

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 develop an individual-based model in which populations of cooperators and defectors evolve and compete in a spatially-structured metapopulation (a collection of populations). Through mutations, individuals gain adaptations to their environment, which increase reproductive fitness, and allow those lineages to rise in abundance. Migration among neighboring populations allows more successful lineages to spread.

We expand upon the model described by Hammarlund et al. (2015) to allow populations to modify their local environment. As this process occurs, environmental changes feed back to affect selection. We perform simulations using this model to explore how niche construction affects this adaptation process and whether selective feedbacks allow cooperation to be maintained.

Model Description

Individual Genotypes and Adaptation

Each individual in a population has a genotype, which is an ordered list of $L+1$ integers, or *loci* (see Table 1 for model parameters and their values). Different

84 values at these loci represent different alleles. A binary allele at locus $L + 1$
 85 determines whether that individual is a defector (0) or a cooperator (0), which
 86 carries fitness cost c . Cooperation is independent from adaptation to the
 87 environment. The first L loci are *adaptive loci*, and are each occupied by 0 or
 88 an integer from the set $\{1, 2, \dots, A\}$. Allele 0 represents a lack of adaptation,
 89 while a non-zero allele represents one of the A possible adaptations at that
 90 locus. The presence of any of these adaptations confers a fitness benefit δ .
 91 We choose $\delta > c$, which allows a minimally adapted cooperator to recoup
 92 the cost of cooperation and gain a fitness advantage. The benefits that these
 93 adaptations engender are purely endogenous, and are not affected by the other
 94 individuals or the state of the environment.

95 Niche Construction and Selective Feedbacks

96 Individual fitness is also affected by the current state of the local environment.
 97 Here, we represent the “niche” implicitly based on the allelic states present in
 98 the population. As allelic states change, populations alter their environment
 99 in different ways, creating a unique niche.

100 We use a form of density dependent selection to favors individuals that better
 101 match their niche. Specifically, the selective value of adaptive allele a at locus l
 102 increases with the number of individuals in the population that have allele $a + 1$
 103 at locus $l + 1$. As a consequence, genotypes with sequentially increasing allelic
 104 states will tend to evolve. We treat both adaptive loci and allelic states as
 105 “circular”, so the selective value of an allele at locus L is affected by the allelic

106 composition of the population at locus 1. Similarly, the selective value of allele
 107 A at any locus increases with the number of individuals carrying allele 1 at
 108 the next locus. This circularity is represented by the function $\beta(x, X)$, which
 109 gives the integer that follows an arbitrary value x in the set $\{1, 2, \dots, X\}$:

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

110 Here, $\text{mod}_X(x)$ is the integer remainder when dividing x by X . Thus, the
 111 selective value of adaptive allele a at locus l increases with the number of
 112 individuals that have allele $\beta(a, A)$ at locus $\beta(l, L)$. The slope of this increase
 113 is ϵ , which specifies the intensity of niche construction.

114 Consider a genotype g with the allelic state at locus l given by $a_{g,l}$; the fitness
 115 of an individual with this genotype is defined as:

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

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

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

118 Thus, an individual's fitness is determined both endogenously by adaptation
 119 (δ) and exogenously by its niche (ϵ).

120 Because mutations occur randomly (see below), each population will evolve
 121 different consecutive sequences. These different sequences represent the unique
 122 niches constructed by populations.

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

124 Cooperation benefits a population by allowing it to reach greater density. This
 125 benefit affects all individuals equally and accumulates linearly with the propor-
 126 tion of cooperators in the population. If p is the proportion of cooperators in
 127 a population at the beginning of a growth cycle, then that population reaches
 128 the following size:

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

129 During growth, individuals compete for inclusion in the resulting population.
 130 Each individual's probability of success is determined by its fitness. The com-
 131 position of a population with size P and cooperator proportion p after growth
 132 is multinomial with parameters and $S(p)$ and $\{\pi_1, \pi_2, \dots, \pi_P\}$, where:

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

133 Here, $W_{\gamma(i)}$ is the fitness of an individual i with genotype $\gamma(i)$ (see Equation 2).
 134 The value π_i represents an individual's reproductive fitness relative to others
 135 in the population.

136 **Mutation**

137 For simplicity, we apply mutations after population growth. Mutations occur
138 independently at each locus and cause an allelic state change. At each adaptive
139 locus, mutations occur at rate μ_a . These mutations replace the existing allele
140 with a random selection from the set $\{0\} \cup \{1, 2, \dots, A\}$. Note that this allows
141 for the possibility of an allele replacing itself, thus slightly reducing the effective
142 mutation rate. At the binary cooperation locus, mutations occur at rate μ_c .
143 These mutations flip the allelic state, causing cooperators to become defectors
144 and vice versa.

145 **Migration**

146 Our simulated environment consists of N^2 patches arranged as an $N \times N$
147 lattice, where each patch can support a population. After mutation, individ-
148 uals emigrate to an adjacent patch at rate m . During each migration event,
149 a single destination patch is randomly chosen with uniform probability from
150 each source patch's Moore neighborhood, which is composed of the nearest
151 8 patches on the lattice. Because the metapopulation lattice has boundaries,
152 patches located on an edge have smaller neighborhoods.

153 **Metapopulation Initialization and Simulation**

154 Metapopulations are initiated in a state that follows an environmental change,
155 which leaves most patches empty. First, populations are seeded at all patches
156 with cooperator proportion p_0 and grown to density $S(p_0)$. An environmental

challenge is then introduced, which subjects the population to a bottleneck. For each individual, the probability of survival is μ_t , which represents the likelihood that a mutation occurs that confers tolerance. Because individuals have not yet adapted to this new environment, the allelic state of each individual's genotype is 0 at each adaptive locus. Following initialization, simulations are run for T cycles, where each discrete cycle consists of population growth, mutation, and migration. At the end of each cycle, populations are thinned to allow for growth in the next cycle. Each individual persists with probability d , regardless of allelic state.

Source Code and Software Environment

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

Results

We follow the evolution of cooperation in a metapopulation consisting of populations connected by spatially-limited migration. Individuals in these populations can gain a limited number of adaptations that confer selective benefits. While the allele at an individual's cooperation locus does not directly affect

177 the value of alleles at adaptive loci, cooperation can have indirect effects on the
 178 process of adaptation. Specifically, because cooperation increases population
 179 density, isolated cooperators experience more mutational opportunities to gain
 180 adaptations. Cooperation can hitchhike along with these adaptations, which
 181 compensate for the cost of cooperation. Additionally, populations alter their
 182 environment. Here, we explore how niche construction can favor the evolution
 183 of cooperation. Our simulation environment is defined by the parameter val-
 184 ues listed in [Table 1](#). Unless otherwise noted, 10 replicate simulations were
 185 performed for each experiment. We quantify cooperator success using the area
 186 under the cooperator proportion curve. This measure of cooperator presence
 187 increases as cooperators rise in abundance or remain in the population longer.

188 **Niche Construction Maintains Cooperation**

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

199 cooperation persists (Figure 1C).

200 **Fitness Increases Alone do not Support Persisting Coop-** 201 **eration**

202 In our model, niche construction introduces additional selective benefits. To
203 determine how these selective effects influence evolutionary outcomes, we per-
204 formed simulations in which the selective effects of niche construction were
205 removed ($\epsilon = 0$), and we instead increased the fitness benefits conferred by
206 adaptation ($\delta = 0.6$). Here, we are conservative by lifting the selective value of
207 exogenous adaptation by the maximum value possible from niche construction.

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

213 **Negative Niche Construction is Critical to Cooperator** 214 **Persistence**

215 Negative niche construction occurs in our model due to selection for
216 sequentially-increasing allelic states and the circular arrangement of these
217 alleles. When the genome length (L) is not evenly divided by the number
218 of adaptive alleles (A), then it is not possible for the population to be fixed

219 for a genotype that is perfectly adapted to the constructed environment.
 220 Technically (in terms of the model) this is because the equality:

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

221 cannot simultaneously hold for all l .

222 For example, consider genotype $(1, 2)$ when $L = 2$ and $A = 3$. Here, allelic
 223 state 2 at locus 2 will be be beneficial, because it follows allelic state 1 at
 224 locus 1. However, due to the circular effects, allelic state 1 at locus 1 will be
 225 deleterious relative to allelic state 3 at locus 1. Yet, fixation for genotype $(3, 2)$
 226 does not solve the problem, because a mutant $(3, 1)$ is fitter, and so on.

227 We first focus on the effects of positive niche construction by removing the
 228 allelic conflict that leads to negative niche construction ($L = 5$, $A = 5$). In
 229 the absence of this conflict, cooperator presence is significantly increased (Fig-
 230 ure 2C). Within these environments, we find that positive niche construction
 231 prolongs the fitness advantage that cooperators have over defectors (Figure
 232 3C).

233 **Positive niche construction is important to cooperator** 234 **persistence**

235 To determine how negative niche construction influences the evolution of co-
 236 operation, we maximize the allelic conflict ($L = 1$, $A = 6$). Here, selection for
 237 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.

NC Prevents Defector Invasion

Figure 5

How Cooperation Fuels all of this

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

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

Discussion

257 Despite their negative effects, deleterious traits can rise in abundance due to
258 genetic linkage with other traits that are strongly favored by selection (May-
259 nard Smith and Haigh, 1974). In a process termed the “Hankshaw effect”,
260 Hammarlund et al. (2015) recently demonstrated that cooperative behaviors
261 can prolong their existence by actively increasing their likelihood of hitchhik-
262 ing with a beneficial trait. While this process does favor cooperation in the
263 short term, it eventually reaches a dead end. When the opportunities for
264 adaptation are exhausted, and cooperators can no longer hitchhike, they face
265 extinction. In this work, we have considered whether niche construction can
266 maintain cooperation indefinitely.

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

281 cooperation.

282 When successful, we observe that populations do not reach the maximum pos-
283 sible fitness (Figure 3A). Although cooperation is the focus of this study, it
284 can be seen as deleterious. Previous work has shown that niche construction
285 can favor deleterious alleles (Laland *et al.*, 1996, 1999). Similarly here, coop-
286 eration is maintained in the presence of niche construction, but lost otherwise.
287 Van Dyken and Wade (2012) showed that when two cooperative behaviors
288 co-evolve and niche construction feedbacks benefit the other type, niche con-
289 struction can increasingly favor these traits, which were otherwise disfavored
290 when alone.

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

299 In our model, the environmental state was implicitly modeled, and depended
300 solely on the current state of the population. In natural settings, however, the
301 timescales at which environments are modified and reproduction are likely to
302 be decoupled. For example, a multitude of factors including protein durabil-
303 ity (Brown and Taddei, 2007; Kümmerli and Brown, 2010), diffusion (Allison,

304 2005; Driscoll and Pepper, 2010), and resource availability (Zhang and Rainey,
 305 2013; Ghoul *et al.*, 2014) influence both the rate and the degree to which public
 306 goods alter the environment. These factors are likely to influence evolution-
 307 ary trajectories (Laland *et al.*, 1996). Lehmann (2007) demonstrated that a
 308 cooperative, niche constructing behavior can be favored when it only affected
 309 selection for future generations, thus reducing the potential for competition
 310 among contemporary kin. The evolutionary inertia that this creates, however,
 311 may ultimately work against cooperators. When public good accumulates in
 312 the environment, cooperators must reduce their investment in production to re-
 313 main competitive (Kümmerli and Brown, 2010; Dumas and Kümmerli, 2012).
 314 Cooperation that occurs facultatively, perhaps by sensing the abiotic (Bernier
 315 *et al.*, 2011; Koestler and Waters, 2014) or biotic environment (Brown and
 316 Johnstone, 2001; Darch *et al.*, 2012), are likely to be favored in these environ-
 317 ments.

318 In many instances of cooperation, the environment is itself a biological entity,
 319 which can produce additional evolutionary feedbacks. As the host population
 320 changes, so too will selection on their symbiont populations. Here, evolution-
 321 ary outcomes depend greatly on the degree of shared interest between the host
 322 and symbiont. For example, the cooperative production of virulence factors by
 323 the human pathogen *P. aeruginosa* in lung infections is harmful to those with
 324 cystic fibrosis (Harrison, 2007). Conversely, cooperative light production by *A.*
 325 *fisheri* is vital for the survival of its host, the Hawaiian bobtail squid (Ruby,
 326 1996). It was recently argued that incorporating the effects of niche construc-
 327 tion is critical for improving our understanding of viral evolution (Hamblin *et*

328 *al.*, 2014) and evolution in co-infecting parasites (Hafer and Milinski, 2015).
329 Incorporating host dynamics, co-evolution, and the feedbacks that they pro-
330 duce into models is likely to be equally important for gaining an understanding
331 of how cooperative behaviors evolve in these host-symbiont settings.

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339 Figures

340 **Figure 1**

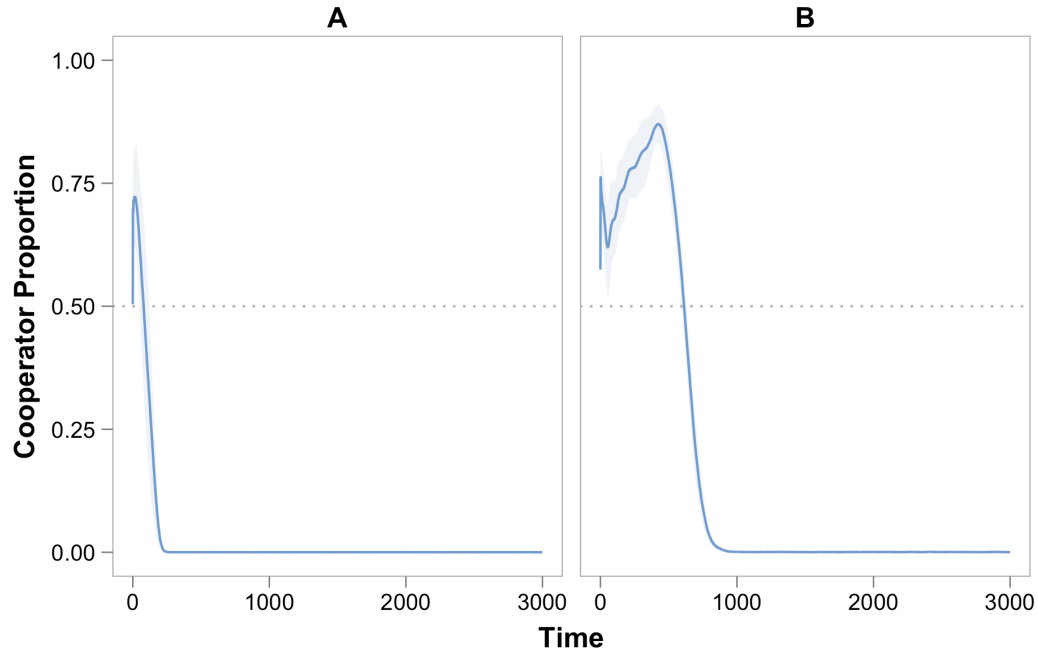


Figure 1: **Adaptation, Hitchhiking, and the Evolution of Cooperation.** The proportion of cooperators present in the population is shown for the duration of simulations. Curves show the average among replicate populations, and shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter values are listed in [Table 1](#). **(A)** Without any opportunity to adapt (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), cooperation hitchhikes along with adaptations, allowing cooperators to temporarily rise in abundance before eventually going extinct.

341 **Figure 2**

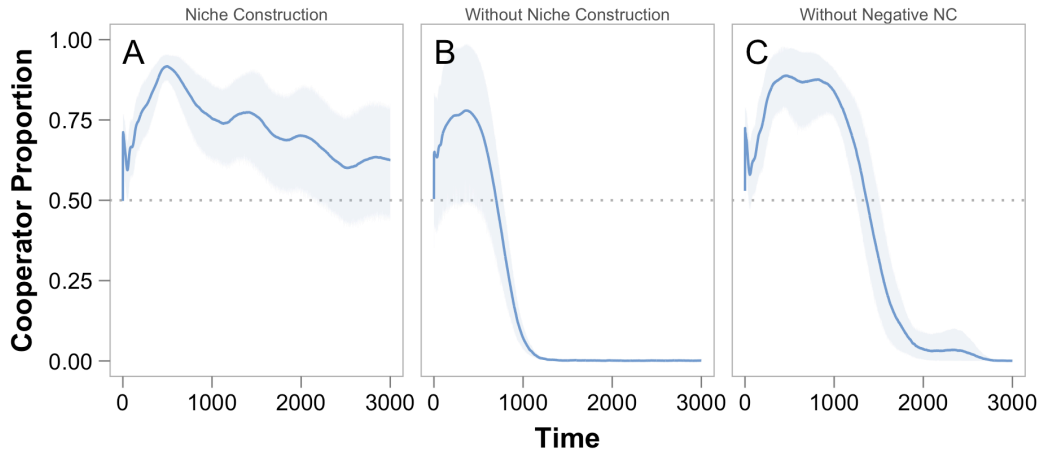


Figure 2: Niche Construction and the Evolution of Cooperation. The proportion of cooperators present in the population is shown for the duration of simulations. Curves show the average among replicate populations, and shaded areas indicate 95% confidence intervals. **(A)** Niche construction enables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

342 **Figure 3**

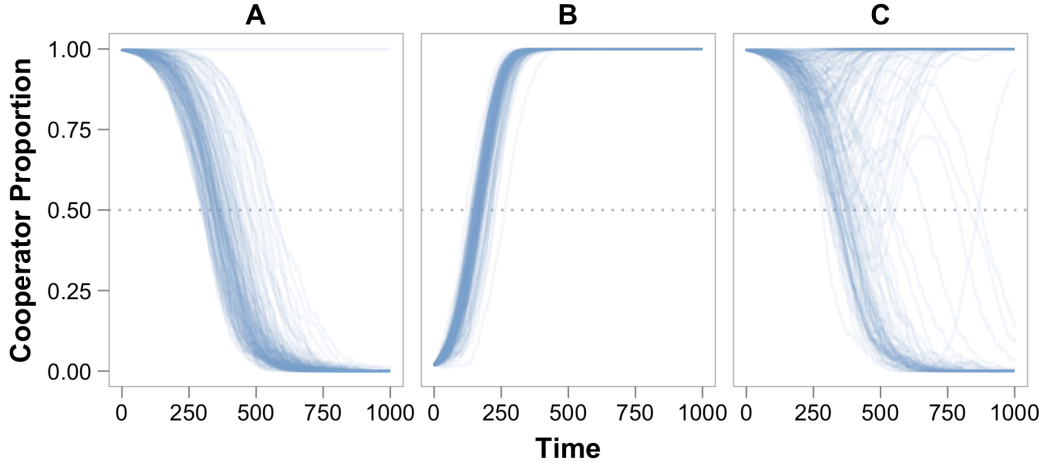


Figure 3: **Niche Construction and Invasion.** Curves trace the proportion of cooperators present in the population for the duration of 160 replicate simulations. These experiments examine whether a strategy initiated at a single population in the center of the metapopulation lattice ($N^2 = 121$) can 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 $[1,2,3,4,5]$) and adaptation can not occur, defectors quickly drive cooperators to extinction due to the cost of cooperation. Defectors were stochastically eliminated in 2 replicate populations. **(B)** However, the adaptive opportunities produced by negative niche construction and density dependence enable 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 initially-matching defectors, which arise via mutation and remain a constant threat. Here, cooperation persisted in 91 populations ($\mu_a = 0.00005$, the base mutation rate).

343 **Figure 4**

344 Cooperators invade defector population. Fully adapted but mismatched. Neg-
345 ative NC.

346 **Figure 5**

347 Defectors invade cooperator population. Fully adapted and matched. Role of
348 Export.

349 **Figure 6**

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

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

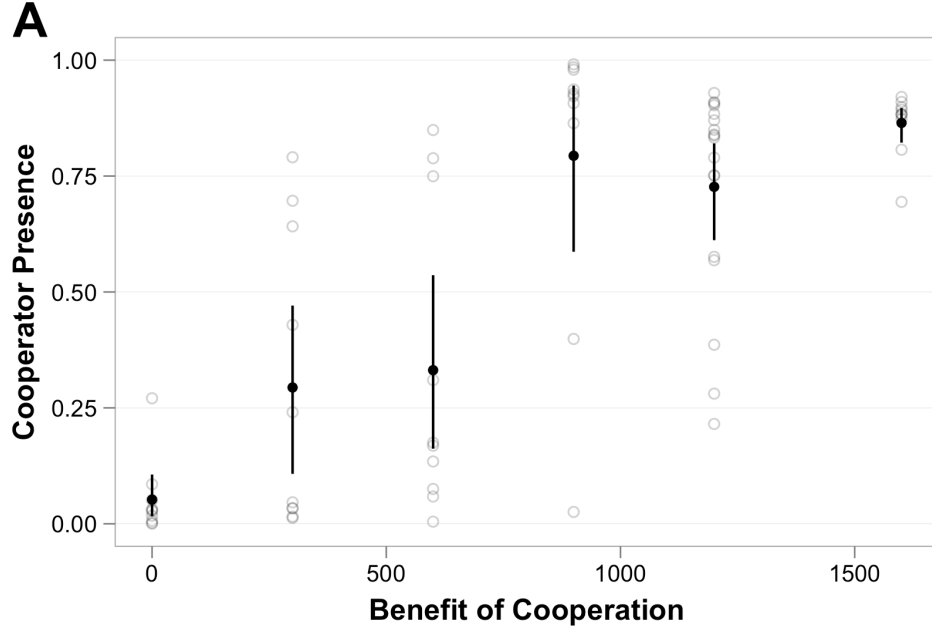


Figure 4: **Cooperator Presence as a Function of Population Size and Migration Rate.** Cooperator presence for each replicate population is shown as an open circle. The mean among these replicates is represented by a filled circle, and bars indicate 95% confidence intervals. **(A)** Cooperator presence 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.

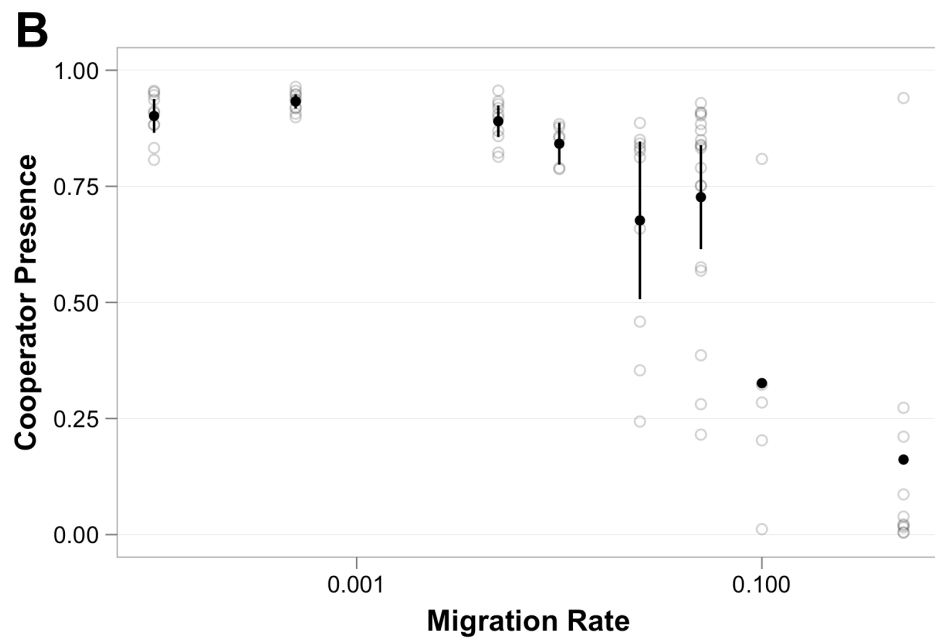


Figure 5: Will share caption with 6A

Table 1: Model parameters and their value

Parameter	Description	Base Value
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}
N^2	Number of metapopulation sites	625
m	Migration rate	0.05
p_0	Initial cooperator proportion	0.5
μ_t	Mutation rate (tolerance to new environment)	10^{-5}
d	Population dilution factor	0.1
T	Number of simulation cycles	1000

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