

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 **Materials and 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 Niche Construction Maintains Cooperation

189 Despite being able to form larger populations, cooperators are swiftly elimi-
190 nated in competition with defectors, despite spatial structuring in the metapop-
191 ulation (Figure 1A). As demonstrated by Hammarlund *et al.* (2015), coopera-
192 tors are temporarily bolstered by the ability to hitchhike along with non-social
193 adaptations (Figure 1B). As shown in Figure 1C, we find that niche hiking can
194 prolong cooperation, perhaps indefinitely (see [Table 1](#) for model parameters).
195 (**TODO** describe the oscillations). We now explore this process further to
196 identify the factors underlying this effect.

197 Not Just Because of Additional Fitness from Epsilon 198 (**TODO title**)

199 In our model, an individual’s fitness is the product of two processes. First,
200 mutations engender environmental adaptations, which are represented by non-

201 zero alleles. These adaptations create the transient lift in cooperation seen in
 202 Figure 1B. The second process that contributes to fitness is niche construc-
 203 tion. Selection favors individuals with sequentially-increasing alleles. Because
 204 larger populations will have a greater effect on their environment, this bene-
 205 fit is density dependent. In our experiments, this positive niche construction
 206 contributed equally to fitness when all individuals shared the same allele in a
 207 population at maximum carrying capacity. To determine whether cooperation
 208 was maintained simply due to the higher selective values made possible by this
 209 second source of fitness, we compared our results against the results of exper-
 210 iments in which the ordering of alleles did not matter, and the fitness benefit
 211 provided by adaptation was doubled ($\epsilon = 0$, $\delta = 0.6$). That this doubling is an
 212 over estimate of the magnitude of fitness contributions that arise from niche
 213 construction, since these values would only occur in populations at maximum
 214 carrying capacity, which does not occur in the presence of defectors. Never-
 215 theless, Figure 2 shows that higher selective values have little effect (columns
 216 A and C) and do not explain the maintenance of cooperation that we observe
 217 when niche construction occurs (column B).

218 Although we have seen that maximum fitness does not substantially effect the
 219 maintenance of cooperation, perhaps the rate at which fitness accumulates in
 220 cooperator and defector populations matters. When we compare the accumu-
 221 lation of fitness via adaptation in the presence of niche construction (Figure
 222 3A) against simulations in which selective values are doubled (Figure 3B), two
 223 features emerge. In both scenarios, cooperators gain adaptations more quickly
 224 than defectors due to their size. When niche construction is not present, co-

operator fitness is eventually surpassed by that of defectors (Figure 3B). As described by Hammarlund et al. (2015), this leads to the demise of cooperators. In contrast, cooperator fitness is never surpassed when niche construction is present (Figure 3A), which allows cooperation to persist.

TODO: discuss time at which fitness plateaus?

TODO: describe how maximum fitness is calculated?

Negative Niche Construction Plays a Key Role (TODO title)

Figure 3A also shows that niche-constructing populations never reach maximum fitness. One major contributor to this is the density dependence of the benefit provided by niche construction. Because defectors remain present (Figure 1C), the smaller populations that result are unable to unlock the full benefit of niche construction. The second contributor to the reduced fitness that we observe is negative niche construction. This occurs in our model due to selection for sequentially-increasing allelic states and the circular arrangement of these alleles. When the genome length (L) is not evenly divided by the number of non-zero alleles (a_{max}), a conflict arises when the allelic state at locus 1 is not 1 larger than the allelic state at locus L . For example, consider genotype $(1, 2)$ when $L = 2$ and $a_{max} = 3$. Here, allelic state 2 at locus 2 will be beneficial, because it follows allelic state 1 at locus 1. However, due to the circular effects, allelic state 1 at locus 1 will be deleterious, because it does not follow 2.

247 To isolate the effect of negative niche construction, we compare our results
248 against those from simulations in which this allelic conflict was absent ($L = 5$,
249 $a_{max} = 5$). Figure 2 shows that although positive niche construction still led
250 to an increase in cooperation (column D), these populations were not able to
251 maintain the same level of cooperation seen in the presence of negative niche
252 construction (column B). We find that because this lack of conflict allows
253 populations to reach a fully-adapted state, cooperators once again acquire
254 these adaptations more quickly but are eventually driven from the population
255 (Figures 3C and 1X). These results indicate that both positive and negative
256 niche construction is required to maintain cooperation.

257 **(TODO: explain why defector fitness doesn't reach 4 (density de-**
258 **pendent fitness)** maybe better in figure caption?)

259 To further explore the influence of negative niche construction, we performed
260 experiments in which the positive effects of niche construction were removed.
261 Here, individuals had a single adaptive locus that was constantly in conflict
262 ($L = 1$, $a_{max} = 6$). As seen in Figures 2 (column E) and 3D, the constant
263 source of adaptation that is provided by negative niche construction is not
264 sufficient to maintain cooperation via hitchhiking, and cooperators are quickly
265 purged from the population. This offers further evidence that feedbacks from
266 both positive and negative niche construction are required for cooperation to
267 persist.

268 NC Enables Cooperator Spread

269 Figure 4

270 NC Prevents Defector Invasion

271 Figure 5

272 How Public Good Fuels all of this

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

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

286 To address how migration affects the evolutionary process in this system, we
287 vary the rate at which migration occurs (m). As seen in Figure 6B, cooperation

288 decreases as migration rate increases. This is likely because migration defines
289 the spatial structuring in this system. As migration increases, the population
290 becomes more like a well-mixed system, where defectors are better able to
291 exploit the benefits of cooperation (Griffin *et al.*, 2004; Kümmerli *et al.*, 2009).

292 # Discussion

- 293 • summary of results
- 294 • similarities/differences from previous work
 - 295 – Schwilk and Kerr (2002)
 - 296 – 10.1073/pnas.0812644106
- 297 • negative/positive NC
 - 298 – laland1996evolutionary
- 299 • public goods as niche construction
- 300 • future QS or other environmental sensing
- 301 • Facultative cooperation
 - 302 – Rodrigues (2012)
 - 303 – Dumas and Kümmerli (2010)
 - 304 – Kümmerli and Brown (2010)
 - 305 – Darch/Diggle
 - 306 – QS?
 - 307 – Environmental Sensing? - (Koestler and Waters, 2014, Bernier et
 - 308 al. (2011))

- Negative Niche construction as a strategy? - would those that create this constant pressure (L=5, A=6) do better than those that do not (L=5, A=5)?

Niche construction and selective feedbacks Niche construction and other social interactions

Public Goods

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

By their very nature, public goods benefit populations by making their environment more hospitable. For example, bacteria produce 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), among many others (West *et al.*, 2007a). While many studies have explored how the environment affects the evolution of cooperative behaviors, relatively few have examined how those behaviors affect the environment and the resulting change in evolutionary trajectories. Lehmann (2007) demonstrated analytically that when niche construction act benefits future generations, cooperation is favored due to reduced competition among kin. When rate-benefitting and yield-benefitting altruistic acts co-evolve, Van Dyken and Wade (2012) showed that “reciprocal niche construction”, where the selective feedbacks produced by one act benefitted the other, can lead to increased selection for both traits.

330 While these studies have focused on the niche constructing effects of cooper-
331 ation, we instead focus our attention here on how niche construction enables
332 cooperators to escape defection by hitchhiking along with non-social traits.

333 **Primacy/Recency**

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

345 **Cooperative Niche Construction**

346 While our focus for this work has been on the eco-evolutionary feedbacks cre-
347 ated by non-social traits, it would also be interesting to explore how this
348 system is affected by the timescale at which carrying capacity at a given patch
349 is increased by public goods. In natural settings, a multitude of factors in-
350 cluding 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 and symbiont. For example, the cooperative production of virulence factors by the human pathogen *P. aeruginosa* in lung infections is harmful to those with cystic fibrosis (Harrison, 2007). Conversely, cooperative light production by *A. fischeri* is vital for the survival of its host, the Hawaiian bobtail squid (Ruby, 1996). It was recently argued that incorporating the effects of niche construction is critical for improving our understanding of viral evolution (Hamblin *et*

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

377 Acknowledgments

- 378 • TODO: Organizers?
- 379 • TODO: lab comments

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385 and do not necessarily reflect the views of the National Science Foundation.
386 Computational resources were provided by an award from Google (to BDC
387 and BK).

388 **Figures**

389 **Figure 1**

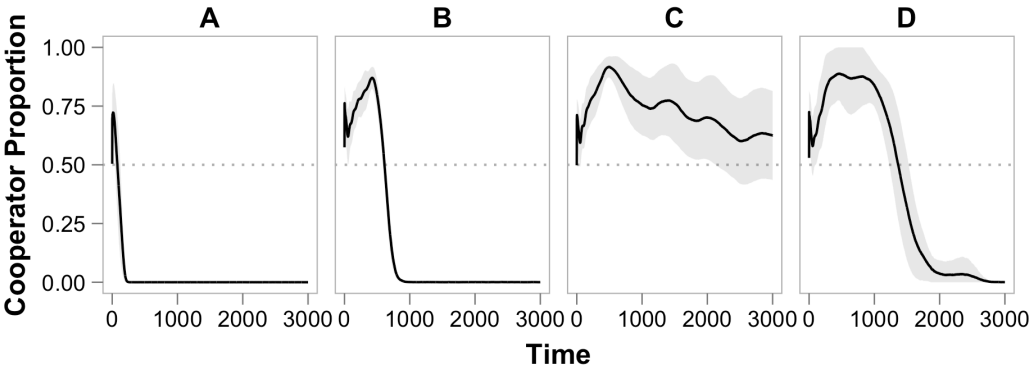


Figure 1: Proportion of cooperators over time TODO

390 **Figure 2**

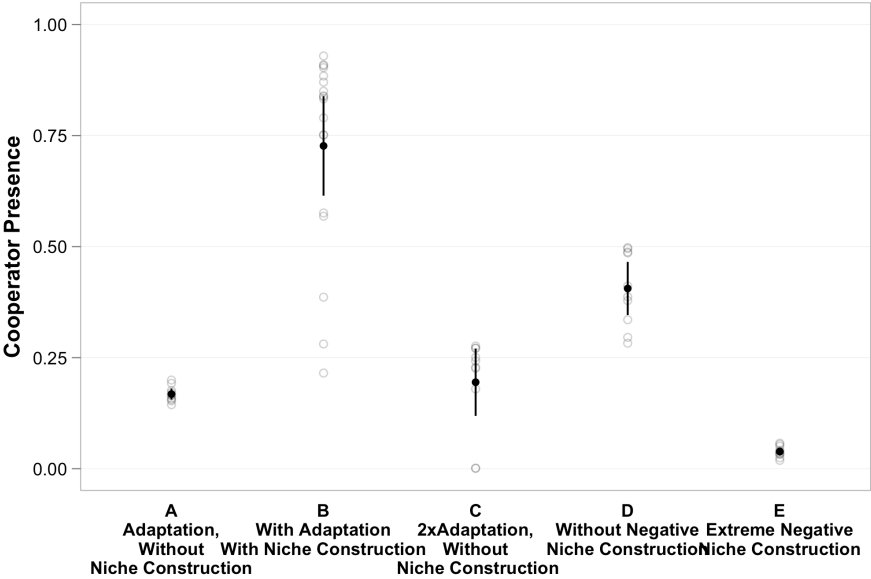


Figure 2: Cooperator Presence TODO

391 **Figure 3**

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

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

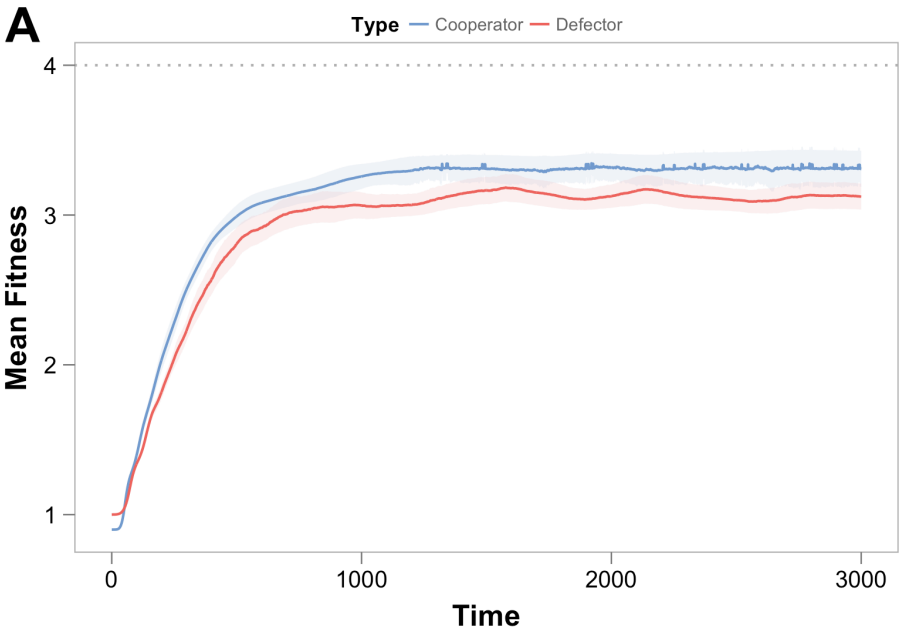


Figure 3: Grand mean Fitness of cooperators and defectors TODO

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

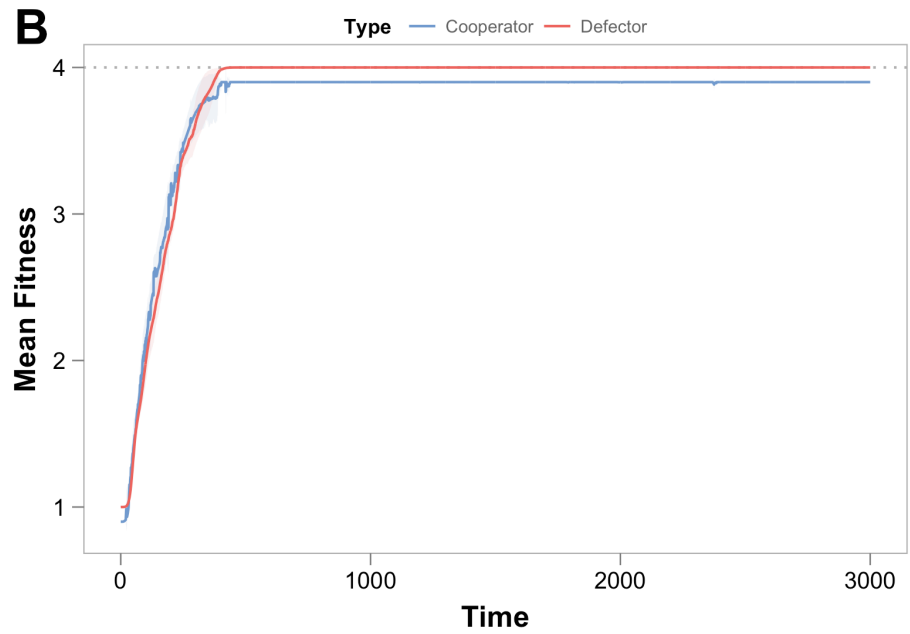


Figure 4: Grand mean Fitness of cooperators and defectors, double delta, no epsilon TODO

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

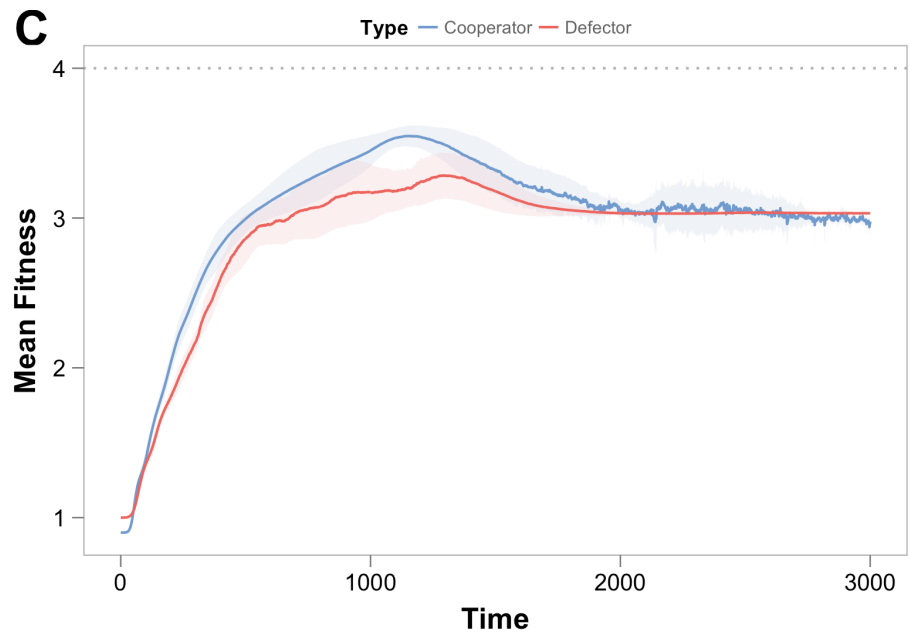


Figure 5: Grand mean Fitness of cooperators and defectors, no negative niche construction TODO

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

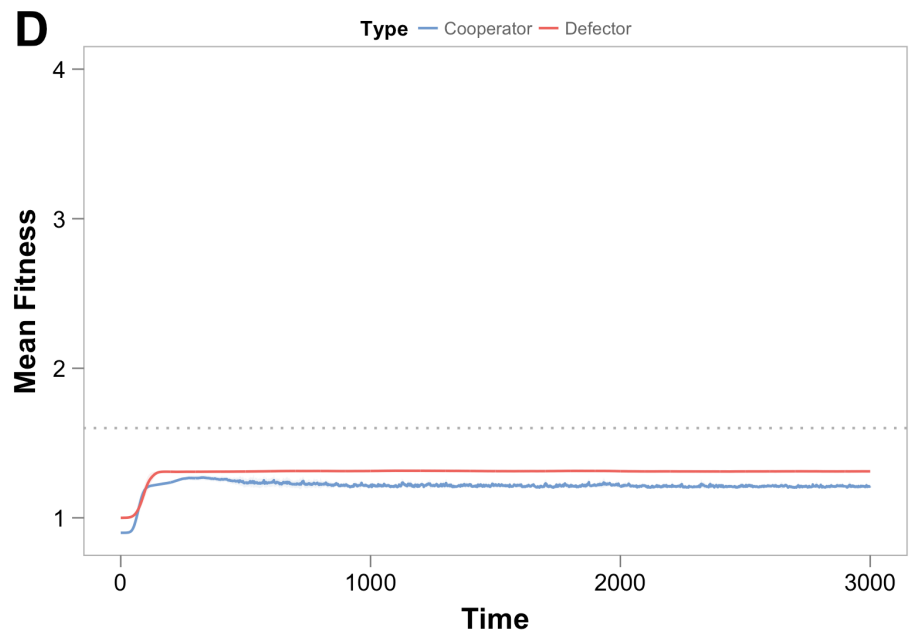


Figure 6: Grand mean Fitness of cooperators and defectors, extreme negative niche construction TODO

398 **Figure 4**

399 Cooperators invade from single population

400 **Figure 5**

401 Defectors are kept at bay

402 **Figure 6**

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

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

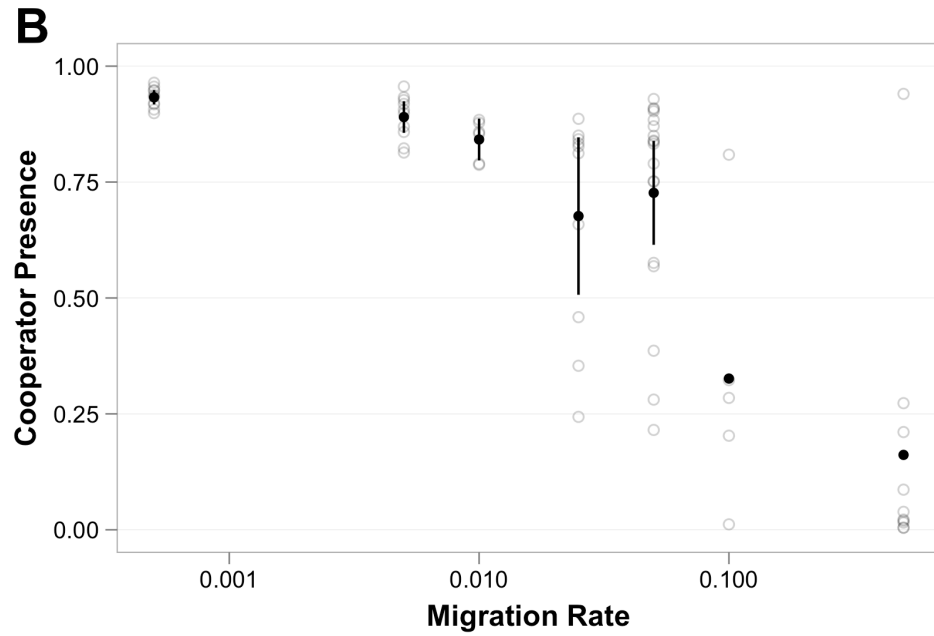


Figure 7: TODO Cooperator Presence for different migration rates

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

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