

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

4 TODO

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

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

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

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

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

65 populations produce more emigrants, these populations will exert a stronger in-
66 fluence on neighboring populations, effectively exporting their niche. Because
67 of these potential benefits, we also focus our attention on how population size
68 and migration rate influence evolutionary outcomes in these environments.

69 **Methods**

70 We build upon the model described in Hammarlund et al. (2015), in which
71 cooperators and defectors compete and evolve in a metapopulation (a collec-
72 tion of populations). Individuals in each of the populations reproduce, mutate,
73 and migrate to neighboring populations. Importantly, adaptation can occur.
74 In our model here, we further allow populations to modify their local environ-
75 ment, and these modifications feed back to affect selection.

76 **Model Description**

77 Our simulated environment consists of N^2 patches arranged as an $N \times N$ lattice
78 (see [Table 1](#) for model parameters and their values), where each patch can
79 support a population. Each individual in a population has a genotype, which
80 is an ordered list of $L + 1$ integers (loci). The first L loci are *adaptive loci*, and
81 are each occupied by 0 or an integer from the set $\{1, 2, \dots, A\}$, where A is the
82 number of alleles conferring a selective benefit. Specifically, the presence of
83 any non-zero allele at any of these loci represents an adaptation that confers
84 fitness benefit δ . A binary allele at locus $L + 1$ determines whether or not

85 that individual is a cooperator. Individuals with allelic state 1 at this locus
 86 are cooperators, carrying a cost c , while individuals with allelic state 0 are
 87 defectors. When $\delta \geq c$, a minimally adapted cooperator recoups the cost of
 88 cooperation.

89 Organisms also influence their environment, which, in turn, influences selection.
 90 We model this as a form of density dependent selection. Specifically, the
 91 selective value of adaptive allele a at locus l increases with the number of
 92 individuals in the population that have allele $a - 1$ at locus $l - 1$. We treat
 93 both adaptive loci and allelic states as “circular”, so the allelic state at locus
 94 1 is affected by the allelic composition of the population at locus L , and the
 95 selective value of allele 1 at any locus increases with the number of individuals
 96 carrying allele A at the previous locus. For the remainder of this section, this
 97 circularity is represented by the function below, which gives the integer below
 98 x in the set $\{1, 2, \dots, X\}$.

$$\beta(x, X) = \text{mod}_X(x - 2 + X) + 1 \quad (1)$$

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

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

104 where z is a baseline fitness, and $I_A(a)$ indicates whether an adaptive allele is
 105 non-zero:

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

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

111 Cooperators produce a public good that is equally accessible to all members
 112 of the population. This public good increases the carrying capacity at that
 113 patch, allowing the population to reach greater density. This benefit increases
 114 linearly with the proportion of cooperators. Thus, if p is the proportion of
 115 cooperators in a population at the beginning of a growth cycle, then that
 116 population reaches the following size during the growth phase:

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

117 The function $S(p)$ reflects the benefit of public good production. A popu-
 118 lation composed entirely of defectors reaches size S_{min} , while one composed
 119 entirely of cooperators reaches size S_{max} (with $S_{max} \geq S_{min}$). During growth,
 120 individuals compete for inclusion in the resulting population. The composi-

tion of a population with size P and cooperator proportion p after growth is multinomial with parameters $S(p)$ and $\{\pi_1, \pi_2, \dots, \pi_P\}$, where:

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

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

For simplicity, we apply mutations after population growth. Mutations occur independently at each locus and cause the allelic state to change. Mutations occur at each adaptive locus at rate μ_a , in which a new allele is chosen at random from the set $\{0\} \cup \{1, 2, \dots, A\}$. At the binary cooperation locus, mutations occur at rate μ_c . These mutations flip the allelic state, causing cooperators to become defectors and vice versa. Therefore, the probability that genotype g mutates into genotype g' is given by:

$$\tau_{g \rightarrow g'} = \mu_a^{H_a(g, g')} (1 - \mu_a)^{\{L - H_a(g, g')\}} \mu_c^{H_c(g, g')} (1 - \mu_c)^{\{1 - H_c(g, g')\}} \quad (6)$$

where $H_a(g, g')$ and $H_c(g, g')$ are the Hamming distances between genotypes g and g' at the cooperation locus and adaptive loci, respectively. The Hamming distance is the number of loci at which allelic states differ (Hamming, 1950).

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

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

153 **Source Code and Software Environment**

154 The simulation software and configurations for the experiments reported are
 155 available online. Simulations used Python 3.4.0, NumPy 1.9.1, Pandas 0.15.2
 156 (McKinney, 2010), and NetworkX 1.9.1 (Hagberg *et al.*, 2008). Data analyses
 157 were performed with R 3.1.3 (R Core Team, 2015).

158 Results

159 We use the model described earlier to follow the evolution of cooperation in
160 a metapopulation of populations that are connected by spatially-limited mi-
161 gration. Individuals in these populations gain a limited number of adapta-
162 tions that confer selective benefits. Adaptation is independent of cooperation.
163 However, because cooperation increases population density, these populations
164 experience more mutational opportunities to gain adaptations. Cooperation
165 can hitchhike along with these adaptations, which compensate for the cost
166 of public good production. During this process, populations alter their envi-
167 ronment. This niche construction process can be either positive or negative,
168 depending on its effects on fitness. Here, we explore how niche construction
169 can favor the evolution of cooperation. Our simulation environment is defined
170 by the parameter values listed in [Table 1](#). Unless otherwise noted, 10 replicate
171 simulations were performed for each experiment.

172 Niche Construction Maintains Cooperation

173 Without any opportunity for adaptation ($L = 0$), cooperators are swiftly elim-
174 inated in competition with defectors (Figure 1). Despite an initial lift due
175 to increased productivity, the cost of cooperation becomes disadvantageous
176 as migration mixes the initially isolated populations. When there are oppor-
177 tunities for adaptation ($L = 5$, $\epsilon = 0$), cooperators are maintained transiently
178 (Figure 1B). Here, the additional mutational abilities provided by their larger
179 sizes allows cooperator populations to more quickly adapt to their environment.

As previously described by Hammarlund et al. (2015), however, cooperation is subsequently lost as defector populations become equally adapted. When populations affect their environment and these changes feed back on selection, cooperation persists (Figure 1C, 3A). In these environments, cooperators maintain higher fitness than defectors, which enables their survival (Figure 3A).

Fitness Increases do not Support Cooperation

In our model, niche construction introduces additional selective benefits. To determine how these selective effects influence evolutionary outcomes, we performed simulations in which the selective effects of niche construction were removed ($\epsilon = 0$). As compensation, we increased the fitness benefits conferred by adaptation ($\delta = 0.6$). Here, the selective effects of niche construction are exaggerated, as a fitness benefit of 0.3 (our increase in δ) is the maximum value possible (see 2). To quantify cooperator success and permit comparison, we use the area under the cooperator proportion curve. This measure of *cooperator presence* increases as cooperators rise in abundance or remain in the population longer.

We find that higher selective values do not provide a significant increase in cooperator presence (Figure 2, column C). As shown in Figure 3, cooperators gain adaptations more quickly than defectors, which provides a fitness advantage. However, the cost of cooperation puts defectors at an advantage once these populations become fully adapted.

202 **Positive Niche Construction Prolongs Cooperation**

203 Negative niche construction occurs in our model due to selection for
204 sequentially-increasing allelic states and the circular arrangement of these
205 alleles. When the genome length (L) is not evenly divided by the number of
206 adaptive alleles (A), a conflict arises when the allelic state at locus 1 is not 1
207 larger than the allelic state at locus L . For example, consider genotype (1, 2)
208 when $L = 2$ and $A = 3$. Here, allelic state 2 at locus 2 will be beneficial,
209 because it follows allelic state 1 at locus 1. However, due to the circular
210 effects, allelic state 1 at locus 1 will be deleterious, because it does not follow
211 2.

212 We first focus on the effects of positive niche construction by removing the
213 allelic conflict that leads to negative niche construction ($L = 5$, $A = 5$). In the
214 absence of this conflict, cooperator presence is significantly increased (Figure
215 2, column D). Within these environments, we find that positive niche con-
216 struction prolongs the fitness advantage that cooperators have over defectors
217 (Figure 3C). Nevertheless, cooperators are eventually driven to extinction once
218 defectors gain the fitness advantage.

219 **Negative Niche Construction is not Sufficient**

220 To determine how negative niche construction influences the evolution of co-
221 operation, we maximize the allelic conflict ($L = 1$, $A = 6$). Here, selection for
222 increasing allelic states among the stress loci means that any allelic state will
223 not be greater than at the previous allele (itself), and thus there will always

224 be opportunity for adaptation. Despite this constant opportunity, niche con-
225 struction does not increase cooperator presence (Figure 2, column E). Here,
226 defectors rapidly gain the fitness advantage.

227 **NC Enables Cooperator Spread**

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

229 **NC Prevents Defector Invasion**

230 Figure 5

231 **How Public Good Fuels all of this**

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

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

242 # Discussion

243 Despite their negative effects, deleterious traits can rise in abundance due to
244 genetic linkage with other traits that are strongly favored by selection (May-
245 nard Smith and Haigh, 1974). In a process termed the “Hankshaw effect”,
246 Hammarlund et al. (2015) recently demonstrated that cooperative behaviors
247 can prolong their existence by actively increasing their likelihood of hitchhik-
248 ing with a beneficial trait. While this process favors cooperation in the short
249 term, it eventually reaches a dead end. When the opportunities for adaptation
250 are exhausted and cooperators can no longer hitchhike, they face extinction.
251 In this work, we have considered whether niche construction can maintain
252 cooperation indefinitely.

253 Our results reveal that with niche construction, cooperation can indeed persist
254 (Figure 1C). But what it is it about this process that maintains cooperation?
255 In our model, niche construction introduces additional selective effects that
256 could influence the evolutionary process. However, simply raising the selective
257 benefits provided by adaptations does not significantly increase cooperator
258 presence (Figure 2, columns C and A), and indicates that niche construction
259 plays an important role. Although cooperators benefit greatly from positive
260 niche construction, it does not fully explain our results (Figure 2 D). Indeed,
261 despite an initial increase in abundance, cooperators are eventually driven to
262 extinction when environmental change produces only positive fitness effects
263 (Figure 1D). As with the Hankshaw effect, adaption eventually slows, allowing
264 defectors to outcompete cooperators (Figure 3C). While it does not benefit
265 cooperation when alone (Figure 3E), negative niche construction acts to pre-
266 vent this stasis. Combined, we find that both positive and negative niche

267 construction are required to main cooperation.

268 When successful, we observe that populations do not reach the maximum pos-
269 sible fitness (Figure 3A). Although cooperation is the focus of this study, it
270 can be seen as deleterious. Previous work has shown that niche construction
271 can favor deleterious alleles (Laland *et al.*, 1996, 1999). Similarly here, coop-
272 eration is maintained in the presence of niche construction, but lost otherwise
273 (Figure 2). Van Dyken and Wade (2012) showed that when two cooperative
274 behaviors co-evolve and niche construction feedbacks benefit the other type,
275 niche construction can increasingly favor these traits, which were otherwise
276 disfavored when alone.

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

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

290 2005; Driscoll and Pepper, 2010), and resource availability (Zhang and Rainey,
 291 2013; Ghoul *et al.*, 2014) influence both the rate and the degree to which public
 292 goods alter the environment. These factors are likely to influence evolution-
 293 ary trajectories (Laland *et al.*, 1996). Lehmann (2007) demonstrated that a
 294 cooperative, niche constructing behavior can be favored when it only affected
 295 selection for future generations, thus reducing the potential for competition
 296 among contemporary kin. The evolutionary inertia that this creates, however,
 297 may ultimately work against cooperators. When public good accumulates in
 298 the environment, cooperators must reduce their investment in production to re-
 299 main competitive (Kümmerli and Brown, 2010; Dumas and Kümmerli, 2012).
 300 Cooperation that occurs facultatively, perhaps by sensing the abiotic (Bernier
 301 *et al.*, 2011; Koestler and Waters, 2014) or biotic environment (Brown and
 302 Johnstone, 2001; Darch *et al.*, 2012), are likely to be favored in these fluctuat-
 303 ing environments.

304 In many instances of cooperation, the environment is itself a biological entity,
 305 which can produce additional evolutionary feedbacks. As the host population
 306 changes, so too will selection on their symbiont populations. Here, evolution-
 307 ary outcomes depend greatly on the degree of shared interest between the host
 308 and symbiont. For example, the cooperative production of virulence factors
 309 by the human pathogen *P. aeruginosa* in lung infections is harmful to those
 310 with cystic fibrosis (Harrison, 2007). Conversely, cooperative light produc-
 311 tion by *A. fischeri* is vital for the survival of its host, the Hawaiian bobtail
 312 squid (Ruby, 1996). It was recently argued that incorporating the effects of
 313 niche construction is critical for improving our understanding of viral evolu-

tion (Hamblin *et al.*, 2014) and evolution in co-infecting parasites (Hafer and Milinski, 2015). Incorporating host dynamics, co-evolution, and the feedbacks that they produce into models is likely to be equally important for gaining an understanding of how cooperative behaviors evolve in these host-symbiont settings. # Acknowledgments

- TODO: Organizers?
- TODO: lab comments

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329 Figures

330 **Figure 1**

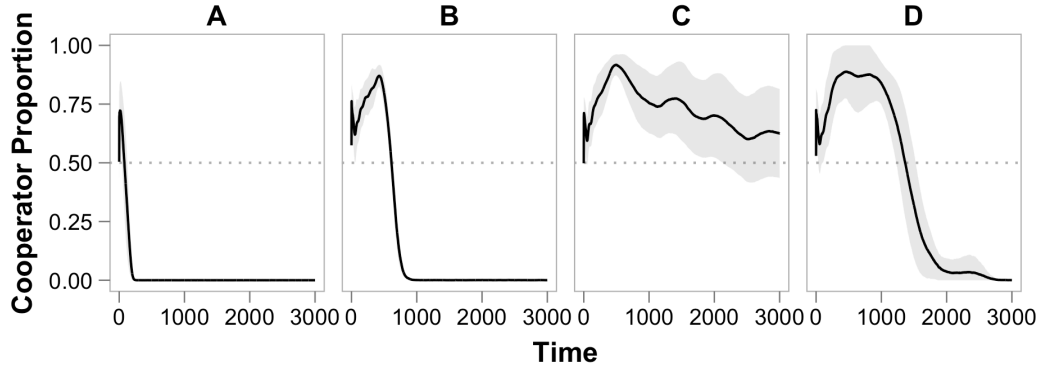


Figure 1: **Adaptation, niche construction, and the evolution of cooperation.** Curves show the average cooperator proportion among replicate populations, while shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter values used are listed in [Table 1](#). **(A)** When there 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)** Selective feedbacks from niche construction allow cooperation to be maintained in 13 of 18 replicate populations. **(D)** While it does contribute to increases in cooperation in other contexts, positive niche construction alone does not maintain cooperation ($A = 5$).

331 **Figure 2**

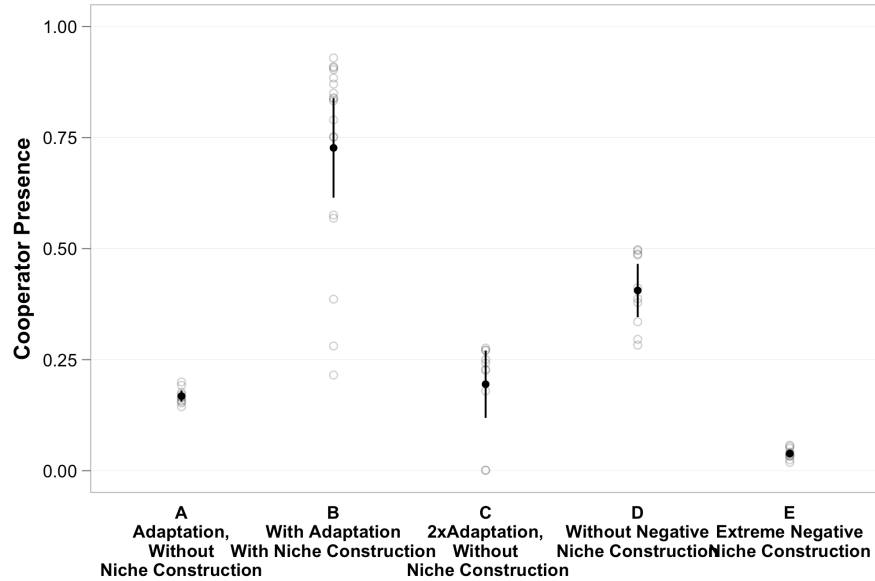


Figure 2: **Evolutionary Processes and their Effect on Cooperator Presence.** Filled circles show the mean cooperator presence among replicate populations, and bars indicate 95% confidence intervals. Individual cooperator presence metrics are shown for each replicate population with an open circle. **(A)** In our model, adaptations allow cooperation to hitchhike. This effect is transient, which limits cooperator presence. **(B)** In the presence of niche construction (positive and negative), cooperator presence is significantly increased. **(C)** When incorporating the potential benefits that it provides, but removing the selective feedback produced by niche construction, cooperator presence is unaffected. **(D)** Positive niche construction increases cooperator proportion, but not to the levels seen in B. **(E)** Negative niche construction alone does not account for the increase in cooperator presence.

332 **Figure 3**

333 Mean fitness over time for the treatments shown in Figure 2

334 **Figure 3A - Fitness for base case: niche construction**

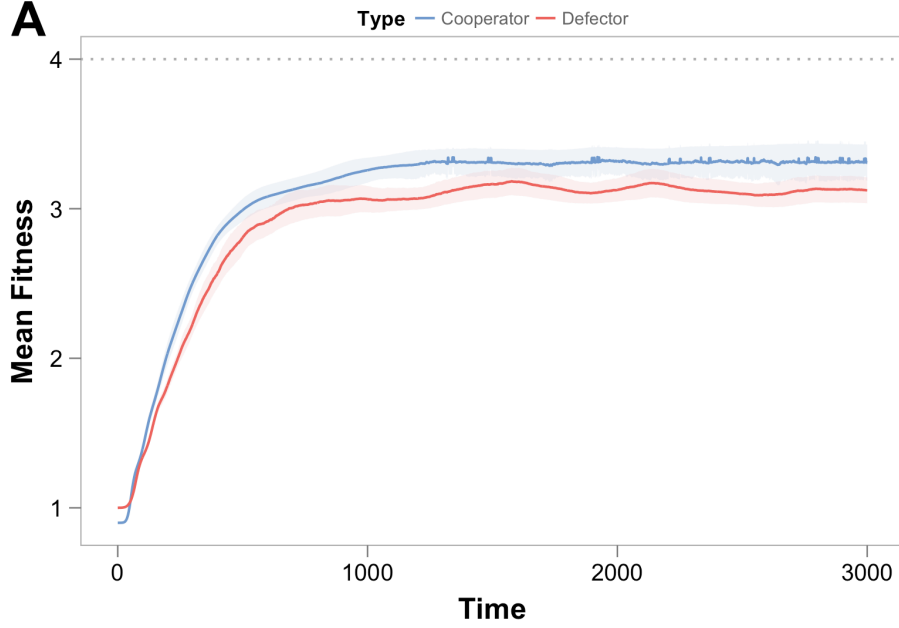


Figure 3: **Fitness Effects of Mutation Accumulation by Cooperators and Defectors.** Lines indicate the grand mean of cooperator (blue) and defector (red) fitness among replicate populations, while shaded areas indicate 95% confidence intervals. Dashed lines indicate the maximum fitness values achievable by cooperators and defectors. **(A)** In the presence of niche construction, cooperators persist in the population by maintaining a greater mean fitness. **(B)** When selective values are increased ($\delta = 0.6$), populations rapidly adapt. In the absence of niche construction ($\epsilon = 0$), defectors eventually become equally adapted and surpass cooperators. At this point, cooperators are driven from the population due to the cost of cooperation. **(C)** With the effects of niche construction removed ($\epsilon = 0$), positive niche construction prolongs the time when cooperators are at an advantage over defectors. Once again, however, defectors eventually become equally adapted, leading to the loss of cooperation. **(D)** Without positive niche construction or further adaptive opportunities ($L = 1$, $a_{max} = 6$) cooperators do not benefit from niche construction.

335 **Figure 3B**

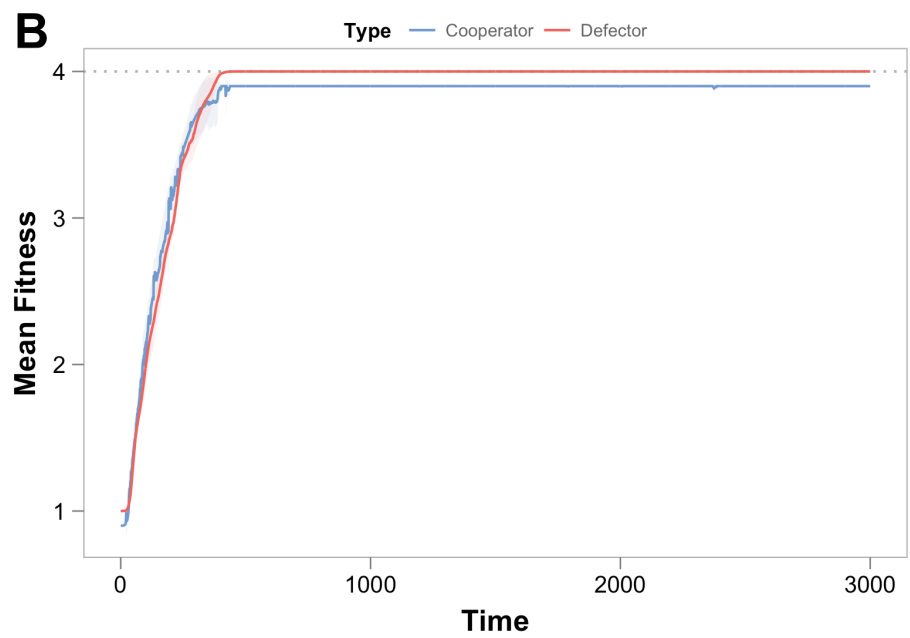


Figure 4: Will share caption with 3A

336 **Figure 3C**

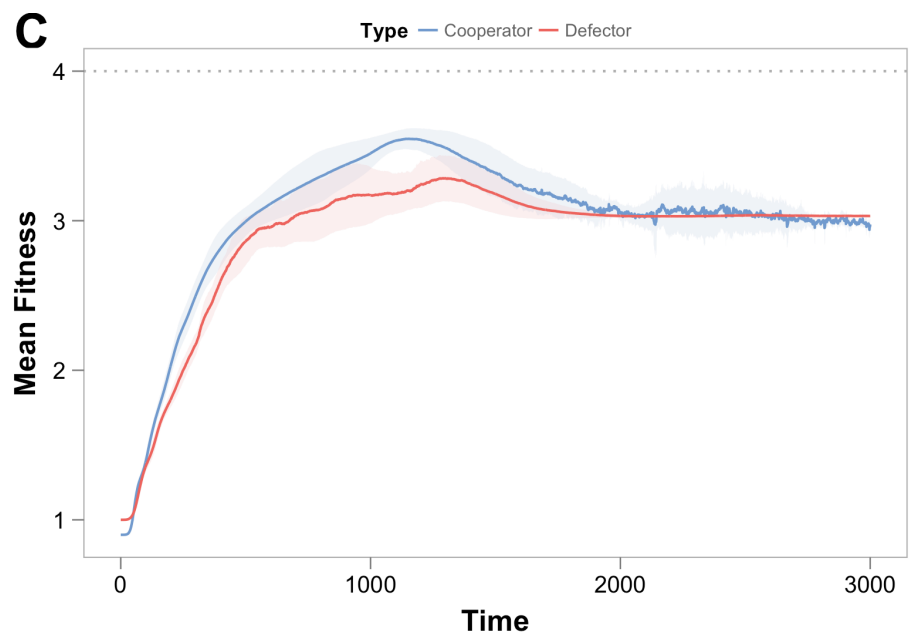


Figure 5: Will share caption with 3A

337 **Figure 3D**

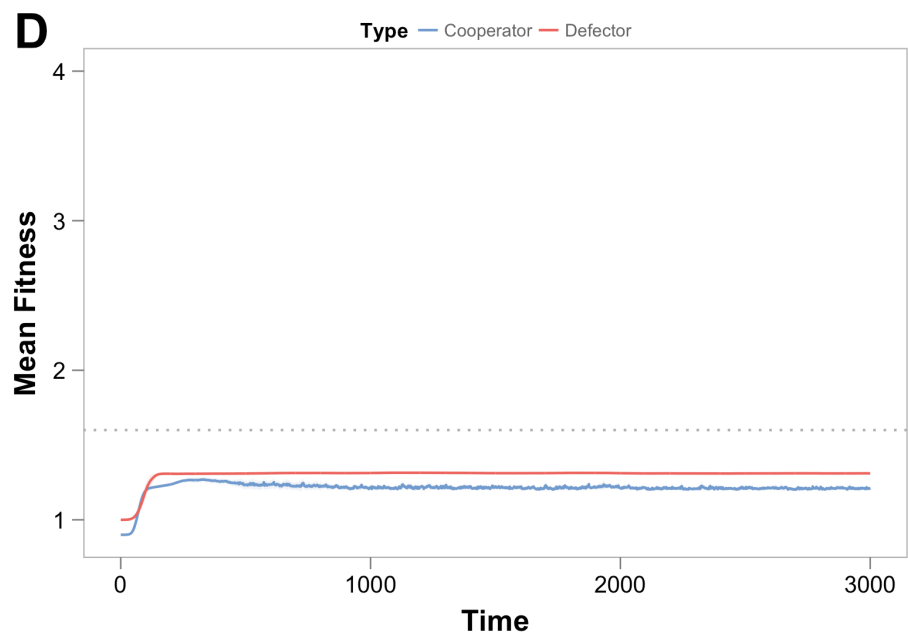


Figure 6: Will share caption with 3A

338 **Figure 4**

339 Cooperators invade defector population. Fully adapted but mismatched. Neg-
340 ative NC.

341 **Figure 5**

342 Defectors invade cooperator population. Fully adapted and matched. Role of
343 Export.

344 **Figure 6**

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

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

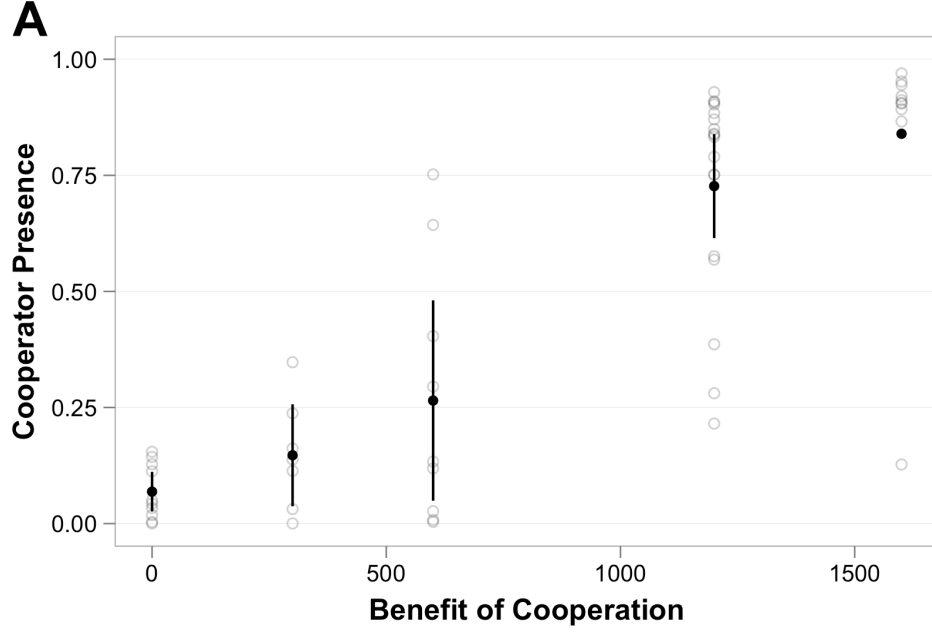


Figure 7: **Cooperator Presence as a Function of Population Size and Migration Rate.** Cooperator presence for each replicate population is shown as an open circle. The mean among these replicates is represented by a filled circle, and bars indicate 95% confidence intervals. **(A)** Cooperator presence increases proportional to increases in population size. Here, the benefit of cooperation (S_{max}) is varied. **(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.

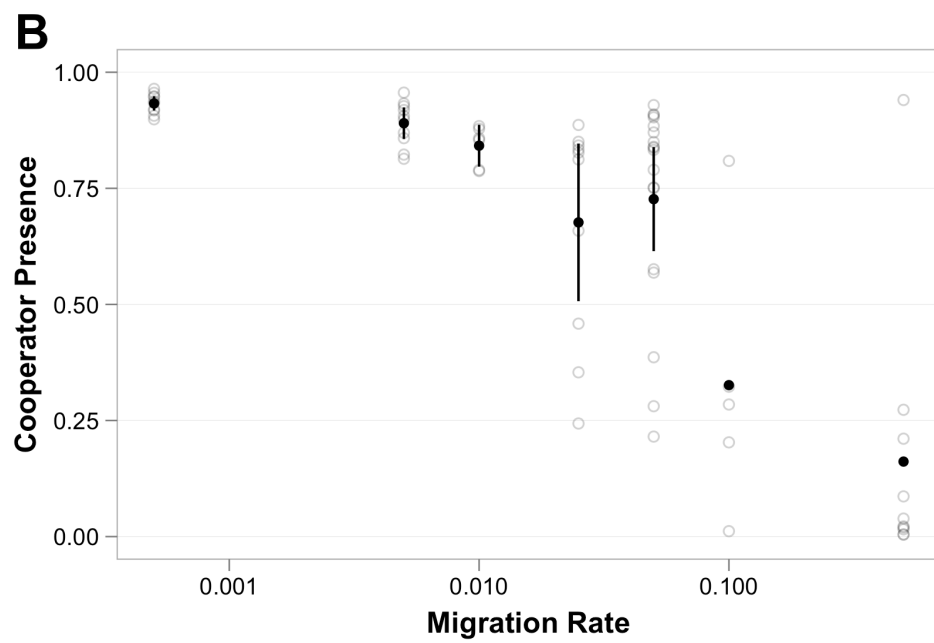


Figure 8: Will share caption with 6A

Table 1: Model parameters and their value

Parameter	Description	Base Value
N^2	Number of metapopulation sites	625
L	Number of adaptive loci	5
A	Number of alleles	6
δ	Fitness benefit, nonzero alleles	0.3
c	Production cost	0.1
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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