

# 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 co-  
71 operators and defectors compete and evolve in a metapopulation (a collection  
72 of populations). Individuals in each of the populations reproduce, mutate, and  
73 migrate to neighboring populations. Importantly, adaptation that is indepen-  
74 dent of cooperation can occur. In our model here, we further allow populations  
75 to modify their local environment, and these modifications feed back to affect  
76 selection.

## 77 **Model Description**

78 Our simulated environment consists of  $N^2$  patches arranged as an  $N \times N$  lattice  
79 (see [Table 1](#) for model parameters and their values), where each patch can  
80 support a population. Each individual in a population has a genotype, which  
81 is an ordered list of  $L + 1$  integers (loci). The first  $L$  loci are *adaptive loci*,  
82 and are each occupied by 0 or an integer from the set  $\{1, 2, \dots, A\}$ , where  $A$  is  
83 the number of alleles conferring a selective benefit. Specifically, the presence  
84 of a non-zero allele at any of these loci represents an adaptation that confers

85 fitness benefit  $\delta$ . A binary allele at locus  $L + 1$  determines whether or not  
86 that individual is a cooperator. Individuals with allelic state 1 at this locus  
87 are cooperators, carrying a cost  $c$ , while individuals with allelic state 0 are  
88 defectors. When  $\delta \geq c$ , a minimally adapted cooperator recoups the cost of  
89 cooperation.

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

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

99 Where  $\text{mod}_Y(y)$  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  $\beta(l, L)$ , which we represent as  $n(a, l)$  below.  
102 The slope of this increase is  $\epsilon$ , which specifies the intensity of niche construction.  
103 Consider a genotype  $g$  with allelic state at locus  $l$  given by  $a_{g,l}$ ; its fitness is  
104 defined as:

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

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

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

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

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

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

118 The function  $S(p)$  reflects the benefit of public good production. A popu-  
 119 lation composed entirely of defectors reaches size  $S_{min}$ , while one composed

entirely of cooperators reaches size  $S_{max}$  (with  $S_{max} \geq S_{min}$ ). During growth, individuals compete for inclusion in the resulting population. The composition 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  $\pi_i$  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  $\mu_a$ , 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  $\mu_c$ . 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

138 patch’s Moore neighborhood, which is composed of the nearest 8 patches on the  
139 lattice. Because the metapopulation lattice has boundaries, patches located  
140 on an edge have smaller neighborhoods.

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

## 154 **Source Code and Software Environment**

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



## Results

We use the model described earlier to follow the evolution of cooperation in a metapopulation of populations that are connected by spatially-limited migration. Individuals in these populations gain a limited number of adaptations that confer selective benefits. Adaptation is independent of cooperation. However, because cooperation increases population density, these populations have more mutational opportunities to gain adaptations. Cooperation can hitchhike along with these adaptations, which compensate for the cost of public good production. During this process, individuals also alter their environment based on the genotypes present in the population. This niche construction process can be either positive or negative, depending on its effects on fitness. Here, we explore how niche construction can favor the evolution of cooperation. Our simulation environment is defined by the parameter values listed in [Table 1](#).

### Niche Construction Maintains Cooperation

Without the opportunity for adaptation ( $L = 0$ ), cooperators are swiftly eliminated in competition with defectors (Figure 1). Despite an initial lift due to increased productivity, the cost of cooperation becomes disadvantageous as migration mixes the initially isolated populations. With adaptive opportunities ( $L = 5$ ,  $\epsilon = 0$ ), cooperators are maintained transiently (Figure 1B). Here, the additional mutational abilities provided by their larger sizes allows cooperator populations to more quickly adapt to their environment. As previously described by Hammarlund et al. (2015), however, this advantage diminishes

181 as defector populations become equally adapted, and cooperators are outcom-  
 182 peted. When populations affect their environment and these changes feed  
 183 back on selection, we find that cooperation can persist, perhaps indefinitely  
 184 (Figure 1C, 3A). In these environments, cooperators maintain higher fitness  
 185 than cooperators, which enables survival (Figure 3A).

## 186 **Fitness Increases do not Support Cooperation**

187 In our model, niche construction provides additional selective benefits. To  
 188 determine how these selective effects contribute to our results, we performed  
 189 simulations in which the selective effects of niche construction were removed  
 190 ( $\epsilon = 0$ ). As compensation, we increased the fitness benefits conferred by adap-  
 191 tation ( $\delta = 0.6$ ). Here, the selective effects of niche construction are exag-  
 192 gerated, as a fitness benefit of 0.3 (our increase in  $\delta$ ) is the maximum value  
 193 possible (see 2). To quantify cooperator success and permit comparison, we  
 194 use the area under the cooperator proportion curve. This measure of *coop-*  
 195 *erator presence* increases as cooperators rise in abundance or remain in the  
 196 population longer.

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

## 202 **Positive Niche Construction Prolongs Cooperation but** 203 **is not Sufficient**

204 We first focus on the effects of positive niche construction by removing the  
205 allelic conflict that leads to negative niche construction ( $L = 5$ ,  $A = 5$ ). In the  
206 absence of this conflict, cooperator presence is significantly increased (Figure  
207 2, column D). Within these environments, we find that positive niche con-  
208 struction prolongs the fitness advantage that cooperators have over defectors  
209 (Figure 3C). Nevertheless, cooperators are eventually driven to extinction once  
210 defectors gain the fitness advantage.

## 211 **Negative Niche Construction is not Sufficient**

212 To determine how negative niche construction influences the evolution of co-  
213 operation, we maximize the allelic conflict ( $L = 1$ ,  $A = 6$ ). However, selection  
214 for increasing allelic states among the stress loci means that any allelic state  
215 will not be greater than at the previous allele (itself), and thus there will al-  
216 ways be opportunity for adaptation. Despite this constant opportunity, niche  
217 construction does not increase cooperator presence (Figure 2, column E). Here,  
218 defectors rapidly gain the fitness advantage.

## 219 **NC Enables Cooperator Spread**

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

## 221 NC Prevents Defector Invasion

222 Figure 5

## 223 How Public Good Fuels all of this

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

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

## 234 # Discussion

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

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

245 Our results reveal that with niche construction, cooperation can indeed persist  
246 (Figure 1C). But what it is about this process that maintains cooperation?

247 In our model, niche construction introduces additional selective effects that  
248 could influence the evolutionary process. However, simply raising the selective  
249 benefits provided by adaptations does not significantly increase cooperator  
250 presence (Figure 2, columns C and A), and indicates that niche construction  
251 plays an important role. Although cooperators benefit greatly from positive  
252 niche construction, it does not fully explain our results (Figure 2 D). Indeed,  
253 despite an initial increase in abundance, cooperators are eventually driven to  
254 extinction when environmental change produces only positive fitness effects  
255 (Figure 1D). As with the “Hankshaw effect”, adaption eventually slows, al-  
256 lowing defectors to outcompete cooperators (Figure 3C). While it does not  
257 benefit cooperation when alone (Figure 3E), negative niche construction acts  
258 to prevent this stasis. Combined, we find that both positive and negative niche  
259 construction are required to main cooperation.

260 When successful, we observe that populations do not reach the maximum pos-  
261 sible fitness (Figure 3A). Although cooperation is the focus of this study, it  
262 can be seen as deleterious. Previous work has shown that niche construction  
263 can favor deleterious alleles (Laland *et al.*, 1996, 1999). Similarly here, coop-  
264 eration is maintained in the presence of niche construction, but lost otherwise  
265 (Figure 2). Van Dyken and Wade (2012) showed that when two cooperative  
266 behaviors co-evolve and niche construction feedbacks benefit the other type,

267 niche construction can increasingly favor these traits, which were otherwise  
268 disfavored when alone.

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

277 In our model, the environmental state was implicitly modeled, and depended  
278 solely on the current state of the population. In natural settings, however, the  
279 timescales at which environments are modified and reproduction are likely to  
280 be decoupled. For example, a multitude of factors including protein durabil-  
281 ity (Brown and Taddei, 2007; Kümmerli and Brown, 2010), diffusion (Allison,  
282 2005; Driscoll and Pepper, 2010), and resource availability (Zhang and Rainey,  
283 2013; Ghoul *et al.*, 2014) influence both the rate and the degree to which public  
284 goods alter the environment. These factors are likely to influence evolution-  
285 ary trajectories (Laland *et al.*, 1996). Lehmann (2007) demonstrated that a  
286 cooperative, niche constructing behavior can be favored when it only affected  
287 selection for future generations, thus reducing the potential for competition  
288 among contemporary kin. The evolutionary inertia that this creates, however,  
289 may ultimately work against cooperators. When public good accumulates in  
290 the environment, cooperators must reduce their investment in production to re-

291 main competitive (Kümmerli and Brown, 2010; Dumas and Kümmerli, 2012).  
292 Cooperation that occurs facultatively, perhaps by sensing the abiotic (Bernier  
293 *et al.*, 2011; Koestler and Waters, 2014) or biotic environment (Brown and  
294 Johnstone, 2001; Darch *et al.*, 2012), are likely to be favored in these fluctuat-  
295 ing environments.

296 In many instances of cooperation, the environment is itself a biological entity,  
297 which can produce additional evolutionary feedbacks. As the host population  
298 changes, so too will selection on their symbiont populations. Here, evolution-  
299 ary outcomes depend greatly on the degree of shared interest between the host  
300 and symbiont. For example, the cooperative production of virulence factors  
301 by the human pathogen *P. aeruginosa* in lung infections is harmful to those  
302 with cystic fibrosis (Harrison, 2007). Conversely, cooperative light produc-  
303 tion by *A. fischeri* is vital for the survival of its host, the Hawaiian bobtail  
304 squid (Ruby, 1996). It was recently argued that incorporating the effects of  
305 niche construction is critical for improving our understanding of viral evolu-  
306 tion (Hamblin *et al.*, 2014) and evolution in co-infecting parasites (Hafer and  
307 Milinski, 2015). Incorporating host dynamics, co-evolution, and the feedbacks  
308 that they produce into models is likely to be equally important for gaining  
309 an understanding of how cooperative behaviors evolve in these host-symbiont  
310 settings. # Acknowledgments

- 311 • TODO: Organizers?
- 312 • TODO: lab comments

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318 and do not necessarily reflect the views of the National Science Foundation.  
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## 321 Figures

322 **Figure 1**

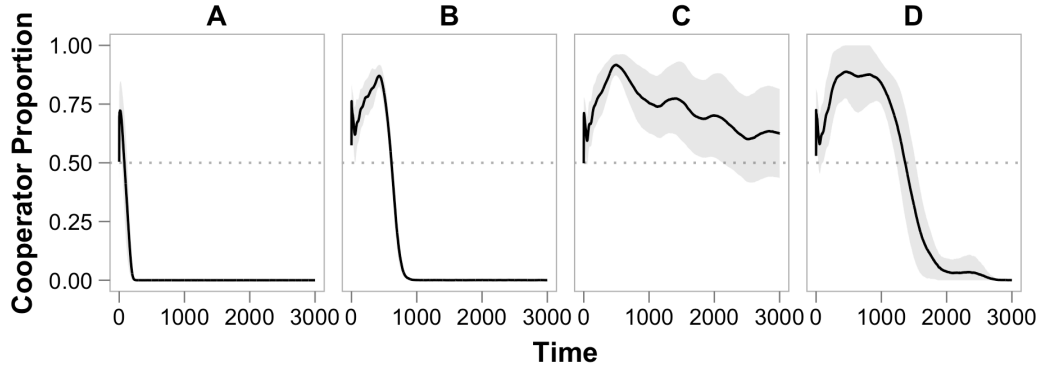
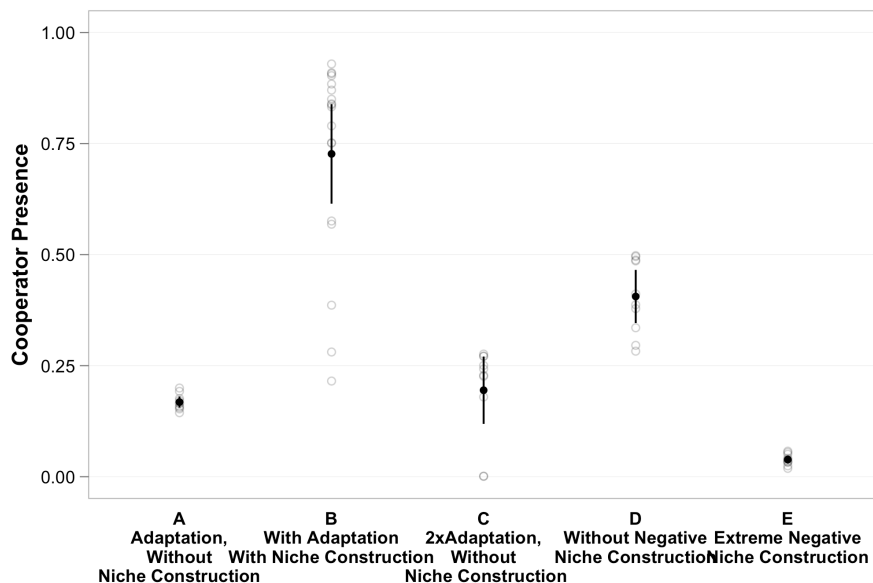


Figure 1: **Adaptation, niche construction, and the evolution of co-operation.** Curves show the average cooperator proportion among replicate populations, while shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter values used are listed in [Table 1](#). **(A)** When there 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 ( $\epsilon$ , the intensity of niche construction, is zero), cooperators temporarily rise in abundance before eventually going extinct. **(C)** Selective feedbacks from niche construction allows cooperation to be maintained in 13 of 18 replicate populations. **(D)** While it does contribute to success, positive niche construction alone does not maintain cooperation ( $A = 5$ ).

323 **Figure 2**



**Figure 2: Evolutionary Processes and their Effect on Cooperator Presence.** For each process shown, the cooperator presence among each replicate population is shown as an open circle. Their mean is showed as a filled circle, and bars indicate 95% confidence intervals. **(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.

324 **Figure 3**

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

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

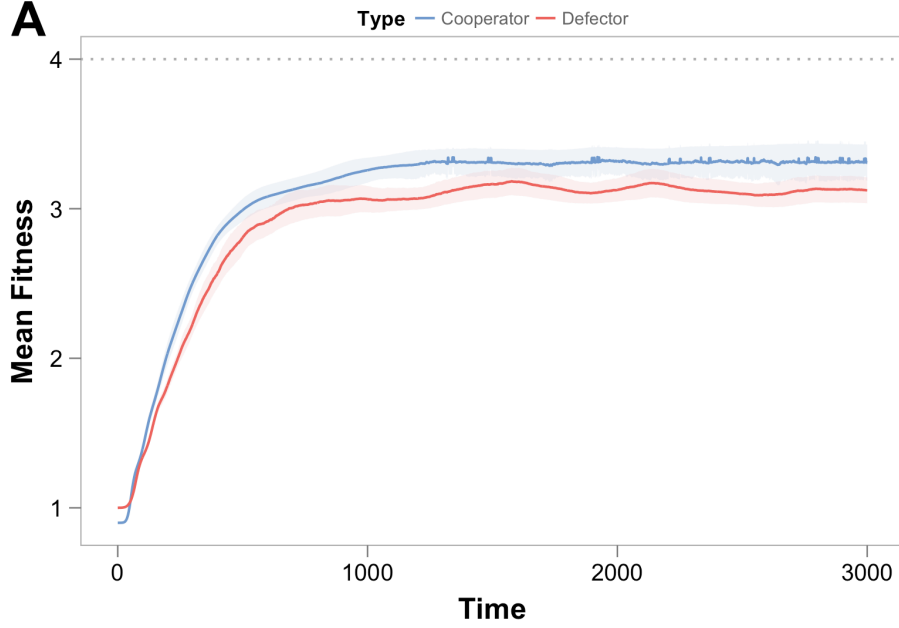


Figure 3: **Fitness Effects of Mutation Accumulation by Cooperators and Defectors.** Lines indicate the grand mean of cooperator (blue) and defector (red) fitness among replicate populations, while shaded areas indicate 95% confidence intervals. Dashed lines indicate the maximum fitness values achievable 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.

327 **Figure 3B**

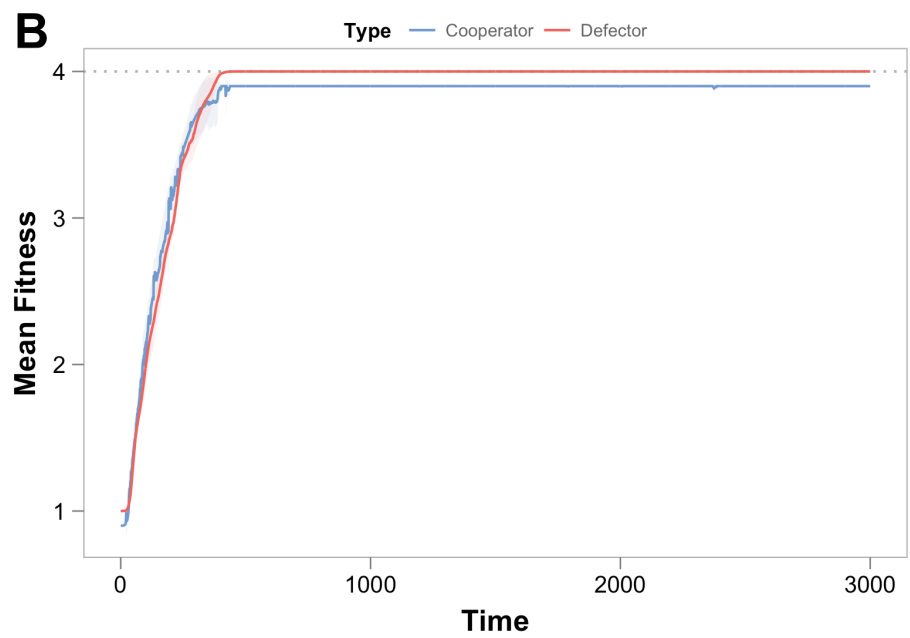


Figure 4: Will share caption with 3A

328 **Figure 3C**

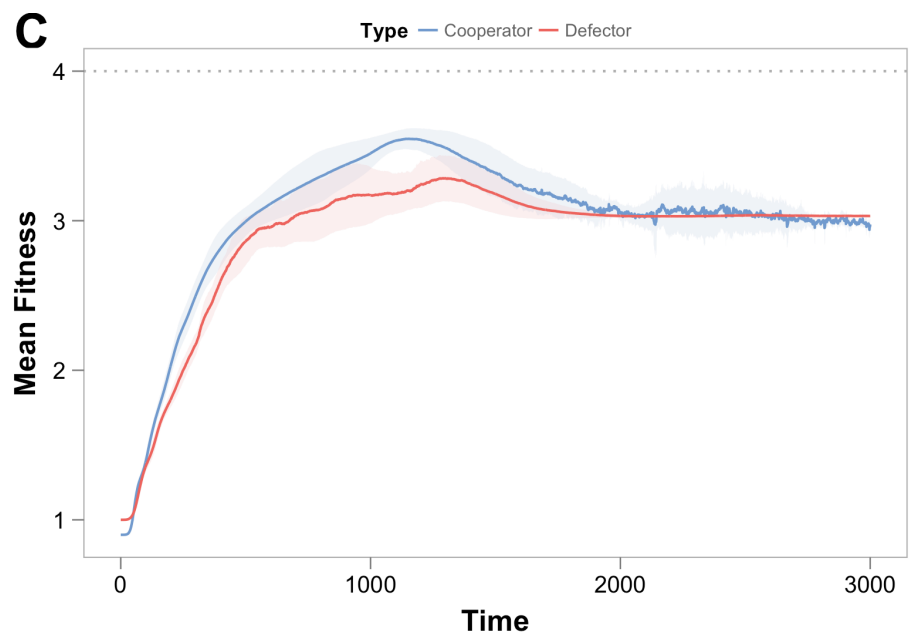


Figure 5: Will share caption with 3A

329 **Figure 3D**

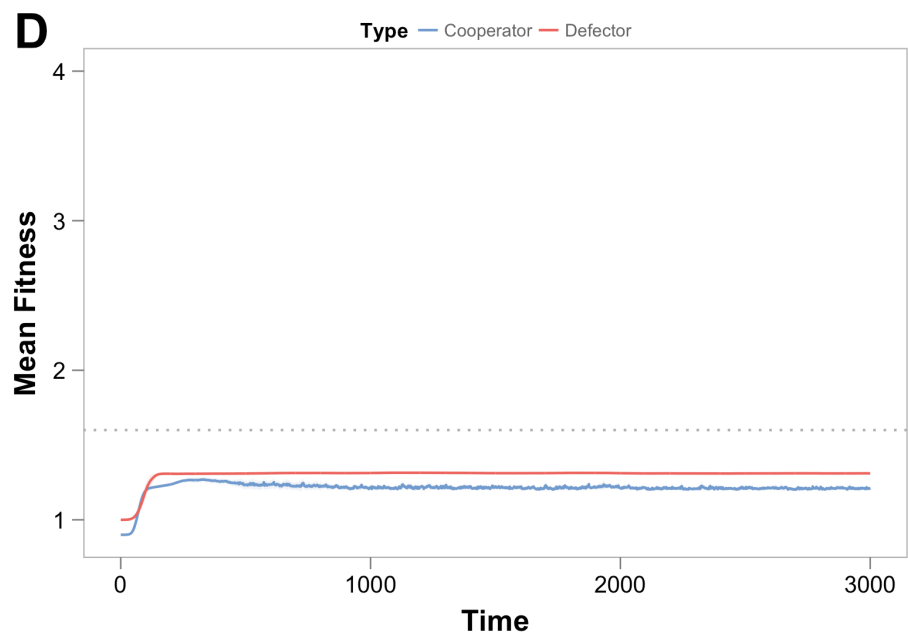


Figure 6: Will share caption with 3A

330 **Figure 4**

331 Cooperators invade defector population. Fully adapted but mismatched. Neg-  
332 ative NC.

333 **Figure 5**

334 Defectors invade cooperator population. Fully adapted and matched. Role of  
335 Export.

336 **Figure 6**

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

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



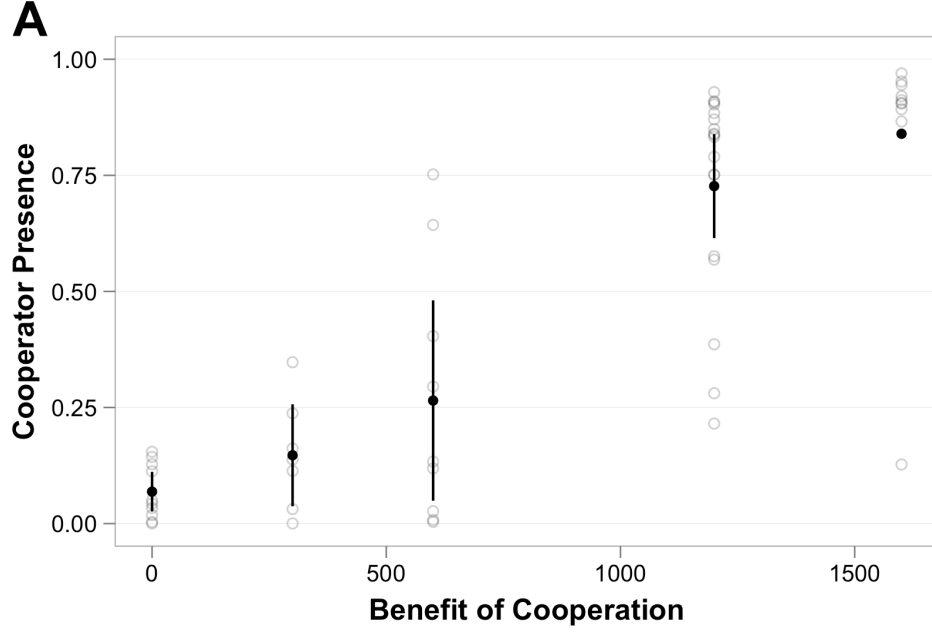


Figure 7: **Cooperator Presence as a Function of Population Size and Migration Rate.** Cooperator presence for each replicate population is shown as an open circle. The mean among these replicates is represented by a filled circle, and bars indicate 95% confidence intervals. **(A)** Cooperator presence 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.

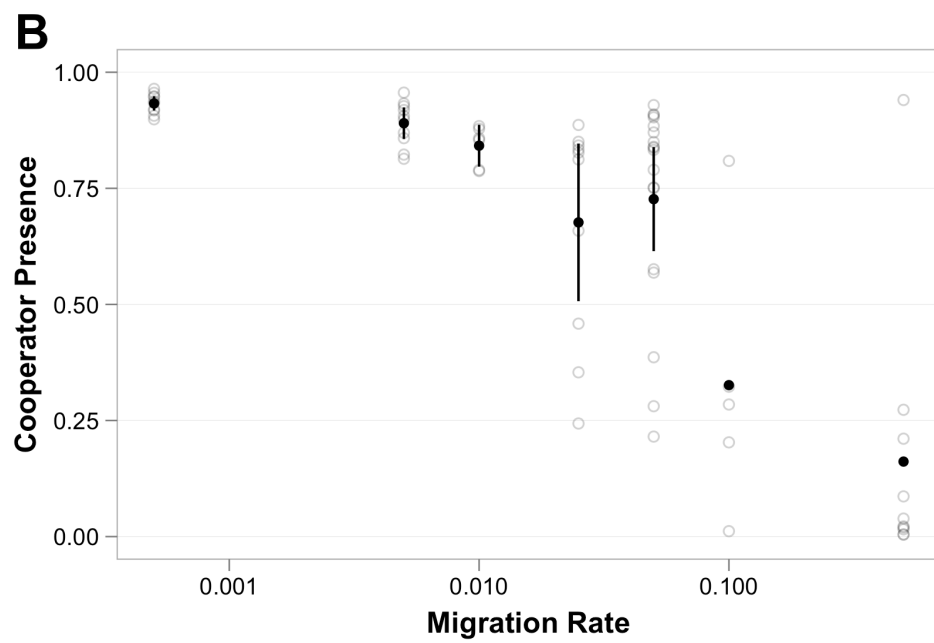


Figure 8: Will share caption with 6A

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
$\delta$	Fitness benefit, nonzero alleles	0.3
$c$	Production cost	0.1
$\epsilon$	Fitness benefit, sequential alleles	0.00015
$z$	Baseline fitness	1
$S_{min}$	Minimum population size	800
$S_{max}$	Maximum population size	2000
$\mu_a$	Mutation rate (adaptation)	$10^{-5}$
$\mu_c$	Mutation rate (cooperation)	$10^{-5}$
$m$	Migration rate	0.05
$p_0$	Initial cooperator proportion	0.5
$\mu_t$	Mutation rate (tolerance to new environment)	$10^{-5}$
$T$	Number of simulation cycles	1000
$d$	Population dilution factor	0.1

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