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The evolution of habitat construction with and without phenotypic plasticity*

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Habitat construction and phenotypic plasticity are alternative responses to variable environments. We explored evolution along an environmental gradient of habitat construction alone and in combination with phenotypic plasticity using individual-based simulations that manipulated the fitness benefit of construction and whether construction maintained or eliminated that gradient. Construction was favored when its benefits were more likely to flow to the immediate offspring of the constructing individuals. Habitat construction and phenotypic plasticity traded off against each other or plasticity was selected against, depending on how the optimum environment varied and with the fitness value of construction. When selection favored differences in the amount of construction along the environmental gradient, genetic differentiation for habitat construction increased as the fitness value of construction increased. The degree to which each adaptive response was likely to evolve also depended on the precise ordering of life history events. Adaptive habitat construction does not always occur and may be selected against.

KEY WORDS: Habitat construction, model, niche construction, phenotypic plasticity.

Given a mismatch between an individual's phenotype and the optimal trait value for its environment, one response is to make the environment more favorable: habitat construction. Habitat construction can take many different forms (see review in Sultan 2015). A robin or an alligator that builds a nest is engaging in habitat construction, but the altered habitat persists for just a short period of time and affects (to first order) only the constructing individual and its immediate offspring. The construction of a beaver dam has more long-lasting effects as it can persist for several generations (Collen and Gibson 2000). The dam affects the physical environment by turning a stream into a pond that in turn affects vegetation in the pond's vicinity. That altered vegetation then feeds back on the suitability of the environment for the beaver, its offspring, and future generations. Other types of habitat construction can affect the fitness of unrelated individuals in a population. As each earthworm alters soil texture, it changes the environment for all other earthworms in its local population—not just its own offspring and close relatives (Darwin 1892; Lavelle 1988). Although the focus of research on the evolution of construction has been on those types that affect the fitness of the constructing individual, environmental changes can also be a simple by-product of an organism's actions. Some types of habitat construction can have consequences over geological time scales (e.g., the build-up of oxygen in the atmosphere, soil formation arising from vegetation-bedrock-climate interactions); our analyses are focused at more modest temporal and spatial scales and intraspecific evolutionary dynamics.

Despite such convincing examples of the existence and ecological importance of habitat construction, the general evolutionary conditions that favor or disfavor construction are still unresolved. Models are one route to that resolution as they permit the exploration of a much larger span of parameter space than a collection of empirical studies, and avoid the problem of comparisons across systems that differ in multiple ways. To date, there have been only a handful of models of the evolution of habitat construction (see review in Odling-Smee et al. 2013). Those models show that habitat construction should be favored when the altered habitat results in an increase in the fitness of an individual or its near kin, taking into account potential construction costs (Post and Palkovacs 2009; Chisholm et al. 2018; Relyea et al. 2018).

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An alternative evolutionary response to a mismatch between an individual's phenotype and its environment is to alter the phenotype through plasticity (see reviews in DeWitt and Scheiner 2004; Pfennig 2021). Given the existence of environmental heterogeneity causing variation in optimal trait values, phenotypic plasticity is expected to be favored when there is a reliable signal at the time of development that predicts the environmental state and the resulting optimal trait value at the time of selection (Berrigan and Scheiner 2004; Scheiner 2019). Still unknown is whether and under what conditions, if both habitat construction and phenotypic plasticity are potential outcomes, each alone would be favored, or when a mix of responses might evolve. The potential for such a mixed outcome has implications for theories of the evolution of the extended phenotype (Brodie 2005).

The term "habitat construction"—where organisms alter their physical environments in ways that directly affect those organisms—was coined by Sultan (2015) to distinguish it from other types of niche construction. The term "niche construction" is sometimes defined to include habitat choice and environmental changes that have no effect on the constructing organisms (Post and Palkovacs 2009; Sultan 2015), a definition criticized by some as being overly broad (Kylafis and Loreau 2008). For example, phenotypic plasticity itself is included as a type of niche construction in some of the most expansive definitions. Such a sweeping definition fails to distinguish the very different requirements, physiological and behavioral mechanisms, and evolutionary dynamics of these different responses, a contrast that we make and explore here (see also the discussions in Edelaar and Bolnick 2019; S. M. Scheiner et al. unpubl. ms.).

Motivating the Model

To motivate our model, consider two real-world examples. We emphasize that our model is not meant to match faithfully these examples; rather, these examples help to illustrate the general features of habitat construction and phenotypic plasticity that we wish to explore. Our model is instead meant as a "proof-of-concept" examination (Servedio et al. 2014), and an initial exploration of the evolutionary interaction between habitat construction and phenotypic plasticity.

The first example involves nitrogen fixation by bacteria and its use by plants (see review by Sachs et al. 2018). This example, cited in a prior model of the evolution of habitat construction (Lehmann 2008), provides a reasonably concrete context for examining the interplay of habitat construction and phenotypic plasticity. Nitrogen is an essential nutrient for plant growth and is the limiting resource in many plant communities (for a review, see Bingham and Cotrufo 2015). Plants respond to variation in available nitrogen by plastically altering their traits (e.g., by increasing the percentage of root mass at low nitrogen levels; Tonsor et al. 2013). Nitrogen is very abundant in the atmosphere, but mostly as N_2, a form that plants cannot directly access. Some bacteria can convert N_2 into nitrates and ammonium that plants can incorporate. Some plants, notably legumes, form symbiotic relationships with some of these bacteria. The bacteria reside in specialized root structures (nodules) and exchange nitrogenous compounds for carbohydrates from the host plant. Because of this exchange, the maintenance of the symbiosis is costly to the host plant and abandoned when nitrates and ammonium are readily available in the soil. Habitat construction occurs as parts of the plant (e.g., leaves) are shed or the entire plant dies and decays, enriching the soil. Nitrogenous compounds in the plant are processed by soil microbes and made available to the entire plant community, including other individuals of the same species. Those conspecifics gain the benefit of the soil nitrogen enrichment without encumbering the costs of the symbiosis. Finally, soil nitrogen can be lost either by leaching into ground water or conversion back into N_2. The optimal amount of soil N might vary along an environmental gradient where growth is also limited by some other factor, such as soil phosphorus, or it might have a single optimum in all environments if N is the only limiting factor.

The second example involves African cichlid fish (Kornfield and Smith 2000; Seehausen 2006). Habitat construction in this system is indirect. Cichlids feed on many food types, including algae scraped from rocks. Some species are territorial, thereby controlling algal resources (Genner et al. 1999). Algae biomass increases through growth, and decreases due to consumption and mortality. An individual can affect the amount, growth, and composition of the algal community within its territory by selectively grazing some species and reducing grazing by other cichlids. Territories can vary in their suitability for algal growth (Hata et al. 2014; Vadeboncoeur and Power 2017), and guarding behavior is costly in time and energy. Finally, the efficiency of feeding on algae depends on jaw morphology, which is phenotypically plastic in response to feeding regimes (Bouton et al. 2002). So an individual can modify its habitat to match its jaw morphology, or plastically modify its jaw morphology in response to the habitat.

Such combinations of factors can be found in other systems. For example, spider mites, which are herbivores of tomato plants, can downregulate the plants' defenses against herbivores, thus increasing mite fitness (Sarmento et al. 2011; Glas et al. 2014; Godinho et al. 2016). See Odling-Smee et al. (2003) for references to other plausible examples.

From such real-world examples, we abstract the following ingredients that will be used in our model for the joint evolution of habitat construction and phenotypic plasticity. Individuals reside in a series of demes that differ in their environment (i.e.,

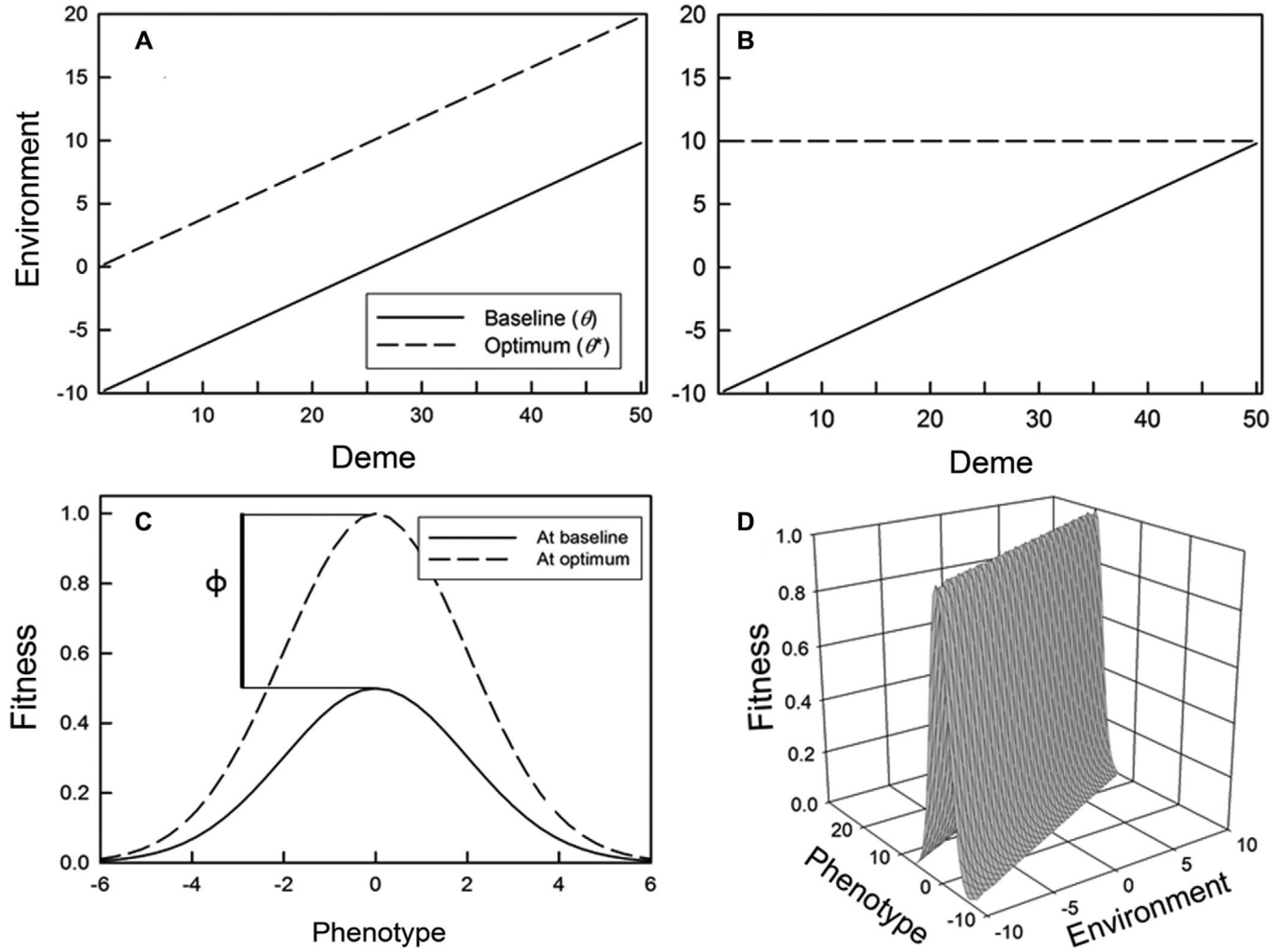

Figure 1. **(A) Both the baseline (θ) and optimal (θ^*) environments vary along a gradient (parallel optimum). (B) The baseline varies, but there is a single optimum for all demes (single optimum). (C) The fitness function in a given deme when the environment equals the optimum, and the decrease in fitness (ϕ) when the environment equals the baseline (for the single optimum case, this is the decrease for the middle of the gradient, which is also the average decrease across all demes), if the optimum phenotype is 0; shown is a value of $\phi = 50\%$. Trait values are in the same units as the environment. (D) The survival probability (W_t) along the environmental gradient when the environment of selection (S_t) and, thus, the optimal phenotype ($T_{\text{opt},t}$) matches the optimum (θ^*) shown in panel A, and assuming no cost of construction. The ridge of the survival probability corresponds to the optimal phenotype ($T_{\text{opt},t}$).**

spatial heterogeneity). The environment in each deme has a baseline state (its state with no construction) that varies linearly along a gradient (indexed by the deme number), and an optimal state that can either parallel the baseline environment (Fig. 1A), or be independent of that baseline and the location along the gradient (Fig. 1B). An individual has some genetic propensity to change the state of its deme's environment (construction). The total amount of construction that occurs in a deme in a given generation is determined by the aggregated construction propensities of all of the individuals in that deme. Those construction effects can carry over from one generation to the next (ecological inheritance sensu Odling-Smee et al. 2003), with some reversion back toward the baseline (decay). Construction and decay each occur once per generation. The equilibrium state of the environment is determined by the relative rates of construction and decay.

Generations are discrete. Within a generation, individuals are born, develop a phenotype, and experience viability selection, the survivors of which disperse, mate and reproduce, and then die (Fig. 2A). The environment can affect each individual at two points in its life cycle: during development if the individual is phenotypically plastic, and during viability selection. Individuals affect the environment through habitat construction, the timing of which depends on the simulation. The simulations we report here considered evolution of (1) habitat construction alone, and (2) habitat construction combined with phenotypic plasticity (and plasticity alone).

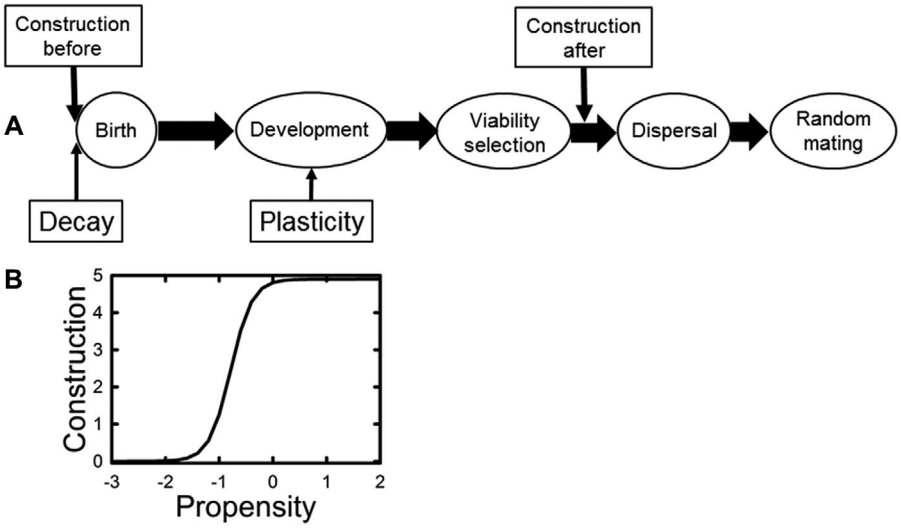

Figure 2. **(A) The order of life history events is as follows: birth, selection, dispersal, and reproduction. Environmental change occurs at two times for a given simulation: decay to the baseline environment, which occurs before birth, and construction, which can occur either before birth (after decay) or after selection. (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.**

Our model expands on previous efforts in various ways. First, previous models have been either optimality models (i.e., no genetics; Lehmann 2008; Krakauer David et al. 2009; Chisholm et al. 2018) or two-locus, two-allele models (Laland et al. 1996; Silver and Di Paolo 2006). In our model, traits are multilocus (as are most actual traits of ecological relevance) allowing for a continuous distribution of genotypic and phenotypic values. With only two alleles at each locus, the only thing that can evolve at each is the probability of one allele (which of course must be between 0 and 1), which determines the distribution of the three possible genotypes. With a multilocus model and an infinite number of possible alleles at each locus, evolution can affect not only the mean genotype, but the entire distribution of genotypes over the population, a distribution that is also affected by processes, such as recombination, not possible with a single locus model. Second, we took an approach to bounding construction that focused on individual limits, rather than on environmental limits. In our model, the environment resulting from construction had no upper bound. An upper bound to the constructed environment may or may not exist depending on the type of habitat construction. Soil N levels can potentially increase well beyond the maximal amounts needed for optimal plant growth; in contrast, a bird building a nest will stop once the nest reaches an optimal size. Two prior models have likewise had no fixed upper bound on construction (Lehmann 2008; Chisholm et al. 2018), whereas others had an upper bound (Laland et al. 1996; Silver and Di Paolo 2006; Kylafis and Loreau 2008; Krakauer David et al. 2009). In our model, we bounded the amount of construction that any individual and group of individuals could accomplish in a given generation. It is unrealistic to expect that the capacity of an individual to fix N or to build a nest has no upper limit. Combined with a fixed decay rate back to the baseline environment, such individual constraints create a maximal cumulative construction that can be sustained by a population. At equilibrium, the amount of construction each generation will equal the amount of decay. We chose a decay rate such that construction alone would modify the environment to approximately match the optimal environment. Third, our model includes multiple demes and environmental heterogeneity. The effects of spatial structure on the evolution of construction have been examined by just two other models (Silver and Di Paolo 2006; Lehmann 2008), and in both of those, all demes had the same baseline environment (viz., no spatial gradient). Finally, our model is the first to contrast the evolution of habitat construction with that of phenotypic plasticity.

Questions Addressed

Using this modeling scenario, we varied the value of habitat construction—the amount by which it increases fitness within a deme—and considered the following issues. First, we considered the behavior of the model when only habitat construction was present (construction-alone strategy) for two effects of construction on environmental heterogeneity: "parallel optimum" (Fig. 1A) and "single optimum" (Fig. 1B). The two differ in that the former has the same amount of construction occurring in all demes to reach the optimal environmental state, whereas the latter requires different amounts of construction among demes.

We predict that in the latter scenario, genetic differentiation among populations across the spatial gradient for the propensity to perform construction will increase as the value of construction increases.

Second, we contrasted the construction-alone strategy with the joint evolution of habitat construction and (noncostly) irreversible phenotypic plasticity (mixed construction + plasticity strategy). The question is whether the evolution of construction or plasticity is altered by the presence of the other process. We already know that the evolution of plasticity is affected by the ordering of life history events (development, dispersal, and selection, e.g., Scheiner and Holt 2012). Here, we explore how the timing of construction might change that evolution by contrasting the mixed strategy with a plasticity-only strategy.

Phenotypic plasticity is favored by evolution when there is environmental heterogeneity, and when the environment at the time of phenotypic determination reliably predicts the environment at the time of selection (Scheiner 2019). Construction might affect selection for plasticity by affecting either of those requirements: environmental heterogeneity or environmental predictability. Construction can increase within- and among-generation environmental heterogeneity because it alters the environment and might do so to different extents in different demes, thereby selecting for increased plasticity (Fig. 1A). Conversely, when construction favors a single optimum in all locations, it decreases environmental heterogeneity (Fig. 1B), selecting for decreased plasticity. The timing of construction creates a different sort of dynamic. When construction happens before the birth of the next generation, it links the environment of development to the environment of selection, selecting for plasticity. When construction happens after selection and before dispersal, it can increase among-generation environmental heterogeneity, also selecting for plasticity but for a different reason. How these two factors—the pattern of heterogeneity and the timing of construction—might interact is not obvious and will be explored by our model.

Table 1. Variables and parameters for the model simulations.

Symbol	Meaning	Value
T	Phenotype of an individual	
G	Nonplastic allelic value	
P	Plastic allelic value	
C	Construction allelic value	
A	Construction propensity of an individual	
B	Amount of construction by an individual	
θ	Baseline environment in each deme	
E	Environment in each deme at the end of each generation	
δ	The rate of decay of the environment to the baseline	50%
ΔH	The total construction in a deme in each generation	
D	Environment in each deme at the time of development	
S	Environment in each deme at the time of selection	
c	Plasticity scaling factor	10
T_{opt}	Optimum phenotype in each deme	
ϕ	Average fitness decrease in the baseline environment (construction value)	10-80%
W	Individual survival probability from juvenile to adult	
i	Subscript for ith deme	
j	Subscript for jth individual	
k	Subscript for kth allele	
t	Subscript for the tth generation	
	Number of nonplastic loci	5
	Number of plastic loci	5
	Number of construction loci	5
ω	Strength of selection	4
	Dispersal rate	41%
γ	Cost of construction	1% (maximum)
	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

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 1. The model was implemented in Fortran 77 (available from GitHub: https://github.com/sscheiner1/Plasticity-models/releases). The genotype of an individual consisted of three types of loci. Two types determined the phenotype: (1) genes whose expressions were independent of the environment (nonplastic loci), and (2) genes whose expressions were dependent on the environment (plastic loci). The third type of locus determined the amount of change in the habitat that an individual would make (construction loci).

DETERMINING THE ENVIRONMENT

The metapopulation consisted of a linear array of 50 demes (indexed by i from 1 to 50; Fig. 1). We consider the simplest case in which the environment is represented by a single scalar quantity (such as soil N or algal biomass). A baseline environmental gradient (environment in the absence of construction; Figs. 1A and 1B, solid lines) was created by varying the environmental value (θ_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; the environments in adjacent demes differed by 0.4 units [$\theta_i = 0.4(i - 25.5)$]. Each deme also had an optimal environment (θ_i^*) that was either 10 units above the baseline (Fig. 1A, dashed line) or fixed at 10 units (Fig. 1B, dashed line). Habitat construction increased the environmental value away from the baseline, and subsequent decay moved it back toward the baseline.

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 (ΔE_{it}) was

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

where $E_{i(t-1)}$ is the environment in deme i at the end of the generation $t-1$ and δ (= 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 after decay occurred and before reproduction ("construction before") or just after selection and before dispersal ("construction after"), depending on the simulation (Fig. 2A). (A third possibility is for construction to occur after development and before selection. We examined this scenario, but as those results were nearly identical to the "construction after" scenario, they are omitted for simplicity.) The amount of habitat construction that occurred in each deme in each generation was determined by two functions: the amount of construction attempted by each 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:

$$A_{ijt} = \sum_{k=1,10} C_{ijkt}, \tag{2}$$

where C_{ijkt} is the allelic value of the kth construction allele of the jth individual in the ith deme in generation t and A_{ijt} is that individual's construction propensity. The amount of construction (B_{ijt}) by an individual was a logistic function of its construction propensity:

$$B_{ijt} = 5/\left[1 + exp\left(-5A_{ijkt}\right)\right] \tag{3}$$

(Fig. 2B). The total construction in the ith deme in generation t (ΔH_{it}) was a saturating function of the sum of the construction of all N_i individuals in the deme:

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

The maximal amount of construction in a single generation was 5.0 units; the mean optimum environment was 10 units greater than the baseline environment (Figs. 1A and 1B). Thus, the environment in the ith deme at the end of generation t was

$$E_{it} = E_{i(t-1)} + \Delta E_{it} + \Delta H_{it}. \tag{5}$$

The environment at the time of development (D_{it}) and at the time of selection (S_{it}) depended on the order of life history events (Fig. 2). If construction occurred before development (construction before):

$$D_{it} = S_{it} = E_{i(t-1)} + \Delta E_{it} + \Delta H_{it}. \tag{6}$$

If construction occurred after selection and before dispersal (construction after):

$$D_{it} = S_{it} = E_{i(t-1)} + \Delta E_{it}. \tag{7}$$

For this last life history ordering, the effects of construction in the previous generation are contained in the environment at the end of this generation ($E_{i(t-1)}$), which affects the current generation. (Our choice of specific parameter values here and below affects the quantitative details of our conclusions, but not the overall qualitative patterns.)

DETERMINING THE PHENOTYPE

An individual's phenotype (trait value) was determined once during its life, at the time of development (before dispersal and selection), by 10 unlinked diploid loci: five nonplastic loci and five plastic loci. Loci contributed additively to the trait, which for simplicity was a scalar with the same units as the environment. Allelic values at the plastic loci were multiplied by the environmental value at the time of development before summing all allelic values. The phenotype of each individual was therefore determined as

$$T_{ijt} = \sum_{k=1,10} G_{ijkt} + D_{it} \sum_{k=1,10} cP_{ijkt}, \tag{8}$$

where T_{ijt} is the phenotype of the jth individual that develops in the ith deme in generation t, G_{ijkt} and P_{ijkt} are the allelic values of the kth nonplastic and plastic alleles of that individual, respectively, D_{it} is the environment of the ith deme at the time of development, and c is a factor that arbitrarily scales the magnitude of the expression of the plasticity loci so that the absolute magnitude

of the nonplastic and plastic loci would be similar for perfectly adapted individuals. There was no random component of phenotypic variation. For a given genotype, the quantity ΣG_{ijk} can be thought of as the intercept of its reaction norm at the point along the gradient where the environment is 0 (the reference environment), and the slope of $D_{it}\Sigma cP_{ijkt}$ calculated across demes can be thought of as the slope of its reaction norm. For simulations that explored the effects of habitat construction in the absence of plasticity, the phenotype was determined only by the nonplastic loci.

SELECTION

Life history events occurred in the following sequence (Fig. 2A): birth, development, selection, dispersal, and then reproduction. (This is the "select first" sequence of our previous papers.) 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 deme i at time t ($T_{\text{opt},it}$) (first term) minus the cost of construction (second term):

$$W_{ijt} = f_{it} \cdot \exp\left\{-\frac{1}{2}\left(\frac{T_{ijt} - T_{\text{opt},it}}{\omega}\right)^2\right\} - \gamma B_{ijt}, \qquad (9)$$

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. 1C) and ω determines the strength of selection on the phenotype (a lower value being stronger selection; Fig. 1D). Because we set units of trait values equal to environmental units, $T_{\text{opt},it}$ equals S_{it}. 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 (2ω). Habitat construction was costly; γ 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 in the simulations this cost function allowed for the possibility of negative fitness values, such negative values simply meant that an individual had a 0% probability of survival.

For habitat construction to be selected for, construction has to increase fitness. That construction benefit was embodied in the f term in equation (9), which was calculated as

$$f_{it} = 1 - \varphi\left|\frac{\theta_i^* - S_{it}}{\theta_0^* - \theta_0}\right|, \qquad (10)$$

where $\theta_0{}^*$ and θ_0 are the optimal and baseline environments at the center of the gradient; the difference (denominator) equals 10 for these simulations. This function equals 1.0 when the environment in the ith deme at the time of selection (S_{it}) equals the optimum environment in that deme ($\theta_i{}^*$), falls linearly with the absolute value of the difference between S_{it} and $\theta_i{}^*$, and reaches a minimum of $1 - \phi$ when S_{it} is at the baseline (θ_i) in the center of the gradient (Fig. 1B). The reduction in fitness at the baseline is highest on the left of the gradient and lowest on the right, with ϕ being the average across all demes. The greater the value of ϕ, the greater the strength of selection on construction. In these simulations, ϕ varied from 10% to 80%.

DISPERSAL

Dispersal occurred in a stepping-stone pattern. The dispersal probability was determined using a zero-mean, unit-variance Gaussian random number, which in turn determined the number of demes through which an individual moved; the integer part of the random number determined the number of demes moved and the sign determined the direction of movement (see fig. 1 of Scheiner and Holt 2012). The result was that the probability of moving (41%) and the average number of demes moved were correlated, with most individuals only moving one deme. Individuals who would have moved beyond either end of the gradient stopped at the end deme. The propensity to disperse was fixed (nonevolving), dispersal probabilities were identical for all individuals, and dispersal per se had no cost—survival during dispersal was 100%.

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 within each deme because population size (after reproduction) was determined independently of the outcome of selection; because individuals within a deme compete to produce successful offspring, such a procedure 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%. When a mutation occurred, the allelic value was changed by adding a Gaussian deviate (mean of 0 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. Both the plastic and nonplastic loci—and the subsequent phenotypes—could take any value from $-\infty$ to ∞. Similarly, the construction loci could take any value from $-\infty$ to ∞. In general, lower mutation rates simply lengthen the timescale over which evolution happens

without affecting the eventual outcome, for the kinds of models considered here (Scheiner and Holt 2012).

INITIAL CONDITIONS

Each simulation was initialized with 16 individual newborns in each deme. For each individual in the initial generation, allelic values for the plastic, nonplastic, 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 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_{ij0}) of each individual equal to 2.5 (Fig. 2B). There was therefore a significant amount of construction in early generations. That is, we biased our initial conditions to favor construction.

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 and slope of the total construction within demes (E_{it}) along the gradient, the mean and slope of the phenotype (T_{it}) along the gradient, the mean and slope of the construction propensity of individuals (A_{it}) along the gradient, the mean amount of phenotypic plasticity (ΣcP_{ijkt}), and the mean fitness (W_t). 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 construction propensity a linear regression was performed on the deme averages, and the resulting slope was standardized relative to the slope of the baseline environment (Fig. 1A).

For total construction, the environmental values (E_{it}) were averaged across all demes. This average was divided by 10, so a value of 1.0 indicates that habitat construction moved the average environment to match the optimum at the midpoint of the environmental gradient, which was always 10 units higher than the baseline; no construction would result in a value of 0. A linear regression was performed on the average value in each deme, and the resulting slope was standardized relative to the slope of the baseline environment. For the parallel optimum, a slope of 1 indicates that habitat construction matched the slope of the optimal environment across the gradient; for the single optimum, a slope of 0 indicates that habitat construction caused the environment to match the slope of the optimal environment across the gradient.

The mean and slope of the phenotype indicate whether the mean trait values in each deme (T_{it}) matched the selective optimum ($T_{\text{opt},it}$). The T_{ijt} values were averaged within demes and slopes across demes calculated as above. A slope of 0 indicates that the population was phenotypically uniform across the gradient, a jack-of-all-trades outcome. A slope of 1 indicates a pure genetic differentiation outcome when plasticity is absent. In the presence of plasticity, it can also indicate a pure plasticity outcome, which can be determined by examining relative plasticity (see below). A slope < 1 indicates an outcome intermediate between a jack-of-all-trades and either genetic differentiation or plasticity.

For phenotypic plasticity, the reaction norm describes the phenotypes that are actually or potentially expressed by a given genotype in all environments. For a reaction norm that is linear over an environmental gradient, its plasticity can be well characterized by its slope over this gradient. In this model, if the nonplastic loci do not contribute to the phenotype differentially among demes, the slope of the reaction norm for a genotype is the sum of the plastic allelic values (ΣcP_{ijkt}, the right-hand component of eq. 8) when normalized against the rate of environmental change along the gradient. The ΣcP_{ijkt} values were averaged as above and standardized relative to the slope of the baseline environment. A relative plasticity of 1 indicates a pure plasticity outcome in the absence of construction, whereas a relative plasticity of 0 indicates a pure genetic differentiation outcome.

Results

HABITAT CONSTRUCTION

We first consider just the evolution of construction in the absence of plasticity for the two patterns of environmental heterogeneity—parallel optimum and single optimum (Figs. 1A and 1B). The amount of construction depended on the pattern of life history events (Fig. 3). When construction happened before reproduction (solid circles), construction resulted in moving the environment most of the way toward the mean optimum (relative value of 1.0), regardless of the value of construction (ϕ). In contrast, when construction happened after selection (solid triangles), as ϕ increased the mean amount of construction moved the environment closer and closer to the optimum.

How the amount of construction changes along the gradient is measured by the construction slope (Figs. 3C and 3D). We expected that for the parallel option that amount should be the same everywhere, whereas for the single optimum it should decrease in demes at the right end of the gradient resulting in a negative slope (Fig. 1B). As expected, the slope of the constructed envi-

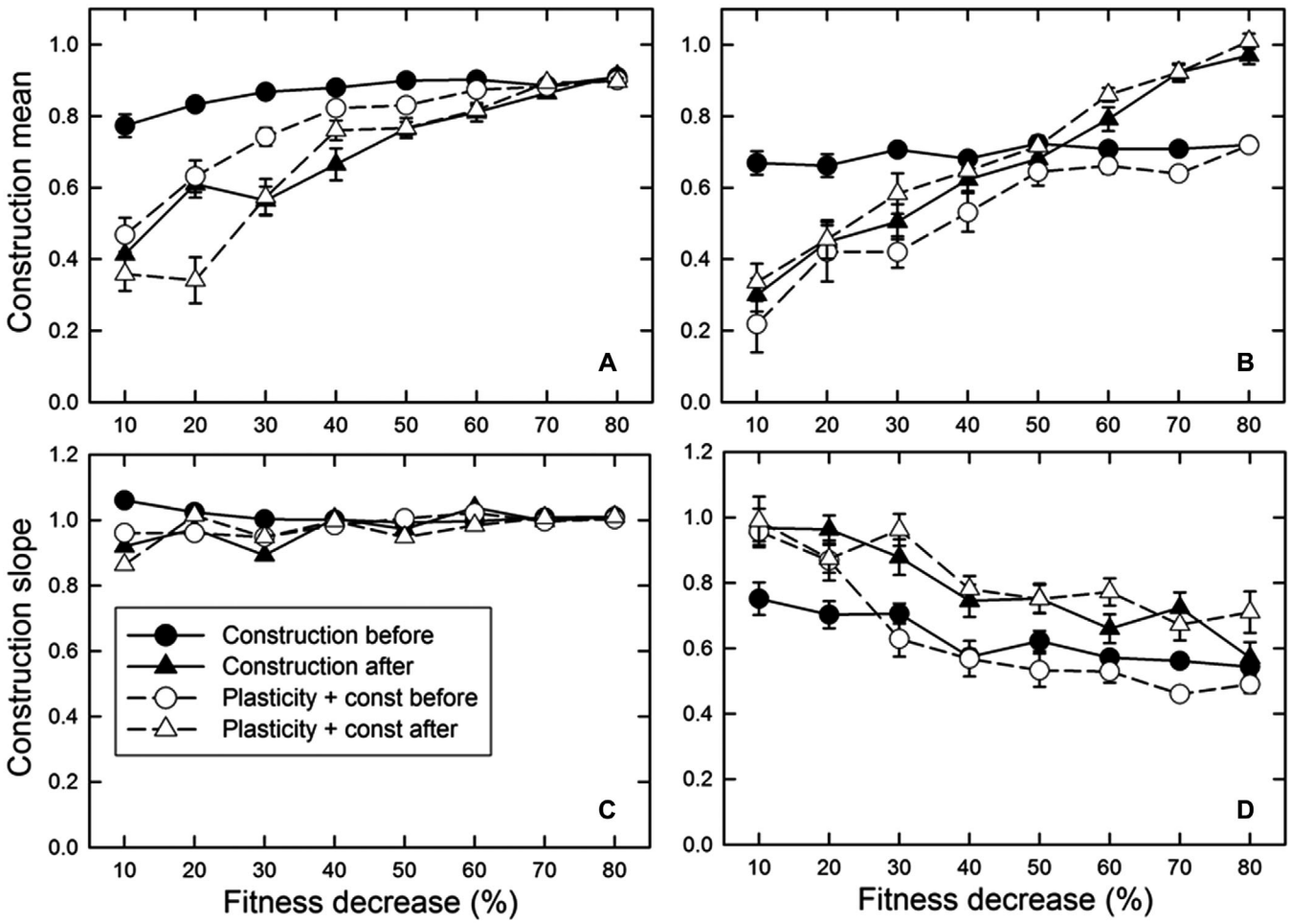

Figure 3. The effect of the fitness decrease (ϕ) on final relative construction environmental mean (mean E_{it}/10) (A and B) and slope (slope E_{it}/0.4) (C and D) for the (A and C) parallel optimum and (B and D) single optimum patterns of environmental heterogeneity. Shown are means and standard errors of 20 replicates; when error bars are absent, they are smaller than the symbol.

ronment was close to 1.0 for the parallel optimum, indicating that the constructed environment was mirroring the pattern of the optimal environment. In contrast, for the single optimum the slope declined from 1.0 as ϕ increased, but never reached a value of 0.0, the optimal pattern.

Construction propensity generally increased with an increase in the value of construction (ϕ), with greater responses for the parallel optimum (Figs. 4A and 4B). Regarding genetic differentiation for construction propensity, with the parallel optimum the slope was close to 0 (Fig. 4C), indicating no differentiation. For the single optimum, differentiation for construction propensity (Fig. 4D) largely followed the patterns of construction itself (Fig. 3D).

THE FIT OF THE PHENOTYPE TO THE CONSTRUCTED HABITAT

The amount of construction sets the conditions for the evolution of the phenotype. For the parallel optimum (Figs. 5A and 5C) when construction happened before reproduction (solid circles), both the relative mean and slope of the phenotype were close to 1.0, mirroring the way that construction moved the environment close to the optimum. Similarly, for the single optimum (Figs. 5B and 5D), the relative mean and slope again mirrored the amount and pattern of construction (Figs. 3B and 3D).

When construction happened after reproduction (solid triangles), the slopes again matched that of the constructed environment. Although the mean increased with the value of construction (ϕ), it was generally lower than the mean that would match the constructed environment. This lower mean occurred because when construction happens after selection in a given generation, decay occurs prior to selection in the following generation so that the environment at the time of selection will have decayed partially back to the baseline and away from the optimum.

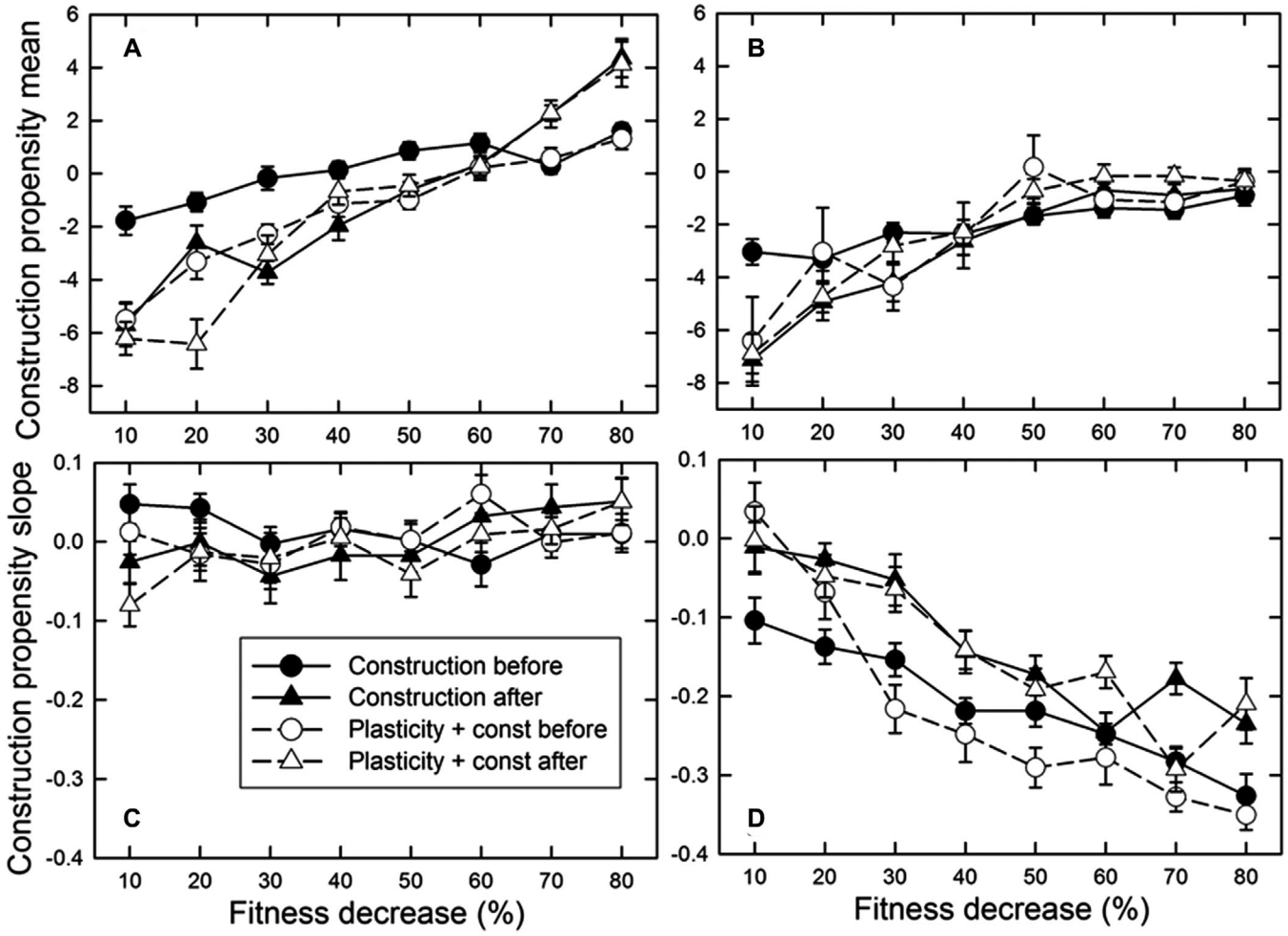

Figure 4. The effect of the fitness decrease (ϕ) on final construction propensity mean (mean A_{ijt}/10) (A and B) and slope (slope A_{ijt}/0.4) (C and D) for the (A and C) parallel optimum and (B and D) single optimum patterns of environmental heterogeneity. Shown are means and standard errors of 20 replicates; when error bars are absent, they are smaller than the symbol.

THE INTERPLAY OF HABITAT CONSTRUCTION AND PHENOTYPIC PLASTICITY

We next consider how the joint presence of habitat construction and phenotypic plasticity influences the evolution of each other—the mixed construction + plasticity strategy (Figs. 3–6, open symbols). If construction happened after selection, neither trait affected the evolution of the other (i.e., in Figs. 3–5, the open and closed triangles, and in Fig 6, the triangles and squares, were generally close to each other). This was not the case if construction occurred before reproduction and development. For small values of ϕ, construction was depressed for both the parallel optimum and the single optimum (open circles, Figs. 3A, 3B, 4A, and 4B). In contrast, plasticity was enhanced for the parallel optimum (especially for small values of ϕ; Fig. 6A) and nearly eliminated for the single optimum (Fig. 6B). That is, as expected, if construction acted to eliminate environmental heterogeneity prior to development, the value of plasticity was also eliminated. Conversely, adding plasticity to construction before development resulted in less construction, unless ϕ was large (Fig. 3B).

THE TRADE-OFF BETWEEN CONSTRUCTION AND PLASTICITY

If mean fitness is greater for a given strategy, that strategy will be favored by selection. Whether construction or plasticity are favored depends on the timing of construction (Fig. 7). First, we contrast the two pure strategies—construction-alone and plasticity-alone; we then consider a mixed construction + plasticity strategy.

When construction happened before reproduction and development, construction-alone (Fig. 7, solid circles) always had a higher fitness than plasticity-alone (Fig. 7, open squares), except for $\phi = 10\%$, for both the parallel optimum and single optimum. In contrast, when construction happened after development (Fig. 7, solid triangles), for the parallel optimum the plasticity-alone strategy had a higher fitness for small values of ϕ, with that

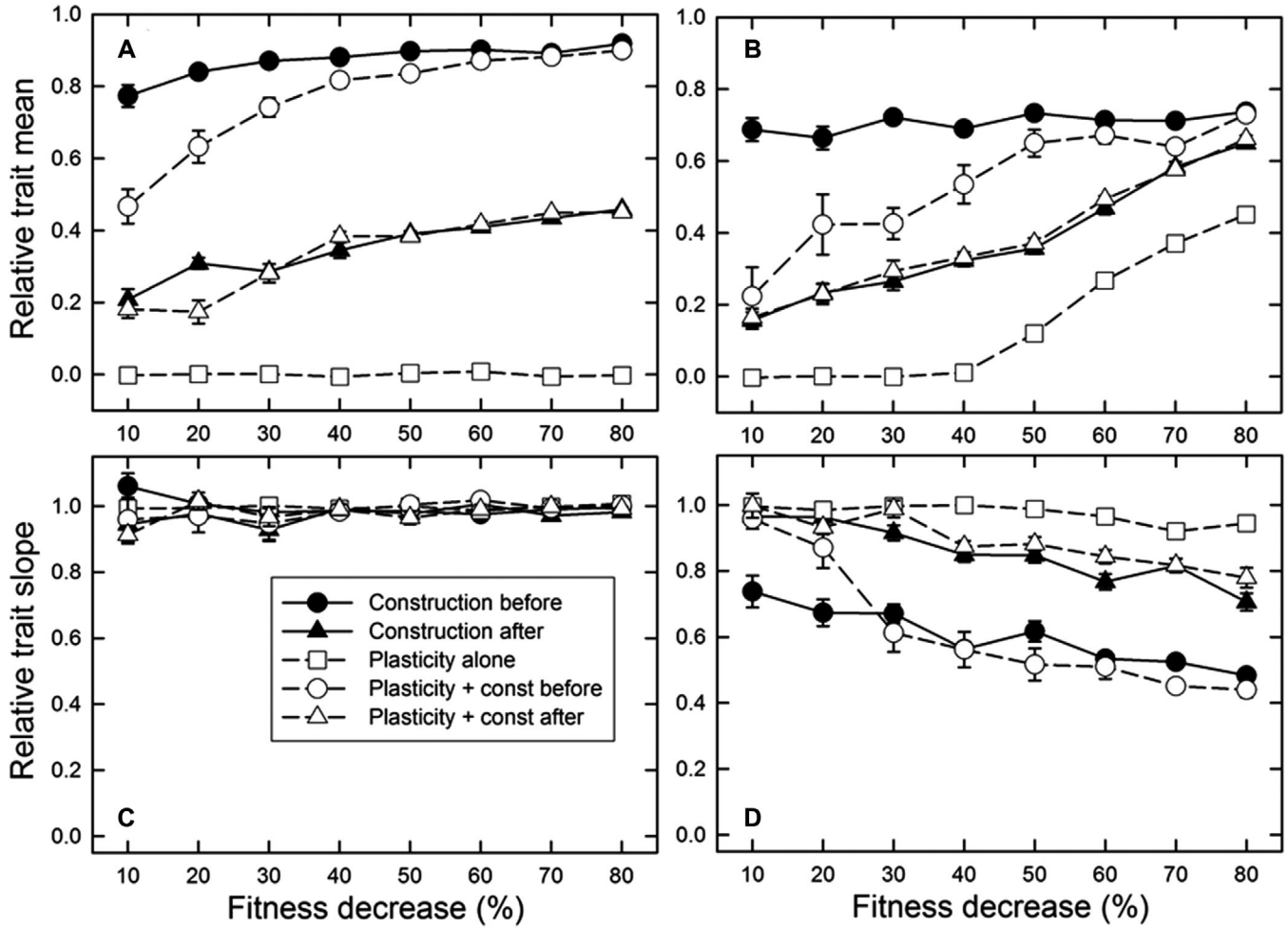

Figure 5. The effect of the fitness decrease (ϕ) on final relative trait mean (mean T_{ijt}/10) (A and B) and slope (slope T_{ijt}/0.4) (C and D) for the (A and C) parallel optimum and (B and D) single optimum patterns of environmental heterogeneity. Shown are means and standard errors of 20 replicates; when error bars are absent, they are smaller than the symbol.

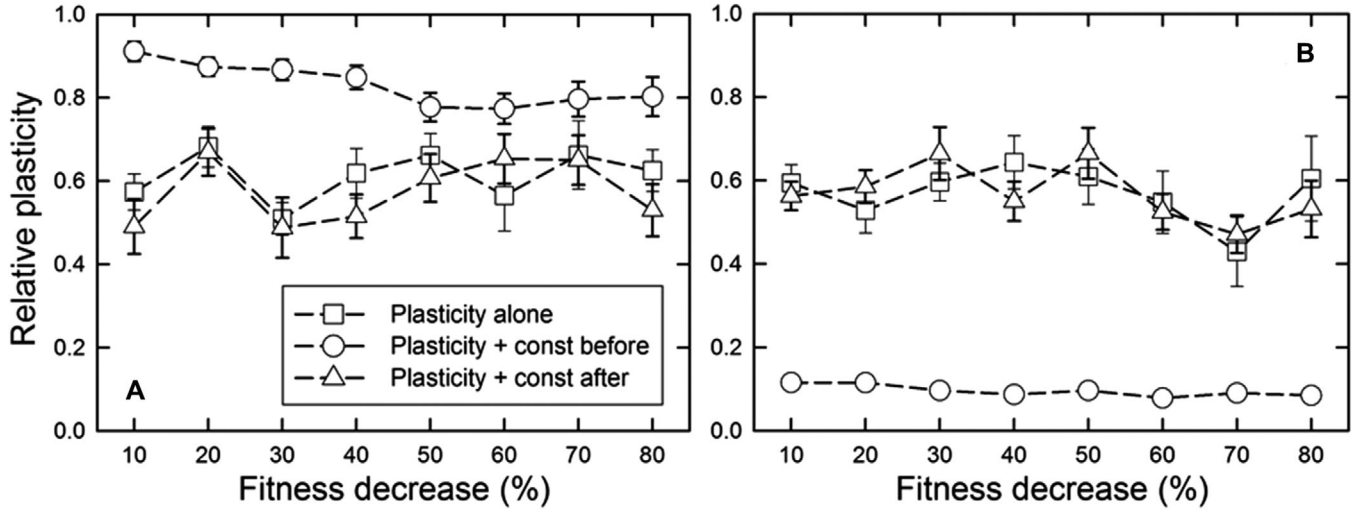

Figure 6. The effect of the fitness decrease (ϕ) on final phenotypic plasticity (mean ΣcP_{ijk}) for the (A) parallel optimum and (B) single optimum patterns of environmental heterogeneity. Shown are means and standard errors of 20 replicates; when error bars are absent, they are smaller than the symbol.

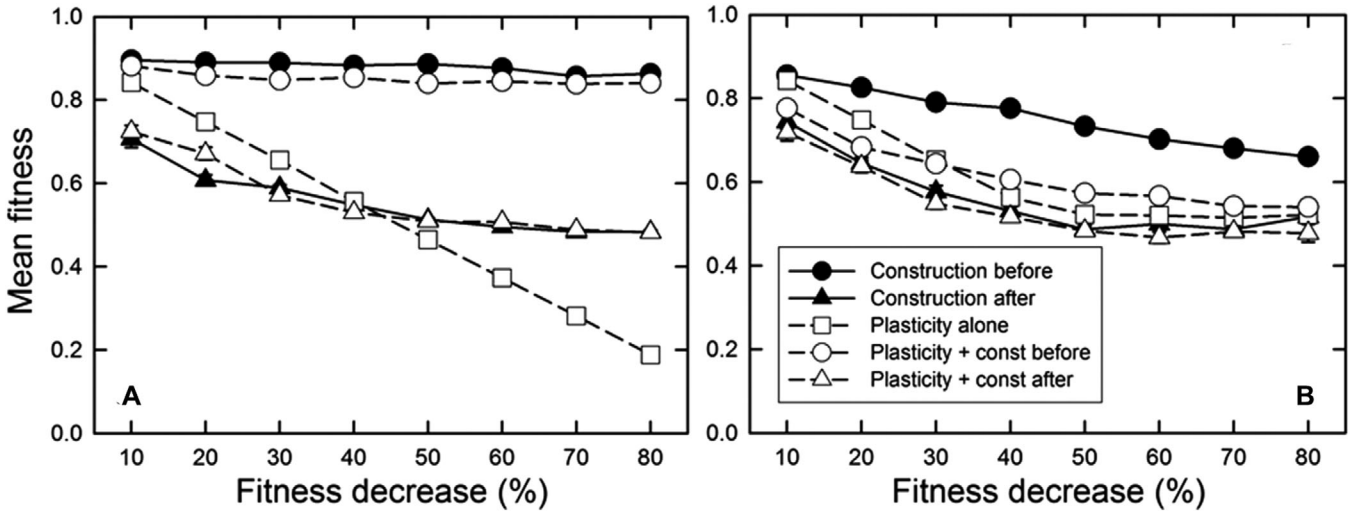

Figure 7. **The effect of the fitness decrease (ϕ) on final mean fitness (W_{ijt}) for the (A) parallel optimum and (B) single optimum patterns of environmental heterogeneity. Shown are means and standard errors of 20 replicates; when error bars are absent, they are smaller than the symbol.**

relative fitness advantage reversing as ϕ increased. For the single optimum, again the plasticity-alone strategy had a higher fitness for small values of ϕ with the fitnesses converging as ϕ increased. Thus, which strategy will be favored depends on the pattern of environmental heterogeneity, the value of construction, and the life history pattern.

A mixed construction + plasticity strategy never had a fitness greater than a construction-alone strategy. When construction happened after development, mean fitness was the same whether plasticity was present or absent for both the parallel optimum and the single optimum scenarios. In contrast, for the parallel optimum when construction happened before reproduction and development, the fitnesses of the two strategies are nearly identical, but for the single optimum the mixed strategy decreased fitness. Thus, plasticity is unlikely to evolve when construction is already present. However, construction might evolve in the presence of plasticity under some circumstances.

Discussion

We made three predictions: (1) that genetic differentiation along a spatial gradient for the propensity to perform construction would increase as the value of construction increases, (2) that selection on construction and plasticity would be synergistic when construction precedes development, because construction would increase among-generation environmental heterogeneity, and (3) that selection would be antagonistic when construction favors a single optimum in all locations because construction decreases environmental heterogeneity.

HABITAT CONSTRUCTION ALONE

When habitat construction evolved in isolation, our results confirm our first prediction. When maximizing fitness required different amounts of construction in different demes (Fig. 1B), genetic differentiation increased with the value of construction (Fig. 4D). However, even a very high value for construction failed to create sufficient differentiation to match the optimum across the entire gradient (Fig. 3D). This limitation of genetic differentiation for construction was not due to the rate of dispersal per se. The slope for the phenotype of the trait under direct selection was near 1.0 for the parallel optimum (Fig. 5C). The strength of selection was great enough to result in genetic differentiation for the primary trait despite high dispersal rates, and mirrors those in previous simulations using this model (e.g., Scheiner 2013). However, similar genetic differentiation did not occur for the propensity for construction even for much lower dispersal rates (results not shown).

This lesser differentiation for construction likely occurred because selection on construction propensity is indirect. Although the costs are borne by the individual, the benefits accrue to the entire deme. Construction should be more favored when the benefits are more likely to be directed to self or near kin as predicted by inclusive fitness and multilevel selection theory (Hamilton 1964; Wilson 1983). We found exactly that. Construction after selection but before dispersal (Fig. 2A) means that the benefits of construction may not accrue to the offspring of the constructing individuals. When the value of construction (ϕ) was low, construction after selection generally resulted in selection for less construction than construction before selection (Figs. 3A and 3B). A decrease in deme size would have similar effects (results not shown). These results are congruent with those of

previous habitat construction models (Laland et al. 1996; Silver and Di Paolo 2006; Kylafis and Loreau 2008; Lehmann 2008; Krakauer David et al. 2009; Chisholm et al. 2018).

HABITAT CONSTRUCTION VERSUS PHENOTYPIC PLASTICITY

The interaction of habitat construction and phenotypic plasticity is somewhat complex, as it depended on the pattern of spatial variation and the timing of life history events. When selection on construction and plasticity were potentially synergistic (parallel optimum and construction before; Figs. 3A, 3C, and 6A), the presence of both construction and plasticity resulted in greater plasticity and less construction at lower values of construction. So, the expectation of synergistic selection was only partially upheld, as the effects were positive only on plasticity and only under some conditions. In contrast when construction happened after selection, the traits evolved independently because plasticity is most favored when the phenotype matches the current environment of selection rather than the future constructed environment.

Selection on construction and plasticity were potentially antagonistic when construction favored a single optimum in all locations because the effect of such construction is to decrease environmental heterogeneity. This is exactly what we found (Fig. 6B, circles). Construction after selection (triangles) did not have this effect, because the decay process recreated the environmental gradient prior to the next selection episode.

Based on differences in mean fitnesses of the two strategies alone or in combination (Fig. 7), it is clear that the circumstances that would favor both strategies in combination are more limited than instances where either of the pure strategies are favored. We therefore predict that natural populations are likely to exhibit either phenotypic plasticity or habitat construction, but not typically both. A fruitful starting point would be to examine the many examples of habitat construction previously cited with an eye toward examining the plasticity of traits whose fitness is determined by the environmental factor(s) modified by that construction. Table 2.3 in Odling-Smee et al. (2003) provides a lengthy list of anatomical and behavioral traits that have plausibly evolved in response to habitat construction, all of which in principle could be examined for their plasticity.

In our model, we considered a limited set of life history patterns, patterns of environmental heterogeneity, deme sizes, and construction timings. How other conditions might affect the interaction of construction and plasticity can be gauged by how those alternatives affect the evolution of plasticity alone. Other simulations have considered the alternative life history patters, specifically the effects of dispersal occurring before selection (Scheiner and Holt 2012). The life history pattern explored in this article is the one most favorable for the evolution of plasticity, and thus other life history patterns are likely to favor construction over plasticity even more so. Similarly, spatial heterogeneity, which was explored here, more strongly favors plasticity than does temporal heterogeneity (Scheiner 2013); thus, temporal heterogeneity is again likely to favor construction. Smaller deme sizes favor construction (results not shown), and the size used here ($n = 16$) was chosen to be small enough to favor the evolution of construction, but not so small as to result in high amounts of local extinction due to stochastic effects. Those other results suggest that the overall patterns seen here would not differ for alternative deme sizes. It would be interesting, however, to consider scenarios in which construction increased local population size, which might tend to limit the evolution of construction. Similarly, the two timings of construction were chosen to contrast conditions that would favor or disfavor construction, with construction at other points in the life cycle not changing the general conclusions about how the evolution of construction and plasticity might interact. In a similar way, other parameters (e.g., the rate of environmental decay, the probability of dispersal) were chosen to highlight this interaction. Changing those parameters to favor or disfavor one or the other process would change the outcome, but in ways that were consistent with what is known about the conditions that favor either process. For example, adding a cost of plasticity would have decreased the absolute amount of plasticity selected for, but not have changed the pattern of response with respect to varying the fitness value of construction. It is also possible that other types of models with very different sorts of assumptions (e.g., an analytic model rather than an individual-based simulation) might reach other conclusions; the robustness of model conclusions is always best tested by addressing a question using a variety of different approaches.

IMPLICATIONS FOR THE EVOLUTION OF ADAPTIVE HABITAT CONSTRUCTION

Discussions about the evolutionary importance of habitat construction (Odling-Smee et al. 2013; Laland et al. 2015) often simply assume that construction occurs, and then proceed to explore its evolutionary consequences. The results of our model for habitat construction largely accord with standard examples of habitat construction. Examples of habitat construction described in Odling-Smee et al. (2003) include nests of cooperatively breeding birds, middens of woodrats, and burrows of mole rats. In such cases, the benefits of habitat construction are likely realized mainly by the constructing individual or its near kin. That is not to say that habitat construction cannot also benefit other unrelated individuals of the same or even different species. What needs to be established is the extent to which such additional benefits are sufficiently strong and consistent to affect the evolutionary trajectories of those species (Odling-Smee et al. 2003, pp. 298–301).

Our results suggest that the occurrence of adaptive habitat construction is not assured and may even be selected against,

depending on the order of life history events. Our model considered the effects of spatial, but not temporal, heterogeneity. Thus, the types of construction that we might expect and the consequent evolutionary dynamic might be very different for organisms with different life histories or with different types of environmental variation. For example, in our model the amount of construction was not directly regulated by environmental conditions. We found that selection was unable to result in complete genetic differentiation across a gradient for the amount of construction. Given the ubiquity of environmental heterogeneity, these results suggest that selection on habitat construction may be constrained to reflect the average conditions in a landscape, rather than producing fine-tuned results. This prediction can be tested by looking for genetic differentiation in the amount of habitat construction. If the evolutionary feedback favoring the evolution of construction includes a coevolving, biotic component—unlike our model—that feedback may be even weaker, further diminishing the potential for adaptive habitat construction. A better understanding of the evolution of adaptive habitat construction awaits more detailed models combined with empirical data.

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.

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