

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

85 that confers fitness benefit δ . A binary allele at locus $L+1$ determines whether
 86 or not that individual is a cooperator. Individuals with allelic state 1 at this
 87 locus are cooperators, carrying a cost c , while individuals with allelic state 0
 88 are defectors. When $\delta \geq c$, a minimally adapted cooperator recoups the cost
 89 of cooperation. Equation 1 defines function $n(a, l)$, which gives the number
 90 of individuals in the population with allelic state a at locus l . $I_x(y)$ indicates
 91 whether the allelic state y matches allelic state x (1) or not (0), and $\gamma(i)$ is
 92 the genotype of individual i .

$$n(a, l) = \sum_{i \in P} I_{a_{\gamma(i), l}}(a_{\gamma(i), l}) \quad (1)$$

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

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

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

$$W_g = z + \delta \sum_{l=1}^L I_A(a_{g,l}) + \epsilon \sum_{l=1}^L n(\beta(a_{g,l}, a_{max}), \beta(l, L)) - ca_{g,L+1} \quad (3)$$

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

$$I_A(a) = \begin{cases} 1 & \text{if } a \in A \\ 0 & \text{otherwise} \end{cases} \quad (4)$$

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

115 Cooperators produce a public good that is equally accessible to all members
 116 of the population. This public good increases the carrying capacity at that
 117 patch, allowing the population to reach greater density. This benefit increases
 118 linearly with the proportion of cooperators. Thus, if p is the proportion of
 119 cooperators in a population at the beginning of a growth cycle, then that

120 population reaches the following size during the growth phase:

$$S(p) = S_{min} + p(S_{max} - S_{min}) \quad (5)$$

121 The function $S(p)$ reflects the benefit of public good production. A population
 122 composed entirely of defectors reaches size S_{min} , while one composed entirely
 123 of cooperators reaches size S_{max} (with $S_{max} \geq S_{min}$). During growth, indi-
 124 viduals compete for inclusion in the resulting population. The composition of
 125 population P with cooperator proportion p after growth is multinomial with
 126 parameters and $S(p)$ and $\{\pi_1, \pi_2, \dots, \pi_{|P|}\}$, where:

$$\pi_i = \frac{W_{\gamma(i)}}{\sum_{j \in P} W_{\gamma(j)}} \quad (6)$$

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

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

$$\tau_{g \rightarrow g'} = \mu_a^{H_a(g, g')}(1 - \mu_a)^{\{L - H_a(g, g')\}} \mu_c^{H_c(g, g')}(1 - \mu_c)^{\{1 - H_c(g, g')\}} \quad (7)$$

136 where $H_a(g, g')$ and $H_c(g, g')$ are the Hamming distances between genotypes g
 137 and g' at the cooperation locus and adaptive loci, respectively. The Hamming
 138 distance is the number of loci at which allelic states differ (Hamming, 1950).
 139 After mutation, individuals emigrate to an adjacent patch at rate m . The
 140 destination patch is randomly chosen with uniform probability from the source
 141 patch's Moore neighborhood, which is composed of the nearest 8 patches on the
 142 lattice. Because the metapopulation lattice has boundaries, patches located
 143 on an edge have smaller neighborhoods.
 144 Metapopulations are initiated in a state that follows an environmental change.
 145 First, populations are seeded at all patches with cooperator proportion p_0 and
 146 grown to density $S(p_0)$. An environmental challenge is then introduced, which
 147 subjects the population to a bottleneck. For each individual, the probability
 148 of survival is μ_t , which represents the likelihood that a mutation occurs that
 149 confers tolerance. Survivors are chosen by binomial sampling. Because indi-
 150 viduals have not yet adapted to this new environment, the allelic state of each
 151 individual's genotype is set to 0 at each adaptive locus. Following initializa-
 152 tion, simulations are run for T cycles, where each discrete cycle consists of
 153 growth, mutation, and migration. At the end of each cycle, populations are
 154 thinned to allow for growth in the next cycle. The individuals that remain are
 155 chosen by binomial sampling, where each individual persists with probability
 156 d , regardless of allelic state.

157 Source Code and Software Environment

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

162 Results

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

175 **Niche Construction Maintains Cooperation**

176 Without the opportunity for adaptation ($L = 0$), cooperators are swiftly elim-
177 inated in competition with defectors (Figure 1). Despite an initial lift due to
178 increased productivity, the cost of cooperation becomes disadvantageous as
179 migration mixes the initially isolated populations. With adaptive opportuni-
180 ties ($L = 5$, $\epsilon = 0$), cooperators are maintained transiently (Figure 1B). Here,
181 the additional mutational abilities provided by their larger sizes allows coop-
182 erator populations to more quickly adapt to their environment. As previously
183 described by Hammarlund et al. (2015), however, this advantage diminishes
184 as defector populations become equally adapted, and cooperators are outcom-
185 peted. When populations affect their environment and these changes feed
186 back on selection, we find that cooperation can persist, perhaps indefinitely
187 (Figure 1C, 3A). In these environments, cooperators maintain higher fitness
188 than cooperators, which enables survival (Figure 3A).

189 **Fitness Increases do not Support Cooperation**

190 In our model, niche construction provides additional selective benefits. To
191 determine how these selective effects contribute to our results, we performed
192 simulations in which the selective effects of niche construction were removed
193 ($\epsilon = 0$). As compensation, we increased the fitness benefits conferred by adap-
194 tation ($\delta = 0.6$). Here, the selective effects of niche construction are exag-
195 gerated, as a fitness benefit of 0.3 (our increase in δ) is the maximum value
196 possible (see 3). To quantify cooperator success and permit comparison, we

197 use the area under the cooperator proportion curve. This measure of *coop-*
198 *erator presence* increases as cooperators rise in abundance or remain in the
199 population longer.

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

205 **Positive Niche Construction Prolongs Cooperation but** 206 **is not Sufficient**

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

214 **Negative Niche Construction is not Sufficient**

215 To determine how negative niche construction influences the evolution of coop-
216 eration, we maximize the allelic conflict ($L = 1$, $a_{max} = 6$). However, selection

217 for increasing allelic states among the stress loci means that any allelic state
218 will not be greater than at the previous allele (itself), and thus there will al-
219 ways be opportunity for adaptation. Despite this constant opportunity, niche
220 construction does not increase cooperator presence (Figure 2, column E). Here,
221 defectors rapidly gain the fitness advantage.

222 **NC Enables Cooperator Spread**

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

224 **NC Prevents Defector Invasion**

225 Figure 5

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

227 To directly explore how the increase in population size affects evolutionary
228 outcomes, we vary the maximum size that a population can reach (S_{max} , see
229 Equation 5). Figure 6A shows the result of these simulations. (**TODO** de-
230 scription of results)

231 To address how migration affects the evolutionary process in this system, we
232 vary the rate at which migration occurs (m). As seen in Figure 6B, cooperation
233 decreases as migration rate increases. This is likely because migration defines
234 the spatial structuring in this system. As migration increases, the population
235 becomes more like a well-mixed system, where defectors are better able to

236 exploit the benefits of cooperation (Griffin *et al.*, 2004; Kümmerli *et al.*, 2009).

237 # Discussion

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

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

benefit cooperation when alone (Figure 3E), negative niche construction acts to prevent this stasis. Combined, we find that both positive and negative niche construction are required to maintain cooperation.

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

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

In our model, the environmental state was implicitly modeled, and depended solely on the current state of the population. In natural settings, however, the timescales at which environments are modified and reproduction are likely to

283 be decoupled. For example, a multitude of factors including protein durabil-
284 ity (Brown and Taddei, 2007; Kümmerli and Brown, 2010), diffusion (Allison,
285 2005; Driscoll and Pepper, 2010), and resource availability (Zhang and Rainey,
286 2013; Ghoul *et al.*, 2014) influence both the rate and the degree to which public
287 goods alter the environment. These factors are likely to influence evolution-
288 ary trajectories (Laland *et al.*, 1996). Lehmann (2007) demonstrated that a
289 cooperative, niche constructing behavior can be favored when it only affected
290 selection for future generations, thus reducing the potential for competition
291 among contemporary kin. The evolutionary inertia that this creates, however,
292 may ultimately work against cooperators. When public good accumulates in
293 the environment, cooperators must reduce their investment in production to re-
294 main competitive (Kümmerli and Brown, 2010; Dumas and Kümmerli, 2012).
295 Cooperation that occurs facultatively, perhaps by sensing the abiotic (Bernier
296 *et al.*, 2011; Koestler and Waters, 2014) or biotic environment (Brown and
297 Johnstone, 2001; Darch *et al.*, 2012), are likely to be favored in these fluctuat-
298 ing environments.

299 In many instances of cooperation, the environment is itself a biological entity,
300 which can produce additional evolutionary feedbacks. As the host population
301 changes, so too will selection on their symbiont populations. Here, evolution-
302 ary outcomes depend greatly on the degree of shared interest between the host
303 and symbiont. For example, the cooperative production of virulence factors
304 by the human pathogen *P. aeruginosa* in lung infections is harmful to those
305 with cystic fibrosis (Harrison, 2007). Conversely, cooperative light produc-
306 tion by *A. fischeri* is vital for the survival of its host, the Hawaiian bobtail

307 squid (Ruby, 1996). It was recently argued that incorporating the effects of
308 niche construction is critical for improving our understanding of viral evolu-
309 tion (Hamblin *et al.*, 2014) and evolution in co-infecting parasites (Hafer and
310 Milinski, 2015). Incorporating host dynamics, co-evolution, and the feedbacks
311 that they produce into models is likely to be equally important for gaining
312 an understanding of how cooperative behaviors evolve in these host-symbiont
313 settings. # Acknowledgments

- 314 • TODO: Organizers?
- 315 • TODO: lab comments

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324 Figures

325 **Figure 1**

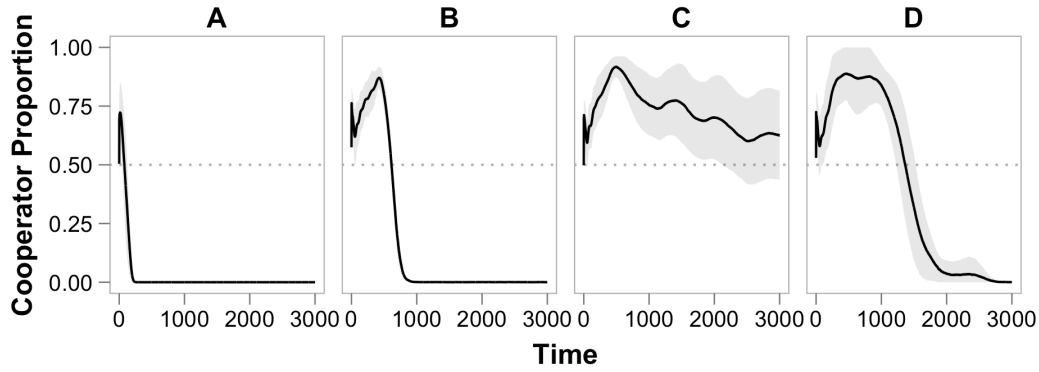


Figure 1: **Adaptation, niche construction, and the evolution of co-operation.** Curves show the average cooperator proportion among replicate populations, while shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter values used are listed in [Table 1](#). **(A)** When there 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 (ϵ , 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 ($A = 5$).

326 **Figure 2**

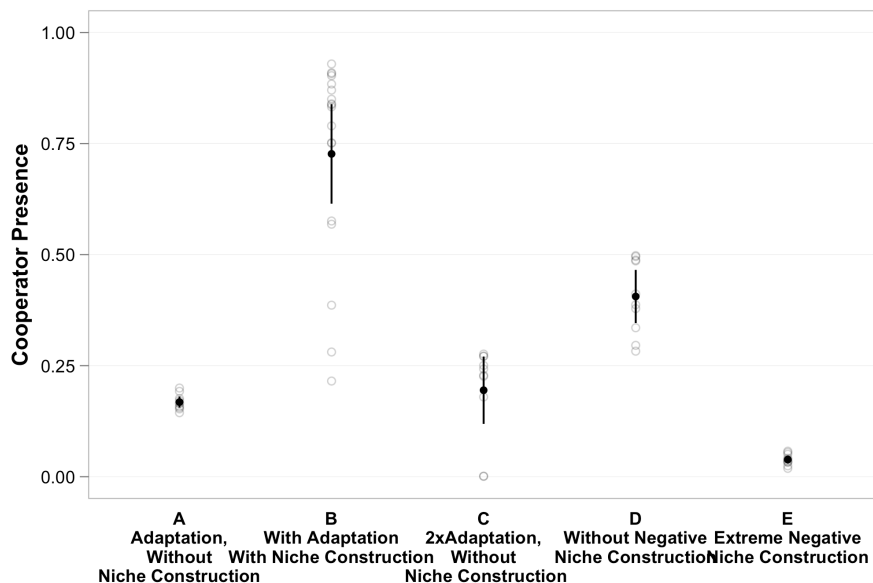


Figure 2: Evolutionary Processes and their Effect on Cooperator Presence. For each process shown, the cooperator presence among each replicate population is shown as an open circle. Their mean is showed as a filled circle, and bars indicate 95% confidence intervals. **(A)** In our model, adaptations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

327 **Figure 3**

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

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

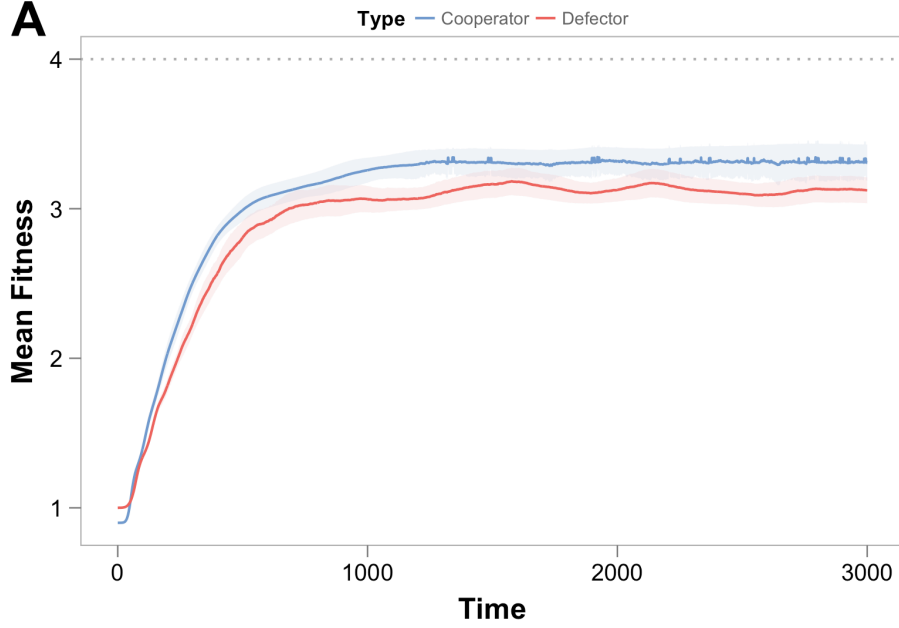


Figure 3: **Fitness Effects of Mutation Accumulation by Cooperators and Defectors.** Lines indicate the grand mean of cooperator (blue) and defector (red) fitness among replicate populations, while shaded areas indicate 95% confidence intervals. Dashed lines indicate the maximum fitness values achievable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

330 **Figure 3B**

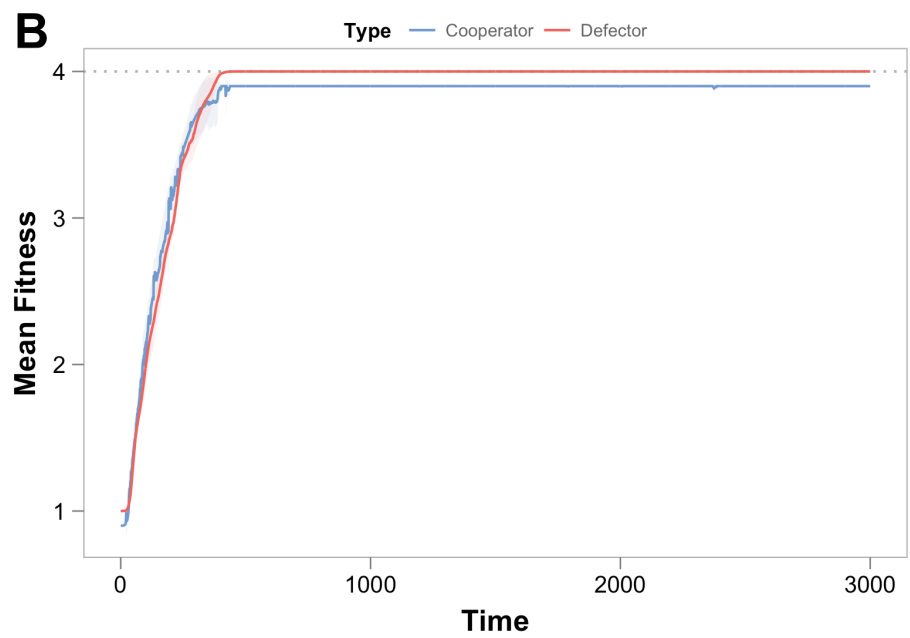


Figure 4: Will share caption with 3A

331 **Figure 3C**

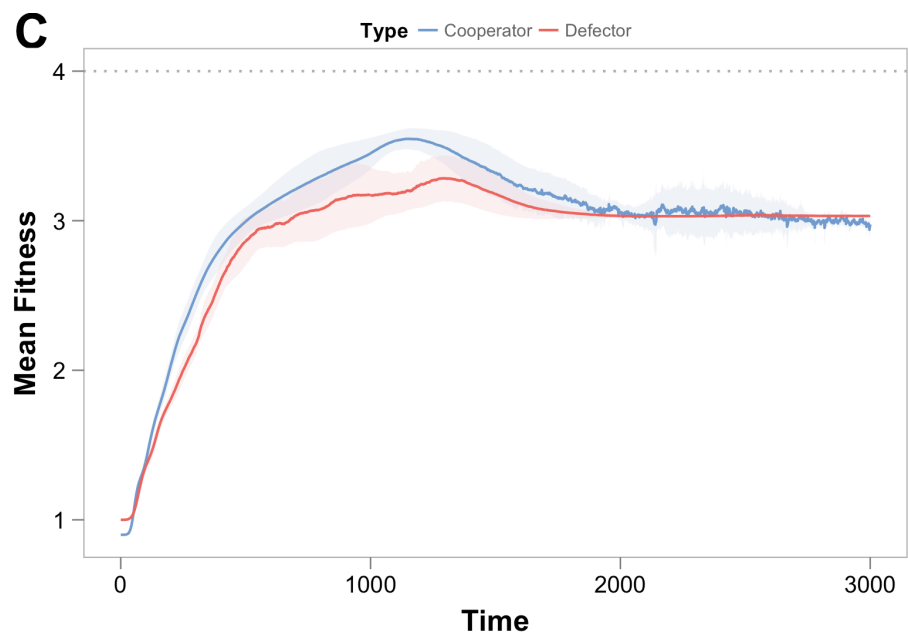


Figure 5: Will share caption with 3A

332 **Figure 3D**

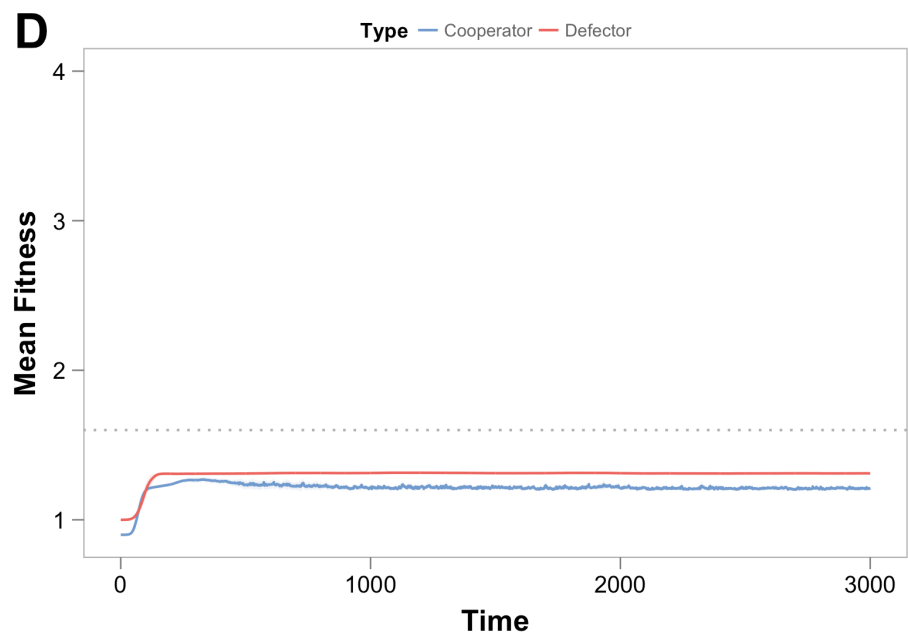


Figure 6: Will share caption with 3A

333 **Figure 4**

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

336 **Figure 5**

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

339 **Figure 6**

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

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

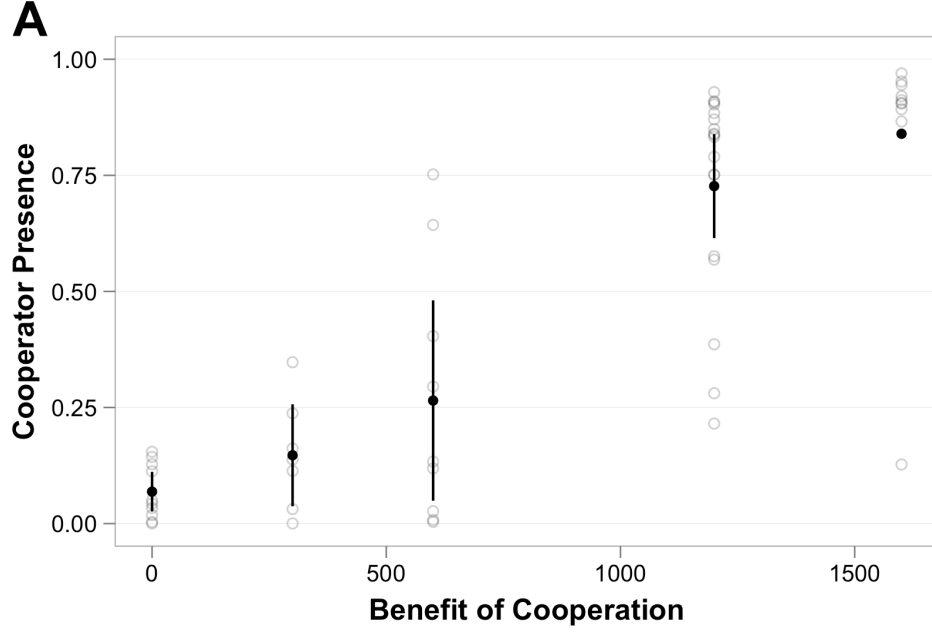


Figure 7: **Cooperator Presence as a Function of Population Size and Migration Rate.** Cooperator presence for each replicate population is shown as an open circle. The mean among these replicates is represented by a filled circle, and bars indicate 95% confidence intervals. **(A)** Cooperator presence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

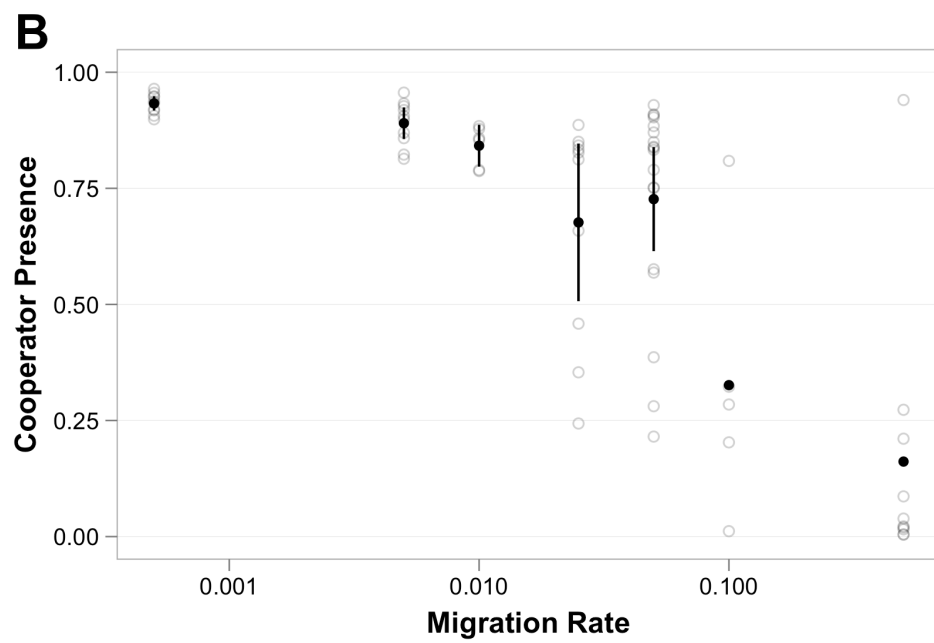


Figure 8: Will share caption with 6A

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_{max}	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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