

1 A Combination of Positive and Negative Niche 2 Construction Favors the Evolution of 3 Cooperation

4
5 **Abstract**

6 TODO

7 **Introduction**

8 Cooperative behaviors are common across all branches of the tree of life. In-
9 sects divide labor within their colonies, plants and soil bacteria exchange es-
10 sential nutrients, birds care for others' young, and the trillions of cells in the
11 human body restrain their growth and coordinate to provide vital functions.
12 Each instance of cooperation presents an evolutionary challenge: How can in-
13 dividuals that sacrifice their own well-being to help others avoid subversion by
14 those that do not? Over time, we would expect these *defectors* to rise in abun-
15 dance at the expense of others, eventually driving cooperators—and perhaps
16 the entire population—to extinction.

17 Several factors can prevent this *tragedy of the commons* (Hamilton, 1964;
 18 Hardin, 1968; Nowak, 2006; West *et al.*, 2007b). One important factor in-
 19 volves non-random social interaction, in which cooperators benefit more from
 20 the cooperative act than defectors. This can occur when cooperators are clus-
 21 tered together in spatially-structured populations (Fletcher and Doebeli, 2009;
 22 Nadell *et al.*, 2010; Kuzdzal-Fick *et al.*, 2011) or when cooperators use com-
 23 munication (Brown and Johnstone, 2001; Darch *et al.*, 2012) or other cues
 24 (Sinervo *et al.*, 2006; Gardner and West, 2010; Veelders *et al.*, 2010) to coop-
 25 erate conditionally with kin. Cooperation can also be bolstered by pleiotropic
 26 connections to personal benefits (Foster *et al.*, 2004; Dandekar *et al.*, 2012) or
 27 alleles encoding self-benefitting traits (Asfahl *et al.*, 2015). In the latter case,
 28 the alleles may provide (private) benefits that are completely independent from
 29 the (public) benefits of cooperation. In a population of both cooperators and
 30 defectors, this sets the stage for an “adaptive race” in which both types vie
 31 for the first highly beneficial adaptation (Waite and Shou, 2012; Morgan *et*
 32 *al.*, 2012). The tragedy of the commons can be deferred if a cooperator, by
 33 chance, wins the adaptive race.

34 Hammarlund et al. (2015) recently showed that in spatially structured popu-
 35 lations, cooperators can gain a substantial leg up on defectors in an adaptive
 36 race. Specifically, cooperation increases local population density, thus increas-
 37 ing the likelihood of acquiring beneficial mutations. By hitchhiking along with
 38 these adaptations, the cooperative trait can rapidly rise in abundance. Never-
 39 theless, this advantage is fleeting. As soon as the opportunities for adaptation
 40 are exhausted, cooperators are once again at a disadvantage against adapted

41 defectors. However, Hammarlund et al. (2015) demonstrated that cooperation
42 can be maintained indefinitely when frequent environmental changes produce
43 a steady stream of adaptive opportunities. Although organisms typically find
44 themselves in dynamic environments, change might not occur at a rate that
45 provides sufficient adaptive opportunities to ensure long-term cooperator per-
46 sistence.

47 In this work, we explore whether cooperation can be maintained indefinitely
48 by niche construction. We expand upon the model presented in Hammarlund
49 et al. (2015) to allow populations to alter their local environment. As environ-
50 ments change, so too does selection, which creates an eco-evolutionary feedback
51 whereby selection is dependent on the genotypes present in the population, and
52 the composition of genotypes is dependent on selection. Niche construction
53 can be positive or negative, depending on whether the environmental change
54 increases or decreases the fitness of the niche-constructing individual. We in-
55 vestigate whether these selective feedbacks can act as a continual source of
56 adaptive opportunities for cooperators.

57 Although niche construction occurs independently of cooperation in our model,
58 the increase in density that results from cooperation has a profound effect on
59 how populations evolve in the presence of selective feedbacks. First, these pop-
60 ulations exert greater influence on their environments, which better enables
61 them to benefit from positive niche construction. Additionally, as environ-
62 ments change, either through negative niche construction or external influ-
63 ences, these larger populations can adapt more quickly. Finally, because large
64 populations produce more emigrants, these populations will exert a stronger in-

fluence on neighboring populations, effectively exporting their niche. Because of these potential benefits, we also focus our attention on how population size and migration rate influence evolutionary outcomes in these environments.

Methods

We build upon the model described in Hammarlund et al. (2015), in which cooperators and defectors compete and evolve in a metapopulation (a collection of populations). Individuals in each of the populations reproduce, mutate, and migrate to neighboring populations. Importantly, adaptation can occur. In our model here, we further allow populations to modify their local environment, and these modifications feed back to affect selection.

Model Description

Our simulated environment consists of N^2 patches arranged as an $N \times N$ lattice (see Table 1 for model parameters and their values), where each patch can support a population.

Individuals and Genotypes

Each individual in a population has a genotype, which is an ordered list of $L + 1$ integers (loci). A binary allele at the last locus ($L + 1$) determines whether that individual is a cooperator (1) or a defector (0). Cooperators incur a fitness cost c . The first L loci are *adaptive loci*, and are each occupied

by 0 or an integer from the set $\{1, 2, \dots, A\}$, where A is the number of alleles conferring a selective benefit. Specifically, the presence of any non-zero allele at any of these loci represents an adaptation that confers a fitness benefit δ . We choose $\delta > c$, which allows a minimally adapted cooperator to recoup the cost of cooperation. The fitness benefits of these adaptations are purely endogenous, and are not affected by other individuals or the environment.

Niche Construction

Populations also influence their environment, which feeds back to affect selection. This process adds a second, exogenous component to each individual's fitness. Here, the “niche” is defined implicitly by the allelic states present in the population. As allelic states change, a population constructs its unique niche. We use a form of density dependent selection to increasingly favors individuals that match their niche.

Specifically, the selective value of adaptive allele a at locus l increases with the number of individuals in the population that have allele $a + 1$ at locus $l + 1$. We treat both adaptive loci and allelic states as “circular”, so the allelic state at locus L is affected by the allelic composition of the population at locus 1, and the selective value of allele A at any locus increases with the number of individuals carrying allele 1 at the next locus. For the remainder of this section, this circularity is represented by the function below, which gives the integer that follows an arbitrary value x in the set $\{1, 2, \dots, X\}$.

$$\beta(x, X) = \text{mod}_X(x) + 1 \quad (1)$$

Here, $\text{mod}_Y(y)$ is the integer remainder when dividing y by Y . Thus, the selective value of adaptive allele a at locus l increases with the number of individuals that have allele $\beta(a, A)$ at locus $\beta(l, L)$. The slope of this increase is ϵ , which specifies the intensity of niche construction. Consider a genotype g with allelic state at locus l given by $a_{g,l}$; its fitness is defined as:

$$W_g = z + \delta \sum_{l=1}^L I(a_{g,l}) + \epsilon \sum_{l=1}^L n(\beta(a_{g,l}, A), \beta(l, L)) - ca_{g,L+1} \quad (2)$$

where z is a baseline fitness, and $I(a)$ indicates whether a given adaptive allele is non-zero:

$$I(a) = \begin{cases} 1 & \text{if } a \in \{1, 2, \dots, A\} \\ 0 & \text{otherwise} \end{cases} \quad (3)$$

As a consequence of this form of density dependent selection, genotypes with sequentially increasing allelic states will tend to evolve. Because mutations are random (see below), each population will evolve different consecutive sequences. These different sequences represent the unique niches constructed by populations.

117 **Population Growth and the Benefit of Cooperation**

118 Cooperation allows the population to reach greater density. If p is the propor-
119 tion of cooperators in a population at the beginning of a growth cycle, then
120 that population reaches the following size:

$$S(p) = S_{min} + p(S_{max} - S_{min}) \quad (4)$$

121 The function $S(p)$ reflects the benefit of cooperation. During growth, individ-
122 uals compete for inclusion in the resulting population. The composition of a
123 population with size P and cooperator proportion p after growth is multino-
124 mial with parameters $S(p)$ and $\{\pi_1, \pi_2, \dots, \pi_P\}$, where:

$$\pi_i = \frac{W_{\gamma(i)}}{\sum_{j=1}^P W_{\gamma(j)}} \quad (5)$$

125 Here, $W_{\gamma(i)}$ is the fitness of an individual i with genotype $\gamma(i)$ (see Equation
126 2). The value π_i therefore reflects an individual's reproductive fitness relative
127 to others' in the population.

128 **Mutation**

129 For simplicity, we apply mutations after population growth. Mutations occur
130 independently at each locus and cause an allelic state change. At each adaptive
131 locus, mutations occur at rate μ_a . These mutations replace the current allele
132 with a random selection from the set $\{0\} \cup \{1, 2, \dots, A\}$. Note that this allows

133 for the possibility of an allele replacing itself, thus slightly reducing the effective
134 mutation rate. At the binary cooperation locus, mutations occur at rate μ_c .
135 These mutations flip the allelic state, causing cooperators to become defectors
136 and vice versa.

137 **Migration**

138 After mutation, individuals emigrate to an adjacent patch at rate m . The
139 destination patch is randomly chosen with uniform probability from the source
140 patch's Moore neighborhood, which is composed of the nearest 8 patches on the
141 lattice. Because the metapopulation lattice has boundaries, patches located
142 on an edge have smaller neighborhoods.

143 **Metapopulation Initialization and Simulation**

144 Metapopulations are initiated in a state that follows an environmental change.
145 First, populations are seeded at all patches with cooperator proportion p_0 and
146 grown to density $S(p_0)$. An environmental challenge is then introduced, which
147 subjects the population to a bottleneck. For each individual, the probability
148 of survival is μ_t , which represents the likelihood that a mutation occurs that
149 confers tolerance. Survivors are chosen by binomial sampling. Because indi-
150 viduals have not yet adapted to this new environment, the allelic state of each
151 individual's genotype is set to 0 at each adaptive locus. Following initializa-
152 tion, simulations are run for T cycles, where each discrete cycle consists of
153 population growth, mutation, and migration. At the end of each cycle, popu-

154 lations are thinned to allow for growth in the next cycle. The individuals that
155 remain are chosen by binomial sampling, where each individual persists with
156 probability d , regardless of allelic state.

157 **Source Code and Software Environment**

158 The simulation software and configurations for the experiments reported are
159 available online. Simulations used Python 3.4, NumPy 1.9.1, Pandas 0.15.2
160 (McKinney, 2010), and NetworkX 1.9.1 (Hagberg *et al.*, 2008). Data analyses
161 were performed with R 3.1.3 (R Core Team, 2015). Confidence intervals were
162 estimated by bootstrapping with 1000 resamples.

163 **Results**

164 We follow the evolution of cooperation in a metapopulation consisting of pop-
165 ulations connected by spatially-limited migration. Individuals in these popu-
166 lations can gain a limited number of adaptations that confer selective benefits.
167 While the allele at an individual’s cooperation locus does not directly affect
168 the value of alleles at adaptive loci, cooperation can have indirect effects on the
169 process of adaptation. Specifically, because cooperation increases population
170 density, isolated cooperators experience more mutational opportunities to gain
171 adaptations. Cooperation can hitchhike along with these adaptations, which
172 compensate for the cost of cooperation. Additionally, populations alter their
173 environment. Here, we explore how niche construction can favor the evolution

174 of cooperation. Our simulation environment is defined by the parameter val-
 175 ues listed in [Table 1](#). Unless otherwise noted, 10 replicate simulations were
 176 performed for each experiment. We quantify cooperator success using the area
 177 under the cooperator proportion curve. This measure of cooperator presence
 178 increases as cooperators rise in abundance or remain in the population longer.

179 **Niche Construction Maintains Cooperation**

180 Without any opportunity for adaptation ($L = 0$), cooperators are swiftly elim-
 181 inated in competition with defectors (Figure 1A). Despite an initial lift due
 182 to increased productivity, the cost of cooperation becomes disadvantageous as
 183 migration mixes the initially isolated populations. When there are opportu-
 184 nities for adaptation ($L = 5$) but no niche construction ($\epsilon = 0$), cooperators are
 185 maintained transiently (Figure 1B). Here, the additional mutational oppor-
 186 tunities provided by their larger sizes allows cooperator populations to more
 187 quickly adapt to their environment. As previously described by Hammarlund
 188 et al. (2015), however, cooperation is subsequently lost as *adapted* defector
 189 populations arise via mutation. When niche construction is incorporated,
 190 cooperation persists (Figure 1C).

191 **Fitness Increases Alone do not Support Persisting Coop-** 192 **eration**

193 In our model, niche construction introduces additional selective benefits. To
 194 determine how these selective effects influence evolutionary outcomes, we per-

195 formed simulations in which the selective effects of niche construction were
 196 removed ($\epsilon = 0$), and we instead increased the fitness benefits conferred by
 197 adaptation ($\delta = 0.6$). Here, we are conservative by lifting the selective value of
 198 exogenous adaptation by the maximum value possible from niche construction.

199 We find that higher selective values do not provide a significant increase in
 200 cooperator presence (Figure 2B). As shown in Figure 3, cooperators gain adap-
 201 tations more quickly than defectors, which provides a fitness advantage. How-
 202 ever, the cost of cooperation puts defectors at an advantage once these popu-
 203 lations become fully adapted.

204 **Negative Niche Construction is Critical to Cooperator** 205 **Persistence**

206 Negative niche construction occurs in our model due to selection for
 207 sequentially-increasing allelic states and the circular arrangement of these
 208 alleles. When the genome length (L) is not evenly divided by the number
 209 of adaptive alleles (A), then it is not possible for the population to be fixed
 210 for a genotype that is perfectly adapted to the constructed environment.
 211 Technically (in terms of the model) this is because the equality:

$$\beta(a_{g,l}, A) = a_{g,\beta(l,L)}$$

212 cannot simultaneously hold for all l .

213 For example, consider genotype $(1, 2)$ when $L = 2$ and $A = 3$. Here, allelic

state 2 at locus 2 will be beneficial, because it follows allelic state 1 at locus 1. However, due to the circular effects, allelic state 1 at locus 1 will be deleterious relative to allelic state 3 at locus 1. Yet, fixation for genotype (3, 2) does not solve the problem, because a mutant (3, 1) is fitter, and so on.

We first focus on the effects of positive niche construction by removing the allelic conflict that leads to negative niche construction ($L = 5$, $A = 5$). In the absence of this conflict, cooperator presence is significantly increased (Figure 2C). Within these environments, we find that positive niche construction prolongs the fitness advantage that cooperators have over defectors (Figure 3C).

Positive niche construction is important to cooperator persistence

To determine how negative niche construction influences the evolution of co-operation, we maximize the allelic conflict ($L = 1$, $A = 6$). Here, selection for increasing allelic states among the adaptive loci means that any allelic state will not be greater than at the previous allele (itself), and thus there will always be opportunity for adaptation. Despite this constant opportunity, niche construction does not increase cooperator presence (Figure 2D).

NC Enables Cooperator Spread

Figure 4 - if not, could be why thinning is a must.

234 NC Prevents Defector Invasion

235 Figure 5

236 How Cooperation Fuels all of this

237 To directly explore how the increase in population size affects evolutionary
238 outcomes, we vary the maximum size that a population can reach (S_{max} , see
239 Equation 4). Figure 6A shows the result of these simulations. (TODO de-
240 scription of results)

241 To address how migration affects the evolutionary process in this system, we
242 vary the rate at which migration occurs (m). As seen in Figure 6B, cooperation
243 decreases as migration rate increases. This is likely because migration defines
244 the spatial structuring in this system. As migration increases, the population
245 becomes more like a well-mixed system, where defectors are better able to
246 exploit the benefits of cooperation (Griffin *et al.*, 2004; Kümmerli *et al.*, 2009).

247 # Discussion

248 Despite their negative effects, deleterious traits can rise in abundance due to
249 genetic linkage with other traits that are strongly favored by selection (May-
250 nard Smith and Haigh, 1974). In a process termed the “Hankshaw effect”,
251 Hammarlund *et al.* (2015) recently demonstrated that cooperative behaviors
252 can prolong their existence by actively increasing their likelihood of hitchhik-
253 ing with a beneficial trait. While this process does favor cooperation in the
254 short term, it eventually reaches a dead end. When the opportunities for
255 adaptation are exhausted, and cooperators can no longer hitchhike, they face

extinction. In this work, we have considered whether niche construction can maintain cooperation indefinitely.

We demonstrate that when niche construction occurs, cooperation can indeed persist (Figure 1C). But what aspects of niche construction produce this result? In our model, niche construction introduces additional selective effects that could influence the evolutionary process. However, simply raising the selective benefits provided by adaptations does not significantly increase cooperator presence (Figure 2B), and indicates that niche construction plays an important role. Although cooperators benefit greatly from positive niche construction, it does not fully explain our results (Figure 2C). Indeed, despite an initial increase in abundance, cooperators are eventually driven to extinction when environmental change produces only positive fitness effects. As with the Hankshaw effect, adaption eventually slows, allowing defectors to outcompete cooperators (Figure 3C). While it does not benefit cooperation when alone (Figure 3E), negative niche construction acts to prevent this stasis. Combined, we find that both positive and negative niche construction are required to maintain cooperation.

When successful, we observe that populations do not reach the maximum possible fitness (Figure 3A). Although cooperation is the focus of this study, it can be seen as deleterious. Previous work has shown that niche construction can favor deleterious alleles (Laland *et al.*, 1996, 1999). Similarly here, cooperation is maintained in the presence of niche construction, but lost otherwise. Van Dyken and Wade (2012) showed that when two cooperative behaviors co-evolve and niche construction feedbacks benefit the other type, niche con-

struction can increasingly favor these traits, which were otherwise disfavored when alone.

By their very nature, public goods benefit populations by making their environment more hospitable (West *et al.*, 2007a). For example, bacteria produce a host of extracellular products that find soluble iron (Griffin *et al.*, 2004), digest large proteins (Diggle *et al.*, 2007; Darch *et al.*, 2012), and reduce the risk of predation (Cosson *et al.*, 2002). While many studies have explored how the environment affects the evolution of cooperative behaviors such as these, relatively few have examined how those behaviors affect the environment and how the resulting feedbacks influence evolutionary trajectories.

In our model, the environmental state was implicitly modeled, and depended solely on the current state of the population. In natural settings, however, the timescales at which environments are modified and reproduction are likely to be decoupled. For example, a multitude of factors including protein durability (Brown and Taddei, 2007; Kümmerli and Brown, 2010), diffusion (Allison, 2005; Driscoll and Pepper, 2010), and resource availability (Zhang and Rainey, 2013; Ghoul *et al.*, 2014) influence both the rate and the degree to which public goods alter the environment. These factors are likely to influence evolutionary trajectories (Laland *et al.*, 1996). Lehmann (2007) demonstrated that a cooperative, niche constructing behavior can be favored when it only affected selection for future generations, thus reducing the potential for competition among contemporary kin. The evolutionary inertia that this creates, however, may ultimately work against cooperators. When public good accumulates in the environment, cooperators must reduce their investment in production to re-

304 main competitive (Kümmerli and Brown, 2010; Dumas and Kümmerli, 2012).
305 Cooperation that occurs facultatively, perhaps by sensing the abiotic (Bernier
306 *et al.*, 2011; Koestler and Waters, 2014) or biotic environment (Brown and
307 Johnstone, 2001; Darch *et al.*, 2012), are likely to be favored in these environ-
308 ments.

309 In many instances of cooperation, the environment is itself a biological entity,
310 which can produce additional evolutionary feedbacks. As the host population
311 changes, so too will selection on their symbiont populations. Here, evolution-
312 ary outcomes depend greatly on the degree of shared interest between the host
313 and symbiont. For example, the cooperative production of virulence factors by
314 the human pathogen *P. aeruginosa* in lung infections is harmful to those with
315 cystic fibrosis (Harrison, 2007). Conversely, cooperative light production by *A.*
316 *fischeri* is vital for the survival of its host, the Hawaiian bobtail squid (Ruby,
317 1996). It was recently argued that incorporating the effects of niche construc-
318 tion is critical for improving our understanding of viral evolution (Hamblin *et*
319 *al.*, 2014) and evolution in co-infecting parasites (Hafer and Milinski, 2015).
320 Incorporating host dynamics, co-evolution, and the feedbacks that they pro-
321 duce into models is likely to be equally important for gaining an understanding
322 of how cooperative behaviors evolve in these host-symbiont settings.

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330 Figures

331 **Figure 1**

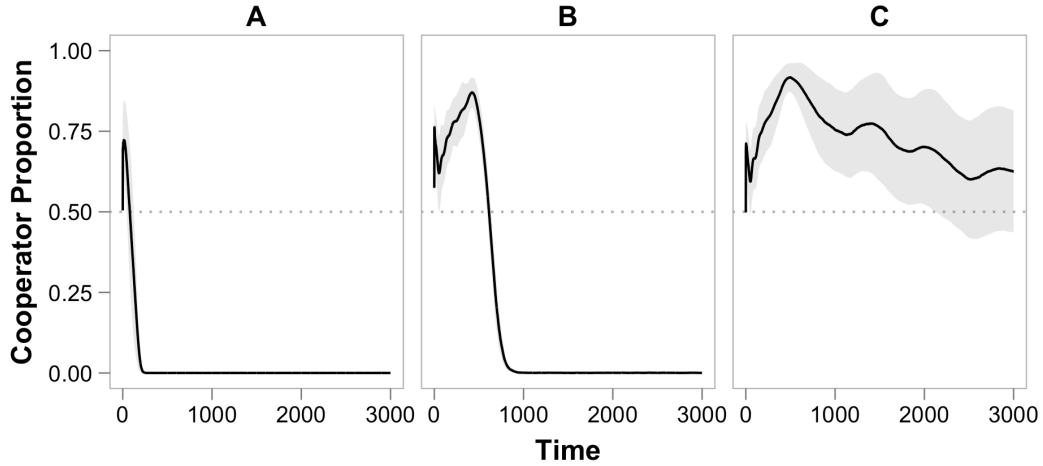


Figure 1: **Adaptation, niche construction, and the evolution of cooperation.** The proportion of cooperators present in the population is shown for the duration of simulations. Curves show the average among replicates, and shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter values used are listed in [Table 1](#). **(A)** When there is no opportunity for adaptation (L , the number of adaptive loci, is zero), cooperation is quickly lost. **(B)** When adaptation can occur ($L = 5$), but populations do not alter their environment (ϵ , the intensity of niche construction, is zero), cooperators temporarily rise in abundance before eventually going extinct. **(C)** Niche construction enables cooperation to be maintained indefinitely. After 3000 cycles, cooperation was the dominant phenotype in 13 of 18 replicate populations.

332 **Figure 2**

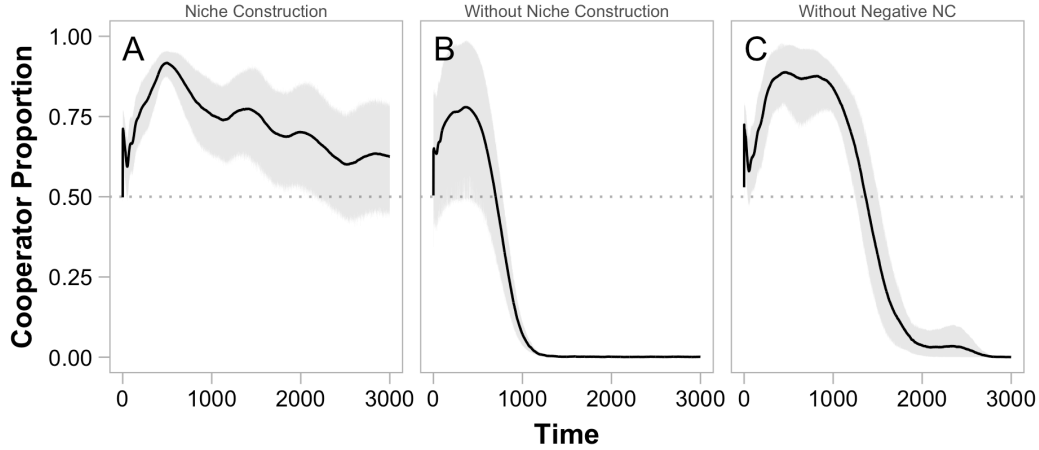


Figure 2: Niche Construction and the Evolution of Cooperation. The proportion of cooperators present in the population is shown for the duration of simulations. Curves show the average among replicates, and shaded areas indicate 95% confidence intervals. **(A)** Niche construction enables cooperation to be maintained indefinitely. In the majority of populations, cooperation remained as the dominant strategy. **(B)** When niche construction is removed ($\epsilon = 0$) and the fitness benefit of adaptation is increased as compensation ($\delta = 0.6$), cooperation is quickly lost when adapted defectors arise. **(C)** Without negative niche construction, cooperation is not maintained ($A = 5$). Here again, cooperation is driven to extinction by equally-adapted defectors.

333 **Figure 3**

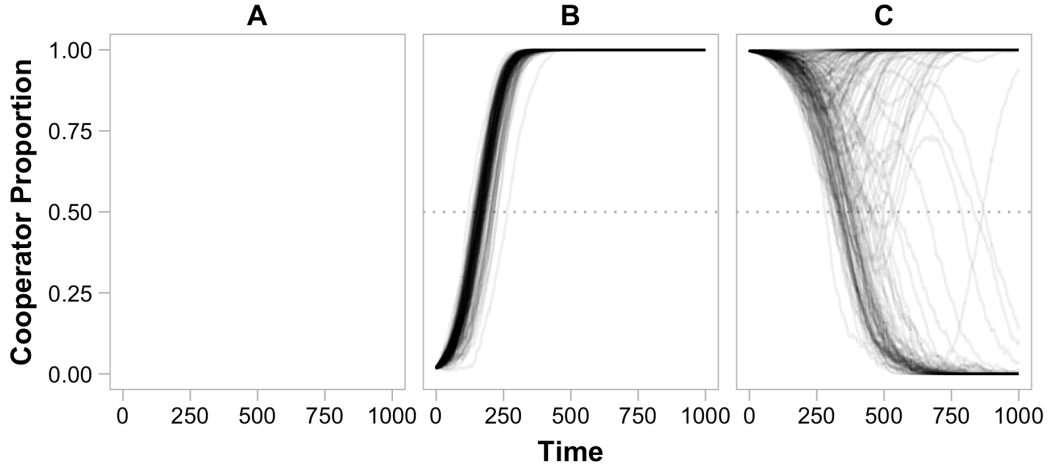


Figure 3: **Niche Construction and Invasion.** Curves trace the proportion of cooperators present in the population for the duration of 160 replicate simulations. In these experiments, we examined whether a strategy initiated at a single population in the center of the metapopulation lattice ($N = 11$) can invade. Unless otherwise noted, we disable mutations ($\mu_a = 0, \mu_c = 0$) to focus on how invasion depends on particular combinations of genotypes. **(A)** When cooperators and defectors are matched (i.e., genotypes $[1, 2, 3, 4, 5]$), defectors quickly drive cooperators to extinction due to the cost of cooperation. **(B)** However, the adaptive opportunities produced by negative niche construction and density dependence can allow an adapted cooperator (genotype $[1, 2, 3, 4, 6]$) to invade a population of defectors. **(C)** These same adaptive opportunities can allow cooperators to resist invasion by matching defectors, which arise via mutation and remain a constant threat. Here, adaptation allows cooperation to persist in 91 populations ($\mu_a = 0.00005$).

334 **Figure 4**

335 Cooperators invade defector population. Fully adapted but mismatched. Neg-
336 ative NC.

337 **Figure 5**

338 Defectors invade cooperator population. Fully adapted and matched. Role of
339 Export.

340 **Figure 6**

341 **Figure 6A - Effect of Public Good Benefit ($S_{\max}-S_{\min}$)**

342 **Figure 6B - Effect of Migration Rate (m)**

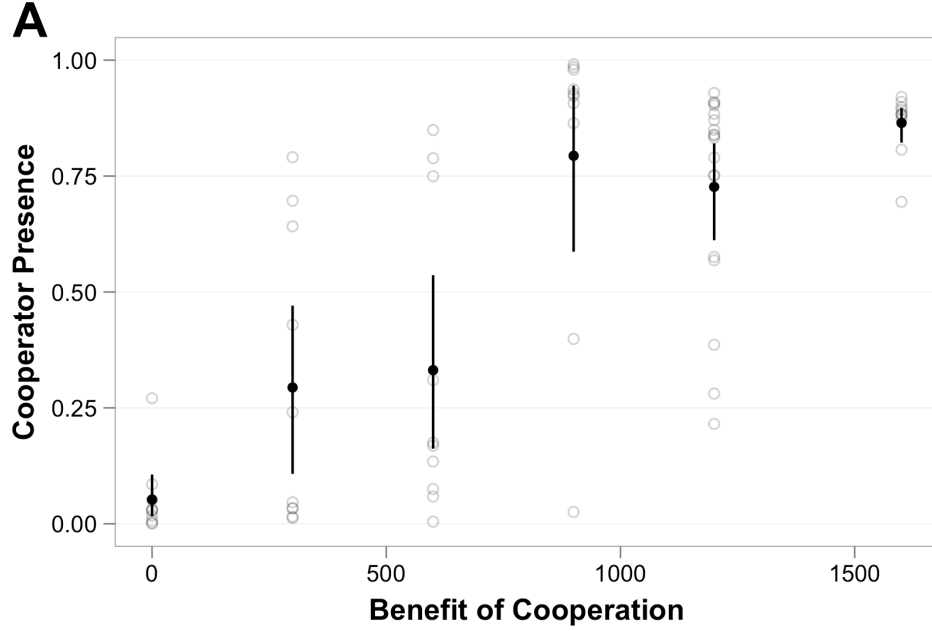


Figure 4: **Cooperator Presence as a Function of Population Size and Migration Rate.** Cooperator presence for each replicate population is shown as an open circle. The mean among these replicates is represented by a filled circle, and bars indicate 95% confidence intervals. **(A)** Cooperator presence increases proportional to increases in population size. Here, the benefit of cooperation (S_{max}) is varied (the density-dependent fitness effects of niche construction are adjusted accordingly in the model parameter ϵ). **(B)** Cooperator presence decreases with migration rate (m). When migration is low, cooperators can not export their niche, which limits expansion. When migration is high, the defectors immigrate into populations more quickly than cooperators can adapt.

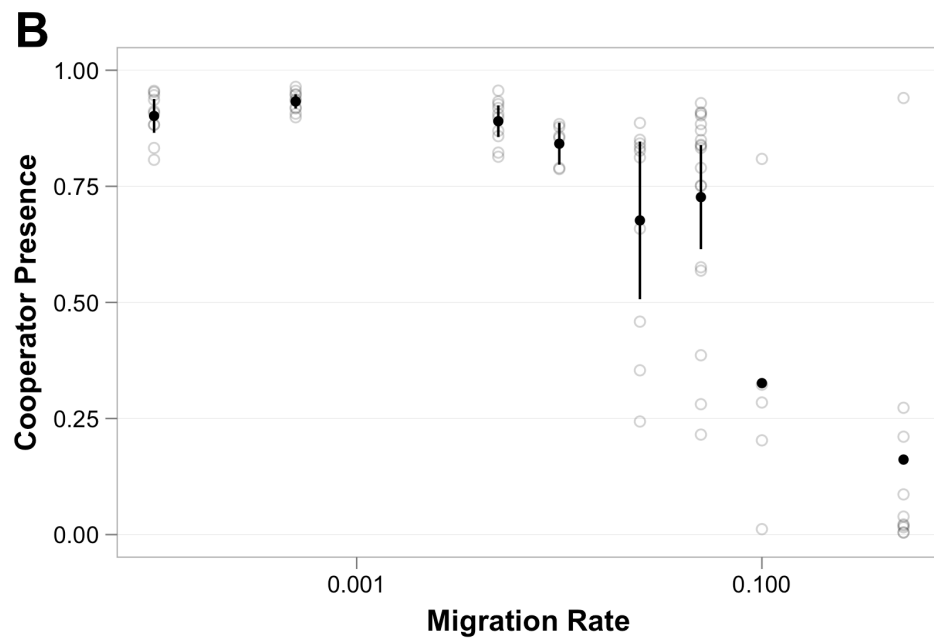


Figure 5: Will share caption with 6A

Table 1: Model parameters and their value

Parameter	Description	Base Value
N^2	Number of metapopulation sites	625
L	Number of adaptive loci	5
c	Fitness cost of cooperation	0.1
A	Number of alleles	6
δ	Fitness benefit, nonzero alleles	0.3
ϵ	Fitness benefit, sequential alleles	0.00015
z	Baseline fitness	1
S_{min}	Minimum population size	800
S_{max}	Maximum population size	2000
μ_a	Mutation rate (adaptation)	10^{-5}
μ_c	Mutation rate (cooperation)	10^{-5}
m	Migration rate	0.05
p_0	Initial cooperator proportion	0.5
μ_t	Mutation rate (tolerance to new environment)	10^{-5}
T	Number of simulation cycles	1000
d	Population dilution factor	0.1

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