

# Do I build or do I move? Adaptation by habitat construction versus habitat choice\*

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Trait adaptation to a heterogeneous environment can occur through six modes: genetic differentiation of those traits, a jack-of-all-trades phenotypic uniformity, diversified bet-hedging, phenotypic plasticity, habitat choice, and habitat construction. A key question is what circumstances favor one mode over another, and how they might interact if a system can express more than one mode at a time. We examined the joint evolution of habitat choice and habitat construction using individual-based simulations. We manipulated when during the life cycle construction occurred and the fitness value of construction. We found that for our model habitat construction was nearly always favored over habitat choice, especially if construction happened after dispersal. Because of the ways that the various modes of adaptation interact with each other, there is no simple answer as to which will be favored; it depends on details of the biology and ecology of a given system.

**KEY WORDS:** Generalist, habitat choice, habitat construction, jack-of-all-trades, model, niche construction, specialist.

Understanding the process of trait evolution through selection and adaptation has been one of the core concerns of evolutionary biology ever since Charles Darwin, with evolutionary models tracing to the pioneering efforts of R. A. Fisher, Sewall Wright, and J. B. S. Haldane (Provine 1971). There are numerous models of the processes of trait adaptation in a population inhabiting a uniform environment (e.g., Mather and Jinks 1982; Feldman 1989; Falconer and Mackay 1996; Gillespie 1998; Rice 2004; Vincent and Brown 2005; Charlesworth and Charlesworth 2012). Still developing is an understanding of the multifarious modes of trait adaptation of species whose populations inhabit a heterogeneous environment. By “heterogeneous environment,” we mean those aspects of the environment that are external to the population itself, such as the abiotic environment or other species, and vary over space, time, or a combination of the two.

Trait adaptation to a heterogeneous environment can occur through six distinct modes: genetic differentiation of traits among subpopulations, a jack-of-all-trades phenotypic uniformity, diversified bet-hedging, phenotypic plasticity, habitat choice, and

habitat construction. By “mode” we mean the genotypes and phenotypes of the adapted individuals, not the consequences of those phenotypes (e.g., the distinction between the propensity to perform habitat construction versus the change in the environment due to that construction). There is a considerable and still growing literature on each of these, considered separately, but in many taxa more than one could operate at a time. Saltz and Nuzhdin (2014), for instance, suggest that habitat construction can influence the evolution of phenotypic plasticity. A key question then is what circumstances favor one mode over another, and how they might interact if a system can respond in more than one way at a time. The answer is important because different modes have different implications for other processes such as divergence among populations (e.g., Schlichting 2004; Edelaar et al. 2008; Krakauer et al. 2009; Thibert-Plante and Hendry 2011; Schmid and Guillaume 2017), speciation (e.g., De Meeûs et al. 1993; West-Eberhard 2003; Peterson 2011; Nonaka et al. 2015), predator-prey cycles (e.g., Mougi et al. 2011), and competition (e.g., Connell 1980; Post and Palkovacs 2009; Jacob et al. 2018). A full answer requires that we not just study each mode in isolation; we also need to allow them to evolve in tandem to see if the modes have nonadditive effects on each other such that the presence of one enhances or suppresses the potential

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for another. In this article, we present results concerning interactions of two of those modes of adaptation—habitat construction and habitat choice—and place them in the context of all of those modes so as to help crystalize that understanding.

The first models of trait adaptation in a heterogeneous environment date to the 1950s and focus on genetic differentiation and the jack-of-all-trades, which were typically framed as the evolution of specialists versus generalists (e.g., Levene 1953; Dempster 1955; Levins 1962; Haldane and Jayakar 1963), although only a few of these models explicitly include traits (e.g., Gilchrist 1995). When genetic differentiation is favored, the resulting population consists of individuals that are genetically variable (specialists) with each genotype expressing a different trait value. When dispersal is limited and localized in space, this will often lead to local adaptation (Kawecki and Ebert 2004), with each population being dominated by genotypes that have the highest fitness in its environment. In this article, however, we consider systems in which the dispersal distance is much larger than the grain of the environment or is otherwise not spatially restricted. Although such global (nonlocal) dispersion can also lead to local adaptation if selection is sufficiently strong, it can also result in a jack-of-all-trades (generalist) that consists of a single genotype and phenotype. When such a generalist is favored, it may not reach the fitness maximum in any single environment; rather, it will have a greater fitness than any specialist when averaged appropriately across environments. More formally, the jack-of-all-trades has a greater geometric mean fitness even if it has a lower arithmetic mean fitness, relative to specialized individuals. This type of generalist is favored when environmental heterogeneity is temporal because fitnesses are multiplied across generations. The end result of evolution could be a population consisting of all specialists, all generalists, or some mixture of both types (see reviews by Hedrick 1986; Wilson and Yoshimura 1994).

The jack-of-all-trades is sometimes referred to as conservative bet-hedging because of the trade-off between geometric and arithmetic mean fitness (Starrfelt and Kokko 2012). A similar trade-off is expressed by diversified bet-hedging, in which a single genotype expresses variable phenotypes due to developmental instability (Slatkin 1974; Philippi and Seger 1989; Simons and Johnston 1997; Starrfelt and Kokko 2012). This phenotypic variation is random, that is, not dependent on environmental inputs, and sometimes referred to as “adaptive coin flipping” (Kaplan and Cooper 1984). Diversified bet-hedging is more likely to be favored by temporal heterogeneity than by spatial heterogeneity (Starrfelt and Kokko 2012; Poethke et al. 2016; Haaland et al. 2019), and a combination of spatial and temporal heterogeneity can act synergistically to further favor diversified bet-hedging (Scheiner 2014a). As with genetic differentiation, diversified bet-hedging results in phenotypic trait variation. The difference is that with genetic differentiation the phenotypic variation

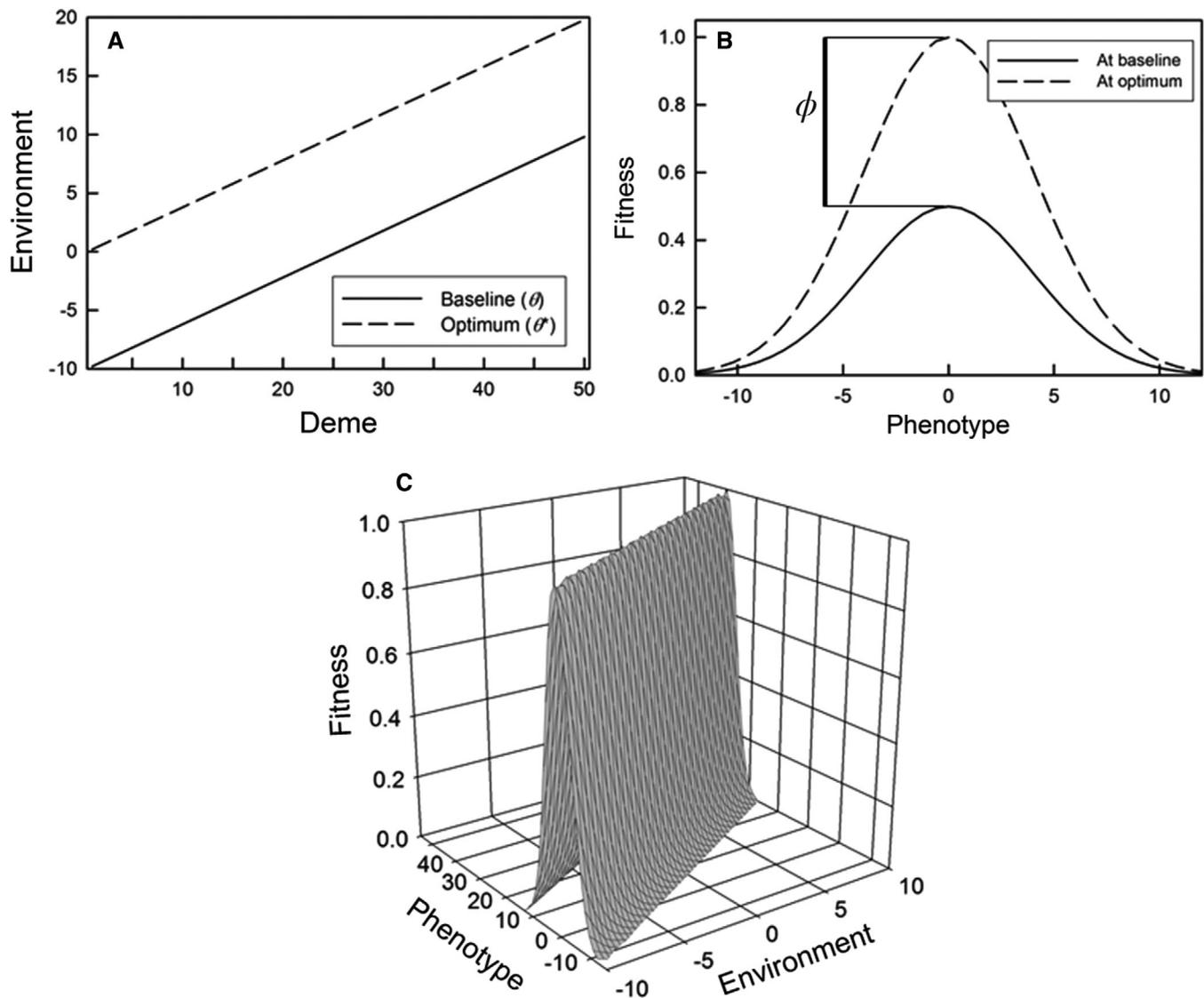
occurs among lineages in a population, whereas with diversified bet-hedging the phenotypic variation is within each lineage.

A different mode of adaptation is phenotypic plasticity, which is the expression of multiple phenotypes from a single genotype (Schlichting and Pigliucci 1998; DeWitt and Scheiner 2004). Plasticity differs from diversified bet-hedging in that the phenotypic variability depends on environmental inputs. In some instances when temporal and spatial variation are very high, plasticity can act as a form of bet-hedging (Scheiner 2014b; Haaland et al. 2021). More typically, however, this mode of adaptation can potentially result in an “ideal” generalist, a genotype that is capable of expressing the optimal trait value in all environments. That we rarely see such individuals in nature then raises questions of what costs or limitations prevent such adaptation, but that issue is beyond the scope of this article (see Reed et al. 2010; Chevin and Lande 2011; Frankenhuis and Panchanathan 2011; Scheiner 2013; Fischer et al. 2014; Hendry 2016; Scheiner 2019). As with diversified bet-hedging, phenotypic variation is within, rather than among, lineages.

For the four modes detailed above, the only evolution is of the focal trait whose optimal value varies across environments. However, adaptation by phenotypic plasticity is different from the other three modes because it can involve loci in addition to those that determine mean trait values (e.g., Weber and Scheiner 1992; Morgante et al. 2015; Kusmec et al. 2017). The existence of both environmentally sensitive loci (plasticity genes) and nonsensitive loci can result in different evolutionary outcomes than if there are only plasticity genes (Scheiner 1998).

The other two modes of adaptation—habitat choice and habitat construction—differ from the previous four in that evolution can happen to a second trait (or set of traits) that determines the choice or construction process, which might also result in a different evolutionary dynamic. Edelaar and Bolnick (2019) classified the processes that improve fitness using two criteria: what changes (the trait or the environment) and how it changes (through selection and through alteration; see their Fig. 1). However, their figure does not emphasize the distinction between those processes that occur within a single generation (developmental plasticity, habitat choice, habitat construction) and what is changed by those processes versus those that occur across many generations (evolution by natural selection) and the subsequently evolving traits. Even for very quickly evolving systems, evolutionary changes are generally on longer time scales than the one or a few generations of potential carryover of plasticity, choice, and construction. We expand and clarify their classification by making clearer this distinction between within- and among-generation processes (Table 1) and by highlighting critical distinctions among the six modes of adaptation.

Habitat choice is predicted to favor genetic differentiation and local adaptation over a generalist, jack-of-all-trades strategy



**Figure 1.** (A) Both the baseline ( $\theta$ ) and optimal ( $\theta^*$ ) environment vary along a gradient. (B) The fitness function in a deme with  $T_{opt,t} = 0$  when the environment equals the optimum, and the fitness ( $\phi = 50\%$ ) when the environment equals the baseline. Trait values are in the same units as the environment. (C) The survival probability ( $W_t$ ) along the environmental gradient when the environment of selection ( $S_t$ ) and, thus, the optimal phenotype ( $T_{opt,t}$ ) matches the optimum ( $\theta^*$ ) shown in panel A, and assuming no cost of construction. The ridge of the survival probability corresponds to the optimal phenotype ( $T_{opt,t}$ ).

(Edelaar and Bolnick 2012; Scheiner 2016; Nicolaus and Edelaar 2018), and in source-sink scenarios habitat choice can foster habitat specialization (Holt 1987). Habitat construction is predicted to be favored when the benefits of habitat construction are enjoyed either by the individuals that bore the costs of construction or their close relatives (e.g., offspring) (Laland et al. 1996; Silver and Di Paolo 2006; Kylafis and Loreau 2008; Lehmann 2008; Krakauer et al. 2009; Chisholm et al. 2018). None of those models of habitat construction considered the effects of environmental heterogeneity and so did not address the issue of genetic differentiation versus a jack-of-all-trades for a trait affected by that construction.

A few models have looked at the joint evolution of habitat choice or habitat construction and plasticity. Under some conditions, habitat choice and plasticity can jointly enhance genetic differentiation (Nonaka et al. 2015). Other models (Scheiner 2016; Edelaar et al. 2017) found that habitat choice suppresses the evolution of phenotypic plasticity and favors genetic differentiation when there is only spatial variation, but that the addition of temporal variation allows selection for a generalist plastic strategy. One article (Scheiner et al. 2021) has considered the joint evolution of construction and plasticity. It concluded that construction and plasticity can trade off against each other, or interfere with each other, depending on the temporal ordering of

**Table 1.** A classification of the processes that improve fitness in heterogeneous environments, modified from Edelaar and Bolnick (2019).

A. What changes within a generation	
The focal trait	The environment
No change	Habitat choice
Plastic development	Habitat construction
B. What evolves among generations	
The focal trait	Other traits
Mean trait values (1,2)	Propensity to disperse or related behaviors (5)
Variability of trait values (1,3)	
The reaction norm (4)	Propensity to construct or related behaviors (6)

We make a distinction between those processes that occur within a single generation, and the parallel evolutionary trait changes that occur across generations. (A) These are changes in phenotype or the environment that might occur within a well-adapted population of individuals living in a heterogeneous environment. “No change” equates to past selection for among-individual variability so that individuals have a fixed phenotype that results in high fitness for each individual in some part of the heterogeneous environment. (B) These are the past evolutionary changes that lead to the population characteristics in panel (A). The numbers map the six modes of adaptation: (1) genetic differentiation of traits among subpopulations, (2) a jack-of-all-trades phenotypic uniformity, (3) diversified bet-hedging, (4) phenotypic plasticity, (5) habitat choice, and (6) habitat construction. Variability of trait values can refer to either adaptive differences (genetic differentiation) or random variation (bet hedging).

development, construction, dispersal, and selection. In the current article, we examine the remaining possible joint evolutionary process: what happens when habitat construction and habitat choice are both potential modes of adaptation in a single system.

### MODELING HABITAT CONSTRUCTION AND HABITAT CHOICE

In our model, construction increases fitness within a deme and could occur either prior to dispersal or after dispersal. The form of habitat construction that we model can be referred to as “undirected construction” in that the effects are shared by all individuals in a deme. For example, nitrogen fixation by symbiotic bacteria (see review by Sachs et al. 2018) can be considered a form of habitat construction by the host plant that benefits other plants as leaves are shed or the entire plant dies (Lehmann 2008; Scheiner et al. 2021). Earthworms altering soil texture is another such example (Darwin 1892; Lavelle 1988). These examples contrast with “directed construction” in which the effects largely go to just the constructing individual or perhaps its offspring or sib-

lings. Examples of this sort include the building of bird nests, termite mounds, and rodent burrows. The two forms overlap because the effects of undirected construction might still go just to near kin if the size of each population (deme) is very small. In our current model, deme size was 16, so effects were undirected. Because the benefits of habitat construction were also enjoyed by individuals other than those doing the construction, its evolution was determined, in part, by any inclusive fitness effects through a structured population selection process (Hamilton 1964; Wilson 1983). Habitat construction in our model was costly with a linear decrease in fitness as the amount of construction increased.

The form of habitat construction that we model also can be referred to as “unresponsive” as the amount of construction performed by an individual is based solely on its genotype. Although construction was not responsive to the environment, it was limited. We modeled a saturating function for the amount of construction conducted by an individual. This function was premised on the notion that a single individual cannot perform an unlimited amount of construction due to energy, time, or other constraints. The alternative would be responsive construction in which the individual assesses the state of the environment and the amount of construction that is done is that which is necessary to move the environment as close to the optimal state as possible. Again, both nitrogen fixation and soil conditioning by earthworms are forms of unresponsive construction. In the former case, the amount of nitrogen fixation that occurs is unresponsive to the levels of nitrogen in the soil over a broad range of concentrations; in the latter case, the effects of earthworms on the soil are fundamental to their biology and are not dependent on the state of the soil.

However, we did have a version of responsiveness in our model in that the total amount of construction within a deme was also a saturating function. The latter was premised on there being some type of feedback among individuals limiting what any single individual could accomplish. This feedback could be as simple as negative density dependence, for example, earthworm burrowing is reduced as their density increases, or direct behavioral feedbacks. Such a limitation also prevented the amount of construction from massively overshooting the optimal environmental condition as we did not directly limit the state of the environment. We emphasize that the results of our modeling are dependent on all of these choices. Models based on other types of habitat construction might reach different conclusions.

The form of habitat choice that we model is often referred to as “adaptive habitat choice” in which individuals choose habitats because that choice potentially increases their fitness. (For a list of alternative terminology, see Edelaar et al. [2008] or Bolnick and Otto [2013].) Each individual assessed its environment, and its probability of moving increased with greater deviations of its

phenotype from the current optimum for its environment. After moving, a new assessment occurred, and the individual could decide to keep moving. That movement probability, however, also was conditioned on the individual's genetic propensity to disperse, which could evolve. Selection favoring habitat choice results in the evolution of a higher propensity to disperse, which creates greater opportunities for choice. Movement was assumed to be costly, with a fixed chance of dying with each dispersal event.

In our model, in one sense choice itself is not evolving. Choice either exists or it does not; the dispersal of an individual is either dependent on its assessment of the environment or it is not, and what evolves is the propensity to disperse. We also emphasize that in our model an optimal environment can occur only with habitat construction. We modeled choice in this way because the focus of these simulations is on how choice might interact with construction; the choice-alone scenario exists so that the effects of choice can be observed separately from those of construction. For the evolution of habitat choice of this type but without the need for construction to match the optimum, see Scheiner (2016). Other forms of habitat choice could have been modeled. For example, we could have modeled the evolution of the assessment of the local environment, which in turn would affect the probability of dispersal. Again, we emphasize that our results are specific to our model and that models based on other types of habitat choice might reach different conclusions.

### **HABITAT CHOICE VERSUS HABITAT CONSTRUCTION**

Our model and others that allow for multiple modes of trait adaptation are needed to address the question posed above of what circumstances favor one mode over another. Does the presence of one mode enhance or inhibit the likelihood of adaptation by another? Modes of adaptation that concern the evolution of just the trait that is directly linked to fitness such as genetic differentiation and phenotypic plasticity have to trade off against each other. But such trade-offs are not inherent when the modes of adaptation involve the joint evolution of that focal trait and other traits that determine processes such as construction and choice. Both processes can occur within a single system. For example, the building of dams by beavers is the paradigmatic example of habitat construction, and habitat quality is one factor that affects when and where juvenile beavers disperse (Hartman 1996; McNew Jr. and Woolf 2005). In cooperatively breeding birds and burrowing mammals, habitat choice can determine where nest or burrows are constructed, and these structures can be passed on to future generations. See Odling-Smee et al. (2003) for references to these and many other plausible examples.

It is likely that choice and construction, especially the timing of one versus the other, will create nonadditive effects. Previous models of the evolution of habitat choice showed that ran-

dom temporal variation in the environment after dispersal selects against choice and favors a jack-of-all-trades because such environmental variation negates the value of moving (Edelaar and Bolnick 2012; Scheiner 2016; Nicolaus and Edelaar 2018). In a similar fashion, habitat construction could change the accuracy of choice if that construction changes the environment after the choice occurs. Therefore, we predict that for our model construction after dispersal will act like temporal variation and select against dispersal. In our model, the baseline environment is always below the optimal environment (Fig. 1A), so in the absence of construction fitness is always less than the maximum (Fig. 1B), and there is always selection for habitat choice by individuals seeking a habitat with higher fitness. However, if construction occurs before dispersal, construction should weaken that selection by increasing the maximum fitness within a location.

Previous models of the evolution of habitat construction show that when dispersal occurs after construction, construction is selected against because any benefits go to other individuals (Lehmann 2008); if habitat choice increases dispersal rates, it will indirectly cause selection against construction. Even when dispersal occurs before construction, higher dispersal rates can select against construction. When the effects of construction carry across generations, kin selection can operate on offspring and later generations to favor or disfavor construction. Therefore, we predict that for our model greater habitat choice will select against construction, and both habitat choice and habitat construction may interfere with the evolution of each other.

Our model examines the potential for this interference by examining the joint evolution of habitat choice and habitat construction with spatial variation. No previous model of the evolution of habitat construction has considered the effects of an evolving dispersal rate. To fully examine how habitat choice and habitat construction might jointly evolve, we considered scenarios where dispersal happens then construction occurs, and alternatively where construction occurs and then dispersal. We recognize that the latter scenario seems unlikely. Why would an individual engage in costly construction and then disperse? We include that scenario, however, to be able to understand how the two modes of adaptation interact with each other. Because the goal of these simulations is to examine how each process might affect the other, parameter values were chosen to maximize adaptation of each in the absence of the other process.

## *The Model*

### **MODEL STRUCTURE**

The model was a discrete-time, individual-based simulation using a gene-based model of adaptation to a heterogeneous environment. The variables and parameters are listed in Table 2.

**Table 2.** Variables and parameters for the model simulations.

Symbol	Meaning	Value
$T$	Phenotype of an individual	
$G$	Trait allelic value	
$M$	Dispersal allelic value	
$C$	Construction allelic value	
$A$	Construction propensity of an individual	
$B$	Amount of construction by an individual	
$\theta$	Baseline environment in each deme	
$E$	Environment in each deme at the end of each generation	
$\delta$	The rate of decay of the environment to the baseline	50%
$\Delta H$	The total construction in a deme in each generation	
$S$	Environment in each deme at the time of selection	
$T_{\text{opt}}\phi$	Optimum phenotype in each deme/Fitness decrease in the baseline environment	10–70%
$W$	Individual survival probability from juvenile to adult	
$i$	Subscript for $i$ th deme	
$j$	Subscript for $j$ th individual	
$k$	Subscript for $k$ th allele	
$t$	Subscript for the $t$ th generation	
	Number of trait loci	5
	Number of migration loci	5
	Number of construction loci	5
$\omega$	Strength of selection (smaller is stronger selection)	4
	Mortality rate during dispersal with habitat choice	10%
$\gamma$	Cost of construction	1%
	Per-generation per-locus mutation rate	0.1
	Variance of mutation effect	0.01
	Number of demes	50
$N$	Number of individuals per deme after reproduction	16

The model was implemented in Fortran 77. The genotype of an individual consisted of three types of loci that were unlinked within and among types. One type determined the phenotype (trait loci), one type determined the amount of change to the habitat that an individual would cause (construction loci), and one type determined the propensity to disperse (choice loci). Thus, four of the six modes of adaptation—genetic differentiation, a jack-of-all-trades, habitat construction, and habitat choice—and their interactions were possible.

### DETERMINING THE ENVIRONMENT

The metapopulation consisted of a linear array of 50 demes (indexed by  $i$  from 1 to 50; Fig. 1). We considered the simplest case in which the environment is represented by a single scalar quantity. A baseline environmental gradient (environment in the absence of construction; Fig. 1A, solid line) was created by varying the environmental value ( $\theta_i$ ) in a linearly increasing fashion along the array from approximately  $-10$  arbitrary units at one end of the gradient to about  $+10$  units at the other; therefore, environments in adjacent demes differed by 0.4 units [ $\theta_i = 0.4(i - 25.5)$ ]. Each deme also had an optimal environment ( $\theta_i^*$ ) that was 10 units

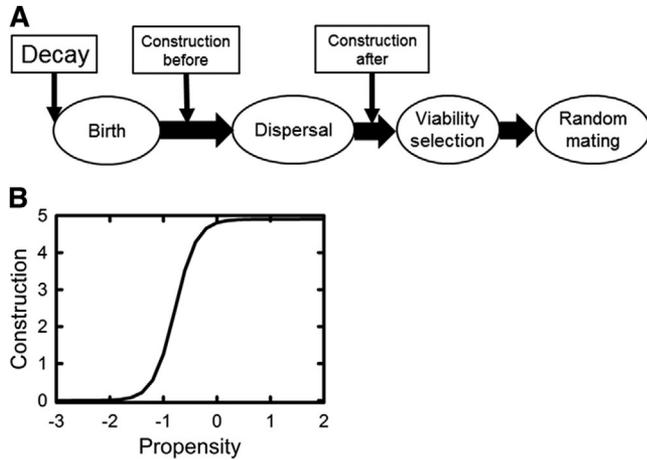
above the baseline (Fig. 1A, dashed line). Habitat construction increased the environmental value away from the baseline, and subsequent decay moved it back toward the baseline. (Here and below, the specific parameter values we chose have a quantitative but not qualitative effect on our conclusions.)

Between generations, the environment in each deme ( $i$ ) decayed back toward its baseline state. The decay between the end of generation  $t - 1$  and the start of generation  $t$  ( $\Delta E_{it}$ ) was as follows:

$$\Delta E_{it} = -\delta(E_{i(t-1)} - \theta_i), \quad (1)$$

where  $E_{i(t-1)}$  is the environment in deme  $i$  at the end of the generation  $t - 1$  and  $\delta$  ( $= 50\%$  for all simulations) is the rate of decay. This produced an environment of  $E_{i(t-1)} + \Delta E_{it}$  before construction.

Habitat construction could occur at one of two times during the life cycle, either just before or just after dispersal, depending on the simulation (Fig. 2A). The amount of construction that occurred in each deme in each generation was determined by two functions: the amount of construction attempted by each



**Figure 2.** (A) The order of life history events is as follows: birth, dispersal, selection, and reproduction. Environmental change occurs at two times for a given simulation: during decay to the baseline environment, which occurs before birth, and during construction, which can occur either before or after dispersal. (B) The total construction in a given generation by 16 individuals all with the same construction propensity (sum of the construction alleles) as a function of that propensity.

individual (a function of its genotype) and the amount of construction by the entire deme (a function of the individual constructions). The construction propensity of an individual was the sum of five unlinked diploid loci:

$$A_{ijt} = \sum_{k=1,10} C_{ijk t}, \quad (2)$$

where  $C_{ijk t}$  is the allelic value of the  $k$ th construction allele of the  $j$ th individual in the  $i$ th deme in generation  $t$  and  $A_{ijt}$  is that individual's construction propensity. The amount of construction ( $B_{ijt}$ ) by the individual was a logistic function of its construction propensity:

$$B_{ijt} = 5 / [1 + \exp(-5A_{ijk t})] \quad (3)$$

(Fig. 2B). The total construction in the  $i$ th deme in generation  $t$  ( $\Delta H_{it}$ ) was a saturating function of the sum of the construction of all  $N_i$  individuals in the deme:

$$\Delta H_{it} = \left( \sum_{j=1, N_i} B_{ijt} \right) / \left( 1 + 0.2 \sum_{j=1, N_i} B_{ijt} \right). \quad (4)$$

The maximal amount of construction in a single generation was 5.0 units; the optimum environment was 10 units greater than the baseline environment (Fig. 1A). The environment in the  $i$ th deme at the time of selection was as follows:

$$S_{it} = E_{i(t-1)} + \Delta E_{it} + \Delta H_{it}, \quad (5)$$

which was also the environment at the end of generation  $t$  ( $E_{it}$ ). Even though the only extrinsically imposed variation was spatial, this dynamic of construction and decay produced temporal variation within each deme.

## DETERMINING THE PHENOTYPE

An individual's phenotype (trait value) was determined at birth by five unlinked diploid loci. The loci contributed additively to the trait, which for simplicity was a scalar with the same units as the environment:  $T_{ijt} = \sum_{k=1,10} G_{ijk t}$ , where  $T_{ijt}$  is the phenotype of the  $j$ th individual that develops in the  $i$ th deme in generation  $t$ , and  $G_{ijk t}$  is the value of the  $k$ th trait allele of that individual. There was no random component of phenotypic variation.

## SELECTION

Life history events occurred in the following sequence: birth, dispersal, selection, and reproduction after which all adults die (Fig. 2A). This is the "move first" sequence of previous articles (e.g., Scheiner and Holt 2012). Selection occurred during survival from juvenile to adult. The survival probability of each individual was a Gaussian function of the difference between its phenotype and the optimum phenotype in its deme (deme  $i$ ) at time  $t$  ( $T_{opt, it}$ ) (first term) minus the cost of construction (second term):

$$W_{ijt} = f_{it} \cdot \exp \left\{ -\frac{1}{2} \left( \frac{T_{ijt} - T_{opt, it}}{\omega} \right)^2 \right\} - \gamma B_{ijt}, \quad (6)$$

where  $f$  is a function (see below) that accounts for a decrease in fitness due to the difference between the current environment and the optimum environment (Fig. 1B) and  $\omega$  determines the strength of selection on the phenotype (a lower value being stronger selection, Fig. 1C). Because we set units of trait values equal to environmental units,  $T_{opt, it}$  equals  $S_{it}$ . When the environment in a deme equaled the optimum environment ( $\theta_i^*$ ), the survival probability (in the absence of construction costs) was 1.0 for an individual with trait  $T_{ijt}$  equal to the optimum ( $T_{opt, it}$ ), and decreased as the difference between  $T_{ijt}$  and  $T_{opt, it}$  increased. For all simulations,  $\omega = 4$ ; the length of the spatial gradient across all demes was approximately 2.5 times the width of the within-deme selection function ( $2\omega$ ). Habitat construction was costly;  $\gamma$  was the per-unit construction cost, which was multiplied by the construction trait as defined in equation (3). Costs were scaled to the percentage decrease in total fitness (survival probability) for individuals that expressed the optimum phenotype. An individual that contributed the maximal construction would experience a 1% decrease in fitness. Although this cost function allowed for the possibility of negative fitness values if overall fitness was low enough, such negative values simply meant that an individual had a 0% probability of survival. Increasing the cost of construction would lower the absolute fitness of individuals, but would not change the relative effects of construction on choice.

For selection to act on habitat construction, construction has to affect fitness. That construction effect was embodied in the  $f$  term in equation (6), which was calculated as

$$f_{it} = 1 - \phi \left| \frac{\theta_i^* - S_{it}}{\theta_0^* - \theta_0} \right|, \quad (7)$$

where  $\theta_0^*$  and  $\theta_0$  are the optimal and baseline environments at the center of the gradient, the difference of which equals 10 for these simulations. This function equals 1.0 when the environment in the  $i$ th deme at the time of selection ( $S_{it}$ ) equals the optimum environment in that deme ( $\theta_i^*$ ), it falls linearly with the absolute value of the difference between  $S_{it}$  and  $\theta_i^*$ , and it reaches a minimum of  $1 - \phi$  when  $S_{it}$  is at the baseline ( $\theta_i$ ) (Fig. 1B). Selection on environmental construction is therefore toward the optimum, and the greater the value of  $\phi$ , the greater the strength of selection on that construction. In these simulations,  $\phi$  varied from 10% to 70%. For values above 70%, the metapopulation went extinct for simulations with choice alone and so those values of  $\phi$  were not considered.

## DISPERSAL

Dispersal was not spatially localized. Instead, we assumed that if an individual moved, it had an equal probability of moving to any of the other demes in the metapopulation, also known as an island dispersal pattern. Thus, the mean distance of dispersal was much greater than the grain of the environment. An individual's probability of moving was determined both by its fitness in its current deme (higher probability for lower fitness) and by its genetic propensity to disperse. An individual's propensity to disperse was determined by five diploid, unlinked loci,  $M_{ijt} = \sum_{k=1,10} M_{ijk t}$ , where  $M_{ijk t}$  is the allelic value of the  $k$ th dispersal allele of the  $j$ th individual in the  $i$ th deme in generation  $t$ ; values of the dispersal alleles ( $M_{ijk t}$ ) were constrained to be between 0 and 0.1 so that  $M_{ijt}$  was always in the interval [0,1]. Dispersal with habitat choice was costly in that individuals had a chance of dying during dispersal; that chance was the same for all individuals regardless of phenotype. The probability that an individual dispersed was as follows:

$$M_{ijt}^* = M_{ijt} (1 - W'_{ijt}), \quad (8)$$

where  $W'_{ijt}$  is the fitness as shown in equation (6), but not including the cost of construction, and represents the probability of the individual surviving if it remained in deme  $i$ . The quantity in parentheses is the individual's assessment of the match between its phenotype and the phenotype that would be optimal ( $T_{\text{opt},it}$ ) in its current habitat ( $S_{it}$ ) as set by the amount of construction and decay that had occurred. The assessment of that match included the fitness penalty; removal of that fitness penalty effect did not change the outcome (results not shown). That assessment was made without error; see Scheiner (2016) for the effects of as-

essment error in this model. The greater the mismatch between an individual's phenotype and the current optimal phenotype in its location, the greater the probability of dispersal (the effective dispersal rate). The "choice" here is thus the decision that an individual makes to leave the habitat it currently occupies, driven by the degree of mismatch between its own phenotype and the current local optimum, a form of condition-dependent dispersal.

The individual moved to a randomly chosen habitat with probability  $M_{ijt}^*$ . If it moved, the individual reassessed its habitat match and moved again with probability  $M_{ijt}^*$  assessed for the new habitat. The individual had a fixed, 10% chance of dying at each movement event. Movement continued until either the individual chose not to move or died during movement. Increasing the cost of movement would decrease selection for dispersal, but would not change the relative effects of choice on construction; a previous model that explored the effects of the cost of dispersal on the evolution of choice found a very weak effect (see Scheiner 2016, Fig. 1A). A value of  $M_{ijt}$  close to 0 meant the individual had a low propensity to disperse regardless of its phenotype, whereas a value of  $M_{ijt}$  close to 1 meant that the propensity to disperse was determined almost entirely by its trait phenotype and subsequent fitness in its current deme. The dispersal propensity of an individual with intermediate values was determined jointly by its trait phenotype and its dispersal genotype. Because in the absence of construction  $W_{ijt} < 1$ , there was always some probability of dispersal under those conditions (unless  $M_{ijt}$  was 0). In simulations without habitat choice, the propensity to disperse ( $M_{ijt}$ ) equaled the probability of dispersal (the individual dispersed if the value of  $M_{ijt}$  was greater than a random deviate from a uniform distribution between 0 and 1) and each individual moved only once.

## REPRODUCTION AND MUTATION

Sexual reproduction of surviving individuals was accomplished by assembling pairs of individuals within a deme at random with replacement (allowing for self-fertilization), with each parent producing a haploid gamete of unlinked alleles. Each pair then produced one offspring. This process was repeated until the carrying capacity of that deme (16) was reached. This procedure assumes soft selection in that local population size (after reproduction) was determined independently of the outcome of selection, and implies that individuals compete to produce successful offspring, which will weakly oppose kin selection when the deme size is very small (Wade 1985). The model assumes that the spatial scale of reproduction and mating matches that of density dependence and the grain of the selective environment.

When new offspring were generated, each allele at each locus mutated with a probability of 10%. In general, lower mutation rates simply lengthen the timescale over which evolution happens without affecting the eventual outcome, for the models

considered here (Scheiner and Holt 2012). When a mutation occurred, the allelic value was changed by adding a Gaussian deviate (mean of zero and a standard deviation of 0.1 units) to the previous allelic value (i.e., this is a continuum-of-alleles model; Kimura 1965). Allelic values were unconstrained for trait and construction loci, and could take any value from  $-\infty$  to  $\infty$ . Allelic values for the dispersal loci were constrained to the interval [0,0.1] so that the sum of the 10 alleles was constrained to the interval [0,1]. When a mutation would have resulted in a value outside that range, the allele was set to either 0 or 0.1, as appropriate.

### INITIAL CONDITIONS

Each simulation was initialized with 16 newborn individuals in each deme, for a total metapopulation size of 800. For each individual in the initial generation, allelic values for the trait and construction loci were chosen independently from the values  $-2$ ,  $-1$ ,  $0$ ,  $1$ , and  $2$ , with each value being equally likely. Even though these alleles were integer-valued initially, their values could assume any real number in subsequent generations due to mutation. The allelic values for the dispersal alleles were all initiated at a value of 0. The environment of each deme was initially equal to its baseline. The initial expected value of construction propensity was 0, so that the initial expected value of potential construction ( $B_{ij}$ ) of each individual was 2.5 (Fig. 2B). There was, therefore, a significant amount of construction in the first generations. That is, initial conditions included the existence of construction so as to maximize the opportunity for it to interact with choice.

### RESPONSE VARIABLES

All simulations were run for 1000 generations to ensure that equilibrium (the point after which all calculated quantities showed no further obvious directional trend) was reached. Each parameter combination was replicated 20 times; the results shown are the means and standard errors of those replicates.

Evolutionary outcomes were assessed by examining the mean construction propensity of individuals ( $A_{it}$ ), the constructed environments within demes ( $E_{it}$ ), the mean dispersal propensity ( $M_{it}$ ), the mean effective dispersal rate ( $M_{it}^*$ ), the mean fitness of the metapopulation ( $W_t$ ), elevation of the mean phenotype ( $T_{it}$ ) at the midpoint of the gradient, and its slope (determined by linear regression) along the gradient. Because each trait consisted of multiple, unlinked loci and the mutation rate was high, the genetic correlation among the three traits (phenotype, construction propensity, and dispersal propensity) was effectively zero.

At the end of 1000 generations, there was one last round of mating and reproduction (without environmental decay) to return the demes to full size. The parameters then were measured by first averaging among individuals within demes, and then averaging among demes. For total construction, that average was divided

by 10, so a value of 1.0 indicates that habitat construction moved the environment to match the target optimum, which was 10 units higher than the baseline; no construction would result in a value of 0.

For the propensity to disperse, at the end of 1000 generations the  $M_{ijt}$  values were averaged across all individuals and demes. The final effective dispersal rate ( $M_t^*$ ), which measures the rates of dispersal in the presence of habitat choice, was calculated by multiplying that mean value ( $M_t$ ) by  $(1 - W_t)$ . For simulations without habitat choice, the mean dispersal propensities ( $M_t$ ) measure the rates of dispersal.

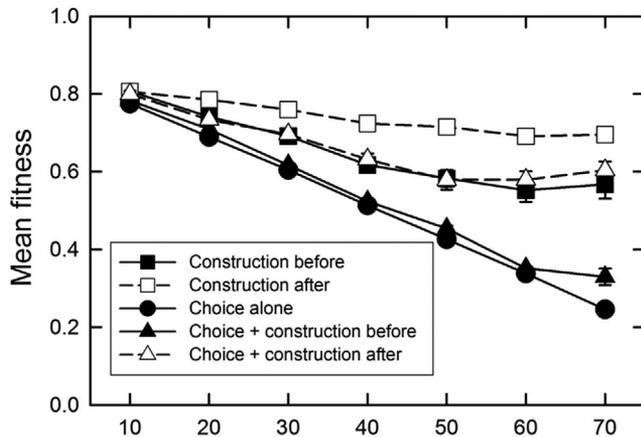
The match of the trait to the selective optimum averaged across the metapopulation was measured by the mean fitness of the metapopulation ( $W_t$ ), which was a function of how closely the mean phenotype of each deme ( $T_{it}$ ) matched the slope and mean elevation of the constructed environment ( $E_{it}$ ) and the fitness penalty due to the deviation of that constructed environment from the optimum ( $\theta_i^*$ ). At the end of 1000 generations, the  $T_{ijt}$  values were averaged across all individuals within each deme, linear regression was performed on the averages, and the resulting slope was standardized relative to the slope of the optimal environment and compared to the slope of the constructed environment. A slope of zero indicates that the population was phenotypically uniform across the gradient, a jack-of-all-trades outcome. A slope matching the constructed environment indicates a pure genetic differentiation outcome. A slope between zero and the matching slope indicates an outcome intermediate between a jack-of-all-trades and genetic differentiation. A relative mean elevation of one indicates that the metapopulation matched the optimum ( $\theta_i^*$ ).

## Results

### PATTERNS OF ADAPTATION

Adaptation was measured by three parameters: the mean fitness of the metapopulation ( $W_t$ ) and the slope and elevation of the mean phenotype ( $T_{it}$ ) along the gradient. Unsurprisingly, in the absence of construction (choice alone, circles) an increase in the fitness penalty ( $\phi$ ) for no construction decreased mean fitness (Fig. 3). The presence of construction alone (squares) increased fitness, with a somewhat greater increase if construction occurred after dispersal (open squares). Choice plus construction that occurred after dispersal (open triangles) resulted in fitnesses intermediate between choice alone (circles) and construction alone (open squares) and similar to that of construction alone before dispersal. Choice plus construction before dispersal (closed triangles) did not differ from choice alone (except at the largest  $\phi$ ).

These fitness effects were primarily due to mismatches in the elevation of the constructed environment ( $E_{it}$ ) relative to that of



**Figure 3.** The effect of the fitness decrease ( $\phi$ ) in the baseline environment on mean fitness ( $W_i$ ). Shown are means and standard errors of 20 replicate simulations; when error bars are absent, they are smaller than the symbol.

the optimal environment ( $\theta_i^*$ ) (Fig. 4). A relative environmental slope and elevation of 1.0 indicates construction to the optimum environment. A match of the trait slope and elevation to that of the constructed environment indicates perfect trait genetic differentiation; a slope of zero indicates a jack-of-all-trades outcome. The relative slopes of the traits were always lower than those of the constructed environment but above that of the optimal environment (Figs. 4A, B). In the case of choice alone, the slope was lower than the optimal environment ( $\theta_i^*$ ). In contrast, the relative elevations of the traits closely matched those of the constructed environments (Figs. 4C, D). Values close to the ideal combination of construction and genetic differentiation (relative slope and elevation all = 1.0) occurred for simulations with construction alone after dispersal (open squares). For choice alone (circles), selection favored genetic differentiation with an elevation near zero as expected in the absence of construction, as did construction before dispersal with choice (solid triangles).

#### EVOLUTION OF DISPERSAL RATE AND HABITAT CHOICE

The evolution of dispersal rate was only weakly affected by the presence of habitat construction, and mostly when construction occurred after dispersal with habitat choice (Fig. 5A, open triangles). In that case, a greater propensity for dispersal—and thus habitat choice—was favored than when there was habitat construction and no choice (Fig. 5A, open squares). The effective dispersal rate is the product of the genetic propensity to disperse and the perceived match between an individual and its environment fitness (eq. 8); in the absence of choice, the effective dispersal rate equals the dispersal rate propensity. Individuals that are highly adapted to their natal habitats have no need to disperse, despite their genetic propensity to do so. In general, the effective

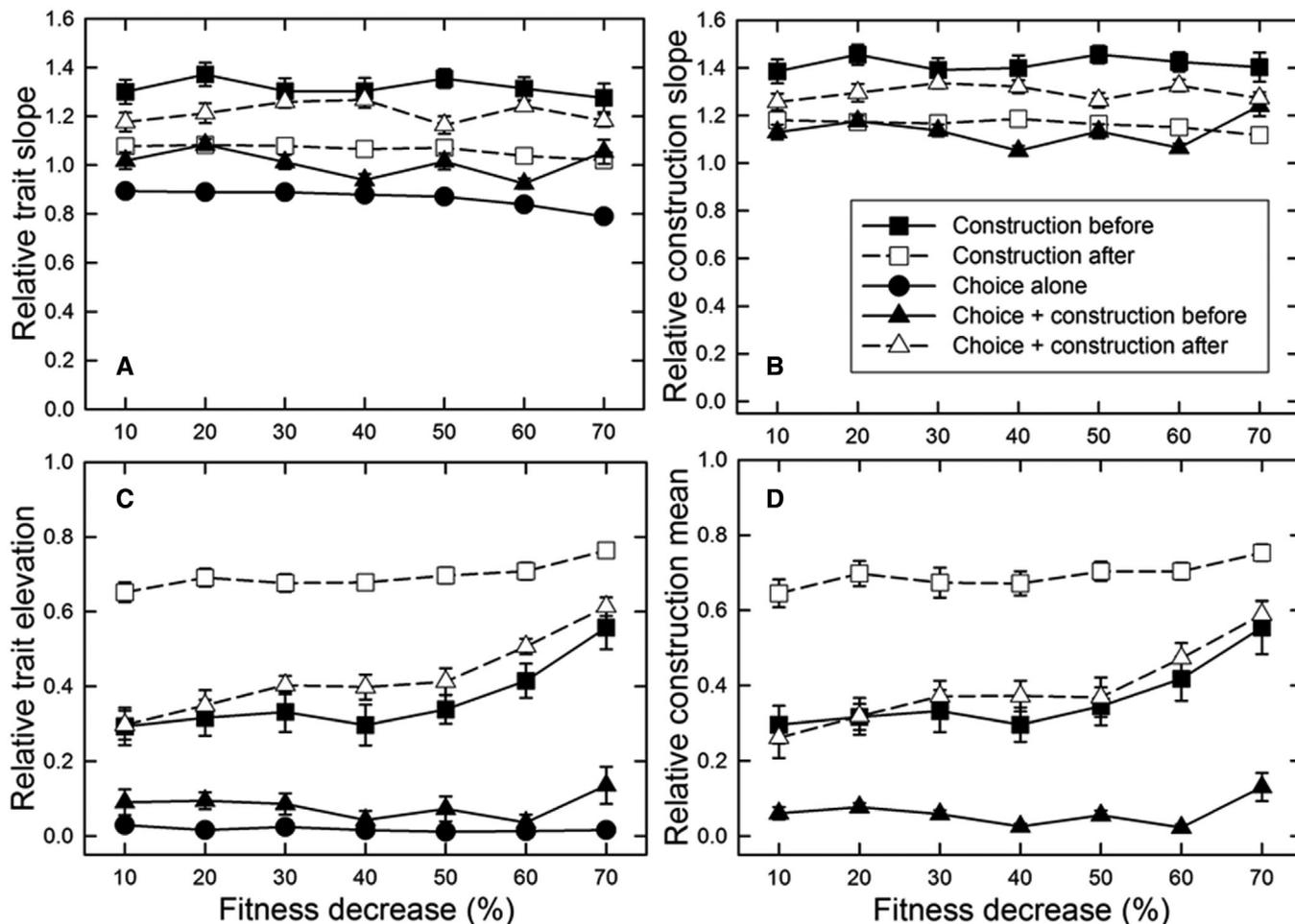
dispersal rate increased with increasing values of  $\phi$  (Fig. 5B), consistent with the lower fitness at those larger values (Fig. 3). (In the absence of any increase in fitness due to construction, the dispersal rate propensity will evolve to approximately 50% and the effective dispersal rate to approximately 4%; see fig. 1A in Scheiner [2016].) However, when choice was combined with construction after dispersal (open triangles), the effective dispersal rate slightly decreased at very high values of  $\phi$ , despite the greater propensity for dispersal, again consistent with the greater fitness under these conditions.

#### EVOLUTION OF CONSTRUCTION

Construction alone after dispersal (open squares), as expected, selected for the greatest propensity for construction (Fig. 5C) and actual construction (Fig. 4D) so that the environment neared the optimum (a relative value of 1.0). When construction occurred before dispersal, the benefits of construction were less likely to accrue to the constructing individual. As a result, for construction alone that occurred before dispersal (closed squares), individuals had a lower propensity for construction and less construction occurred, although these both increased as the value of construction ( $\phi$ ) increased. When habitat construction was combined with habitat choice (triangles), both the propensity for construction and the amount of construction were decreased relative to construction alone, especially for construction before dispersal. In this last scenario, construction was disfavored even for large values of the fitness penalty, because higher fitness could be achieved by moving rather than constructing.

#### Discussion

We predicted that habitat choice and habitat construction would each interfere with adaptation of the other mode in a way that depended on the timing of life history events. For our model, selection for habitat choice means selection for an increased propensity to disperse. Construction after dispersal was predicted to select for habitat construction and against habitat choice; construction before dispersal was predicted to select against habitat construction and for habitat choice. These predictions were only partially met. For habitat choice, the propensity to disperse was nearly identical for all scenarios, except for being slightly higher when construction happened after dispersal (Fig. 5A), contrary to both predictions. For habitat construction, the presence of choice always decreased construction (Fig. 4D), contrary to one prediction and in agreement with the other. This negative synergy between the two modes was due to the fact that the construction plus decay process creates temporal variation that increases selection for the propensity to disperse (see below), which in turn reduces the relatedness of the individual doing the construction and the individuals gaining its benefits. This link could be severed if



**Figure 4.** The effect of the fitness decrease ( $\phi$ ) in the baseline environment on (A) the relative slope along the gradient of the mean phenotypes of the selected trait ( $T_{it}$ ), (B) the relative slope of the constructed environment ( $E_{it}$ ), (C) the relative mean phenotype of the selected trait, and (D) the relative mean of the constructed environment ( $E_{it}/10$ ). In the absence of construction, the relative slope and elevation of the environment are 1.0 and 0.0, respectively. Shown are means and standard errors of 20 replicate simulations; when error bars are absent, they are smaller than the symbol.

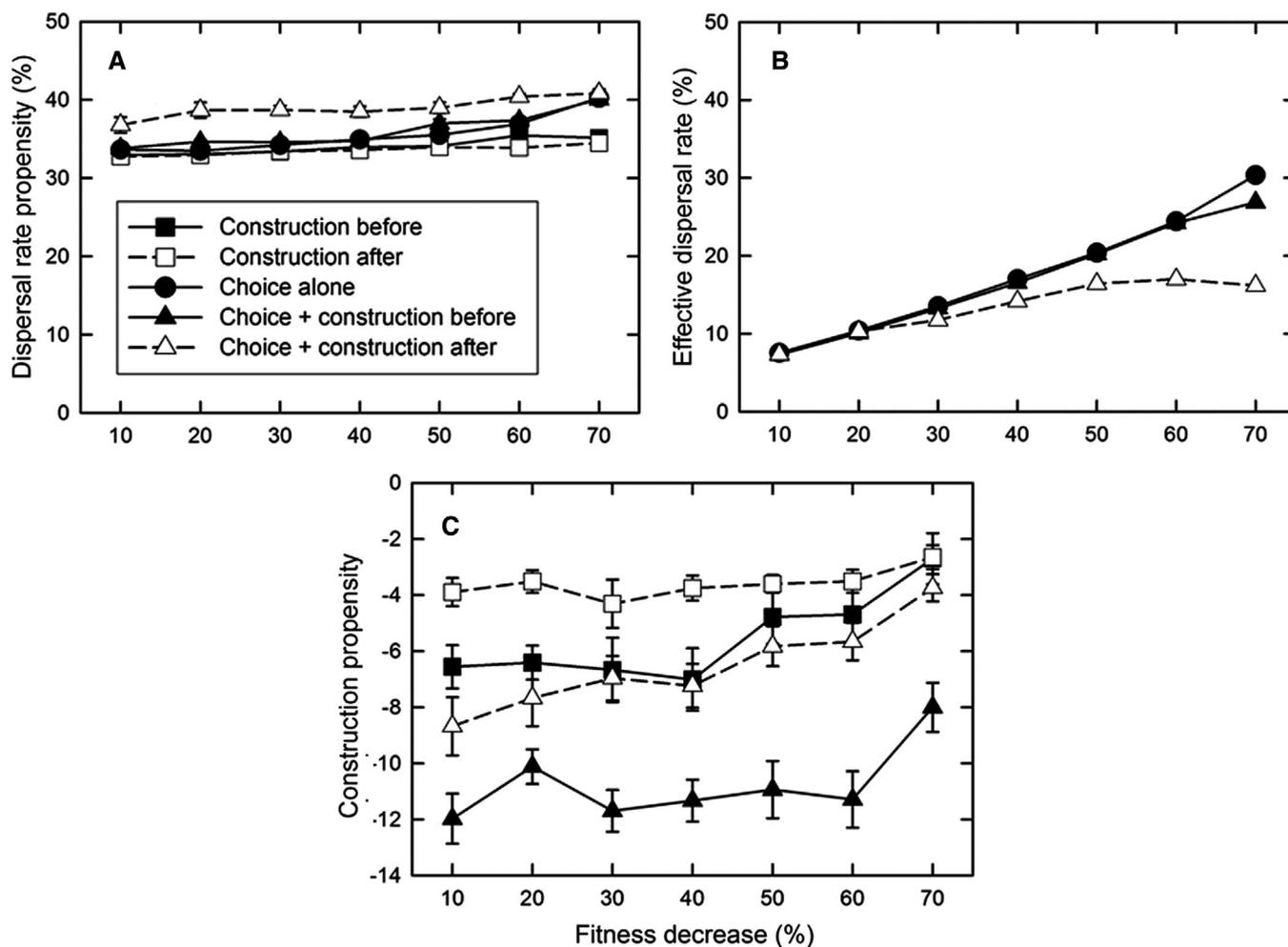
construction were eliminated, but in our model construction always increases fitness.

We can assess the conditions that would favor one combination of traits over another by looking at the overall fitness of each strategy (Fig. 3). For construction alone, as expected, construction after dispersal always had higher fitness than construction before selection, except for the smallest fitness value of construction. Construction alone always had a higher fitness than either choice alone or a mixed construction + choice strategy, except for very small fitness values of construction, and these differences increased as the fitness value of construction increased. Thus, if habitat construction exists and can increase fitness, it is unlikely that habitat choice would also evolve, at least for the model structure we have assumed here. Conversely, habitat choice could be displaced by habitat construction. We modeled undirected and nonresponsive habitat construction; directed or responsive con-

struction would likely only amplify these results. Evolution in one modality thus alters the likelihood and ultimate outcome of evolution in another, as we conjectured.

#### INTERACTIONS AMONG MODES OF ADAPTATION

The results of the simulations presented here, along with previous models by us and others, are beginning to fill in the picture of how the various modes of adaptation might interact with each other (Table 1). Critical to that interaction is the type of environmental heterogeneity: spatial or temporal. That distinction mirrors earlier models that found that (crudely) adaptation by genetic differentiation versus a jack-of-all-trades was alternatively favored by spatial and temporal variation, respectively. In a similar fashion, in the presence of habitat choice temporal variation selects for a propensity for dispersal, thus favoring a jack-of-all-trades strategy (Scheiner 2016). In our current model, the combination of



**Figure 5.** The effect of the fitness decrease ( $\phi$ ) on (A) mean dispersal propensity ( $M_{it}$ ), (B) the mean effective dispersal rate in the presence of habitat choice ( $M_{it}^*$ ), and (C) the mean construction propensity of individuals ( $A_{it}$ ). The effects on habitat choice and habitat construction are each shown with and without the presence of the other process. In the absence of habitat choice, the dispersal rate propensity equals the effective dispersal rate. Shown are means and standard errors of 20 replicate simulations; when error bars are absent, they are smaller than the symbol.

construction and decay each generation generates that temporal variation, even in the absence of an extrinsic source, and favoring a high propensity for dispersal (Fig. 5A).

The focus of the current model and others has been on how evolution is affected by factors that determine the optimal phenotype and fitness (e.g., spatial and temporal environmental heterogeneity, dispersal rates and patterns). But we also know that the evolution of phenotypic plasticity is affected by factors such as genetic architecture (Scheiner and Holt 2012; Scheiner 2014b; Scheiner et al. 2017) and other types of costs and limitations (DeWitt 1998). Although costs of dispersal and construction are typically considered in models of choice and construction, we are not aware of a systematic examination of other developmental constraints on their evolution. Theoretical and empirical explorations of such factors might prove fruitful.

In this study, we found that the presence of habitat construction disfavored the evolution of habitat choice, because if construction improves survival (which has a maximal value of unity), that construction reduces the potential advantage of moving to other habitats. Previously, it was shown that habitat choice suppresses the evolution of phenotypic plasticity when there is only spatial variation, but that the addition of temporal variation favors selection for plasticity (Scheiner 2016; Edelaar et al. 2017). We have also shown that habitat construction and phenotypic plasticity trade off against each other, or interfere with each other, depending on the ordering of development, construction, dispersal, and selection (Scheiner et al. 2021). Phenotypic plasticity is favored over diversified bet-hedging, but this result depends on whether that developmental instability is genetically independent of plasticity (Scheiner 2014b).

## IMPLICATIONS

There is no simple answer as to the relatively likelihood of the six modes of adaptation: genetic differentiation of those traits, a jack-of-all-trades phenotypic uniformity, diversified bet-hedging, phenotypic plasticity, habitat choice, and habitat construction. All of these modes involve the evolution of traits that may be continuous (Table 1, panel B), so that partial or mixed strategies are possible outcomes. Because both choice and construction are separate traits from the focal trait under selection, their evolution interacts with the evolution of the mean, variability, and plasticity of trait values. In general, choice and construction favor genetic differentiation over either a jack-of-all-trades or plasticity, for the types of choice and construction modeled here, although this result depends on the pattern of environmental heterogeneity and the ordering of life history events. As both construction and choice make the environment experienced by an organism and its offspring more predictable, they also are likely to favor genetic differentiation over diversified bet-hedging, although this is an open question. All of the models by others and us only point to general patterns based on very abstracted models. We also caution that these conclusions are based on a single model. It would be valuable to assess these conclusions in a wider range of models with different assumptions (e.g., hard vs. soft selection, the presence of temporal variability or disturbances). For example, temporal variation can weaken selection for habitat choice (e.g., Scheiner 2016). Predictions about specific empirical systems will require much more tailored models that take into account the biology and ecology of those systems.

Testing our predictions in empirical systems presents an interesting dilemma. If, as predicted, plasticity, choice, and construction tend to interfere with each other, then any given system will likely express just one of those modes of adaptation. How then can we measure the effects of one mode on the other? Experimental systems can be designed that impose adaptive habitat choice by the artificial movement of individuals. Trait plasticity that is otherwise not adaptive in nature can be made adaptive by artificial selection. Either or both of these manipulations could be imposed on a species that otherwise shows random trait variability (diversified bet-hedging) or habitat construction. An alternative approach would be examining the evolution of plasticity, choice, and construction in a phylogenetic context. We predict that within clades that manifest more than one mode of adaptation, those modes will tend to be found on alternative branches. Such phylogenetic comparisons are not without their challenges. We know of only one study that has extensively examined the evolution of plasticity in a phylogenetic framework (Relyea et al. 2018). That system (North American anurans) might be amenable to looking at the joint evolution of plasticity and habitat choice. We challenge the reader to conceive of other systems for exam-

ining such joint evolution in this and other pairs of adaptational modes.

## AUTHOR CONTRIBUTIONS

SMS conceived the project and executed the software. SMS, MB, and RDH developed the model and wrote the manuscript.

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## DATA ARCHIVING

There are no data to be archived. The program code is available from GitHub: <https://github.com/sscheiner1/Plasticity-models/releases>.

## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## LITERATURE CITED

- Bolnick, D. I., and S. P. Otto. 2013. The magnitude of local adaptation under genotype-dependent dispersal. *Ecol. Evol.* 3:4722–4735.
- Charlesworth, B., and D. Charlesworth. 2012. *Elements of evolutionary genetics*. Roberts and Company, Greenwood Village, CO.
- Chevin, L. M., and R. Lande. 2011. Adaptation to marginal habitats by evolution of increased phenotypic plasticity. *J. Evol. Biol.* 24:1462–1476.
- Chisholm, R. H., B. D. Connelly, B. Kerr, and M. M. Tanaka. 2018. The role of pleiotropy in the evolutionary maintenance of positive niche construction. *Am. Nat.* 192, 35–48.
- Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35:131–138.
- Darwin, C. 1892. The formation of vegetable mould through the action of worms: with observations on their habits. John Murray, Lond.
- De Meeüs, T., Y. Michalakis, F. Renaud, and I. Olivieri. 1993. Polymorphism in heterogeneous environments, evolution of habitat selection and sympatric speciation: soft and hard selection models. *Evol. Ecol.* 7:175–198.
- Dempster, E. R. 1955. Maintenance of genetic heterogeneity. *Cold Spring Harbor Symp. Quant. Biol.* 20:25–32.
- DeWitt, T. J. 1998. Costs and limits of phenotypic plasticity: tests with predator-induced morphology and life history in a freshwater snail. *J. Evol. Biol.* 11:465–480.
- DeWitt, T. J., and S. M. Scheiner. 2004. *Phenotypic plasticity: functional and conceptual approaches*. Oxford Univ. Press, New York.
- Edelaar, P., and D. I. Bolnick. 2012. Non-random gene flow: an underappreciated force in evolution and ecology. *Trends Ecol. Evol.* 27:659–665.
- Edelaar, P., and D. I. Bolnick. 2019. Appreciating the multiple processes increasing individual or population fitness. *Trends Ecol. Evol.* 34:435–446.
- Edelaar, P., R. Jovani, and I. Gomez-Mestre. 2017. Should I change or should I go? Phenotypic plasticity and matching habitat choice in the adaptation to environmental heterogeneity. *Am. Nat.* 190:506–520.

- Edelaar, P., A. M. Siepielski, and J. Clobert. 2008. Matching habitat choice causes directed gene flow: a neglected dimension in evolution and ecology. *Evolution* 62:2462–2472.
- Falconer, D. S., and T. F. C. Mackay. 1996. *Introduction to quantitative genetics*. 4th ed. Longman, Essex, U.K.
- Feldman M. W. (ed.) 1989. *Mathematical evolutionary theory*. Princeton Univ. Press, Princeton, NJ.
- Fischer, B., G. S. van Doorn, U. Dieckmann, and B. Taborsky. 2014. The evolution of age-dependent plasticity. *Am. Nat.* 183:108–125.
- Frankenhuis, W. E., and K. Panchanathan. 2011. Balancing sampling and specialization: an adaptationist model of incremental development. *Proc. Roy. Soc. London B* 278:3558–3565.
- Gilchrist, G. W. 1995. Specialists and generalists in changing environments. I. Fitness landscapes of thermal sensitivity. *Am. Nat.* 146:252–270.
- Gillespie, J. H. 1998. *Population genetics: a concise guide*. Johns Hopkins University Press, Baltimore, MD.
- Haaland, T. R., J. Wright, and I. I. Ratikainen. 2021. Individual reversible plasticity as a genotype-level bet-hedging strategy. *J. Evol. Biol.* 34:1022–1033.
- Haaland, T. R., J. Wright, J. Tufto, and I. I. Ratikainen. 2019. Short-term insurance versus long-term bet-hedging strategies as adaptations to variable environments. *Evolution* 73:145–157.
- Haldane, J. B. S., and S. D. Jayakar. 1963. Polymorphism due to selection of varying direction. *J. Genet.* 58:237–242.
- Hamilton, W. D. 1964. The genetic evolution of social behavior. *I. J. Theor. Biol.* 7:1–16.
- Hartman, G. 1996. Habitat selection by European beaver (*Castor fiber*) colonizing a boreal landscape. *J. Zool.* 240:317–325.
- Hedrick, P. W. 1986. Genetic polymorphism in heterogeneous environments: a decade later. *Annu. Rev. Ecol. Syst.* 17:535–566.
- Hendry, A. P. 2016. Key questions on the role of phenotypic plasticity in eco-evolutionary dynamics. *J. Hered.* 107:25–41.
- Holt, R. D. 1987. Population dynamics and evolutionary processes: the manifold roles of habitat selection. *Evol. Ecol.* 1:331–347.
- Jacob, S., E. Laurent, B. Haegeman, R. Bertrand, J. G. Prunier, D. Legrand, J. Cote, A. S. Chaine, M. Loreau, J. Clobert, et al. 2018. Habitat choice meets thermal specialization: competition with specialists may drive suboptimal habitat preferences in generalists. *Proc. Nat. Acad. Sci.* 115:11988–11993.
- Kaplan, R. H., and W. S. Cooper. 1984. The evolution of developmental plasticity in reproductive characteristics: an application of the “adaptive coin-flipping” principle. *Am. Nat.* 123:393–410.
- Kawecki, T. J., and D. Ebert. 2004. Conceptual issues in local adaptation. *Ecol. Lett.* 7:1225–1241.
- Kimura, M. 1965. A stochastic model concerning the maintenance of genetic variability in quantitative characters. *Proc. Natl. Acad. Sci. USA* 54:731–736.
- Krakauer, D. C., K. M. Page, and D. H. Erwin. 2009. Diversity, dilemmas, and monopolies of niche construction. *Am. Nat.* 173:26–40.
- Kusmec, A., S. Srinivasan, D. Nettleton, and P. S. Schnable. 2017. Distinct genetic architectures for phenotype means and plasticities in *Zea mays*. *Nature Plants* 3:715–723.
- Kylafis, G., and M. Loreau. 2008. Ecological and evolutionary consequences of niche construction for its agent. *Ecol. Lett.* 11:1072–1081.
- Laland, K. N., F. J. Odling-Smee, and M. W. Feldman. 1996. The evolutionary consequences of niche construction: a theoretical investigation using two-locus theory. *J. Evol. Biol.* 9:293–316.
- Lavelle, P. 1988. Earthworm activities and the soil system. *Biol. Fertil. Soils* 6:237–251.
- Lehmann, L. 2008. The adaptive dynamics of niche constructing traits in spatially subdivided populations: evolving posthumous extended phenotypes. *Evolution* 62:549–566.
- Levene, H. 1953. Genetic equilibrium when more than one ecological niche is available. *Am. Nat.* 87:331–333.
- Levins, R. 1962. Theory of fitness in a heterogeneous environment I. The fitness set and adaptive function. *Am. Nat.* 96:361–378.
- Mather, K., and J. L. Jinks. 1982. *Biometrical genetics*. Chapman and Hall, London, U.K.
- McNew, L. B. Jr., and A. Woolf. 2005. Dispersal and survival of juvenile beavers (*Castor canadensis*) in southern Illinois. *Am. Midl. Nat.* 154:217–228.
- Morgante, F., P. Sørensen, D. A. Sorensen, C. Maltecca, and T. F. C. Mackay. 2015. Genetic architecture of micro-environmental plasticity in *Drosophila melanogaster*. *Scientific Reports*, 5, 9785.
- Mougi, A., O. Kishida, and Y. Iwasa. 2011. Coevolution of phenotypic plasticity in predator and prey: why are inducible offenses rarer than inducible defenses? *Evolution* 65:1079–1087.
- Nicolaus, M., and P. Edelaar. 2018. Comparing the consequences of natural selection, adaptive phenotypic plasticity, and matching habitat choice for phenotype–environment matching, population genetic structure, and reproductive isolation in meta-populations. *Ecol. Evol.* 8:3815–3827.
- Nonaka, E., R. Svanbäck, X. Thibert-Plante, G. Englund, and Å. Brännström. 2015. Mechanisms by which phenotypic plasticity affects adaptive divergence and ecological speciation. *Am. Nat.* 186:E126–E143.
- Odling-Smee, F. J., K. N. Laland, and M. W. Feldman. 2003. *Niche construction: the neglected process in evolution*. Princeton Univ. Press, Princeton, NJ.
- Peterson, A. T. 2011. Ecological niche conservatism: a time-structured review of evidence. *J. Biogeogr.* 38:817–827.
- Philippi, T., and J. Seger. 1989. Hedging one’s evolutionary bets, revisited. *Trends Ecol. Evol.* 4:41–44.
- Poethke, H. J., T. Hovestadt, and O. Mitesser. 2016. The evolution of optimal emergence times: bet hedging and the quest for an ideal free temporal distribution of individuals. *Oikos* 125:1647–1656.
- Post, D. M., and E. P. Palkovacs. 2009. Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Philos. Trans. R. Soc. B Biol. Sci.* 364:1629–1640.
- Provine, W. B. 1971. *The origins of theoretical population genetics*. Univ. of Chicago Press, Chicago, IL.
- Reed, T. E., R. S. Waples, D. E. Schindler, J. J. Hard, and M. T. Kinnison. 2010. Phenotypic plasticity and population viability: the importance of environmental predictability. *Proc. R. Soc. Lond. B* 277:3391–3400.
- Relyea, R. A., P. R. Stephens, L. N. Barrow, A. R. Blaustein, P. W. Bradley, J. C. Buck, A. Chang, J. P. Collins, B. Crother, J. Earl, et al. 2018. Phylogenetic patterns of trait and trait plasticity evolution: insights from amphibian embryos. *Evolution* 72:663–678.
- Rice, S. 2004. *Evolutionary theory: mathematical and conceptual foundations*. Sinauer Associates, Sunderland, MA.
- Sachs, J. L., K. W. Quides, and C. E. Wendlandt. 2018. Legumes versus rhizobia: a model for ongoing conflict in symbiosis. *New Phytol.* 219:1199–1206.
- Saltz, J. B., and S. V. Nuzhdin. 2014. Genetic variation in niche construction: implications for development and evolutionary genetics. *Trends Ecol. Evol.* 29:8–14.
- Scheiner, S. M. 1998. The genetics of phenotypic plasticity. VII. Evolution in a spatially structured environment. *J. Evol. Biol.* 11, 303–320.
- . 2013. The genetics of phenotypic plasticity. XII. Temporal and spatial heterogeneity. *Ecol. Evol.* 3:4596–4609.

- . 2014a. Bet-hedging as a complex interaction among developmental instability, environmental heterogeneity, dispersal, and life history strategy. *Ecol. Evol.* 4:505–515.
- . 2014b. The genetics of phenotypic plasticity. XIII. Interactions with developmental instability. *Ecol. Evol.* 4:1347–1360.
- . 2016. Habitat choice and temporal variation alter the balance between adaptation by genetic differentiation, a jack-of-all-trades strategy, and phenotypic plasticity. *Am. Nat.* 187:633–646.
- . 2019. The theory of the evolution of plasticity. In: *The theory of evolution* (eds. Scheiner SM & Mindell DP). Univ. of Chicago Press, Chicago, pp. 254–272.
- Scheiner, S. M., and R. D. Holt. 2012. The genetics of phenotypic plasticity. X. Variation versus uncertainty. *Ecol. Evol.* 2:751–767.
- Scheiner, S. M., M. Barfield, and R. D. Holt. 2017. The genetics of phenotypic plasticity. XV. Genetic assimilation, the Baldwin effect, and evolutionary rescue. *Ecol. Evol.* 7:8788–8803.
- . 2021. The evolution of habitat construction with and without phenotypic plasticity. *Evolution* 75:1650–1664.
- Schlichting, C. D. 2004. The role of phenotypic plasticity in diversification. In: *Phenotypic plasticity: functional and conceptual approaches* (eds. DeWitt TJ & Scheiner SM). Oxford Univ. Press, New York, pp. 191–200.
- Schlichting, C. D., and M. Pigliucci. 1998. *Phenotypic evolution: a reaction norm perspective*. Sinauer Associates, Sunderland, MA.
- Schmid, M., and F. Guillaume. 2017. The role of phenotypic plasticity on population differentiation. *Heredity* 119:214–225.
- Silver, M. & E. Di Paolo. 2006. Spatial effects favour the evolution of niche construction. *Theor. Popul. Biol.* 70:387–400.
- Simons, A. M., and M. O. Johnston. 1997. Developmental instability as a bet-hedging strategy. *Oikos* 80:401–406.
- Slatkin, M. 1974. Hedging one's evolutionary bets. *Nature* 250:704–705.
- Starrfelt, J., and H. Kokko. 2012. Bet-hedging—a triple trade-off between means, variances and correlations. *Biol. Rev.* 87:742–755.
- Thibert-Plante, X., and A. P. Hendry. 2011. The consequences of phenotypic plasticity for ecological speciation. *J. Evol. Biol.* 24:326–342.
- Vincent, T. L., and J. S. Brown. 2005. *Evolutionary game theory, natural selection, and Darwinian dynamics*. Cambridge Univ. Press, Cambridge, U.K.
- Wade, M. J. 1985. Soft selection, hard selection, kin selection, and group selection. *Am. Nat.* 125:61–73.
- Weber, S. L., and S. M. Scheiner. 1992. The genetics of phenotypic plasticity. IV. Chromosomal localization. *J. Evol. Biol.* 5:109–120.
- West-Eberhard, M. J. 2003. *Developmental plasticity and evolution*. Oxford Univ. Press, New York.
- Wilson, D. S. 1983. The group selection controversy: history and current status. *Annu. Rev. Ecol. Syst.* 14:159–187.
- Wilson, D. S., and J. Yoshimura. 1994. On the coexistence of specialists and generalists. *Am. Nat.* 144:692–707.

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