

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

4 TODO

5 **Abstract**

6 Through their interactions, their activities, and even their mere pres-
7 ence, organisms change the environment for themselves and others. This
8 “niche construction” process becomes particularly interesting when it
9 creates evolutionary feedback, whereby selective pressures are altered
10 in response to environmental change. Here we consider how niche con-
11 struction influences the evolution of cooperation, which has been a long-
12 standing challenge to evolutionary theory. We simulate populations of
13 individuals that cooperatively produce a public good that permits in-
14 creased growth in a stressful environment and investigate how local- and
15 global-scale niche construction affects the ability of these populations
16 to resist invasion by non-producing cheats. We find that niche construc-
17 tion profoundly impacts the evolution of cooperation by creating new
18 opportunities for adaptation. Cooperators are able to escape subversion

19 by cheats as long as niche construction clears these paths of adaptation.
20 This work provides a crucial step towards understanding how evolution
21 occurs in complex environments like those found in nature.

22 Introduction

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

32 Several factors can prevent this *tragedy of the commons* (Hamilton, 1964;
33 Hardin, 1968; Nowak, 2006; West *et al.*, 2007b). For example, cooperators
34 must benefit more from the cooperative act than others. This can occur when
35 cooperators are clustered together in spatially structured populations (Fletcher
36 and Doebeli, 2009; Nadell *et al.*, 2010; Kuzdzal-Fick *et al.*, 2011) or when co-
37 operators use communication (Brown and Johnstone, 2001; Darch *et al.*, 2012)
38 or other cues (Sinervo *et al.*, 2006; Gardner and West, 2010; Veelders *et al.*,
39 2010) to cooperate conditionally with kin. Interestingly, cooperation can also
40 be bolstered by genetic linkage with self-benefitting traits (Foster *et al.*, 2004;

41 Dandekar *et al.*, 2012; Asfahl *et al.*, 2015), setting the stage for an “adap-
42 tive race” in which cooperators and defectors vie for the first highly-beneficial
43 adaptation (Waite and Shou, 2012; Morgan *et al.*, 2012).

44 Hammarlund et al. (2015) recently showed that in spatially structured popula-
45 tions, cooperators can gain a substantial leg up on defectors in an adaptive race.
46 Specifically, cooperative behavior increases local population density, thus in-
47 creasing the likelihood of acquiring beneficial mutations. By hitchhiking along
48 with these adaptations, the cooperative trait can rapidly rise in abundance.
49 Nevertheless, this advantage is fleeting. As soon as the opportunities for adap-
50 tation are exhausted, cooperators are once again at a disadvantage against
51 defectors. However, Hammarlund et al. (2015) demonstrated that coopera-
52 tion can be maintained indefinitely when frequent environmental changes pro-
53 duce a steady stream of adaptive opportunities. Although organisms typically
54 find themselves in dynamic environments, change might not occur at a rate
55 that provides sufficient adaptive opportunities to ensure long-term cooperator
56 persistence.

57 In this work, we demonstrate how cooperation can be maintained indefinitely
58 by niche construction. We expand upon the model presented in Hammarlund
59 et al. (2015) to allow populations to alter their local environment. As environ-
60 ments change, so too does selection. This creates an eco-evolutionary feedback
61 whereby selection is dependent on current genotypes, and the composition of
62 genotypes is dependent on selection. Niche construction can be positive or neg-
63 ative, depending on whether the environmental change increases or decreases
64 the fitness of the niche-constructing individual. Although niche construction

65 occurs independently of cooperation in our model, the increase in density that
66 results from cooperation has a profound effect on how populations evolve in
67 the presence of selective feedbacks. First, these populations exert greater in-
68 fluence on their environments, which better enables them to benefit from posi-
69 tive niche construction. And as environments change, either through negative
70 niche construction or external influences, these larger populations can adapt
71 more quickly. We show that it is the combination of these factors that allows
72 cooperation to persist.

73 **Stuff to be cut/integrated above**

74 As populations construct unique niches, they potentially decrease the threat
75 of invasion from neighboring patches. This occurs when the traits that were
76 advantageous in an immigrant’s home niche are maladaptive elsewhere. Be-
77 cause environmental change is influenced solely by non-social phenotypes in
78 this model, this change of invasibility affects cooperators and defectors equally.
79 Here again, however, populations containing a greater number of cooperators
80 may have an advantage. The greater number of individuals that emigrate from
81 these larger populations allow them to “export” their niche—and thus reduce
82 the fitness of neighboring competitors—at a higher rate. We explore whether
83 the range expansion that this process enables provides additional opportunities
84 for cooperation to hitchhike.

85 Finally, we demonstrate how *negative* niche construction, where populations
86 change their environment in ways that reduce fitness, can further support

87 cooperation. Even though the niche construction process creates selective
88 feedbacks, we would expect the magnitude of these feedbacks to decrease as
89 populations evolve. Once individuals can no longer gain adaptations that
90 compensate for the costs of cooperation, they are then outcompeted by non-
91 cooperators. However if populations construct their environment in a way
92 which decreases fitness, cooperation can still hitchhike when this change also
93 creates the opportunity to gain compensatory adaptations.

94 **Methods**

95 We build upon the model described in Hammarlund et al. (2015), in which co-
96 operators and defectors compete and evolve in a metapopulation (a collection
97 of populations). Individuals in each of the populations reproduce, mutate, and
98 migrate to neighboring populations. Importantly, adaptation that is indepen-
99 dent of cooperation can occur. In our model here, we further allow populations
100 to modify their local environment, and these modifications feed back to affect
101 selection.

102 **Model Description**

103 Our simulated environment consists of N^2 patches arranged as an $N \times N$
104 lattice (see [Table 1](#) for model parameters and their values), where each patch
105 can support a population. Each individual in a population has a genotype,
106 which is an ordered list of $L + 1$ integers (loci). The first L loci are *adaptive*

107 *loci*, and are each occupied by 0 or an integer from the set $A \equiv \{1, 2, \dots, a_{max}\}$,
 108 where a_{max} is the number of alleles conferring a selective benefit. Specifically,
 109 the presence of a non-zero allele at any of these loci represents an adaptation
 110 that confers fitness benefit δ . A binary allele at locus $L+1$ determines whether
 111 or not that individual is a cooperator. Individuals with allelic state 1 at this
 112 locus are cooperators, carrying a cost c , while individuals with allelic state 0
 113 are defectors. When $\delta \geq c$, a minimally adapted cooperator recoups the cost
 114 of cooperation. Equation 1 defines function $n(a, l)$, which gives the number
 115 of individuals in the population with allelic state a at locus l . $I_x(y)$ indicates
 116 whether the allelic state y matches allelic state x (1) or not (0), and $\gamma(i)$ is
 117 the genotype of individual i .

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

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

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

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

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

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

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

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

Cooperators produce a public good that is equally accessible to all members of the population. This public good increases the carrying capacity at that patch, allowing the population to reach greater density. This benefit increases

linearly with the proportion of cooperators. Thus, if p is the proportion of cooperators in a population at the beginning of a growth cycle, then that population reaches the following size during the growth phase:

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

The function $S(p)$ reflects the benefit of public good production. A population 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 population P with cooperator proportion p after growth is multinomial with parameters $S(p)$ and $\{\pi_1, \pi_2, \dots, \pi_{|P|}\}$, where:

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

Here, $W_{\gamma(i)}$ is the fitness of an individual i with genotype $\gamma(i)$ (see Equation 3). 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 $\{0\} \cup A$. 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:

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

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

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

169 Metapopulations are initiated in a state that follows an environmental change.
 170 First, populations are seeded at all patches with cooperator proportion p_0 and
 171 grown to density $S(p_0)$. An environmental challenge is then introduced, which
 172 subjects the population to a bottleneck. For each individual, the probability
 173 of survival is μ_t , which represents the likelihood that a mutation occurs that
 174 confers tolerance. Survivors are chosen by binomial sampling. Because indi-
 175 viduals have not yet adapted to this new environment, the allelic state of each
 176 individual's genotype is set to 0 at each adaptive locus. Following initializa-
 177 tion, simulations are run for T cycles, where each discrete cycle consists of
 178 growth, mutation, and migration. At the end of each cycle, populations are
 179 thinned to allow for growth in the next cycle. The individuals that remain are
 180 chosen by binomial sampling, where each individual persists with probability
 181 d , regardless of allelic state.

182 Source Code and Software Environment

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

187 Results

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

200 **Niche Construction Maintains Cooperation**

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

214 **Fitness Increases do not Support Cooperation**

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

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

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

230 **Positive Niche Construction Prolongs Cooperation but** 231 **is not Sufficient**

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

239 **Negative Niche Construction is not Sufficient**

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

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

247 **NC Enables Cooperator Spread**

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

249 **NC Prevents Defector Invasion**

250 Figure 5

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

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

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

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

262 # Discussion

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

273 Our results reveal that with niche construction, cooperation can indeed persist
274 (Figure 1C). But what it is it about this process that maintains cooperation?
275 In our model, niche construction introduces additional selective effects that
276 could influence the evolutionary process. However, simply raising the selective
277 benefits provided by adaptations does not significantly increase cooperator
278 presence (Figure 2, columns C and A), and indicates that niche construction
279 plays an important role. Although cooperators benefit greatly from positive
280 niche construction, it does not fully explain our results (Figure 2 D). Indeed,
281 despite an initial increase in abundance, cooperators are eventually driven to
282 extinction when environmental change produces only positive fitness effects
283 (Figure 1D). As with the “Hankshaw effect”, adaption eventually slows, al-
284 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 main cooperation.

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- similarities/differences from previous work
 - Schwilk and Kerr (2002)
 - 10.1073/pnas.0812644106
- negative/positive NC
 - laland1996evolutionary
- public goods as niche construction
- future QS or other environmental sensing
- Facultative cooperation
 - Rodrigues (2012)
 - Dumas and Kümmerli (2010)
 - Kümmerli and Brown (2010)
 - Darch/Diggle
 - QS?
 - Environmental Sensing? - (Koestler and Waters, 2014, Bernier et al. (2011))
- Negative Niche construction as a stragegy? - would those that create this constant pressure (L=5, A=6) do better than those that do not (L=5, A=5)?

307 Niche construction and selective feedbacks Niche construction and other social
308 interactions

309 The production of public goods has played a central role in all of the results that
310 we have presented. By enabling populations to reach larger sizes, these public
311 goods have effectively increased the rate of evolution for these populations. As
312 a result, larger populations are able to gain adaptations more quickly, both in
313 response to their environment and the environmental changes brought about
314 by niche construction. Additionally, these larger populations more effectively
315 “export” their niche. As more individuals migrate to neighboring patches, these
316 emigrants exert greater selective pressure. Here, we examine how population
317 size and migration rate influence these processes.

318 **Public Goods**

319 TODO: merge this in with the “Cooperative Niche Construction” section
320 **TEST**

321 By their very nature, public goods benefit populations by making their environ-
322 ment more hospitable. For example, bacteria produce extracellular products
323 that find soluble iron (Griffin *et al.*, 2004), digest large proteins (Diggle *et al.*,
324 2007; Darch *et al.*, 2012), and reduce the risk of predation (Cosson *et al.*, 2002),
325 among many others (West *et al.*, 2007a). While many studies have explored
326 how the environment affects the evolution of cooperative behaviors, relatively
327 few have examined how those behaviors affect the environment and the result-
328 ing change in evolutionary trajectories. Lehmann (2007) demonstrated analyti-

329 cally that when niche construction act benefits future generations, cooperation
330 is favored due to reduced competition among kin. When rate-benefitting and
331 yield-benefitting altruistic acts co-evolve, Van Dyken and Wade (2012) showed
332 that “reciprocal niche construction”, where the selective feedbacks produced
333 by one act benefitted the other, can lead to increased selection for both traits.
334 While these studies have focused on the niche constructing effects of cooper-
335 ation, we instead focus our attention here on how niche construction enables
336 cooperators to escape defection by hitchhiking along with non-social traits.

337 **Primacy/Recency**

338 In our model, alterations to the environment were immediately echoed by
339 changes in selection. However, decoupling the timescales on which these pro-
340 cesses occur can have substantial effects (Laland *et al.*, 1996). By integrating
341 past allelic states into Equation 3, we can begin to explore how the cumulative
342 effects of niche construction affect the creation of non-social adaptive oppor-
343 tunities and the benefits that they offer cooperation. Here, how these past
344 allelic states are integrated will play an important role. For example, when
345 the effects of earlier generations are weighted more heavily, the influence of
346 migration may be diminished. While this will reduce the threat of emigration
347 by defectors, cooperator populations will also be less effective at exporting
348 their niche.

Cooperative Niche Construction

While our focus for this work has been on the eco-evolutionary feedbacks created by non-social traits, it would also be interesting to explore how this system is affected by the timescale at which carrying capacity at a given patch is increased by public goods. In natural settings, a multitude of factors including protein durability (Brown and Taddei, 2007; Kümmerli and Brown, 2010), diffusion (Allison, 2005; Driscoll and Pepper, 2010), and resource availability (Zhang and Rainey, 2013; Ghoul *et al.*, 2014) influence both the rate and the degree to which public goods alter the environment (and thereby selection). Lehmann (2007) demonstrated that a cooperative, niche constructing behavior can be favored when it only affected selection for future generations, thus reducing the potential for competition among contemporary kin. The evolutionary inertia that this creates, however, may ultimately work against cooperators. When public good accumulates in the environment, cooperators must reduce their investment in production to remain competitive (Kümmerli and Brown, 2010).

TODO: wrap up. Facultative cooperation requires sensing.

Host-Symbiont

In many instances of cooperation, the environment is itself a biological entity, which can produce additional evolutionary feedbacks. As the host population changes, so too will selection on their symbiont populations. Here, evolutionary outcomes depend greatly on the degree of shared interest between the host

371 and symbiont. For example, the cooperative production of virulence factors by
372 the human pathogen *P. aeruginosa* in lung infections is harmful to those with
373 cystic fibrosis (Harrison, 2007). Conversely, cooperative light production by *A.*
374 *fischeri* is vital for the survival of its host, the Hawaiian bobtail squid (Ruby,
375 1996). It was recently argued that incorporating the effects of niche construc-
376 tion is critical for improving our understanding of viral evolution (Hamblin *et*
377 *al.*, 2014) and evolution in co-infecting parasites (Hafer and Milinski, 2015).
378 Incorporating host dynamics, co-evolution, and the feedbacks that they pro-
379 duce into models is likely to be equally important for gaining an understanding
380 of how cooperative behaviors evolve in these host-symbiont settings.

381 Acknowledgments

- 382 • TODO: Organizers?
- 383 • TODO: lab comments

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389 and do not necessarily reflect the views of the National Science Foundation.
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391 and BK).

392 Figures

393 **Figure 1**

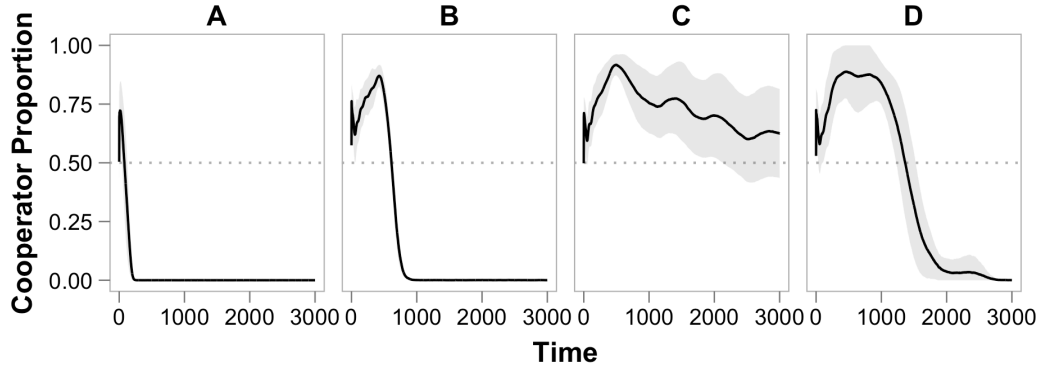


Figure 1: **Adaptation, niche construction, and the evolution of co-operation.** Curves show the average cooperator proportion among replicate populations, while shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter values used are listed in [Table 1](#). **(A)** When there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

394 **Figure 2**

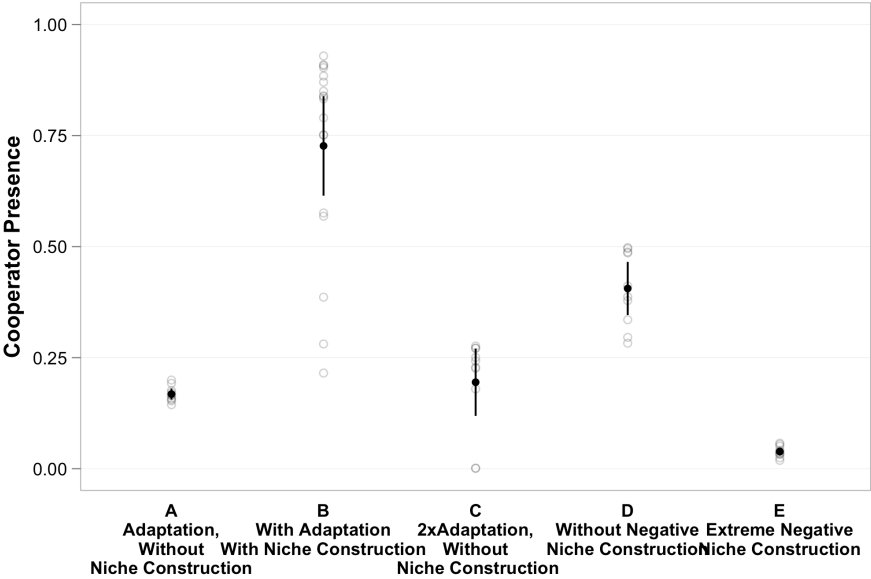


Figure 2: Cooperator Presence TODO

395 **Figure 3**

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

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

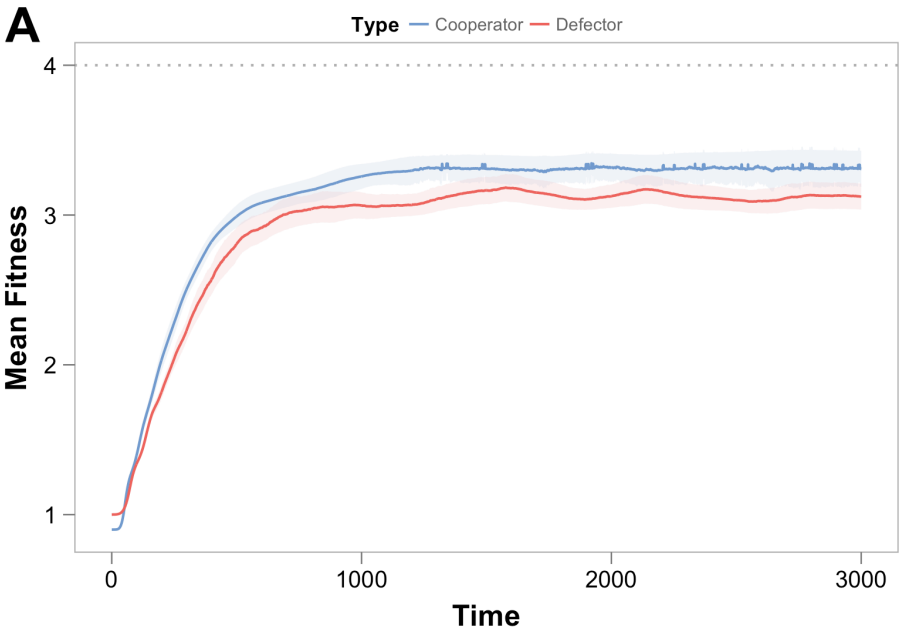


Figure 3: Grand mean Fitness of cooperators and defectors TODO

398 **Figure 3B - Fitness with double delta, no epsilon**

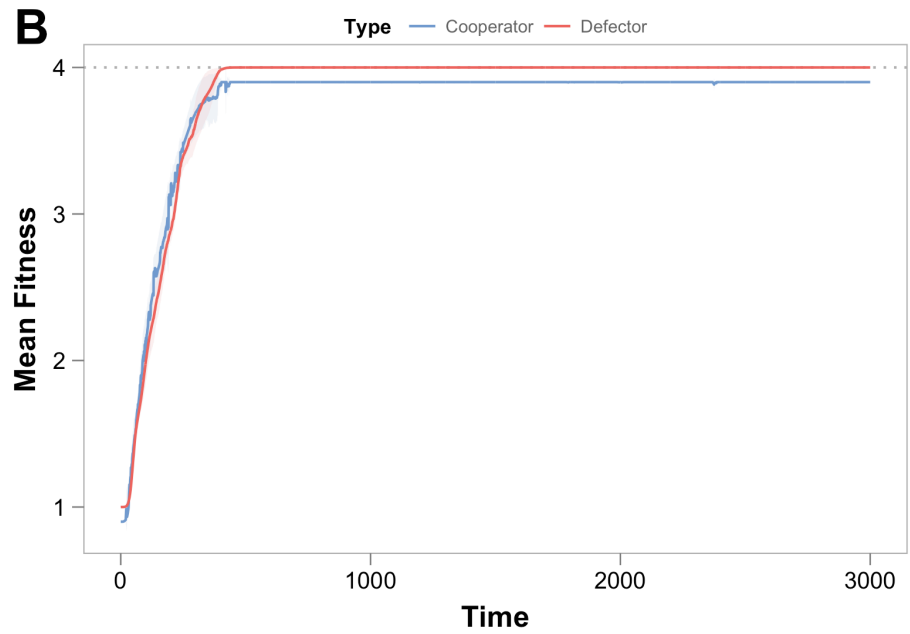


Figure 4: Grand mean Fitness of cooperators and defectors, double delta, no epsilon TODO

399 **Figure 3C - Fitness with no negative niche construction ($L=5$, $A=5$)**

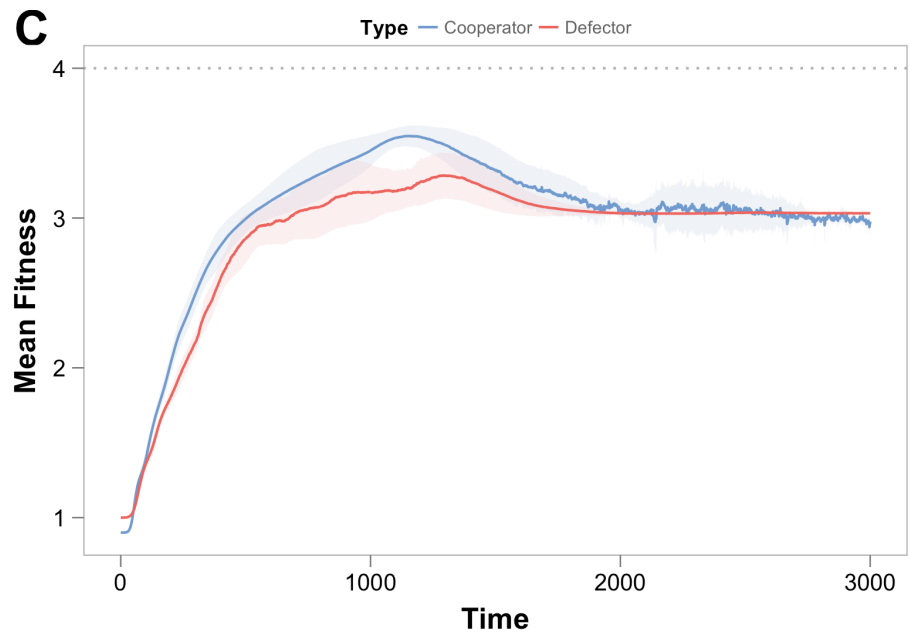


Figure 5: Grand mean Fitness of cooperators and defectors, no negative niche construction TODO

400 **Figure 3D - Fitness with extreme negative niche construction ($L=1$,**
401 **$A=6$)**

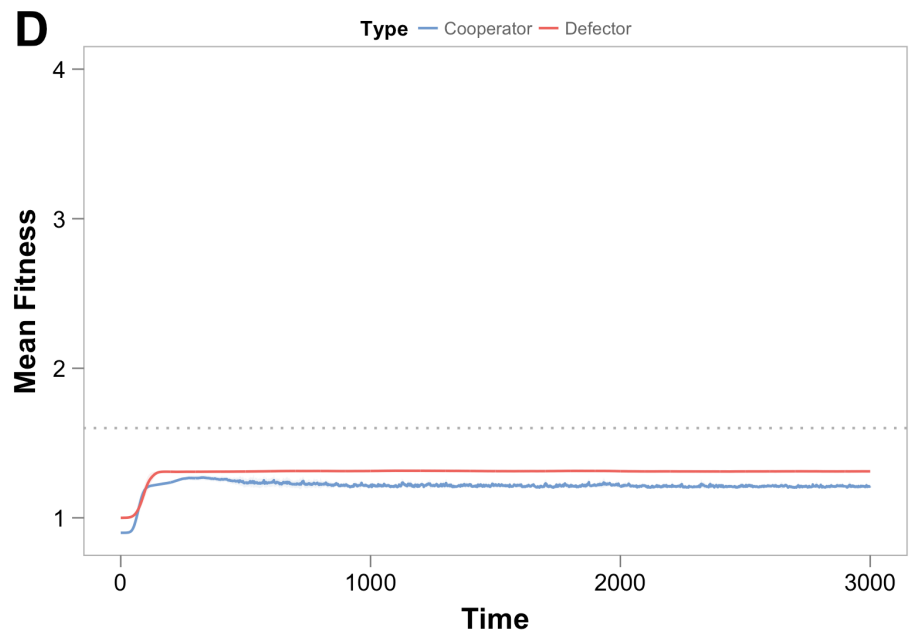


Figure 6: Grand mean Fitness of cooperators and defectors, extreme negative niche construction TODO

402 **Figure 4**

403 Cooperators invade from single population

404 **Figure 5**

405 Defectors are kept at bay

406 **Figure 6**

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

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

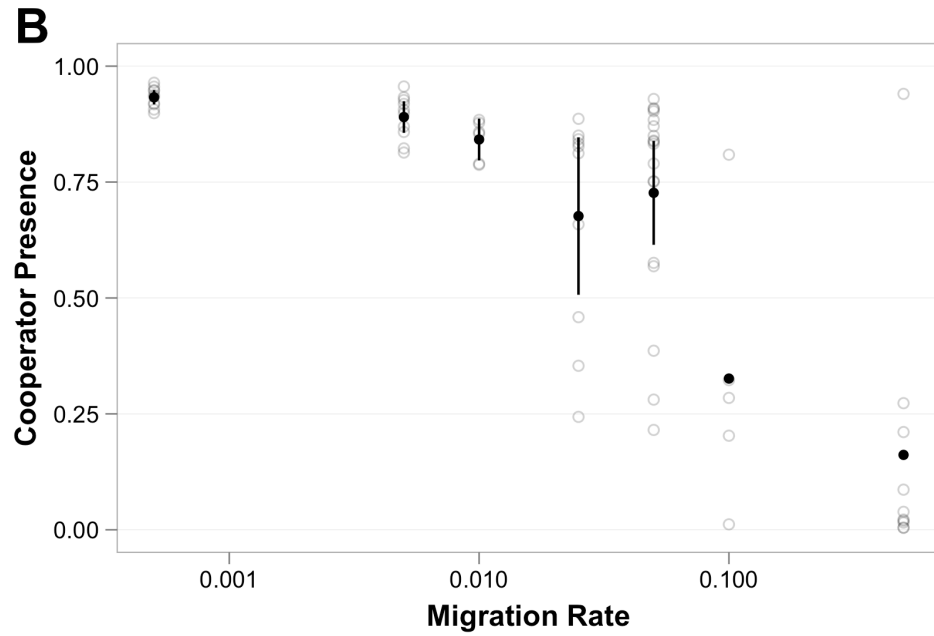


Figure 7: TODO Cooperator Presence for different migration rates

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

References

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