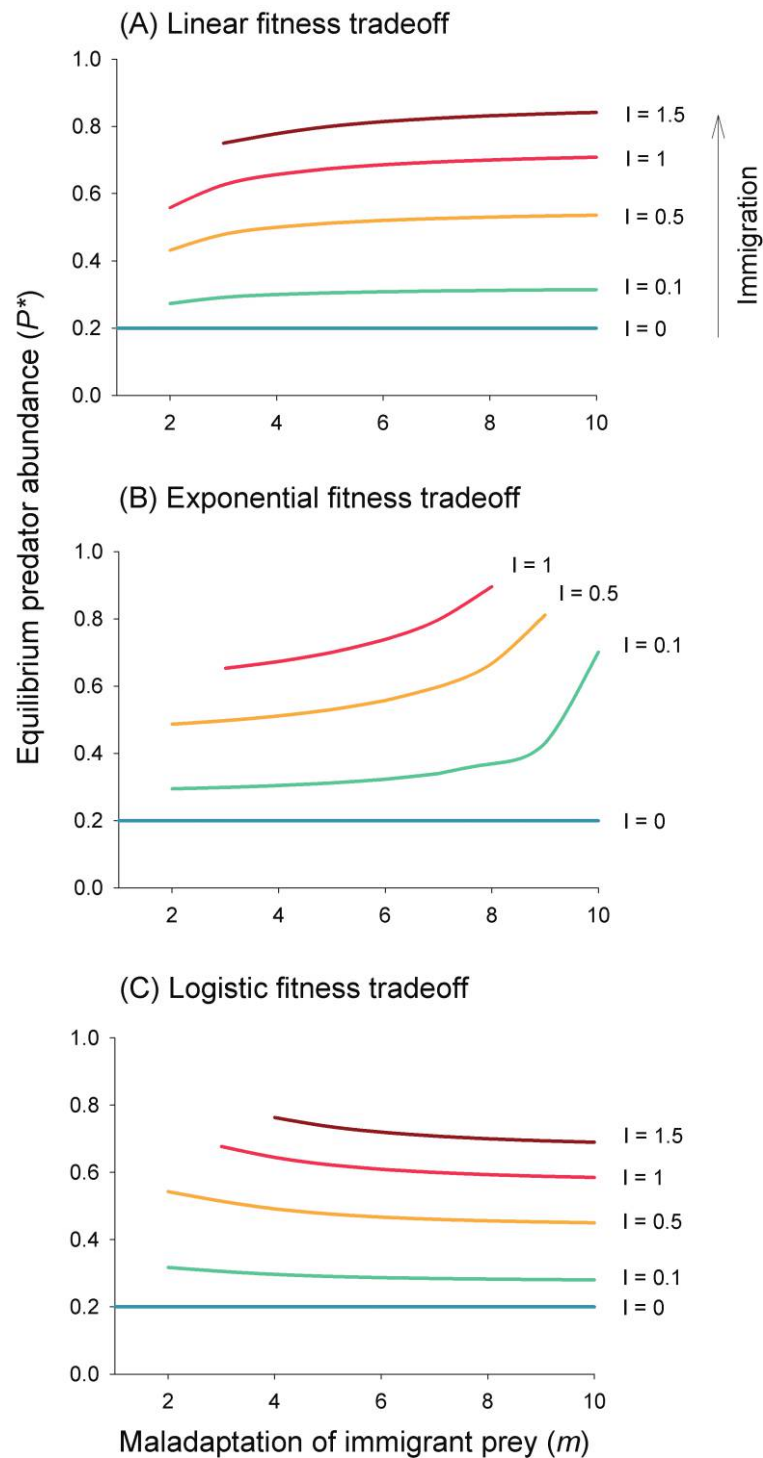
$$\begin{aligned} \frac{dN_{u2}}{dt} = & N_{u2} m \left( cr_d - cr_d \frac{N_{d2} + N_{u2}}{K} \right) - \hat{I} N_{u2} \\ & + \hat{I} N_{u1} + \mu N_{d2} - \mu N_{u2}. \end{aligned} \tag{7d}$$

We used numerical approximations (NDSolve in Mathematica) to solve these linked equations until equilibria were reached in all populations (by 10,000 time steps in all simulations). More maladapted defenses increased predator equilibrium abundances, and this effect was strongest at the highest dispersal levels, consistent with model 2 results with a linear trade-off (fig. 4). However, higher dispersal shifted the relationship between predator abundances and maladapted defenses from a saturating to a sigmoidal curve as predator subsidies were linked increasingly to the dynamics of prey populations in the predator-free patch. Evolution through mutation had little effect on predator abundances even with mutation rates as high as 0.01 (fig. S1; figs. S1–S8 are available online).

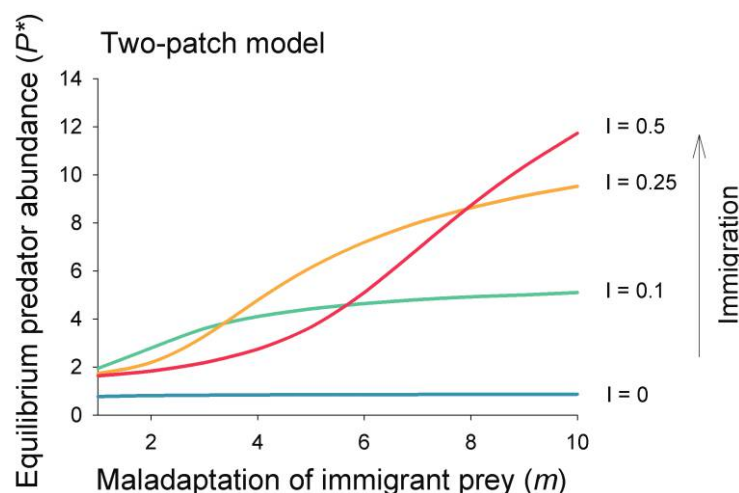
We evaluated the sensitivity of each parameter value on model outcomes by iteratively doubling and halving each variable from a baseline parameterization and normalizing by baseline parameter values to create a dimensionless estimate of sensitivity:

$$S_p^x = \frac{dx}{dp} \frac{p}{x} = \frac{x_2 - x_1}{p_2 - p_1} \frac{p_1}{x_1}, \tag{8}$$

where  $x$  is the equilibrium density of predators or prey with adapted and maladapted defenses in patches 1 and 2 and  $p$  is the altered model parameter. Model outcomes were most sensitive to the linear trade-off slope, level of defensive maladaptation, and attack rate (fig. S2). Maladapted



**Figure 3:** Equilibrium predator abundances in relation to immigration and maladaptation of prey defenses but now including fitness trade-offs. The blue line indicates no immigration ( $I = 0$ ). Predator abundance increases with more prey immigration (an ecological trophic subsidy), as indicated by colored lines from green to red. When prey population growth scales linearly (A) and exponentially (B) with maladapted defenses, this maladaptation increases predator abundances (a spatial genetic subsidy). When prey population growth increases logarithmically with maladapted defenses (C), this maladaptation decreases predator abundances. Parameter values for A:  $r_u = c \cdot m \cdot r_d$ ,  $c = 0.5$ ,  $r_d = 0.1$ ,  $K = 50$ ,  $a_d = 0.1$ ,  $d = 0.4$ ,  $\beta = 0.1$ . Parameter values for B: same as for A except that  $r_u = r_d \cdot e^{(m-1)/4}$ . Parameter values for C: same except that  $r_u = r_d \cdot 2/(1 + e^{-(m-1)})$ . Values are shown only for feasible conditions, including where  $m > g$  and for  $g > 1$  (higher growth rates for undefended prey).



**Figure 4:** Effect of immigration ( $I$ ) and maladapted defenses ( $m$ ) on equilibrium predator abundances in model 3: the two-patch model. The blue line indicates no dispersal ( $I = 0$ ), and colored lines from green to red indicate greater immigration. Predator abundances increase with higher immigration of prey with maladapted defenses but not at all levels of maladaptation. Parameter values:  $\beta = 0.1$ ,  $r_d = 0.1$ ,  $a_d = 0.1$ ,  $c = 0.9$ ,  $d = 0.1$ ,  $K = 50$ ,  $\mu = 0.001$ .

defense level was especially sensitive in determining the abundances of prey adapted to the predator. Predator and prey abundances with adapted defenses were also sensitive to the trade-off slope: increasing the strength of this trade-off elevated predator abundances and decreased adapted prey abundances. The least sensitive parameters were evolutionary rate ( $\mu$ ), prey carrying capacity ( $K$ ), and predator conversion efficiency ( $\beta$ ).

#### Model 4: Prey Evolution across a Predator's Range in an Individual-Based Model

Although simple analytical models provide useful insights into the potential for spatial genetic subsidies, these equations are difficult to solve for the joint spatial, evolutionary, and ecological dynamics that characterize the dynamics of entire species ranges. Particular challenges in developing analytical approaches for these eco-evolutionary models entail incorporating the spatial gradient in environmental conditions that affects the structure of a range. We take advantage of the flexibility offered by individual-based modeling to develop a complementary approach that is spatially explicit and incorporates explicit locus-based evolution of prey defense. By running a suite of experiments using individual-based models, we seek to understand the degree to which our results in models 1–3 are qualitatively robust to simplifying assumptions. Furthermore, we establish how eco-evolutionary dynamics play out across a spatially extended landscape under more complex scenarios, including environmental change. Simulation code has been deposited in the Dryad Digital

Repository (<https://doi.org/10.5061/dryad.13gv04f>; Urban et al. 2019) and is available in a zip file (available online).<sup>1</sup>

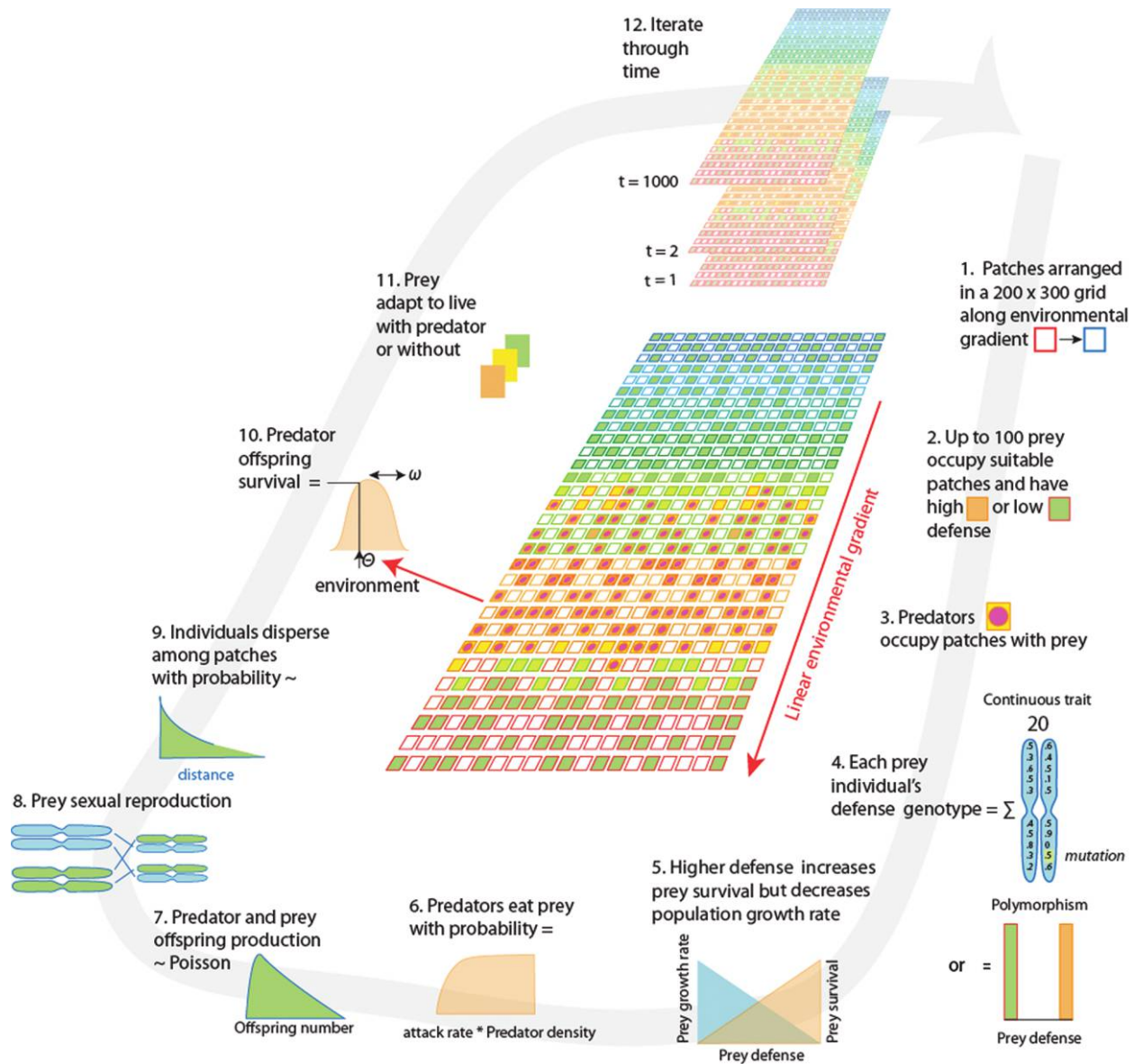
#### Environment

We model a prey and a predator on a 200-column ( $x$ ) by 300-row ( $y$ ) matrix, in which 20% of the cells (100-m resolution) are randomly selected as suitable habitat for both species (fig. 5). We impose a linear environmental gradient  $\theta$  that increases along the  $y$  dimension (e.g., latitude or altitude) by 0.075 units (e.g., °C) per row. The prey are not affected by the environmental gradient and can inhabit all suitable cells across the landscape with a carrying capacity ( $K$ ) equal to 100 individuals per suitable cell. The predator, on the other hand, is limited by abiotic conditions, with an optimal location ( $\Theta = 15$ ) along the environmental gradient where offspring survival is maximal.

#### Population and Community Dynamics

We assumed annual, nonoverlapping generations for both species. We model predator-prey interactions with an individual-based and density-dependent model based on the Hassell-Varley enemy-victim model (Hassell and Varley 1969). Predators first consume prey, and each prey survives predation with probability equal to

1. Code that appears in *The American Naturalist* is provided as a convenience to readers. It has not necessarily been tested as part of peer review.



**Figure 5:** Brief overview of simulation with key sequence of life-history events and interactions among predator and prey indicated. See the main text for details.

$$\zeta = e^{-aP_{x,y,t}^{1-\eta}}, \quad (9)$$

where  $a$  is the predator attack rate;  $P_{x,y,t}$  is the predator population size in cell  $x, y$  at time  $t$ ; and  $\eta$  is the predator interference coefficient that induces negative density dependence in the predator population when  $\eta < 1$ . Each prey  $i$  is assigned a level of defense ( $\delta$ ), which determines its attack rate ( $a$ ) between a fixed range of values ( $a_{\min} = 0.1$ ;  $a_{\max} = 0.5$ ):

$$a = a_{\max} - \delta_i(a_{\max} - a_{\min}). \quad (10)$$

Predator attack rate decreases linearly with prey defense. Prey defense also trades off against prey population growth rate as in the analytical model. Population growth rate  $r$  is constrained between minimum and maximum values ( $r_{\min} = 1.2$ ;  $r_{\max} = 2$ ) and decreases linearly with increasing prey defense:

$$r_i = r_{\max} - \delta_i(r_{\max} - r_{\min}). \quad (11)$$

Each prey that survives mates with a randomly sampled individual from the population (including self-fertilization)



and produces a number of offspring sampled from a Poisson distribution:

$$\text{Off}_{\text{prey},t+1} = \text{Poisson}(e^{r(1-N_{x,y,t}/K)}), \quad (12)$$

where  $N_{x,y,t}$  is the prey population size in cell  $x, y$  at time  $t$ . Concurrently, each predator mates with a randomly sampled individual (including self-fertilization) and produces a number of offspring sampled from

$$\text{Off}_{\text{predator},t+1} = \text{Poisson}\left(\frac{\beta E_{x,y,t}}{P_{x,y,t}}\right), \quad (13)$$

where  $\beta$  is the predator conversion coefficient ( $\beta = 0.45$ ) and  $E_{x,y,t}$  is the total prey consumed at time  $t$  by predators ( $P_{x,y,t}$ ). After reproduction, both predator and prey adults die and their offspring disperse with probabilities  $I_{\text{predator}}$  and  $I_{\text{prey}}$ . If an individual disperses, the new location is determined by drawing the distance moved from a negative exponential distribution with means  $\Delta_{\text{prey}}$  and  $\Delta_{\text{predator}}$  and the direction from the uniform distribution  $(0, 2\pi)$ . If the individual disperses into unsuitable habitat, it dies, and if the new location falls out of the landscape, distance and direction are resampled. After dispersal, predator offspring undergo viability selection by a Gaussian function of their optimal environment ( $\Theta$ ) in relation to the local environment ( $\theta_y$ ):

$$\zeta = e^{-((\Theta-\theta_y)^2/2\omega^2)}, \quad (14)$$

where  $\omega^2$  represents the breadth of the predator's environmental niche ( $\omega^2 = 5$ ).

#### *Prey Defense Evolution*

We first model prey evolution as a distinct polymorphism to extend the analytical results (model 3) to a spatially explicit context and to calibrate the individual-based model against previous ones. The polymorphism is determined by a single haploid locus with two alleles coding for a defended and an undefended prey phenotype. The two alleles mutate into each other with probability  $\mu$  ( $10^{-7}$ ). In this first case, we maintained the predator and prey population dynamics as described above, but we model the trade-offs between attack rate and growth rate as in the analytical model to facilitate comparison. Therefore, prey maladaptation to the predator is the ratio of maladapted to adapted attack rates on the two prey types  $m = a_u/a_d$  ( $a_d = 0.1$ ), and the growth rate of the maladapted prey type is given by  $r_u = c \cdot m \cdot r_d$  ( $r_d = 1.2$ ,  $c = 1$ ; cf. fig. 3).

Next, we develop a quantitative genetics model of defense evolution in which prey defense  $\delta$  is a trait with a diploid autosomal additive genetic architecture. Each prey individual carries  $L$  ( $= 10$ ) unlinked loci with a continuous distribution of alleles and no pleiotropy. Each individual genotypic value

for  $\delta$  is given by the sum of its  $2L$  alleles. The phenotype equals the genotype (i.e., no environmental variance) but is constrained to  $0 \leq \delta \leq 1$ . At  $t = 0$ , alleles are initialized with values sampled from a normal distribution with mean 0.5 and standard deviation 0.1. Alleles mutate with a probability of 0.001 per generation. When mutation occurs, a random normal deviate with mean zero and standard deviation 0.0005 is added to the allele value.

#### *Simulations*

We initialize each simulation with a prey and predator population in every suitable cell at  $K$  and one-tenth  $K$ , respectively. We ran simulations until 2,500 years, when they reached a quasi equilibrium determined by no further directional change in predator-prey and evolutionary dynamics. We explored the effect of prey defense evolution and prey dispersal on prey abundances and genetics and on predator abundances and range size. We also explored the effect of a changing environment, such as for climate change. Beginning at 2,500 years, we shifted the environment of each cell 0.0375 units per year for 100 years to simulate a total environmental change equal to 3.75°C. The predator's environmental optimum is thus moving in space (toward higher  $y$  values), such that the predator would need to move along the environmental gradient to maintain its fitness. At 2,600 years, the environment became stationary again for another 2,500 years to allow for a new quasi equilibrium to be reached. Parameters for the different simulations are summarized in table 1.

We calculated the boundaries of the predator range using the average of one and 1.5 individuals per patch across simulations. Although defining range boundaries is somewhat arbitrary, a mean of one predator per patch indicates the minimum threshold for observation but also includes the possibility of a sink population. Larger values indicate a greater probability of self-sustaining populations for organisms that cannot self. We measure the mean and among-individual variation in genotypic means (summed across all alleles) for each prey population.

#### **Effect of Local Adaptation and Maladaptation**

To build understanding and bridge between local and landscape dynamics, we first extend the two-patch model 3 to a simulation model with a polymorphic defensive trait that evolves via mutations at a single locus across an environmentally driven cline in predator abundance. The mean proportion of defended prey increases as an adaptive response to predation risk in the center of the gradient (fig. 6). We explored the effects of both greater prey emigration probability and dispersal distance. Higher prey emigration probability increased prey maladaptation, which increased predator abundances, especially in the center of the range.

**Table 1:** Summary of variables and parameters used for the individual-based model

Variable	Description	Parameter value(s)
$K$	Prey carrying capacity	100 individuals
	Proportion of suitable cells	.2
$\Theta$	Predator environmental optimum	15
$\omega^2$	Breadth of predator environmental niche	5
	Environmental gradient increment per row ( $y$ )	.075
	Environmental gradient shifting rate	.0375, .05, .075, .1 per year
	Prey defense-growth trade-off	<b>True</b> , false
	Prey defense-predator attack rate trade-off	<b>True</b> , false
$r_{\min}$	Prey minimum growth rate	1.2
$r_{\max}$	Prey maximum growth rate	2.0
$r_0$	Prey growth rate in the absence of defense-growth trade-off	1.6
$a_{\min}$	Predator minimum attack rate	.1
$a_{\max}$	Predator maximum attack rate	.5
$\beta$	Predator conversion coefficient	.4
$\eta$	Predator interference coefficient	.85
$I_{\text{prey}}$	Prey emigration probability	.1, <b>.2</b> , .3
$I_{\text{predator}}$	Predator emigration probability	.1, <b>.2</b>
$\Delta_{\text{prey}}$	Prey mean dispersal distance	100, <b>400</b>
$\Delta_{\text{predator}}$	Predator mean dispersal distance	50, 100, 200, <b>400</b>
$\delta_{\text{const}}$	Nonevolving prey defense	1.0
$\delta$	Evolving prey defense phenotype	$.0 \leq \delta \leq 1.0$
$L$	Number of diploid loci	10
$\delta_0$	Initial genotypic mean for prey defense	.5
$\mu$	Mutation probability (per allele per generation)	<b><math>10^{-3}</math></b> , $10^{-5}$ , $10^{-7}$
	Mean mutational effect	.0
	Standard deviation in mutational effects	.0005
	Initial genotypic standard deviation for prey defense	.1

Note: Values in boldface denote default parameter values.

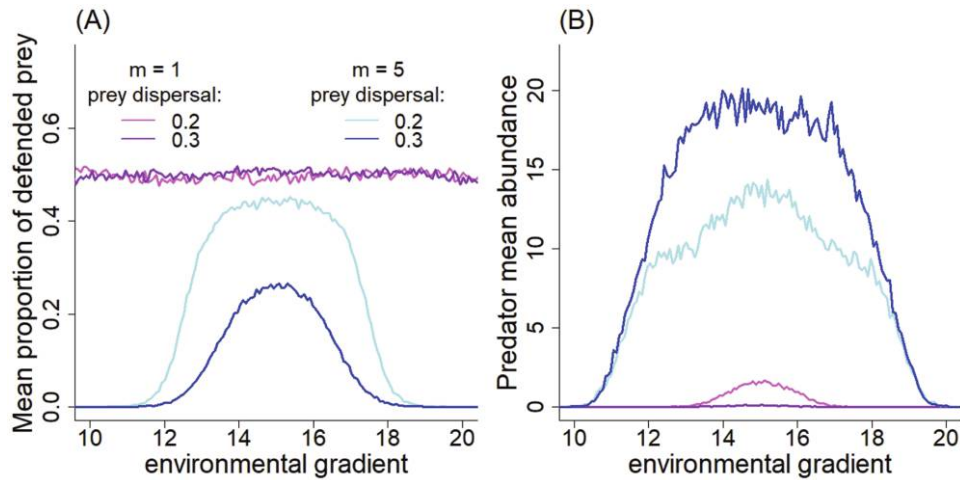
However, higher dispersal distance had more limited effects (fig. S3).

Next, we allow for the evolution of a multilocus quantitative defensive trait that decreases predator attack rate but increases reproductive rate through a trade-off. Prey evolved peak defenses ( $\sim 1.0$ ) in the center of the predator's range (fig. 7A). Because of the assumed trade-off between offspring production and defense, prey evolved lower defenses and higher population growth rates outside the predator's range. Higher prey dispersal distance decreased defense levels inside the predator range, increased them outside the range, and more generally created smoother genetic clines indicative of maladaptive gene flow on prey defenses. Greater prey dispersal increased the genetic load in prey populations, as demonstrated by the increase in genetic variation at the edges of the predator range (fig. 7B).

Gene flow-induced prey maladaptation decreased prey population abundances within the predator range, as predators attacked less defended prey (fig. 7C). This effect was especially pronounced at the edges of the predator's range. Increasing subsidies of maladapted, easily caught prey resulted in greater predator abundances and a larger predator range

extent (figs. 7D, 8). We compared simulations with evolving prey against a baseline model where prey did not evolve and instead had a fixed defense equal to the value that evolved under high predation risk in the center of the predator's range ( $\delta = 1.0$ ). When compared against this fixed defense level, evolutionary models resulted in higher predator abundances near the predator's range edge (fig. 7D), indicating the effect of smoother, maladapted clines in prey defense.

Evolving prey created larger ranges for predators compared to fixed defenses set to maximum defense in all cases (fig. 8, comparing top with bottom). Prey maladaptation increased predator range extent because it provided easily captured prey at the range margins, which increased predator reproduction, and allowed the predator to establish populations even where the abiotic environment caused high mortality. Controlling for the overall subsidy of prey that evolve lower defenses at the edge, we can also observe an effect of dispersal-mediated maladaptation on subsidizing predator ranges, especially from 100 to 400 m when predator range extent was determined by a limit of  $>1.5$  predators per patch (fig. 8, comparing top gray boxes from left to right). However, predator range edges did not differ



**Figure 6:** Simulation results of predator-prey eco-evolutionary dynamics across an environmental cline in predator abundances. Prey defense is modeled as a polymorphism with a trade-off between defense and population growth rate. The purple lines indicate  $m = 1$  or no difference between morphs in defense. Blue lines indicate maladaptation between prey defensive morphs ( $m = 5$ ). Within each color group, lighter lines indicate low prey dispersal (0.2) and darker lines indicate higher prey dispersal (0.3). A higher proportion of defended morphs evolve in response to the predator within its range (A), and greater dispersal probability decreases the extent of this evolutionary response. The evolution of less defended morphs increases predator abundances (B), especially at higher dispersal probabilities. Parameter values are listed in table 1.

for more liberal predator range limits set to more than one predator per patch, which better captures the limits imposed by the abiotic environment and includes sink populations where predators can survive but not reproduce. The reason for this difference is that reproduction is rare at an average of one predator per patch because predator reproduction was the fitness component affected by prey attack rate in the model, whereas predator mortality depends solely on the predator's static responses to the abiotic gradient.

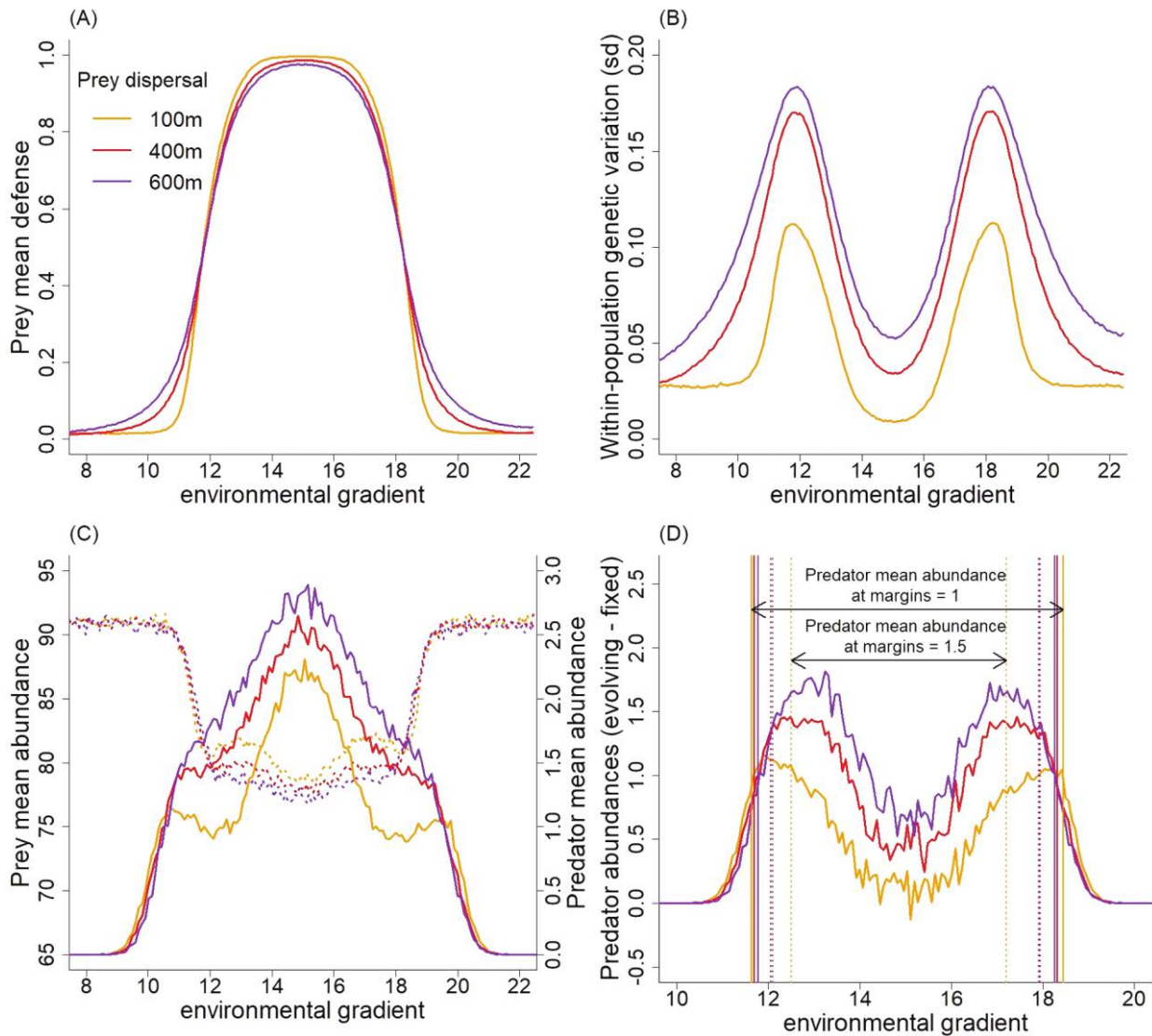
Overall, simulations supported analytical results, suggesting that a trade-off between defense and population growth rate enhances the potential for a spatial genetic subsidy. In particular, the growth-defense trade-off increases predator abundances in marginal habitats, thus greatly expanding the predator's range extent compared to models without a trade-off (fig. S4). Model results were robust to lower mutation rates (fig. S5) because most local genetic variation was generated by migration among spatially varying selection regimes. We also explored results altering emigration probability rather than dispersal distance and found an even greater effect of prey emigration probability on predator range extent (fig. S6 vs. fig. S7 and fig. S7 vs. fig. S8).

#### Range Dynamics with Environmental Change

We next allow the environmental gradient to shift for 100 generations and then restabilize, as might characterize a shift in climate. The predator can now colonize previously unsuitable habitats, which are also inhabited by less defended prey

that are maladapted to predation risk in evolutionary models. Without prey evolution, predator numbers always declined during the environmental change, often substantially, and their range size contracted before rebounding to previous levels (figs. 9, 10, S8). These effects on predators were exaggerated by higher rates of environmental change and lower predator dispersal but were unaffected by dispersal of non-evolving prey (e.g., fig. 9A vs. fig. 9C and fig. 10A vs. fig. 10B). The rate at which the predator shifted its range increased with higher rates of environmental change and higher predator dispersal distance (fig. 11). Without prey evolution, the predator went extinct at rates of change  $>0.0375$  when it dispersed on average 100 m and  $>0.075$  when it dispersed 400 m.

When prey evolved defenses, predator abundances decreased briefly but then rebounded quickly and increased beyond predisturbance abundances (figs. 9, 10). As the predators shifted their range, they encountered not just a subsidy of unexploited prey but also a genetic subsidy of less defended prey adapted to predator-free conditions beyond the predator's historical range. Predator abundances remained high for long periods until prey in these recently colonized areas could evolve defenses against the invading predator. Despite the increase in total abundances, the predator range still shrunk during the environmental shift, especially for poorly dispersing predators, before rebounding to the initial width (fig. S8). For higher rates of environmental change ( $\geq 0.075/\text{year}$ ), the predator range declined dramatically but then reexpanded and exhibited elasticity by overshooting its original range width (fig. S8E–S8H) before returning to quasi equilibrium.

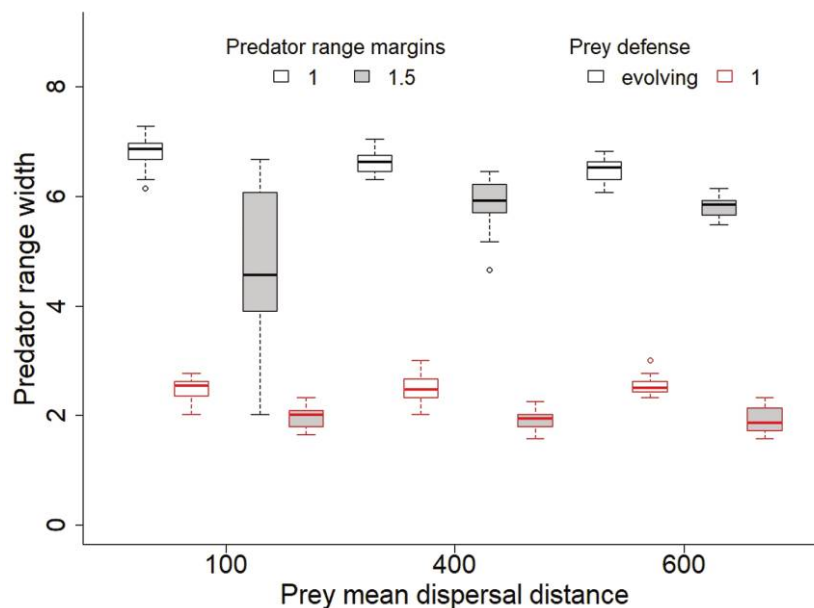


**Figure 7:** Effects of maladaptive gene flow on predator and prey dynamics. Increasing prey dispersal from a mean distance of 100 m (orange) to 600 m (purple) decreased prey defenses in the center of the predator's range and smoothed out genetic clines (A) and increased within-population genetic variation, especially at the edge of the predator range (B). C, Increasing prey dispersal and consequent higher local population maladaptation increased predator abundances (solid lines) and decreased prey population abundances (dotted lines). D, Evolution of less defended prey increased predator mean abundances relative to simulations with fixed defenses ( $\delta_{\text{const}} = 1.0$ , maximum defense that evolved), especially at the predator range margins. As prey dispersed more, their maladapted defenses increased predator range limits set at mean predators per patch = 1.5 (dotted lines) but not at the more liberal limits of one predator on average per patch (solid lines). Results are means across 50 replicate simulations at generation 2,500.

When prey were maladapted to predation risk, the predator shifted its range faster than for fixed defense simulations, and the difference was greater for faster change (fig. 11). Importantly, prey maladapted to predators allowed a poorly dispersing predator species to persist under high rates of environmental change (fig. 11;  $>0.05/\text{year}$ ) where it would otherwise become extinct if it instead encountered prey with fixed defense levels.

During environmental change, higher prey dispersal and subsequent gene flow–induced maladaptation dampened subsidies to predators rather than facilitated them, and predator abundances returned to their lower initial values much faster (fig. 10). This outcome is consistent with results that show that prey defenses evolve to higher levels outside the predator's range when prey disperse greater distances (fig. 6A). Hence, when prey disperse longer distances, they become maladapted





**Figure 8:** Effect of maladapted gene flow on predator's range width in the same environmental gradient units as  $\theta$ . Evolving prey defenses and maladaptive gene flow increased predator ranges relative to nonevolving simulations fixed to maximum defense = 1 (evolving = black border, fixed = red border). More maladapted gene flow increased predator ranges as prey dispersal increased from 100 to 400 m when they were defined as an average of >1.5 individuals per patch (gray boxes) but did not differ when defined as more than one individual per patch (white boxes), where range margins are largely driven by abiotic mortality because reproduction is rare. With strong defenses, greater prey dispersal did not increase predator ranges. Results are presented as median (solid bands), first and third quartiles (box limits), and twice the standard deviation (whiskers) for 50 replicate simulations at generation 2,500.

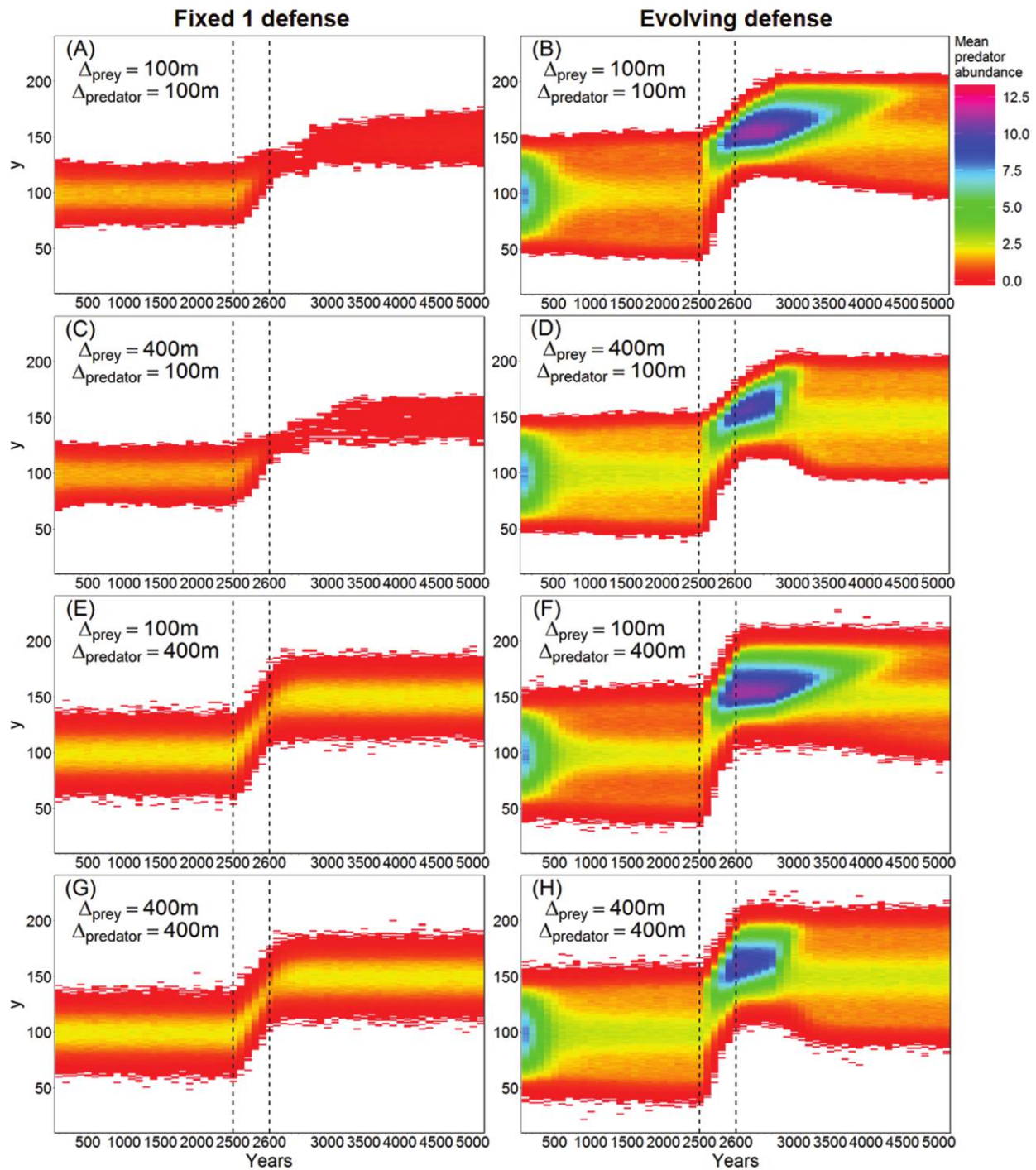
not only to predation within the predator's range but also to predator-free environments outside of it. A rapidly expanding predator will generally meet less defended prey, but those prey will be even less defended if prey disperse less. Hence, the same maladaptation in prey defenses that increases predator abundances during environmental stability decreases it during range expansion. Prey dispersal distance did not significantly affect the rate of range shifting in both evolutionary and non-evolutionary models (fig. 11), suggesting that such impacts weaken the farther the predator gets from the original range boundary. Alternatively, this pattern might occur because of the counteracting effect of prey dispersal and prey maladaptation on the predator: with high prey dispersal, the predator reaches higher abundances and sends out more colonists, but those colonists face better-defended prey.

### Discussion

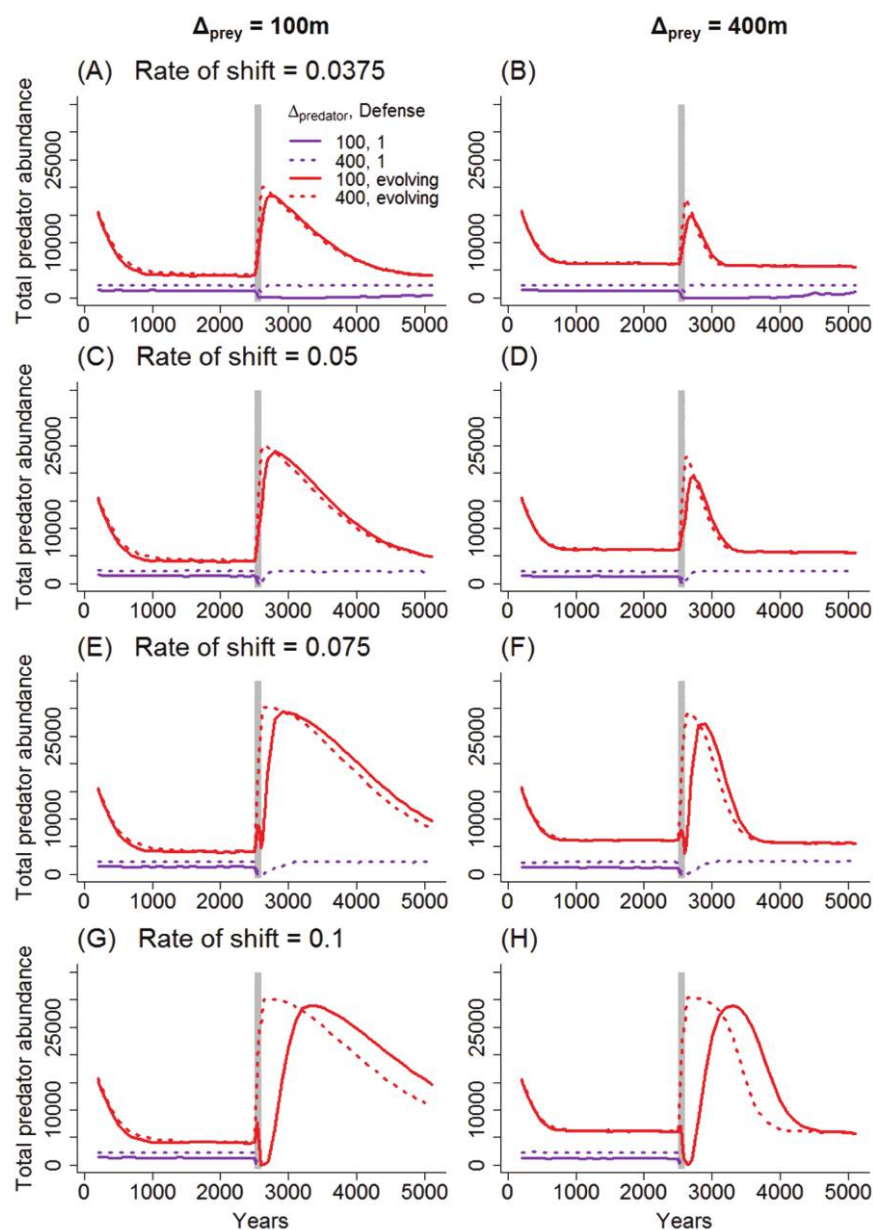
Prey dispersing from predator-free patches often supply a trophic subsidy to predators by providing more prey than are produced locally (Polis et al. 1997; Nakano et al. 1999; Sabo and Power 2002). Such subsidies can increase consumer density or biomass depending on their relative contributions to lo-

cal resources (Marczak et al. 2007). Theory suggests that trophic subsidies not only increase predator densities but stabilize local food web dynamics depending on resource supply and feeding preferences (Huxel and McCann 1998). Spatial subsidies also shifted ecological thinking toward considering communities and ecosystems as open rather than closed via the metacommunity and metaecosystem frameworks (Loreau et al. 2003; Loreau and Holt 2004; Holyoak et al. 2005).

However, this ecological view generally excludes potential impacts from evolutionary dynamics and regional dispersal, a view encapsulated by the evolving metacommunity framework (Urban 2006; Urban and Skelly 2006; Urban et al. 2008). The same predator-free conditions not only can enhance the regional supply of prey but also select for decreased defenses. Prey populations often adapt to predator-free environments and, in doing so, become maladapted to predators via fitness trade-offs. Consequently, prey populations are likely to become increasingly maladapted to predation risk in regions where predators become rare, such as at a predator's range edge (Billerbeck et al. 2000; Laurila et al. 2008). Prey dispersing from a predator-free patch into a patch with predators might be not just plentiful but also maladapted. These maladapted populations could subsidize their enemies and



**Figure 9:** Predator range and abundance responses to environmental change (within dotted vertical lines) for fixed defenses (*left column*) and evolving prey (*right column*). We contrast low (*A–D*; 100 m) versus high (*E–H*; 400 m) predator dispersal and low (*A, B, E, F*; 100 m) versus high (*C, D, G, H*; 400 m) prey dispersal. Colors indicate the mean cell predator abundances across the row (*y*) for 20 replicate simulations. Data are presented at 100-year (generation) intervals, except for between years 2500 and 2600 when they are plotted at 20-year intervals. The initial 1,000 years represent the burn-in period necessary for the model to reach quasi equilibrium, as indicated by stationary ranges.

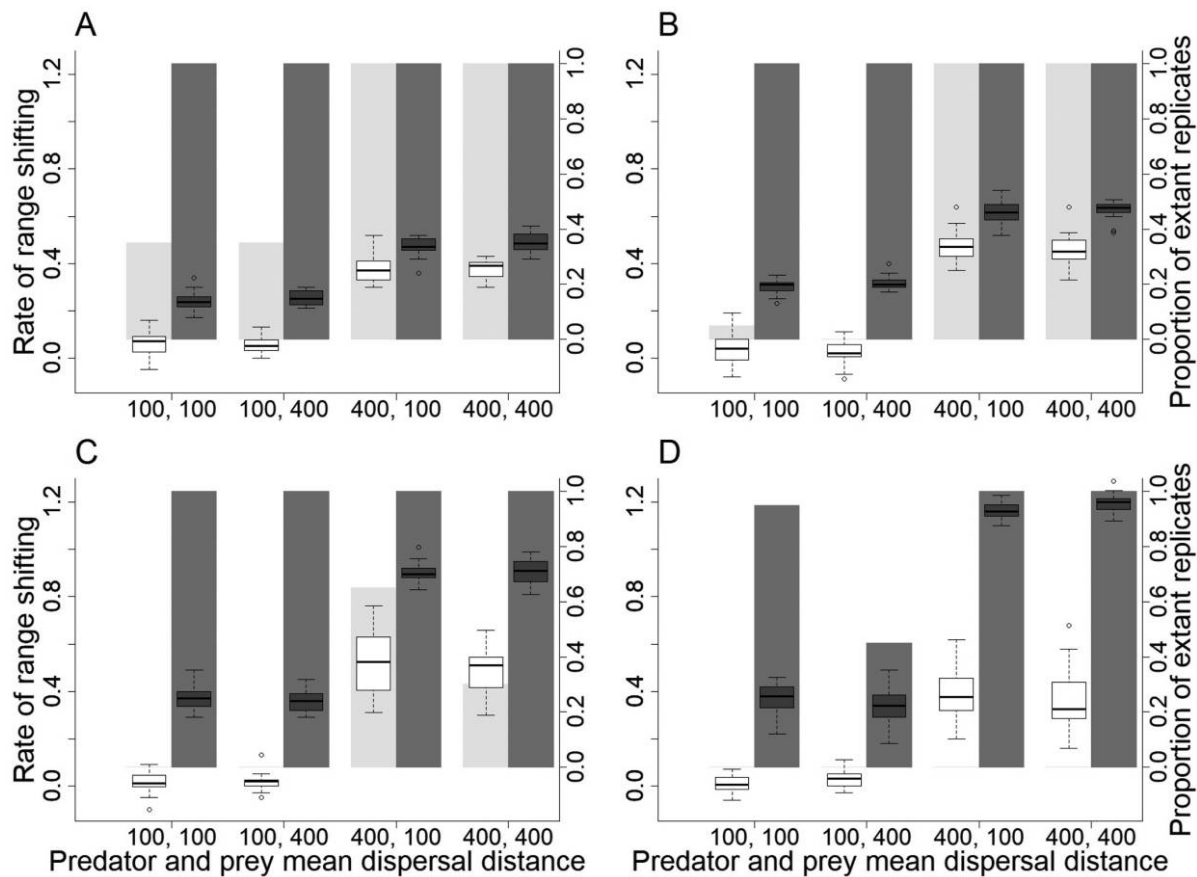


**Figure 10:** Responses of total predator abundances to increasing rates of environmental change: 0.0375 (A, B), 0.05 (C, D), 0.075 (E, F), and 0.1 (G, H) units per year for 100 years (gray vertical band). We contrasted low (left column) versus high (right column) prey dispersal distance ( $\Delta_{\text{prey}}$ ) for fixed, nonevolving defense (= 1; purple) and evolving defense (red). Solid lines indicate low predator dispersal ( $\Delta_{\text{predator}} = 100$  m), and dotted lines indicate high predator dispersal ( $\Delta_{\text{predator}} = 400$  m). Total abundances are presented as means across 20 replicate simulations. The initial 1,000 years represent the burn-in period necessary for the model to reach quasi equilibrium, as indicated by stationary ranges.

increase their abundances, persistence, and range extent. Using complementary analytical, numerical, and individual-based models, we demonstrate that spatial genetic subsidies should be a common outcome of gene flow-induced maladaptation in patchy environments, apply across a range of conditions, and facilitate predator persistence and range shifts during environmental change.

#### *Two-Patch Communities*

Within a community, we demonstrate that the spatial genetic subsidy takes on the properties of a model of apparent competition with dispersal (Holt 1977). Prey immigration introduces a purely ecological trophic subsidy (Polis et al. 1997) by increasing predator abundance in all models. These higher



**Figure 11:** Rate of predator range shifting in  $y$  units per 100 years (box plots) and proportion of simulation runs with persistent predator populations (bars) relative to increasing rates of environmental change: 0.0375 (A), 0.05 (B), 0.075 (C), and 0.1 (D) units per year. Boxes indicate interquartile range, and whisker plots indicate 2 standard deviations. Light boxes and bars symbolize results with fixed prey defenses, and dark boxes and bars symbolize results with evolving defenses. We contrasted low and high predator and prey dispersal within each sub-panel, with the first two groups of bars set to low predator dispersal (100 m) and the second set to high dispersal (400 m). The second and fourth groups of bars represent high prey dispersal (400 m). The rate of range shifting is calculated by dividing the shift in the maximum  $y$  location by 100 years, the duration of the environmental gradient shift.

predator abundances decrease the abundance of the defended prey, consistent with the predictions of apparent competition. Spatial genetic subsidies enhance this ecological effect by increasing the attack rate on undefended, immigrant prey and therefore the subsidy to predators. However, spatial genetic subsidies depend on the absolute difference between undefended and defended prey (model 1).

Assuming linear or accelerating trade-offs between prey defense and growth rate (model 2) ensures a spatial genetic subsidy by allowing undefended prey to recover from high attack rates and equilibrate at sufficient numbers to feed the larger predator population. Such trade-offs between defense evolution and fitness in predator-free environments are a common outcome of adaptive responses to predator and no-predator environments (Lively 1986, 1999; Reznick et al. 1990; Abrams 2000; Lankford et al. 2001; Yoshida et al.

2003; Laurila et al. 2006; Meyer et al. 2006; Becks et al. 2010; Terhorst et al. 2010; Fischer et al. 2014; Hiltunen et al. 2014; Kasada et al. 2014; Urban and Richardson 2015). Numerical results from model 3 confirmed that undefended and maladapted immigrants increase predator abundances, despite including symmetric dispersal, multipatch population dynamics, and evolution via mutation. Hence, at the local scale of linked predator and predator-free patches, spatial genetic subsidies might commonly result from the exchange of less defended prey.

#### *Dynamics across Species' Ranges*

We expanded our general theoretical framework by using individual-based modeling to include predator and prey populations interacting on a landscape and enabling prey



evolution via explicit genetics. Both simulations with discrete and continuous prey defense evolution demonstrated that the basic outcomes from simple theory hold despite the potential for more complex spatial eco-evolutionary dynamics: the genetic subsidy of undefended prey coming from predator-free patches can facilitate more abundant predator populations.

Prey maladaptation also affected predator range limits, although this effect was less pronounced than changes in predator abundance. In simulations, prey evolved defenses in response to the distribution of predator abundances created by the environment, generating a unimodal cline in prey defenses peaking at the center of the predator's range. Prey defenses decline outside of the predator's range because they evolve lower defenses and higher population growth rates according to the assumed trade-off. As prey disperse more, prey populations become more maladapted to both predator and no-predator environments. This maladaptation is reinforced by the asymmetric gene flow from the range edge to the core, where prey numbers are suppressed. Thus, prey evolved lower defenses inside the predator range than optimal, they evolved greater defenses outside the predator range than optimal, and this effect was enhanced by greater maladaptive gene flow. This maladaptive gene flow also increased genetic variation in populations along the steepest parts of the genetic cline, corresponding to regions where predator range extent is determined. These elevated levels of additive genetic variance at the predator's range edge likely enhanced evolutionary rates (Yoshida et al. 2003; Becks et al. 2010; Bolnick et al. 2011; Cortez 2016).

As in the analytical models, less defended prey increased predator abundances through spatial genetic subsidies. These subsidies also expanded the predator's range by increasing predator fitness in marginal abiotic habitats. In particular, decreasing prey defenses and higher intrapopulation genetic variation produced a subsidy of easily captured resources at the edge of the predator's range (fig. 7), which allowed the predator to expand its range until reaching a new fitness limit. Higher prey dispersal and thus more local maladaptation to the predator strengthened the spatial genetic subsidy and increased predator range extents.

#### *Subsidies during Environmental Change*

In a changing environment, predators that attacked nonevolving prey with fixed defenses declined in abundance and sometimes became extinct. However, when prey evolved, they created a reservoir of undefended prey just beyond the predator's original range boundary, which provided a strong subsidy to predators under environmental change. Predator abundances did not decline as much when eating poorly defended prey during the onset of environmental change relative to the nonevolving simulations and subsequently generated preda-

tor abundances higher than before environmental change. This benefit allowed predators to persist under higher levels of environmental change whereas they became extinct when encountering prey with a fixed defense. Interestingly, we also show the emergence of elastic range margins for the predator following environmental change (Holt 2003). Although this phenomenon has been proposed theoretically in single-species models as a consequence of dispersal evolution during range expansion (Holt 2003; Kubisch et al. 2010; Henry et al. 2013), a similar pattern can arise for predator ranges owing to prey maladaptation.

Results suggest that some of the most dramatic effects of spatial genetic subsidies occur when range boundaries are expanding. In a stable environment, the predator reaches an eco-evolutionary equilibrium mediated by prey evolution, prey abundances, and predator abundances. However, when the environment shifts, the predator is temporarily released from its environmental limitations, allowing it to interact with less defended prey and enjoy increased resources. Hence, spatial genetic subsidies could provide an underappreciated but important mechanism facilitating range shifts in response to environmental change. This "resource rescue" could be important for many predators, pathogens, parasites, and grazers during environmental changes such as climate change. More generally, when enemies decline during environmental change, they might often select for the evolution of decreased victim defenses owing to defense-growth trade-offs, thereby producing a community-mediated evolutionary rescue of predators (Yamamichi and Miner 2015).

Few theoretical works have examined how prey defensive maladaptation affects predator abundances, population dynamics, persistence, and range size because most theoretical studies instead focus on how predators affect prey ranges rather than vice versa (e.g., Holt and Barfield 2009; Holt et al. 2011; Osmond et al. 2017). In one exception, Holt (2017) applied a patch-dynamic approach to demonstrate that maladapted prey increased predator persistence in a metacommunity by providing exploitable resources. In a simulated host-pathogen evolving metacommunity, recurrent extirpation and recolonization of patches created susceptible host populations that maintained pathogens, whereas the evolution of resistance in a single patch drove the pathogen extinct (Antonovics et al. 1997). Hochberg and van Baalen (1998) analyzed a predator-prey coevolutionary model along a resource gradient and found that lower resources at either end of the gradient reduced prey densities, which decreased the predator's range. Last, Nuismer and Kirkpatrick (2003) explored a two-patch coevolutionary model of hosts and parasites and found that increasing host gene flow reduced host adaptation and facilitated parasite colonization when the environment was a source for the parasite.

We extend these emerging results to population dynamic models, allow predator survival on defended prey, and include

realistic features such as multilocus genetics, varying dispersal, abiotic clines, and individual-based interactions between predators and prey. This approach allowed us to demonstrate how spatial and genetic subsidies to predators play out in complex landscapes and during environmental change, clarify the role of both predator and prey dispersal, and demonstrate the resulting eco-evolutionary dynamics of predator range shifting and its consequences for prey populations and evolution.

#### *Future Directions for Modeling*

Predator-prey coevolution might often generate negative co-evolutionary feedbacks that dampen environmentally induced changes to their densities (Northfield and Ives 2013) or induce maladaptation because of temporal lags in coadaptation (Lively 1999; Thompson et al. 2002). In one coevolutionary model, gene flow-induced maladaptation prevented host adaptation to parasites when parasites were constrained to a subset of the host's range (Nuismer et al. 2003). Once the parasite range expanded, hosts adapted and parasites became maladapted, potentially constraining their range (Nuismer et al. 2003). In our model, if predators could evolve to counteract prey defenses, then predators should become more abundant in the center of their range. Predators will likely become maladapted to overcoming prey defenses at their range edge with high dispersal, but less defended prey might moderate this effect. Future work is necessary to determine how these dynamics play out with specific parameters.

Future work should also explore constraints on the prey species' ranges. Holt et al. (2011) theoretically demonstrated that predation can modify the interplay between gene flow and selection for prey adapting across an environmental gradient and determine evolutionary constraints on the prey range limits. In particular, a specialist predator might indirectly alter prey local maladaptation by modifying prey abundances and thus reversing maladapted gene flow from the range edges to the center where predators suppress prey. Depending on predator efficacy, form of density dependence, and predator dispersal ability relative to the prey, this effect can either expand or collapse the prey range. Also, during environmental change, prey and predator that share a range boundary might both expand their ranges, such that their eco-evolutionary dynamics depend on relative expansion rates and predator specialization on the prey species.

Future models might also evaluate what happens when prey or predator dispersal evolves. Consumer-resource dynamics can promote or hinder the evolution of increased dispersal depending on the type and complexity of the spatio-temporal ecological dynamics, strength of the interaction, and degree of local adaptation (Savill and Hogeweg 1998; Schreiber and Saltzman 2009; Chaianunporn and Hovestadt 2012; Drown et al. 2013; Travis et al. 2013; Kubisch et al. 2014;

Amarasekare 2016). Single-species models predict that increased dispersal should evolve at an expanding range margin (Travis and Dytham 2002; Phillips et al. 2008; Travis et al. 2009; Henry et al. 2013). However, in a predator-prey model where both species could expand their range into empty habitat, Kubisch et al. (2014) predicted evolution of lower prey emigration rates with a consequent decrease of invasion speed. An interesting future direction would consider coevolution of predator and prey dispersal and prey defense across their ranges and during range shifts. Without environmental change, prey dispersal might decrease to ensure prey adaptation and limit the negative effects of maladapted gene flow. During environmental change, we might expect predators to evolve higher dispersal, which would enhance their impact on maladapted prey. Interestingly, prey defense might sometimes involve enhanced dispersal ability (Siepielski and Beaulieu 2017), thus creating a correlation among the two traits that could alter eco-evolutionary dynamics of both species across their range. Another interesting extension would allow dispersal to evolve as a function of local biotic conditions. For example, predators might evolve to emigrate more in patches with low prey availability, which could result from the evolution of prey defenses (French and Travis 2001). The evolution of these conditional dispersal strategies could also alter the eco-evolutionary dynamics of predator-prey ranges.

#### *Empirical Tests*

Theory predicts that less defended prey will increase predator fitness and abundance. Experiments can test this prediction by contrasting predator population responses to being fed prey adapted or maladapted to the predator. Few such experiments have been performed, perhaps owing to the lack of an appropriate theoretical framework. In one experiment, maladapted hybrids between cottonwood species supported hundreds more mites than pure species (McIntyre and Whitham 2003). In a temporal study, undefended *Chlamydomonas* algae supported higher densities of grazing rotifers, whereas the evolution of better-defended algae decreased grazer densities, thus altering predator-prey oscillatory dynamics (Becks et al. 2010). However, more tests are needed to support the generality of this assumption.

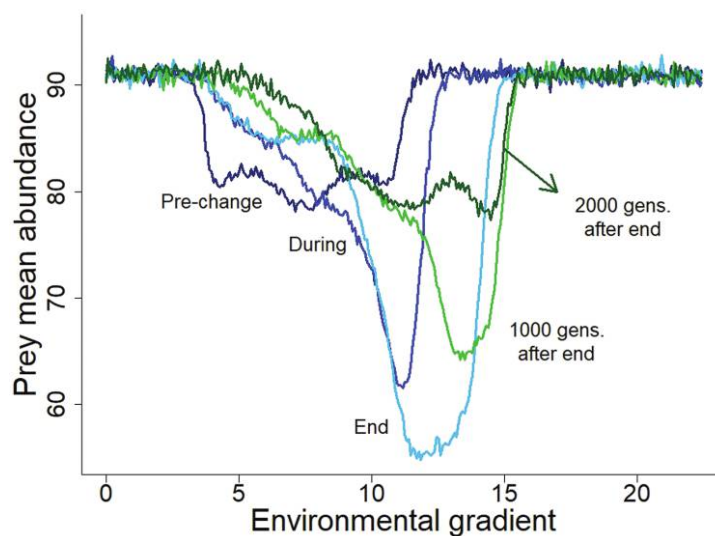
Simulations offer testable predictions about predator range extent, abundance distributions, and responses to environmental change but rely on many untested assumptions. One assumption to test is whether prey differentially adapt to focal predators across their range. In one such study, Laurila et al. (2008) found that *Rana temporaria* tadpoles from high latitude with few predators remained active in the presence of predators and thus suffered higher mortality relative to low-latitude, high-predation populations. Similarly, Toju and Sota (2006) found a latitudinal cline in the Japanese camellia tree's

defenses against an obligate seed predator. Spotted salamanders adapt defensive behaviors within the range of predaceous marbled salamanders depending on local predator densities, adapt weaker defenses to the predator toward the predator's range edge, and do not evolve defenses against this particular predator in populations located beyond the predator's northern range edge (Urban and Richardson 2015). Atlantic silverside fish (*Menidia menidia*) also evolved lower defenses against predators in northern parts of their range with fewer predators (Lankford et al. 2001).

Experiments are needed that evaluate how differential prey adaptation and maladaptation across the range alter predator population and range characteristics. Empiricists can gain inspiration from the many transplant experiments that assess the mechanisms underlying range boundaries (Sexton et al. 2009; Hargreaves et al. 2013). In these experiments, a species is transplanted beyond the range limit to see whether its range limit matches its niche limits or if it simply has not yet dispersed there. A small subset of these studies also manipulate species interactions, and when they do so, a majority find evidence for biotic limitations to range limits (Sexton et al. 2009). Transplants can also be used to test for spatial genetic subsidies across a predator's range. A convincing experiment would evaluate predator population dynamics when raised on prey from central and edge prey populations at both respective locations to account for correlated environmental effects. If maladapted prey expand the predator's current range, then predators should decline toward extirpation when living on defended prey at the range boundary but re-

main stable or increase when raised on undefended prey. To address climate change predictions, predators in a warming experiment conducted beyond the current predator's range should increase more rapidly when fed local, undefended prey than predators fed interior, defended prey. Microcosm experiments could be designed with temperature gradients and prey with and without genetic variation to allow direct tests of these predictions. To our knowledge, no experimental study has demonstrated that increased exploitation of maladapted prey at the range edge increases the predator's population growth rate, overall abundances, range expansion rates, or range limits, but such work could reveal novel insights. The study that comes closest is an observational study on mountain pine beetles. The study found that mountain pine beetles had higher reproductive success on host trees in regions recently colonized due to climate change, which could explain recent outbreaks of beetles and high tree mortality (Cudmore et al. 2010).

Ultimately, we need empirical work that tests spatial genetic subsidies under realistic conditions, such as in enclosure experiments or via whole-ecosystem manipulations. For instance, prey maladapted to predators can be added to existing predator habitats and predator responses followed like those done in classic food supplementation experiments (Boutin 1990; Ruffino et al. 2014). Natural experiments could also provide insights. In one classic example, invasive, maladapted pigs provided a resource that allowed native golden eagles to colonize and surge in numbers on the California Channel Islands (Roemer et al. 2002).



**Figure 12:** Prey mean population abundances along the environmental gradient before, during, and after 0, 1,000, and 2,000 generations of environmental change as colors change from dark blue to dark green. As predators expand their range, they decreased prey beyond their range boundary more than within the existing range, and this asymmetry in prey populations lasted long after the environmental change. Results shown for predator dispersal = 400 m, prey dispersal = 100 m, and rate of environmental change = 0.0375.

### Additional Implications

Theoretical results suggest several additional implications. Predators that eat more dispersive prey should have larger ranges because the prey are more maladapted at range edges. This prediction could be tested using sister taxa that differ in the dispersal distances of their preferred prey. As prey ranges become fragmented and the maladaptive effect of gene flow decreases, predator abundances and ranges might also decrease without the advantage of spatial genetic subsidies. Understanding this contribution requires separating the effects of fragmentation on predator populations versus those on prey maladaptation.

As predators expand their ranges in response to environmental changes such as climate change, they could suppress maladapted prey just at and beyond their range boundary (fig. 12). This zone of prey suppression lasts for many generations in our model, even after environments stabilize. For instance, the asymmetry in prey abundances across the predator range remained for up to 2,000 generations after environments stabilized in our model. These asymmetries in predator numerical effects on prey, when revealed by observations across a predator's range, could indicate past or ongoing environmental change.

Although not directly observed in our model, the potential exists for cycles of predator range expansion followed by prey adaptation and predator range retraction. Such dynamic range boundaries would require sufficient lag times between predator range expansion and prey adaptation, which could be created by any mechanism that prolongs evolutionary dynamics, including lower mutation rates, less genetic variation, overlapping generations, and a greater dependency of predator populations on prey consumption versus abiotic constraints. Coevolutionary dynamics with lag times could also produce these elastic range boundaries. In these cases, predator ranges might show a regular expansion and contraction, independent of environmental change.

### Conclusions

Less defended, maladapted prey might commonly subsidize predator populations and allow them to increase in number and range extent or survive in otherwise unsuitable environments. Although adaptation and maladaptation are simply two sides of the same coin (Hendry and Gonzalez 2008), its effect on ecological properties such as species interactions has largely been ignored (Urban 2006; Farkas et al. 2013, 2015; Hendry 2016). Thus, the regional evolutionary dynamics of maladaptive gene flow might frequently enhance trophic subsidies and explain why these subsidies are so strong and prevalent (Polis et al. 1997; Marczak et al. 2007). Such research places a renewed emphasis on considering how evolution and regional gene flow influence species interactions, as

exemplified by the evolving metacommunity framework, which suggests that communities and populations undergo an analogous tension between local selection on species and population traits versus the dissipative influence of regional mixing of species and genetic pools (Urban and Skelly 2006; Urban et al. 2008; Leibold and Chase 2017). If maladaptation is a natural part of evolution in patchy environments, as theoretical and empirical evidence suggests, then maladaptation might often determine natural ecological dynamics and patterns. By developing theory that integrates maladaptation and community ecology, we offer a number of testable predictions that we hope will encourage future empirical tests.

### Acknowledgments

M.C.U. was supported by National Science Foundation award DEB-1555876 and the James S. McDonnell Foundation, G.B. was supported by the Royal Society University Research Fellowship, and A.S. was supported by Biotechnology and Biological Sciences Research Council grant BB/S507349/1. We thank S. Brady, A. Hendry, and A. Gonzalez for inviting us to present this research at the Maladaptation Symposium at the 2018 meeting of the American Society of Naturalists. We thank J. Travis, three anonymous reviewers, and G. Grant for stimulating discussions of the topic.

*Statement of authorship:* M.C.U., J.M.J.T., and G.B. jointly conceived the study; A.S. and M.C.U. conducted the mathematical analyses; G.B. conducted the individual-based modeling; and M.C.U. led the writing, supported by all other authors.

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Special Feature Editor: Joseph Travis



Theoretical research was inspired by the authors' previous research in *The American Naturalist* (Urban and Richardson 2015) on how prey species adapt or do not adapt defenses against the predator pictured here, a marbled salamander (*Ambystoma opacum*). Photo credit: Mark Urban.