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2 The factors that favor adaptive habitat construction versus non-adaptive environmental
3 conditioning

4 **Running title:** Habitat construction vs environmental conditioning

5
6 Samuel M. Scheiner,¹ Michael Barfield² and Robert D. Holt²

7 ¹*Division of Environmental Biology, National Science Foundation*

8 *4201 Wilson Blvd., Arlington, VA 22230 USA*

9 *E-mail: sscheine@nsf.gov*

10 *Tel: 703-292-7175*

11 ²*Department of Biology, University of Florida*

12 *Gainesville, FL 32611*

13 *E-mail: mjb01@ufl.edu*

14 *E-mail: rdholt@ufl.edu*

15 *Tel: 352-392-6917*

16 **Corresponding author:** sscheine@nsf.gov

17
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30

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32 conditioning

33

34 **Abstract:** Adaptive habitat construction is a process by which individuals alter their
35 environment so as to increase their (inclusive) fitness. Such alterations are a subset of the myriad
36 ways that individuals condition their environment. We present an individual-based model of
37 habitat construction to explore what factors might favor selection when the benefits of
38 environmental alterations are shared by individuals of the same species. Our results confirm the
39 predictions of inclusive fitness and group selection theory and expectations based on previous
40 models that construction will be more favored when its benefits are more likely to be directed to
41 self or near kin. We found that temporal variation had no effect on the evolution of construction.
42 For spatial heterogeneity, construction was disfavored when the spatial pattern of movement did
43 not match the spatial pattern of environmental heterogeneity, especially when there was spatial
44 heterogeneity in the optimal amount of construction. Under those conditions, very strong
45 selection was necessary to favor genetic differentiation of construction propensity among demes.
46 We put forth a constitutive theory for the evolution of adaptive habitat construction that unifies
47 our model with previous verbal and quantitative models into a formal conceptual framework.

48

49 **Key words:** constitutive theory, environmental structure, habitat construction, kin selection,
50 model, niche construction

51 Introduction

52 All organisms, by their very existence, alter their environment as they take in and expel matter
53 and energy. Very often those alterations affect the future fitness of those organisms and others
54 around them. It is therefore unsurprising that natural selection would shape those alterations so
55 as to increase the fitness of the organisms. If those alterations decrease the fitness of the
56 organism, selection typically should act to minimize those effects. (We are ignoring selection for
57 a beggar-thy-neighbor strategy, also known as spite (Hamilton 1970)). In this paper, though, we
58 explore the case where these alterations have positive effects. Such positive effects have been
59 labeled “niche construction” (Odling-Smee *et al.* 2003; Odling-Smee *et al.* 2013); we prefer the
60 terminology of Sultan (2015) – “habitat construction” – as niche construction has been used to
61 refer to a large variety of ways that an organism can alter its fitness, either by changing its own
62 phenotype, or by altering the surrounding environment, or by simply moving to an alternative
63 environment.

64 Habitat (niche) construction activities have been claimed to be adaptations that have come
65 about through natural selection (Odling-Smee *et al.* 2003; Odling-Smee *et al.* 2013; Sultan
66 2015). That claim can be examined based on the form of that construction and the set of
67 individuals that the environmental alterations would affect. Obvious adaptations are the various
68 examples of artifact construction (*sensu* Odling-Smee *et al.* 2013). Such artifacts include bird
69 nests, bee hives, termite mounds, and beaver dams. Despite the costs to the individuals of such
70 elaborate constructions, they also have obvious benefits to those individuals that result in a net
71 increase in fitness.

72 Less obvious as adaptations are instances where individuals simply alter environmental
73 conditions. One hallmark of artifact construction is that its benefits are nearly always directed at
74 the constructing individual or its immediate kin. General alterations of the environment are
75 typically undirected, affecting all individuals in the vicinity of the constructing individual, which
76 may include effects on other species. For example, earthworms, as they burrow through the soil,
77 alter its consistency (Darwin 1892). Elephant browsing can create arboreal nesting sites for
78 lizards (Pringle 2008). Grass can stabilize dune systems, setting the stage for the establishment of
79 other species (Cowles 1899). Some species of chaparral vegetation may have evolved for
80 increased flammability (Schwilk 2003; Cowan & Ackerly 2010), which in turn has multiple
81 effects on the rest of the community (Montenegro *et al.* 2004; Pausas *et al.* 2017). Litter

82 decomposition is a form of environmental conditioning that is potentially a co-evolved
83 relationship between plants and soil microbes. (See Post and Palkovacs (2009) and Sultan (2015)
84 for an extensive list of such types of alterations.) These types of environmental alterations are
85 much more widespread than artifact construction. But are all such alterations adaptations, or are
86 most simply non-adaptive, incidental effects that are not directly selected for? In this paper, to
87 differentiate positively selected, adaptive habitat construction from non-adaptive, incidental
88 effects, we term the latter “environmental conditioning.” Because fitness benefits may extend to
89 unrelated individuals, the conditions that select for such types of habitat construction may be
90 more restricted.

91 The goal of this paper is to explore what factors might favor habitat construction when the
92 benefits of environmental alterations are shared by many individuals of the same species. By
93 determining those conditions, we can set bounds on the likelihood that such alterations are
94 adaptive. Furthermore, the conditions favoring such undirected benefits for a single species are
95 more favorable than those in which the benefits are shared by multiple species where
96 coevolutionary dynamics weaken selection (Trivers 1971; Matessi & Jayakar 1976; Wilson
97 1990). Thus, our results potentially put further restrictions on claims about niche construction as
98 a general, adaptive condition.

99

100 **Questions addressed and model predictions**

101 We use individual-based simulations to explore the factors that might affect selection for or
102 against habitat construction. In our model the environment exists in a baseline state. That state
103 differs from the one that would result in maximal fitness of the individuals. Individuals can alter
104 that environment – do construction – so as to move the environment towards that optimum.
105 Conversely, the environment tends to decay back towards the baseline state. The entire
106 population is divided into multiple demes. Although linked by dispersal, within a deme any
107 alteration of the environment due to construction is independent of such alterations in other
108 demes.

109 We address two broad themes. The first theme examines the factors that determine who
110 receives the benefits of construction: the individuals doing the constructing, their immediate kin,
111 or unrelated individuals. We do that by varying the size of demes, dispersal rates, the timing of
112 dispersal relative to construction and selection, and the temporal sustainability of construction

113 effects (i.e., the decay rate). These factors probe the strength of diffuse selection on groups of
114 potentially related individuals, i.e., kin selection. In the initial simulations the environment was
115 uniform and unstructured; both the baseline and optimal environments were the same in all
116 demes and dispersal was equally likely between all demes.

117 Because construction is costly, it should be favored when the benefits of habitat construction
118 are enjoyed either by the individuals that bore the costs or their close relatives (e.g., offspring);
119 such benefit sharing is a form of inclusive fitness through group selection (Hamilton 1964;
120 Wilson 1983). Based on previous models of the evolution of habitat construction (Laland *et al.*
121 1996; Silver & Di Paolo 2006; Kylafis & Loreau 2008; Lehmann 2008; Krakauer *et al.* 2009;
122 Chisholm *et al.* 2018), we expect that the propensity for construction should increase when the
123 benefits are more likely to be directed to self or near kin in the current or immediately following
124 generations: (1) as the number of individuals in a deme decreases, (2) as the decay rate increases,
125 (3) as the dispersal rate decreases, and (4) when an individual does construction in the same
126 deme as it or its offspring experience selection. We recognize that this first theme is primarily
127 confirming previous results; however, such confirmation is necessary to demonstrate that our
128 model is behaving as expected. Equally important, these initial simulations are necessary to
129 determine and justify the parameter values used in our second theme.

130 The second theme examines how environmental heterogeneity and structure can affect that
131 selection: temporal versus spatial heterogeneity, spatial variation in the optimal amount of
132 construction, and the relative patterns of dispersal and spatial heterogeneity. These factors
133 indicate how narrow or broad are the environmental conditions that will select for construction.
134 In the simulations involving spatial heterogeneity, baseline environmental conditions differed
135 among the demes in a structured way by the existence of an environmental gradient and, for
136 some simulations, dispersal that was limited to demes that were adjacent or very close along that
137 gradient. We predict that selection for construction should be weakened under three conditions:
138 increasing temporal variation, when there is spatial variation in the optimal amount of
139 construction, and when the pattern of dispersal does not match the spatial pattern of
140 environmental heterogeneity.

141

142 **The Model**

143 **Model structure**

144 The model was a discrete-time, individual-based simulation implemented in Fortran 77 that used
 145 a gene-based model of adaptation. The variables and parameters are listed in Table 1. The
 146 genotype of an individual consisted of ten loci – two types of five each – that were unlinked
 147 within and among types: genes determining the phenotype (trait loci) and genes determining the
 148 amount of change in the habitat that an individual would make (construction loci).

149

150 **Determining the environment – structure**

151 For simulations involving an unstructured, uniform environment, all demes consisted of the same
 152 baseline environment. Habitat construction (described below) increased the environmental value
 153 away from the baseline, and subsequent decay moved it back toward the baseline. The optimal
 154 environment was also the same for all demes and 10 units greater than the baseline environment.
 155 The number of demes was either 16, 32, 64, 128, or 256, and the respective carrying capacity for
 156 each deme was 32, 16, 8, 4, or 2; thus, the total metapopulation size (512) was the same for all
 157 simulations.

158 For simulations involving a structured gradient, the metapopulation consisted of a linear array
 159 of 50 demes (indexed by i from 1 to 50; Fig. 1). The carrying capacity for each deme was 8, for a
 160 total metapopulation size of 400. A baseline environmental gradient (environment in the absence
 161 of construction; Figs. 1A, 1B, solid lines) was created by varying the environmental value (θ_i) in
 162 a linearly increasing fashion along the array from approximately -10 arbitrary units at one end of
 163 the gradient to about +10 units at the other; the environments in adjacent demes differed by 0.4
 164 units [$\theta_i = 0.4(i - 25.5)$]. Each deme also had an optimal environment (θ_i^*) that was either 10
 165 units above the baseline (Fig. 1A; dashed line) or fixed at 10 units (Fig. 1B; dashed line). The
 166 optimal amount of construction was, therefore, the same in all demes (Fig. 1A) or varied among
 167 demes (Fig. 1B). Again, habitat construction increased the environmental value away from the
 168 baseline, and subsequent decay moved it back toward the baseline.

169

170 **Determining the environment – construction**

171 Between generations, the environment in each deme (i) decayed back toward its baseline state.
 172 The decay between the end of generation $t - 1$ and the start of generation t (ΔE_{it}) was

$$173 \quad \Delta E_{it} = -\delta (E_{i(t-1)} - \theta_i), \quad (1)$$

174 where $E_{i(t-1)}$ is the environment in deme i at the end of the generation $t - 1$ and δ is the rate of
 175 decay. This produced an environment of $E_{i(t-1)} + \Delta E_{it}$ before construction. For simulations that
 176 explored the effects of decay rate, δ varied from 10% to 100%; otherwise, δ was fixed at 50%.

177 Habitat construction occurred after birth prior to either dispersal or selection (Fig. 2). The
 178 amount of habitat construction that occurred in each deme in each generation was determined by
 179 two functions: the amount of construction attempted by each individual (a function of its
 180 genotype) and the amount of construction by the entire deme (a function of the individual
 181 constructions). The construction propensity of an individual was the sum of 5 unlinked diploid
 182 construction loci:

$$183 \quad A_{ijt} = \sum_{k=1,10} C_{ijk t} \quad (2)$$

184 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
 185 generation t and A_{ijt} is that individual's construction propensity. The amount of construction (B_{ijt})
 186 by an individual was a logistic function of its construction propensity:

$$187 \quad B_{ijt} = 5 / [1 + \exp(-5A_{ijt})] \quad (3)$$

188 (Fig. 2B inset). The construction in the i th deme in generation t (ΔH_{it}) was a saturating function
 189 of the sum of the construction of all N_i individuals in the deme:

$$190 \quad \Delta H_{it} = (\sum_{j=1, N_i} B_{ijt}) / (1 + 0.2 \sum_{j=1, N_i} B_{ijt}). \quad (4)$$

191 The maximal amount of construction in a single generation was 5.0 units; the mean optimum
 192 environment was 10 units greater than the baseline environment (Figs. 1A, 1B).

193 The environment in the i th deme at the time of selection was the environment at the end of the
 194 previous generation plus the changes due to decay and construction:

$$195 \quad S_{it} = E_{i(t-1)} + \Delta E_{it} + \Delta H_{it}, \quad (5)$$

196 which was also the environment at the end of generation t (E_{it}). (Our choice of specific parameter
 197 values here and below affects the quantitative details of our conclusions, but not the overall
 198 qualitative patterns.)

199 The form of habitat construction that we model is “unresponsive” as the amount of
 200 construction performed by an individual is based solely on its genotype. In contrast, “responsive”
 201 construction would entail an individual assessing the state of the environment first, then doing
 202 only that amount of construction necessary to reach the optimal state. We used a different form
 203 of restraint in our model; construction was limited due to the two saturating functions (eqs. 3, 4).
 204 For a deme as a whole, the total amount of construction was a saturating function, premised on

205 there being some type of feedback among individuals limiting what any single individual could
 206 accomplish. For a single individual, the saturating function was premised on the notion that a
 207 single individual cannot perform an unlimited amount of construction due to energy, time, or
 208 other constraints. We emphasize that the results of our modeling are dependent on all of these
 209 choices. Models based on other types of habitat construction might reach different conclusions.
 210

211 **Determining the phenotype**

212 An individual's phenotype (trait value) was determined at birth by 5 unlinked diploid trait loci.
 213 The loci contributed additively to the trait, which for simplicity was a scalar with units of
 214 equivalent magnitude as the environment: $T_{ijt} = \sum_{k=1,10} G_{ijk t}$, where T_{ijt} is the phenotype of the
 215 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
 216 allele of that individual. There was no random component of an individual's phenotype.
 217

218 **Selection**

219 Life history events occurred in one of two sequences (Fig. 2): (1) birth (when the phenotype is
 220 determined), then dispersal, selection, and reproduction (denoted as "move first"); or
 221 alternatively, (2) birth, selection, dispersal, and then reproduction (denote as "select first"). All
 222 individuals die after reproduction. Selection occurred during survival from juvenile to adult. The
 223 survival probability of each individual was a Gaussian function of the difference between its
 224 phenotype and the optimum phenotype in deme i at time t ($T_{opt,it}$) (first term) minus the cost of
 225 construction (second term):

$$226 \quad W_{ijt} = f_{it} \cdot \exp \left\{ -\frac{1}{2} \left(\frac{T_{ijt} - T_{opt,it}}{\omega} \right)^2 \right\} - \gamma B_{ijt}, \quad (6)$$

227 where f is a function (see below) that accounts for a decrease in fitness due to the difference
 228 between the current environment and the optimum environment (Fig. 1C) and ω determines the
 229 strength of selection on the phenotype (a lower value being stronger selection). Because we set
 230 units of trait values to be of equivalent magnitude to environmental units, $T_{opt,it}$ directly equals S_{it}
 231 without need of a transformation. For all simulations, $\omega = 4$. For the structured environment, the
 232 length of the spatial gradient across all demes was approximately 2.5 times the width of the
 233 within-deme selection function (2ω). Habitat construction was costly; γ was the per-unit
 234 construction cost, which was multiplied by the construction trait as defined in equation (3). The

235 cost parameter (γ) chosen was based on the percentage decrease in total fitness (survival
 236 probability) for individuals that expressed the optimum phenotype, so an individual that
 237 contributed the maximal construction would experience a 1% decrease in fitness. Although in the
 238 simulations this cost function allowed for the possibility of negative fitness values, such negative
 239 values simply meant that an individual had a 0% probability of survival.

240 For habitat construction to be selected for, construction has to increase fitness. That
 241 construction benefit was embodied in the f term in equation (6), which was calculated as:

$$242 \quad f_{it} = 1 - \varphi \left| \frac{\theta_i^* - S_{it}}{\theta_0^* - \theta_0} \right|. \quad (7)$$

243 For simulations with unstructured environments: $\theta_0^* - \theta_0 = 10$. For simulations with a gradient,
 244 θ_0^* and θ_0 are the optimal and baseline environments at the center of the gradient (between
 245 demes 25 and 26); the difference (denominator) also equals 10 for these simulations. This
 246 function (f_{it}) equals 1.0 when the environment in the i th deme at the time of selection (S_{it}) equals
 247 the optimum environment in that deme (θ_i^*), falls linearly with the absolute value of the
 248 difference between S_{it} and θ_i^* , and reaches a minimum of $1 - \varphi$ when S_{it} is at the baseline (θ_i) in
 249 the center of the gradient (Fig. 1C). Selection on environmental construction is therefore toward
 250 the optimum, and the greater the value of φ , the greater the strength of selection on that
 251 construction. For the parallel optimum, this reduction in fitness at the baseline is the same in all
 252 demes. For the single optimum, this reduction is highest on the left of the gradient and lowest on
 253 the right, with φ being the average across all demes. The total change in the environment due to
 254 construction was not limited (except by the maximum per-generation construction and the decay
 255 rate); it could increase the selective environment (S_{it}) to be greater than the optimum (θ_i^*), which
 256 would cause a similar reduction in fitness.

257

258 **Temporal variation**

259 In some simulations with the unstructured environment, there was also random variation added
 260 to one of two aspects of that environment, either the selective environment experienced by
 261 individuals (S_{it}), or the optimal environment (θ_i^*). That variation also had two spatial patterns:
 262 either it was independent among demes, i.e., each deme experienced a different pattern of
 263 variation, or all demes experienced the same pattern of variation. Variation in the environment
 264 was added at the time of construction. Random variation within each deme was simulated as a
 265 sequence of independent zero-mean Gaussian random deviates (z_{it}) with a standard deviation of τ

266 that was scaled to be a percentage of the initial difference between the baseline and optimal
 267 environments (10 units for these simulations). If each deme experienced a different pattern of
 268 variation, the environment in the i th deme at the time of selection was:

$$269 \quad S_{it} = E_{i(t-1)} + \Delta E_{it} + \Delta H_{it} + z_{it} \quad (8)$$

270 (compare with eq. 5). If all demes experienced the same pattern of variation, z_{it} was replaced
 271 with z_t , i.e., the same deviation in each deme. Variation in the optimal environment occurred at
 272 the time of selection, using similar Gaussian random deviates ($\theta_{it}^* = \theta_i^* + z_{it}$ or $\theta_{it}^* = \theta_i^* + z_t$),
 273 depending on whether that variation was independent or correlated among demes. Regardless of
 274 the existence of any extrinsically imposed temporal variation, the dynamic of construction and
 275 decay always produced autocorrelated temporal variation within each deme.

276

277 **Environmental structure and dispersal**

278 Dispersal occurred in one of two patterns that corresponded to the two types of environments:
 279 island for the unstructured environment and stepping-stone for the structured environment. For
 280 the island pattern of dispersal, if an individual moved it had an equal probability of moving to
 281 any of the other demes. (In ecology, this pattern is referred to as an unstructured metapopulation
 282 dispersal pattern.) The propensity to disperse was fixed (non-evolving), dispersal probabilities
 283 were identical for all individuals, and dispersal per se had no cost – survival during dispersal was
 284 100%.

285 For the stepping-stone pattern of dispersal, the dispersal probability was determined using a
 286 zero-mean Gaussian random number which in turn determined the number of demes through
 287 which an individual moved; the integer part of the random number determined the number of
 288 demes moved and the sign determined the direction of movement (see Fig. 1 of Scheiner & Holt
 289 2012). The result was that the probability of moving and the average number of demes moved
 290 were correlated, with most individuals that moved only moving one deme and the rest moving at
 291 most a few demes. Individuals who would have moved beyond either end of the gradient stopped
 292 at the end deme. Again, the propensity to disperse was fixed (non-evolving), dispersal
 293 probabilities were identical for all individuals, and dispersal per se had no cost.

294 For simulations that explored the effects of dispersal, the dispersal rate varied from 4% to
 295 100%. Otherwise, the dispersal rate was fixed at 44% for unstructured environments or 41% for

296 structured environments; these values were chosen based on the results of the simulations that
297 examined the effects of dispersal rate.

298

299 **Reproduction and mutation**

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

310 When new offspring were generated, each allele at each locus mutated with a probability of
311 10%. In general, lower mutation rates simply lengthen the time-scale over which evolution
312 happens without affecting the eventual outcome, for the kinds of models considered here
313 (Scheiner & Holt 2012). In addition, this somewhat high mutation rate has the virtue of
314 minimizing linkage disequilibrium. When a mutation occurred, the allelic value was changed by
315 adding a Gaussian deviate (mean of zero and a standard deviation of 0.1 units) to the previous
316 allelic value (i.e., this is a continuum-of-alleles model, Kimura 1965). Allelic values were
317 unconstrained. Trait alleles – and the subsequent phenotypes – could take any value from $-\infty$ to
318 ∞ . Similarly, the construction alleles could take any value from $-\infty$ to ∞ .

319

320 **Initial conditions**

321 Each simulation was initialized with individuals newly born in each deme at that deme's carrying
322 capacity. For each individual in the initial generation, allelic values for the trait and construction
323 loci were chosen independently from the values -2, -1, 0, 1, and 2, with each value being equally
324 likely. Even though these alleles were integer-valued initially, their values could assume any real
325 number in subsequent generations due to mutation. The environment of each deme was initially
326 equal to its baseline. The initial expected value of construction propensity was 0, so that the

327 initial expected value of potential construction (B_{ij0}) of each individual was equal to 2.5 (Fig. 2,
328 inset). There was, therefore, a significant amount of construction in early generations. Such
329 construction lessened the probability of immediate extinction in simulations with large values of
330 ϕ .

331

332 **Response variables**

333 All simulations were run for 1,000 generations to ensure that equilibrium (the point after which
334 all calculated quantities showed no further obvious directional trend) was reached. Each
335 parameter combination was replicated 20 times; the results shown are the means and standard
336 errors of those replicates.

337 To assess evolutionary outcomes, at the end of 1,000 generations there was one last round of
338 mating and reproduction (without environmental decay) to return the demes to full size before
339 parameters were calculated. For unstructured environments, evolutionary outcomes were
340 assessed by examining the mean of the total construction within demes (E_{it}), the mean of the
341 construction propensity of individuals (A_{it}), and the mean fitness (W_{it}). The parameters were
342 measured by first averaging among individuals within demes, and then averaging among demes.
343 For structured environments, for each of these parameters we also examined the slope along the
344 gradient. Slopes were calculated as a linear regression on the deme averages. For construction
345 propensity, the slope was a measure of genetic differentiation among demes. All slopes were
346 standardized relative to the slope of the baseline environment (Figs. 1A, 1B).

347 For total construction, the environmental values (E_{it}) were averaged across all demes. This
348 average was divided by 10, so a value of 1.0 indicates that habitat construction moved the
349 average environment to match the optimum at the midpoint of the environmental gradient, which
350 was always 10 units higher than the baseline; no construction would result in a value of 0. (The
351 amount of construction in deme i is actually $E_{it} - \theta_i$, but since the average θ_i is 0, when this is
352 averaged across demes, it is equal to the average E_{it}). For the parallel optimum, a slope of 1
353 indicates that habitat construction resulted in an environment that matched the slope of the
354 optimal environment across the gradient; for the single optimum, a slope of 0 indicates that
355 habitat construction caused the environment to match the slope of the optimal environment
356 across the gradient.

357

358 Results

359 **Unstructured environments and no environmental heterogeneity**

360 We predicted that habitat construction would be favored when the benefits of construction are
361 more likely to flow to the individual doing the constructing or its close kin. We tested that
362 prediction by manipulating the rate at which the constructed environment reverted to its baseline
363 state, the deme size, and the rate of dispersal. For the “select first” life history pattern, the
364 individual doing the construction always directly benefits from the construction. For the “move
365 first” life history pattern the constructor benefits only if it does not disperse. For both patterns, a
366 lower dispersal rate results in more of the benefits accruing to the constructor’s descendants.
367 Similarly the faster the environment reverts to the baseline state, the more the benefits of
368 construction are focused on one’s direct offspring. We found that all of these factors interacted.

369 Our first set of simulations examined an unstructured environment (i.e., the baseline and
370 optimal environments were the same in all demes) with a matching pattern of dispersal (i.e., an
371 island pattern where all demes were equally distant). If dispersal occurred before selection
372 (“move first”), the greatest propensity for construction (average construction phenotype, mean
373 A_{ijt}) occurred for small population sizes ($N = 4$) at fast rates of decay (Figs. 3C), with a maximum
374 amount of construction (mean $E_{it}/10$) at a decay rate of 40%. (For $N = 2$, the metapopulation
375 simply went extinct under these parameter values.) For intermediate to high decay rates, fitness
376 declined with increasing population size for the smaller deme sizes (4, 8; Fig. 3E).

377 For the largest population size ($N = 32$) there was almost in no construction (mean $E_{it}/10$) at
378 high decay rates, with a peak at 20% (Fig. 3A). That peak was due to a bimodal distribution of
379 environmental construction values with about half near zero and about a third near the maximum
380 possible value (2.4; not shown), suggesting the existence of alternative (quasi-) stable states. The
381 reason for this bimodality is that sometimes the metapopulation is getting “trapped” in an
382 excessive construction phenotype. Because the life history pattern is “move first” and the
383 dispersal rate is 44%, there is a (partial) disconnect between how much construction an
384 individual does and its fitness outcome. In this case, the decay rate is slow enough that once the
385 population is above the optimum it never moves the environment across that optimum threshold
386 back to the state where no construction is selected for. While this result is relevant to only a
387 narrow parameter range in our particular model, it may point at an interesting biological scenario

388 that might possibly be more widespread in other models; analytic treatment of this combination
389 of conditions may be warranted.

390 In contrast, if dispersal occurred after selection (“select first”), the amount of construction
391 (Fig. 3B) and the subsequent fitness (Fig. 3F) were similar for all but the smallest population
392 size, and was highest at an intermediate decay rate. As predicted, the propensity for construction
393 increased with the decay rate at all population sizes (Fig. 3D). Assuming that a steady state is
394 reached, construction must balance decay. Since the maximum construction per generation is 5,
395 and the amount of construction is standardized by dividing by 10, the maximum relative
396 construction is equal to $0.5/\delta$. For larger populations, the decrease in construction with increasing
397 decay rate (for intermediate to high decay rates; Fig. 3B) matched the expected equilibrium
398 pattern. Small population sizes will have a smaller limit; for example, for $N = 2$, the maximum
399 construction is $0.33/\delta$. Thus, construction was not favored at low decay rates because the benefits
400 did not accrue to close kin, while at high decay rates construction was not favored because it was
401 costly while not being able to maintain the demes at the optimum.

402 Dispersal rates had the predicted effect on construction for the “move first” life history
403 pattern, with less construction as rates increased, especially at smaller population sizes (Figs. 4A,
404 4C, 4E). (Again, the smallest population size resulted in metapopulation extinction.) In contrast,
405 for the “select first” life history pattern, dispersal rate had no effect on construction, its
406 propensity, or fitness, except for the smallest population size (Figs. 4B, 4D, 4F). That is, because
407 the constructing individual directly benefited, benefits to other individuals did not change the
408 outcome. Overall, construction was favored the most when it benefits the conditioning individual
409 or its immediate kin.

410 These results were used to set the parameters for the next sets of simulation that explored the
411 effects of environmental structure and patterns of heterogeneity.

412

413 **Unstructured environments and temporal heterogeneity**

414 For the unstructured environment, we looked at the effects of random environmental variation,
415 using parameters that resulted in construction at or close to the optimal amount in the absence of
416 temporal variation (see Figs. 3, 4). We examined temporal variation in either the environment of
417 selection or in the optimal environment. That variation was either independent in each deme or
418 the same across all demes. We had predicted that less construction would evolve with increasing

419 temporal variation. In contrast, we found that for all of those scenarios, there were no effects on
420 the amount or propensity for construction, except for a slightly smaller amount of construction at
421 high rates of temporal variation when it was correlated among demes (Fig. 5).

422

423 **Structured environments and spatial heterogeneity**

424 We considered two types of structured environments, one in which the optimal amount of
425 construction was the same in all demes along the environmental gradient (parallel optimum) and
426 one in which the optimal amount decreased along the gradient (single optimum). In these
427 simulations, the pattern of dispersal was a stepping-stone, thus matching the gradient pattern of
428 heterogeneity in the baseline environment. As with unstructured environments, a structured
429 gradient generally favors construction at lower dispersal rates and when selection happens before
430 dispersal (Figs. 6A, 6C). These effects of dispersal timing could be offset, however, if the fitness
431 benefits of construction were great enough (Figs. 6B, 6D).

432 The difference between the parallel optimum and single optimum scenarios is that the latter
433 requires genetic differentiation in the amount of construction undertaken along the gradient to
434 achieve maximum fitness, with the greatest amount of construction at the left-hand end of the
435 gradient and little to no construction at the right-hand end (Fig. 1B). For the parallel optimum
436 scenario, perfect adaptation would entail a construction slope (normalized by the gradient slope)
437 of 1.0 and a propensity slope of 0.0; for the single optimum scenario, the equivalent values
438 would be 0.0 and -0.5. Values at or close to these ideals occurred only for the “select first”
439 dispersal pattern and parallel optimum scenario (Fig. 7). For the “select first” dispersal pattern
440 and single optimum scenario the construction slope was decreased, but not to zero; the dispersal
441 rate had little effect on this slope (Fig. 7A), but it declined as the fitness benefit of construction
442 increased (Fig. 7B). Genetic differentiation for construction propensity was greatest at lower
443 dispersal rates (except the lowest; Fig. 7C) and for greater fitness benefits (Fig. 7D). For the
444 “move first” dispersal pattern, such differentiation occurred only at the lowest dispersal rates (for
445 the single optimum, of course). As a result, the highest fitnesses were seen for the “select first”
446 dispersal pattern and parallel optimum scenario (Fig. 8). In contrast, for the “move first”
447 dispersal pattern, the two scenarios had similar fitnesses under nearly all conditions, except at
448 very high fitness benefits where the parallel optimum resulted in fitnesses almost identical to
449 those of “select first.”

450

451 **Structured environments and non-structured dispersal**

452 Dispersal pattern and environmental structure can reinforce or oppose each other. A stepping-
453 stone dispersal pattern reinforces a structured environmental gradient in that individuals that
454 move are most likely to land in an environment very similar to the one departed from. In
455 contrast, an island (non-structured) dispersal pattern matches an unstructured environment
456 because traveling a greater distance does not result in traversing a greater environmental space.
457 We tested the effects of a mismatch in these factors by exploring the effects of dispersal rates of
458 an island dispersal pattern in a structured environment. Overall, the level of adaptation was less
459 than for the stepping-stone dispersal pattern (compare Figs. 9A, 9B, 9C, 9D with 6A, 7A, 7C,
460 7C, respectively, and Fig. 8A with Fig. 10).

461 For the single optimum scenario, genetic differentiation for construction propensity failed to
462 occur for the “select first” dispersal pattern (Fig. 9D). Instead, the constructed environment had
463 a mean value that was slightly lower than the optimal mean (Fig 9A) and a slope that matched
464 the baseline slope (1.0, Fig. 9B).

465 For the “move first” dispersal pattern, at high dispersal rates there was selection for little or
466 no construction, especially for the parallel optimum (Figs. 9A, 9C). At low dispersal rates, the
467 slope of the constructed environment was positive (Fig. 9B), as was the slope of the construction
468 propensity (Fig. 9D) for both optimum patterns, but especially for the parallel optimum. These
469 results mean that there was selection for more construction at the right-hand end of the gradient
470 (Figs. 1A, 1B).

471

472 **Discussion**

473 **Theme 1: The recipients of construction benefits**

474 Our results confirm the predictions of inclusive fitness and group selection theory (Hamilton
475 1964; Wilson 1983) and expectations based on previous models (Laland *et al.* 1996; Silver & Di
476 Paolo 2006; Kylafis & Loreau 2008; Lehmann 2008; Krakauer *et al.* 2009; Chisholm *et al.*
477 2018): construction will be more favored when its benefits are more likely to be directed to self
478 or near kin (Figs. 3, 4). Unlike previous models, ours is an individual-based simulation in which
479 both the construction and trait phenotypes are multilocus. The general concordance of our results
480 with those of the previous models suggests that these broad conclusions are robust.

481 The results of our model and others are in general accord with the examples of habitat
482 construction that are typically touted. Examples of habitat construction described in Odling-
483 Smee *et al.* (2003) include: nests of cooperatively breeding birds, middens of woodrats, burrows
484 of mole rats. In such cases of artifact construction, the benefits of habitat construction are likely
485 realized mainly by the constructing individual or its near kin. That is not to say that habitat
486 construction cannot also benefit other individuals of the same or different species through
487 environmental conditioning. What needs to be established is the extent to which such additional
488 benefits are sufficiently strong and consistent to affect the evolution of those other individuals or
489 to feed back on the evolution of construction (Odling-Smee *et al.* 2003, pp. 298-301).

490

491 **Theme 2: Environmental heterogeneity and structure**

492 Our modeling efforts differ from previous ones by also exploring the effects of spatial and
493 temporal variation. While two previous models included spatial structure (Silver & Di Paolo
494 2006; Lehmann 2008), environmental heterogeneity was generated only by the construction
495 itself, as in our models under the first theme. In our simulations, contrary to our prediction,
496 temporal variation had little to no effect on the evolution of construction (Fig. 5). This lack of
497 effects was likely because we focused on just the final equilibrium and temporal variation acted
498 as just background noise. Examination of the dynamics during early generations might show
499 some effects.

500 Spatial heterogeneity did affect construction evolution, but those effects depended on various
501 factors. As before, construction was favored when the timing and rate of dispersal relative to
502 construction and selection resulted in the benefits of construction going to self or near kin.
503 Conversely, construction was disfavored when the spatial pattern of movement did not match the
504 spatial pattern of environmental heterogeneity (Fig. 9). Notably, construction was less favored
505 when there was spatial heterogeneity in the optimal amount of construction, especially as
506 dispersal rates increased (Figs. 6C, 7C). Very strong selection was necessary to favor genetic
507 differentiation of construction propensity among demes (Fig. 7D). This lack of differentiation
508 contrasted with genetic differentiation for the trait itself, which always matched the constructed
509 environment regardless of the pattern or rate of dispersal (results not shown). The reason that
510 similar genetic differentiation did not occur for the propensity for construction is that selection

511 on that trait is indirect, a process analogous to selection on modifier loci, which Wright (1934)
512 showed to be weaker.

513 Because spatial heterogeneity is ubiquitous, the extent to which a lineage experiences that
514 heterogeneity is a function of the rate of dispersal among locations and the distance of that
515 dispersal relative to the grain of the environment. We predict that habitat construction will be
516 greater when dispersal is limited. Because limited dispersal also tends to increase relatedness
517 within demes, a test of this prediction will need to compare multiple populations that vary
518 independently in dispersal rate and population size.

519

520 **Habitat construction or environmental conditioning?**

521 Our simulations suggest that adaptive habitat construction will be favored under a relatively
522 narrow set of circumstances. First, the benefits need to be directed at oneself or near kin. Our
523 model had a relative small cost of construction. Increasing that cost should only further
524 strengthen this requirement. It is notable that the most obvious examples of habitat construction
525 are the creation of artifacts that very clearly fit this stricture: bird nests, bee hives, termite
526 mounds, and beaver dams. That is not to say that termite mounds and beaver dams do not also
527 affect the environments of other species, but most likely those diffuse effects are ancillary and
528 not the result of natural selection for them through those effects (contra Odling-Smee *et al.* 2003,
529 pp. 298-301).

530 Second, the pattern of environmental heterogeneity has to be conducive. Spatial variation in
531 the optimal amount of construction appears to be an impediment to its adaptive evolution
532 (assuming dispersal between locations), for the type of unresponsive construction explored here.
533 For a discussion of responsive versus unresponsive construction in our models, see Scheiner *et*
534 *al.* (2022). Given the ubiquity of environmental heterogeneity, these results suggest that selection
535 on habitat construction may be constrained to reflect the average conditions in a landscape,
536 rather than producing fine-tuned results. This prediction can be tested by looking for genetic
537 differentiation in the propensity for habitat construction. Additionally, the pattern of dispersal
538 needs to conform to the pattern of spatial heterogeneity. That is to say, the indirect nature of
539 selection on construction magnifies the known factors that limit adaptive evolution. More
540 simulation work that delves deeper into those limitations is warranted.

541 On the other hand, habitat construction can create a positive feedback that maintains itself.
542 Once construction exists and trait values evolve to that constructed optimum, joint selection on
543 the trait and the propensity for construction will reinforce each other. Kylafis and Loreau (2008),
544 using a scenario similar to ours, found two equilibrium points for construction, an unstable
545 boundary point and a stable interior point. In our model, populations were initialized with a
546 substantial amount of construction. These initial conditions were thus biased towards that stable
547 interior point and might explain the bimodal result found for one parameter combination (Fig. 3).
548 A positive feedback can also be created between the amount of construction and environmental
549 dynamics; for example, beaver dams can continue to accumulate naturally created woody debris.
550 Such a positive feedback, by maintaining the constructed environment, might stabilize the
551 equilibrium of the trait and construction propensity. On the other hand, if habitat construction is
552 generally favored if and only if it benefits the constructing individual or its immediate kin, then
553 construction that benefits other species beyond tight mutualisms (i.e., community-level
554 selection) will be too diffuse to be selected for. Thus, a better understanding of the evolution of
555 adaptive habitat construction awaits more detailed models combined with empirical data.

556

557 **A constitutive theory of the evolution of habitat construction**

558 A constitutive theory is a set of propositions that serve as guidelines or rules for building models
559 within a defined domain (Scheiner 2010; Scheiner & Willig 2011; Scheiner & Mindell 2019).
560 They can unify a set of seemingly contradictory models (e.g., Scheiner & Willig 2005; Leibold
561 2011), crystalize a field around a theory (Fox & Scheiner 2019; Gillespie *et al.* 2020), make
562 explicit the sometimes tacit assumptions behind a model, reveal unexplored models (Fox *et al.*
563 2011), and help the conversion of a verbal model into a quantitative one. Quantitative models of
564 habitat construction stretch back to 1996 (Laland *et al.* 1996), and there are now a variety of
565 other quantitative models (Silver & Di Paolo 2006; Kylafis & Loreau 2008; Lehmann 2008;
566 Krakauer *et al.* 2009; Chisholm *et al.* 2018; Scheiner *et al.* 2021, 2022), along with verbal
567 summaries of the conditions that should favor the evolution of habitat construction (Odling-Smee
568 *et al.* 2003; Odling-Smee *et al.* 2013). Thus, the time is ripe to formalize a constitutive theory of
569 the evolution of habitat construction.

570 We present the domain and propositions for that theory in Table 2. The domain of this theory
571 is environmental conditioning that increases the inclusive fitness of an individual. That

572 conditioning can consist of changes in the state of the environment (e.g., soil processing by
573 earthworms), resource levels, or the creation of artifacts (e.g., nests, sensu Odling-Smee *et al.*
574 2013). That conditioning must be, at least in part, of the abiotic environment. If the effects of the
575 target species are just on other living organisms, that is more properly the domain of theories of
576 co-evolution. Domains are defined by the nature of the models that they encompass. Models in
577 which the environmental component is strictly abiotic, and therefore cannot also evolve, will be
578 different than those in which other components can evolve. Clearly, though, there is potential
579 overlap in domains if the environment contains both abiotic and biotic components; it is not
580 necessary that theory domains be non-exclusive and some models can fall into more than one
581 domain.

582 All habitat construction models that we are familiar with meet the first four propositions
583 (Table 2). The first two propositions separate instances of adaptive habitat construction from
584 environmental conditioning that is simply a by-product of other adaptations. The third and fourth
585 propositions are statements about components of the model; the latter suggests that this theory
586 could be considered a subdomain of the constitutive theory of evolution by natural selection
587 (Frank & Fox 2019). The last four propositions describe conditions that might favor or disfavor
588 the evolution of adaptive construction, and not all may be relevant to all models. The seventh
589 proposition is not relevant to our model. The eighth proposition is not relevant to the version of
590 our model explored here, although it is relevant to other versions (Scheiner *et al.* 2021, 2022). As
591 with any theory, its components are subject to amendment. We present this constitutive theory in
592 that spirit.
593

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674

675 **Table 1.** Variables and parameters for the model simulations

Symbol	Meaning	Value
A) For all simulations		
T	Phenotype of an individual	
G	Trait 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 a generation	
δ	The rate of decay of the environment to the baseline	50%
ΔH	The total construction in a deme in a generation	
S	Environment in each deme at the time of selection	
T_{opt}	Optimum phenotype in a deme	
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 construction loci	5
ω	Strength of selection	4
γ	Cost of construction	0.002
	Per-generation per-locus mutation rate	0.1
	Variance of mutation effect	0.01
B) For unstructured environment simulations		
ϕ	Average fitness decrease in the baseline environment	50%
	Dispersal rate	4%-100%
	Number of demes	256, 128, 64, 32, 16
N	Number of individuals per deme after reproduction	2, 4, 8, 16, 32

τ	Amount of temporal variation scaled as a percent of the difference between the baseline and the optimum	0%-27.5%
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C) For structured environment simulations

ϕ	Average fitness decrease in the baseline environment	50% or 10%-90%
	Dispersal rate	4%-100% or 41%
	Number of demes	50
N	Number of individuals per deme after reproduction	8

676

677

678 Table 2. A constitutive theory of the evolution of habitat construction
679

680 Domain: Evolutionary change in the propensity of an individual to directly or indirectly alter its
681 abiotic environment so as to increase its inclusive fitness.

682

683 Propositions:

684 1. The state of the environment that would result in the maximal fitness of an
685 individual, group of individuals, or lineage differs from the current state.

686 2. Individuals are able to alter their environment so as to increase the fitness of
687 themselves or other individuals.

688 3. The effects of construction on the environment are self-limiting, either due to
689 feedbacks on the construction process or an upper limit to that construction,
690 and/or are subject to decay.

691 4. The propensity for construction meets the conditions required for evolution by
692 natural selection.

693 5. Construction is favored when its benefits are directed at the constructing
694 individual or its near kin.

695 6. Non-optimal construction may result from costs of construction.

696 7. Non-optimal construction may result from trade-offs between the ability to
697 perform construction and the trait(s) directly affected by the environment.

698 8. Non-optimal construction may result from interactions with other processes that
699 alter the fit of an individual to its environment.

700

701

702 **Figure captions**

703 Figure 1. (A) Both the baseline (θ) and optimal (θ^*) environments vary along a gradient (parallel
 704 optimum). (B) The baseline varies, but there is a single optimum for all demes (single
 705 optimum). (C) The fitness function in a given deme when the environment equals the
 706 optimum, and the decrease in fitness (ϕ) when the environment equals the baseline (for the
 707 single optimum case, this is the decrease for the middle of the gradient, which is also the
 708 average decrease across all demes), if the optimum phenotype is 0; shown is a value of $\phi =$
 709 50%. Trait values are in the same units as the environment.

710 Figure 2. The two life history patterns that were modeled. (A) Birth, construction, dispersal,
 711 selection, reproduction, and death (“move first”). (B) Birth, construction, selection, dispersal,
 712 reproduction, and death (“select first”). Insert: The amount of construction by an individual
 713 as a function of its construction propensity (sum of the construction alleles).

714 Figure 3. For the unstructured, uniform environment, the effect of the decay rate (δ) on (A, B)
 715 the normalized construction environmental mean (mean $E_{it}/10$), (C, D) the mean construction
 716 propensity of individuals (mean A_{ijt}), and (E, F) final mean fitness (W_{ijt}) for the (A, C, E)
 717 “move first” and (B, D, F) “select first” life history patterns, for different population sizes.
 718 Dispersal was the island pattern; the dispersal rate was 44%; the total number of individuals
 719 in the metapopulation was 512 for all population sizes. Shown are means and standard errors
 720 of 20 replicates; when error bars are absent they are smaller than the symbol. If values are
 721 missing, those parameter combinations resulted in extinction of the metapopulation in all of
 722 60 replications.

723 Figure 4. For the unstructured, uniform environment, the effect of the dispersal rate on (A, B) the
 724 normalized construction environmental mean (mean $E_{it}/10$), (C, D) the mean construction
 725 propensity of individuals (mean A_{ijt}), and (E, F) final mean fitness (W_{ijt}) for the (A, C, E)
 726 “move first” and (B, D, F) “select first” life history patterns, for different population sizes.
 727 Dispersal was the island pattern; the decay rate (δ) was 50%; the total number of individuals
 728 in the metapopulation was 512 for all population sizes. Shown are means and standard errors
 729 of 20 replicates; when error bars are absent they are smaller than the symbol. If values are
 730 missing, those parameter combinations resulted in extinction of the metapopulation in all of
 731 60 replications.

732 Figure 5. For the unstructured, uniform environment, the effect of different amounts of temporal
 733 variation on (A) the normalized construction environmental mean (mean $E_{it}/10$) and (B) the
 734 mean construction propensity of individuals (mean A_{ijt}). The variation could occur in the
 735 environment of selection (S_{it} , circles) or in the optimum environment (θ_i^* , squares), and either
 736 vary independently (solid) or be correlate (open) among the demes. The standard deviation of
 737 temporal variation (τ) was scaled as a percentage of the difference between the baseline (θ_i)
 738 and optimum environments (θ_i^*). The life history pattern was “select first”; dispersal was the
 739 island pattern with a rate of 4%. The population size (N) was 8, the number of demes was 64,
 740 and the decay rate (δ) was 50%. Shown are means and standard errors of 20 replicates; when
 741 error bars are absent they are smaller than the symbol.

742 Figure 6. For the structured gradient environment, the effect of the dispersal rate (A, C) and the
 743 fitness decrease (ϕ) (B, D) on (A, B) the normalized construction environmental mean (mean
 744 $E_{it}/10$), and (C, D) the mean construction propensity of individuals (mean A_{ijt}) for the both
 745 patterns of environmental heterogeneity and life history orderings. The population size (N)
 746 was 8 and the decay rate (δ) was 50%. For (A, C) the fitness decrease (ϕ) was 50%; for (B,
 747 D) the dispersal rate was 41%. Dispersal was the stepping-stone pattern. Shown are means
 748 and standard errors of 20 replicates; when error bars are absent they are smaller than the
 749 symbol.

750 Figure 7. For the structured gradient environment, the effect of the dispersal rate (A, C) and the
 751 fitness decrease (ϕ) (B, D) on (A, B) the normalized slope of the constructed environment
 752 (slope $E_{it}/0.4$), and (C, D) the normalized construction propensity slope (slope $A_{ijt}/0.4$) for the
 753 both patterns of environmental heterogeneity and life history orderings. The population size
 754 (N) was 8 and the decay rate (δ) was 50%. For (A, C) the fitness decrease (ϕ) was 50%; for
 755 (B, D) the dispersal rate was 41%. Dispersal was the stepping-stone pattern. Shown are
 756 means and standard errors of 20 replicates; when error bars are absent they are smaller than
 757 the symbol.

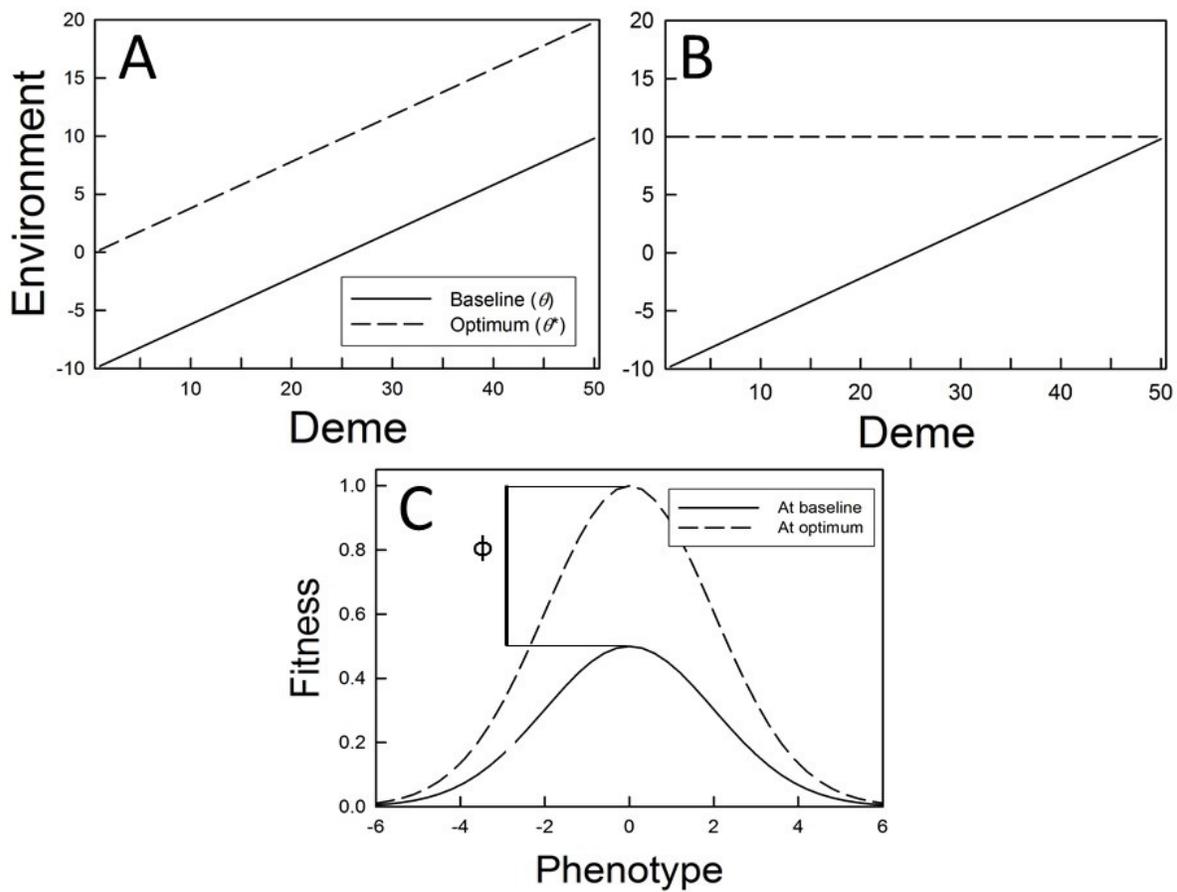
758 Figure 8. For the structured gradient environment, the effect of (A) the dispersal rate and (B) the
 759 fitness decrease (ϕ) on final mean fitness (W_{ijt}) for the both patterns of environmental
 760 heterogeneity and life history orderings. For (A) the fitness decrease (ϕ) was 50%, and for
 761 (B) the dispersal rate was 41%. Dispersal was the stepping-stone pattern. Shown are means

762 and standard errors of 20 replicates; when error bars are absent they are smaller than the
763 symbol.

764 Figure 9. For the structured gradient environment with island-type dispersal, the effect of the
765 dispersal rate on (A) the normalized construction environmental mean (mean $E_{it}/10$) (B) and
766 the normalized relative slope of the constructed environment (slope $E_{it}/0.4$), (C) the mean
767 construction propensity of individuals (mean A_{ijt}) and, (D) the normalized construction
768 propensity slope (slope $A_{ijt}/0.4$) (C, D) for the both patterns of environmental heterogeneity
769 and life history orderings. The fitness decrease (φ) was 50%. Shown are means and standard
770 errors of 20 replicates; when error bars are absent they are smaller than the symbol.

771 Figure 10. For the structured gradient environment with island-type dispersal, the effect of the
772 dispersal rate on final mean fitness (W_{ijt}) for the both patterns of environmental heterogeneity
773 and life history orderings. The fitness decrease (φ) was 50%. Shown are means and standard
774 errors of 20 replicates; when error bars are absent they are smaller than the symbol.

775

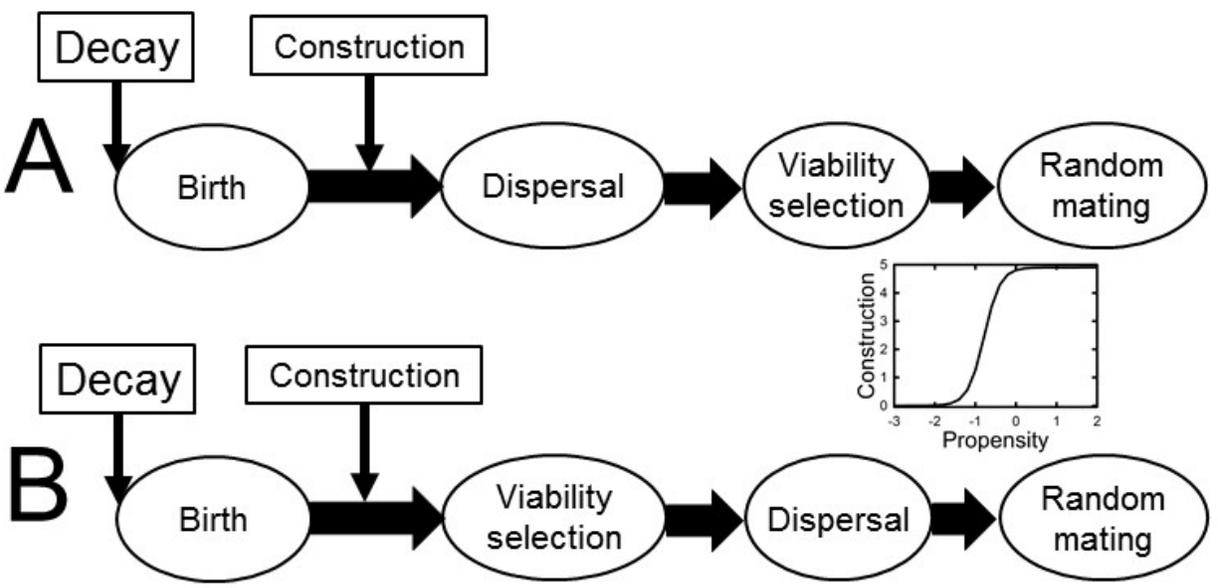


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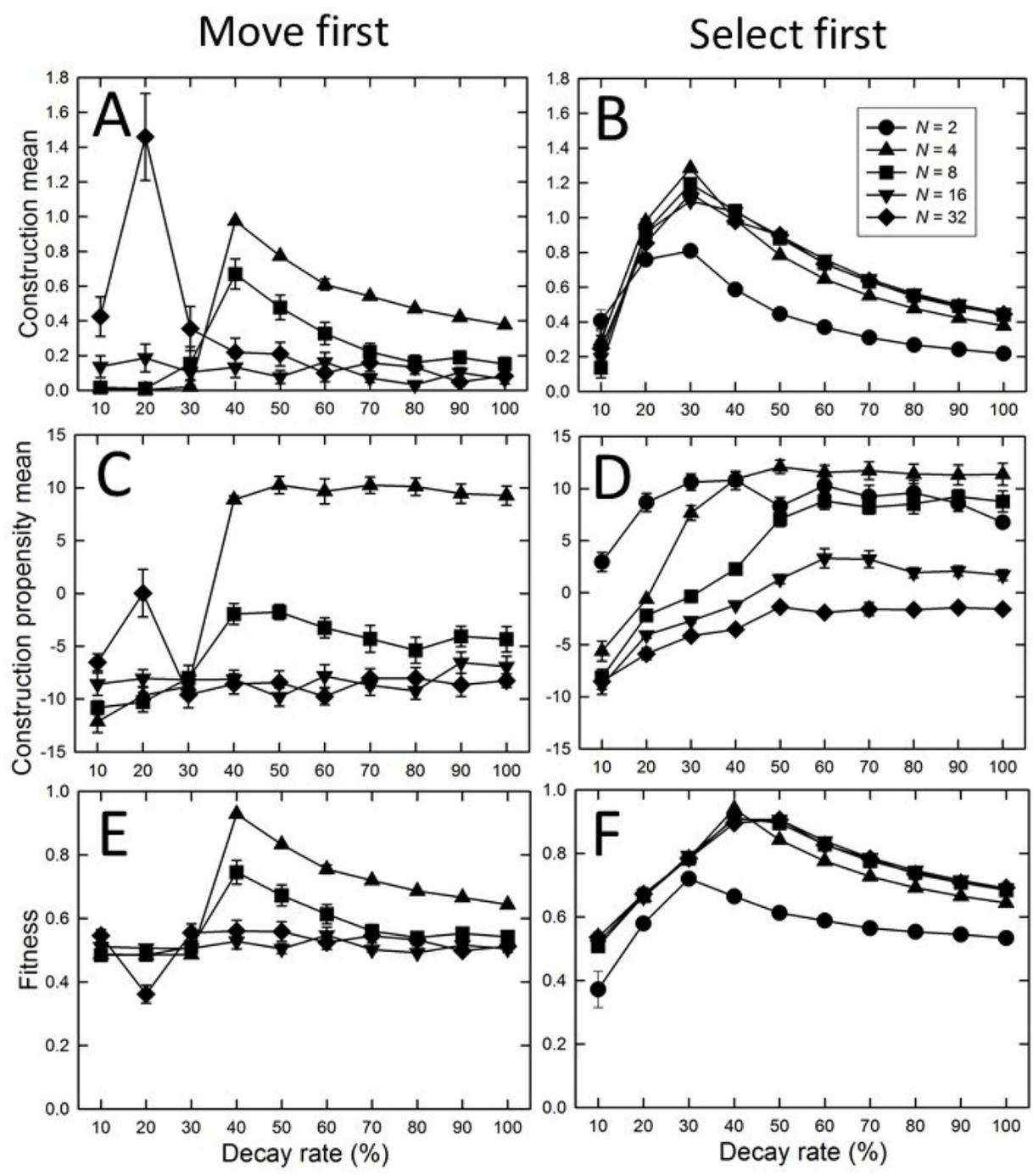
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Figure 1



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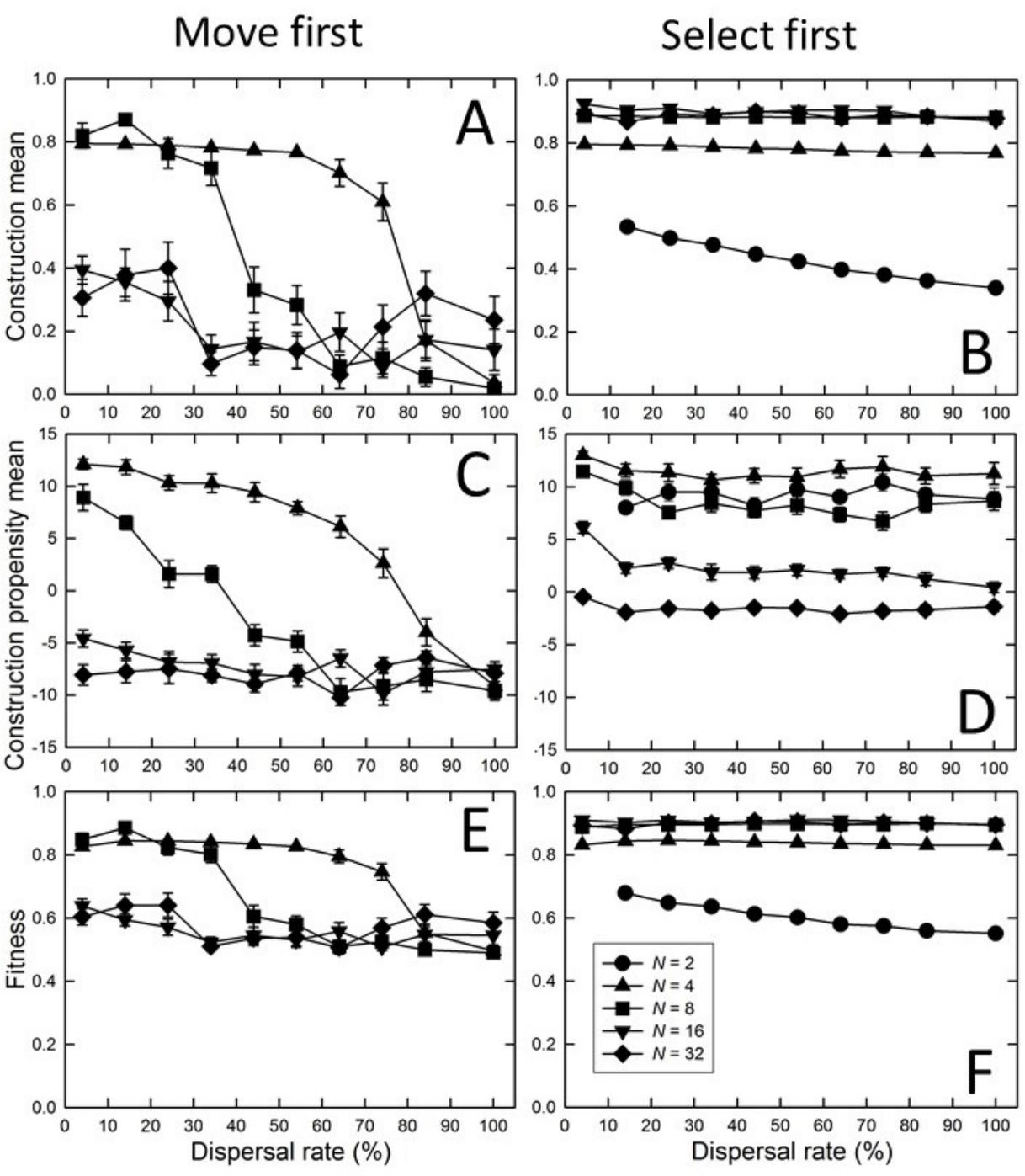
Figure 2



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Figure 3

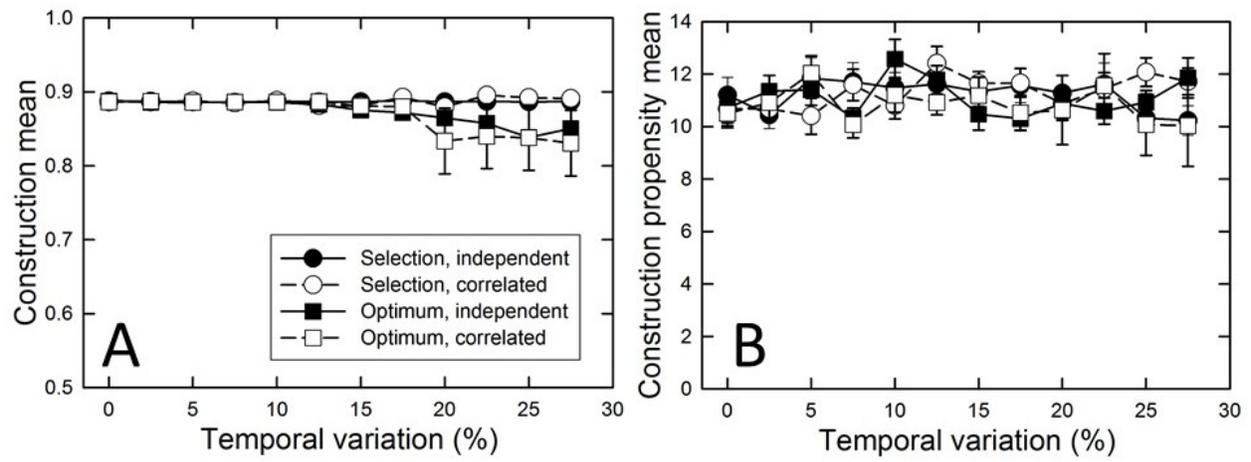


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Figure 4

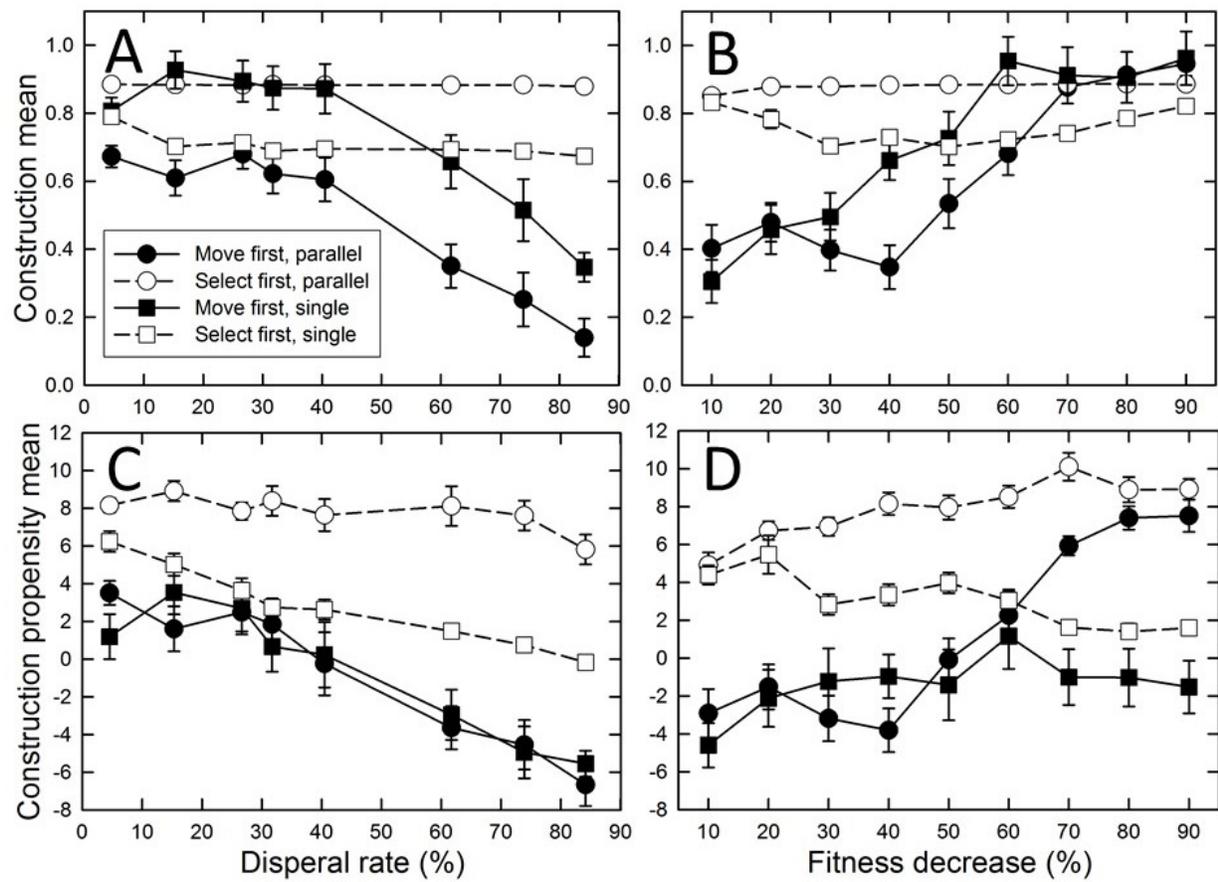
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Figure 5

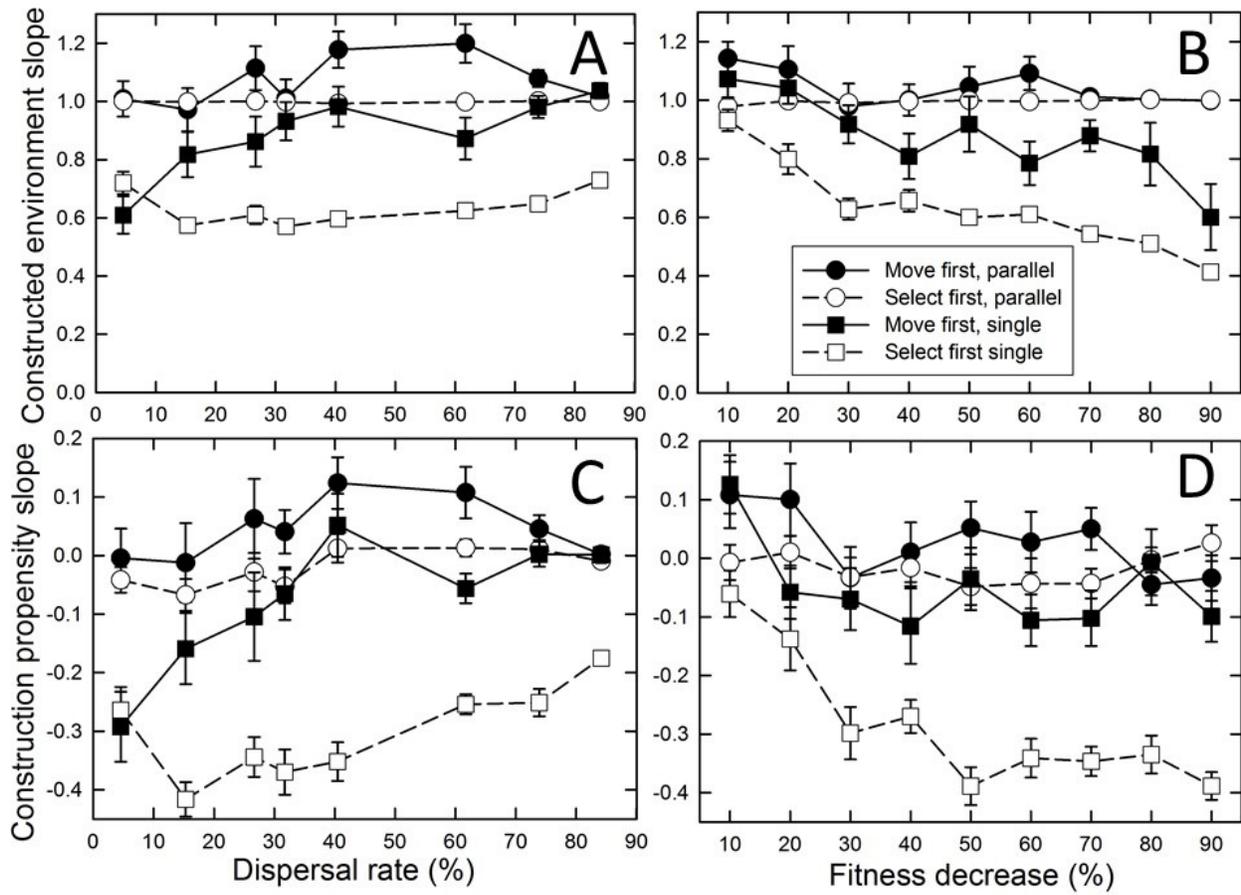


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Figure 6

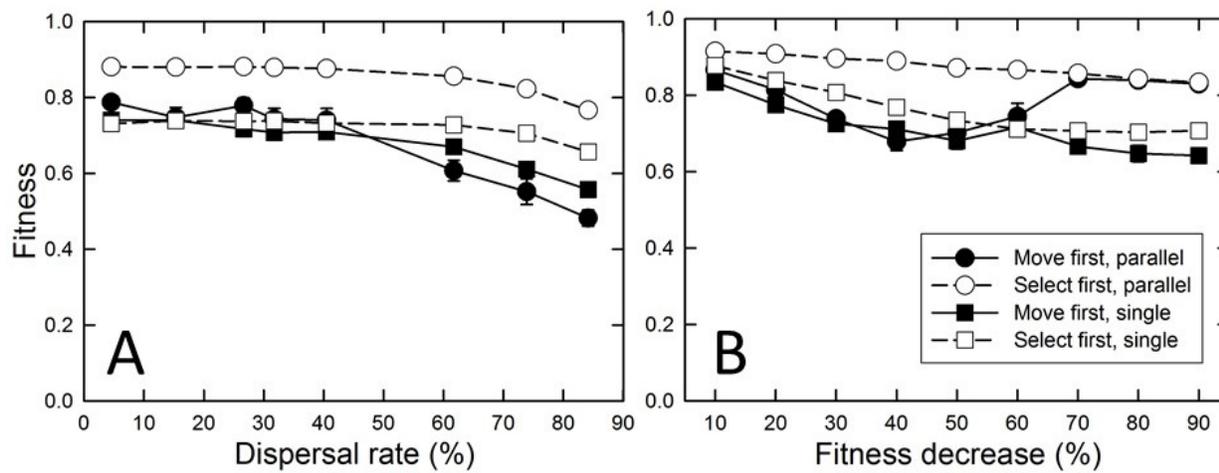


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Figure 7

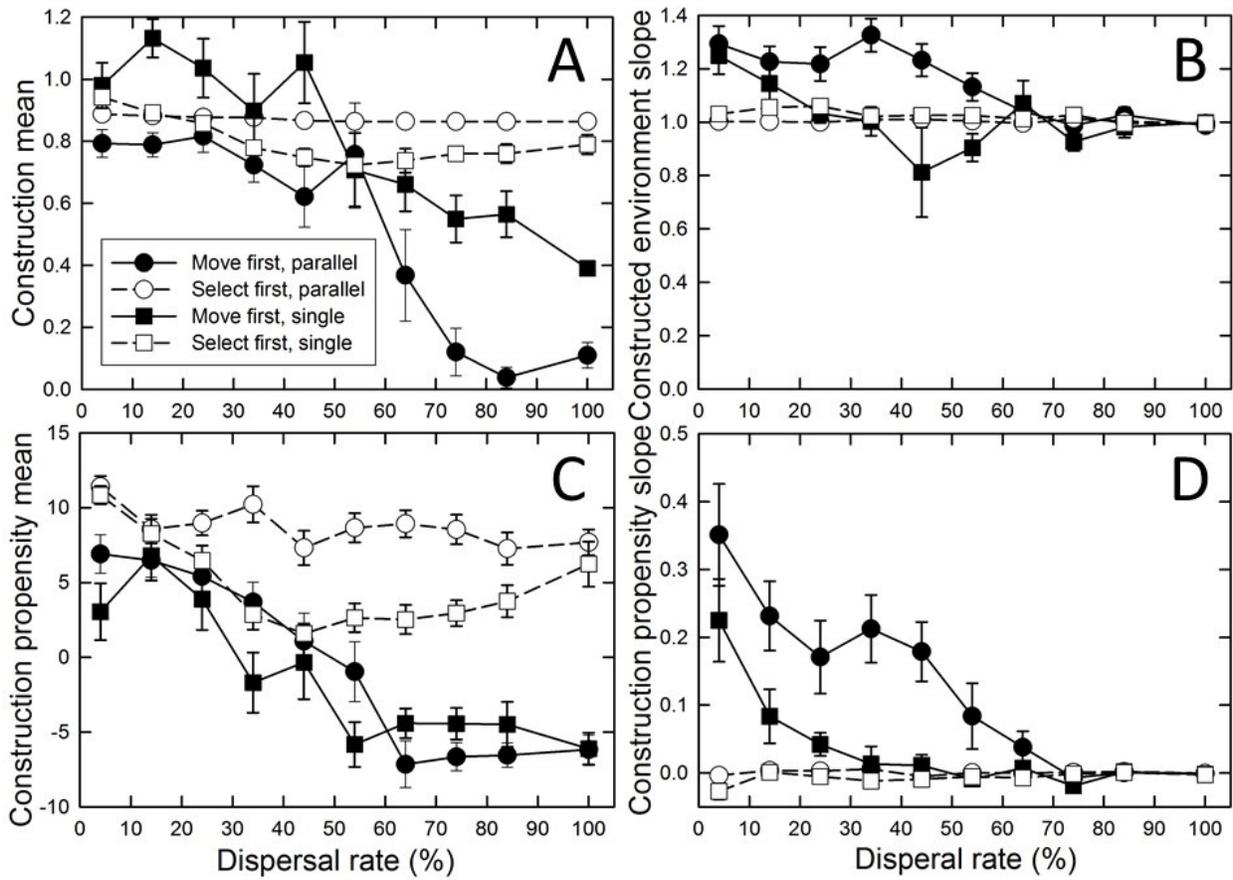


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Figure 8

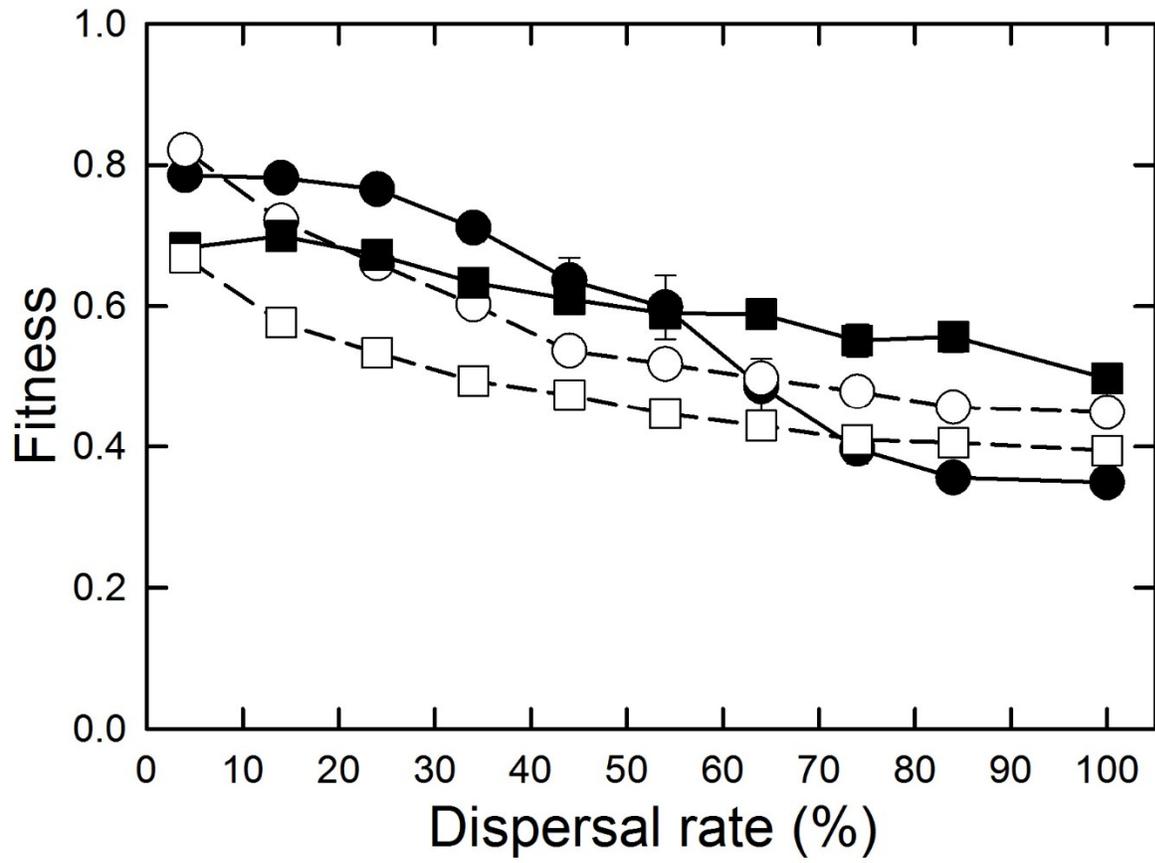


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Figure 9



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Figure 10