

# TODO title

## TODO

### **Abstract**

Through their interactions, their activities, and even their mere presence, organisms change the environment for themselves and others. This “niche construction” process becomes particularly interesting when it creates evolutionary feedback, whereby selective pressures are altered in response to environmental change. Here we consider how niche construction influences the evolution of cooperation, which has been a long-standing challenge to evolutionary theory. We simulate populations of individuals that cooperatively produce a public good that permits increased growth in a stressful environment and investigate how local- and global-scale niche construction affects the ability of these populations to resist invasion by non-producing cheats. We find that niche construction profoundly impacts the evolution of cooperation by creating new opportunities for adaptation. Cooperators are able to escape subversion by cheats as long as niche construction clears these paths of adaptation. This work provides a crucial step towards understanding how evolution occurs in complex environments like those found in nature.

## 20 Introduction

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

30 Several factors can defer this potential *tragedy of the commons* (Hamilton,  
31 1964; Hardin, 1968; Nowak, 2006; West *et al.*, 2007b). For example, coopera-  
32 tors must benefit more from the cooperative act than others. This can occur  
33 when cooperators are clustered together in spatially-structured populations  
34 (Fletcher and Doebeli, 2009; Nadell *et al.*, 2010; Kuzdzal-Fick *et al.*, 2011) or  
35 when cooperators use communication (Brown and Johnstone, 2001; Darch *et*  
36 *al.*, 2012) or other cues (Sinervo *et al.*, 2006; Gardner and West, 2010; Veelders  
37 *et al.*, 2010) to cooperate conditionally with kin. Interestingly, cooperation can  
38 also be bolstered by genetic linkage with self-benefitting traits (Foster *et al.*,  
39 2004; Dandekar *et al.*, 2012; Asfahl *et al.*, 2015), setting the stage for an “adap-  
40 tive race” in which cooperators and defectors vie for the first highly-beneficial  
41 adaptation (Waite and Shou, 2012; Morgan *et al.*, 2012).

42 Hankshaw and Kerr (2015) recently showed that in spatially-structured popula-

tions, cooperators can gain a substantial leg up on defectors in an adaptive race when the cooperative behavior increases local population density, thus increasing the likelihood of acquiring beneficial non-social mutations. By hitchhiking along with these adaptations, the cooperative trait can rapidly rise in abundance. Nevertheless, this advantage is fleeting. As soon as the opportunities for adaptation are exhausted, cooperators are once again at a disadvantage against defectors. However, Hankshaw and Kerr (2015) demonstrated that cooperation can be maintained indefinitely when frequent environmental changes produce a steady stream of non-social adaptive opportunities. Although organisms typically find themselves in dynamic environments, change might not occur at a rate that provides sufficient adaptive opportunities to ensure long-term cooperator survival.

In this work, we demonstrate how cooperation can be maintained indefinitely by niche construction. We expand upon the model presented in Hankshaw and Kerr (2015) to allow populations to alter their local environment. As environments change, so too does selection. This creates an eco-evolutionary feedback whereby selection is altered based on current phenotypes, which changes the composition of phenotypes and their effects. The effect on selection can be either positive or negative, depending on whether the environmental change increases or decreases the fitness of the niche-constructing individual. Although niche construction occurs independently of cooperation in our model, the increase in density that results from public good production has a profound effect on how populations evolve in the presence of selective feedbacks. First, these populations exert greater influence on their environments, which allows them

67 to benefit more from positive niche construction. And as environments change,  
68 either by negative niche construction or external influences, these larger pop-  
69 ulations can adapt more quickly. We show that it is the combination of these  
70 factors that allows cooperation to persist.

## 71 **Description of positive NC effects**

72 Include Smax and m sweeps here, or in a later paragraph?

## 73 **Description of negative NC effects**

74 TODO

## 75 **Stuff to be cut/integrated above**

76 This niche construction creates feedback that increasingly favors the adapta-  
77 tions present in each population. We first examine how the intensity of these  
78 feedbacks affects the hitchhiking process. Because the production of public  
79 goods increases population density, populations containing cooperators will  
80 exert a greater influence on their environment. As a result, these environ-  
81 ments will be more quickly brought to states where fitness is higher.

82 As populations construct unique niches, they potentially decrease the threat  
83 of invasion from neighboring patches. This occurs when the traits that were  
84 advantageous in an immigrant's home niche are maladaptive elsewhere. Be-  
85 cause environmental change is influenced solely by non-social phenotypes in  
86 this model, this change of invasibility affects cooperators and defectors equally.

87 Here again, however, populations containing a greater number of cooperators  
88 may have an advantage. The greater number of individuals that emigrate from  
89 these larger populations allow them to “export” their niche—and thus reduce  
90 the fitness of neighboring competitors—at a higher rate. We explore whether  
91 the range expansion that this process enables provides additional opportunities  
92 for cooperation to hitchhike.

93 Finally, we demonstrate how *negative* niche construction, where populations  
94 change their environment in ways that reduce fitness, can further support  
95 cooperation. Even though the niche construction process creates selective  
96 feedbacks, we would expect the magnitude of these feedbacks to decrease as  
97 populations evolve. Once individuals can no longer gain adaptations that  
98 compensate for the costs of cooperation, they are then outcompeted by non-  
99 cooperators. However if populations construct their environment in a way  
100 which decreases fitness, cooperation can still hitchhike when this change also  
101 creates the opportunity to gain compensatory adaptations.

## 102 **Materials and Methods**

103 We build upon the model described in Hankshaw and Kerr (2015), in which co-  
104 operators and defectors compete and evolve in a spatially-structured metapop-  
105 ulation of populations. Each of these populations grows to carrying capacity,  
106 mutates, and migrates to neighboring patches. During this process, popula-  
107 tions adapt to their local environments. In our extended model, we allow  
108 populations to modify their local environment, and these modifications feed

109 back to affect selection.

## 110 Model Description

111 Our simulated environment consists of  $N^2$  patches arranged as an  $N \times N$   
112 lattice (see [Table 1](#) for model parameters and their values), where each patch  
113 supports a population of zero or more individuals. Each individual in the  
114 population has a genotype, which is an ordered list of  $L + 1$  integers (loci).  
115 The first  $L$  loci are *adaptive loci*, and are each occupied by a 0 or an integer  
116 from the set  $A = \{1, \dots, a_{max}\}$ , where  $a_{max}$  is the number of potential alleles.  
117 At each of these loci, the presence of a non-zero allele represents an adaptation  
118 to the environment that confers fitness benefit  $\delta$ . A binary allele at locus  $L + 1$   
119 determines whether or not that individual is a cooperator. Individuals with  
120 allelic state 1 at this locus are cooperators, carrying a cost  $c$ , while individuals  
121 with allelic state 0 are defectors. When  $\delta \geq c$ , a minimally-adapted cooperator  
122 recoups the cost of cooperation. Equation [1](#) defines function  $n(a, l)$ , which  
123 gives the number of individuals in the population with allelic state  $a$  at locus  
124  $l$ .  $I_x(y)$  indicates whether the allelic state  $y$  matches allelic state  $x$  (1) or not  
125 (0), and  $\gamma(i)$  is the genotype of individual  $i$ .

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

126 Organisms also influence their environment, which, in turn, influences selec-  
127 tion. We model this as a form of frequency dependent selection. Specifically,  
128 the selective value of adaptive allele  $a$  at locus  $l$  increases with the number

129 of individuals in the population that have allele  $a - 1$  at locus  $l - 1$  (note  
 130 that we treat both adaptive loci and allelic states as circular, so the allelic  
 131 state at locus 1 is affected by locus  $L$ , and allele 1 is best preceded by allele  
 132  $a_{max}$ ). The slope of this increase is  $\epsilon$ , which specifies the intensity of niche con-  
 133 struction. As a consequence of this form of frequency dependence, genotypes  
 134 with sequentially-increasing allelic states will tend to evolve. Because muta-  
 135 tions are random, as described later, each population will evolve sequences  
 136 that start with different allelic states. These different sequences represent the  
 137 unique niches constructed by populations. Under this model, the fitness of an  
 138 individual with genotype  $g$  in population  $P$  is:

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

139 where  $z$  is a baseline fitness, and  $a_{g,l}$  represents the allelic state of genotype  $g$   
 140 at locus  $l$ . The function  $I_A(a)$  indicates whether a given allelic state  $a$  is in  $A$   
 141 (i.e., it is non-zero), while the function  $\beta(x, x_{max})$  gives the value below some  
 142 value  $x$  in the circular set  $\{1, \dots, x_{max}\}$  (Equation 3).

$$\beta(x, x_{max}) = \{(x - 2 + x_{max}) \bmod x_{max}\} + 1 \quad (3)$$

143 Cooperators produce a public good that is equally accessible to all members  
 144 of the population. This public good increases the carrying capacity at that  
 145 patch, allowing the population to reach greater density. This benefit increases  
 146 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:

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

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 and  $S(p)$  and  $\{\pi_1, \pi_2, \dots, \pi_{|P|}\}$ , where:

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

Here,  $W_{\gamma(i)}$  is the fitness of an individual  $i$  with genotype  $\gamma(i)$  (see Equation 2).  $\pi_i$  therefore reflects that an individual's ability to persist is proportional to its fitness relative to others'.

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



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

165 where  $H_a(g, g')$  and  $H_c(g, g')$  are the Hamming distances between genotypes  $g$   
 166 and  $g'$  at the cooperation locus and adaptive loci, respectively. The Hamming  
 167 distance is the number of loci at which allelic states differ (Hamming, 1950).  
 168 Because we define no inherent relationship among alleles, each of the  $a_{max} + 1$   
 169 allelic states is equally likely to arise via mutation at a given locus.

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

175 Metapopulations are initiated in a state that follows an environmental change.  
 176 First, populations are seeded at all patches with cooperator proportion  $p_0$  and  
 177 grown to density  $S(p_0)$ . An environmental challenge is then introduced, which  
 178 subjects the population to a bottleneck. For each individual, the probability  
 179 of survival is  $\mu_t$ , which represents the likelihood that a mutation occurs that  
 180 confers tolerance. Survivors are chosen by binomial sampling. Because indi-  
 181 viduals have not yet adapted to this new environment, the allelic state of each  
 182 individual's genotype is set to 0 at each adaptive locus ( $\forall i \in P, l \in \{1, \dots, L\} :$   
 183  $a_{\gamma(i), l} = 0$ ). Following initialization, simulations are run for  $T$  cycles, where  
 184 each discrete cycle consists of growth, mutation, and migration. At the end  
 185 of each cycle, populations are thinned to allow for growth in the next cycle.

186 The individuals that remain are chosen by binomial sampling, where each  
187 individual persists with probability  $d$ , regardless of allelic state.

## 188 **Source Code and Software Environment**

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

## 193 **Results**

### 194 **Niche construction prolongs cooperator survival**

195 “cooperator presence” greater in NC runs than with no-NC (GNH)

### 196 **Negative Niche construction helps**

197 Runs with wraparound persist indefinitely, while those without do not.

198 **NC Prevents/Limits Defector invasion**

199 **NC Enables Cooperator Spread by “exporting” environ-**  
200 **ment**

## 201 **Discussion**

- 202 • summary of results
- 203 • similarities/differences from previous work
  - 204 – Schwilk and Kerr (2002)
  - 205 – 10.1073/pnas.0812644106
- 206 • public goods as niche construction
- 207 • future QS or other environmental sensing
- 208 • Facultative cooperation
  - 209 – Rodrigues (2012)
  - 210 – Dumas and Kümmerli (2010)
  - 211 – Kümmerli and Brown (2010)
  - 212 – Darch/Diggle
  - 213 – QS?
  - 214 – Environmental Sensing? - (Koestler and Waters, 2014, Bernier et
  - 215 al. (2011))
- 216 • Negative Niche construction as a stragegy? - would those that create this
- 217 constant pressure (L=5, A=6) do better than those that do not (L=5,

218 A=5)?

219 Niche construction and selective feedbacks Niche construction and other social  
220 interactions

## 221 **Public Goods**

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

224 By their very nature, public goods benefit populations by making their environ-  
225 ment more hospitable. For example, bacteria produce extracellular products  
226 that find soluble iron (Griffin *et al.*, 2004), digest large proteins (Diggle *et al.*,  
227 2007; Darch *et al.*, 2012), and reduce the risk of predation (Cosson *et al.*, 2002),  
228 among many others (West *et al.*, 2007a). While many studies have explored  
229 how the environment affects the evolution of cooperative behaviors, relatively  
230 few have examined how those behaviors affect the environment and the result-  
231 ing change in evolutionary trajectories. Lehmann (2007) demonstrated analyti-  
232 cally that when niche construction act benefits future generations, cooperation  
233 is favored due to reduced competition among kin. When rate-benefitting and  
234 yield-benefitting altruistic acts co-evolve, Van Dyken and Wade (2012) showed  
235 that “reciprocal niche construction”, where the selective feedbacks produced  
236 by one act benefitted the other, can lead to increased selection for both traits.  
237 While these studies have focused on the niche constructing effects of cooper-  
238 ation, we instead focus our attention here on how niche construction enables  
239 cooperators to escape defection by hitchhiking along with non-social traits.

## Primacy/Recency

In our model, alterations to the environment were immediately echoed by changes in selection. However, decoupling the timescales on which these processes occur can have substantial effects (Laland *et al.*, 1996). By integrating past allelic states into Equation 2, we can begin to explore how the cumulative effects of niche construction affect the creation of non-social adaptive opportunities and the benefits that they offer cooperation. Here, how these past allelic states are integrated will play an important role. For example, when the effects of earlier generations are weighted more heavily, the influence of migration may be diminished. While this will reduce the threat of emigration by defectors, cooperator populations will also be less effective at exporting 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, 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 fa-

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

## 283 Acknowledgments

- 284 • TODO: Organizers?
- 285 • TODO: lab comments

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294 **Figures**

295 **Figure 1**

296 **Figure 1A**

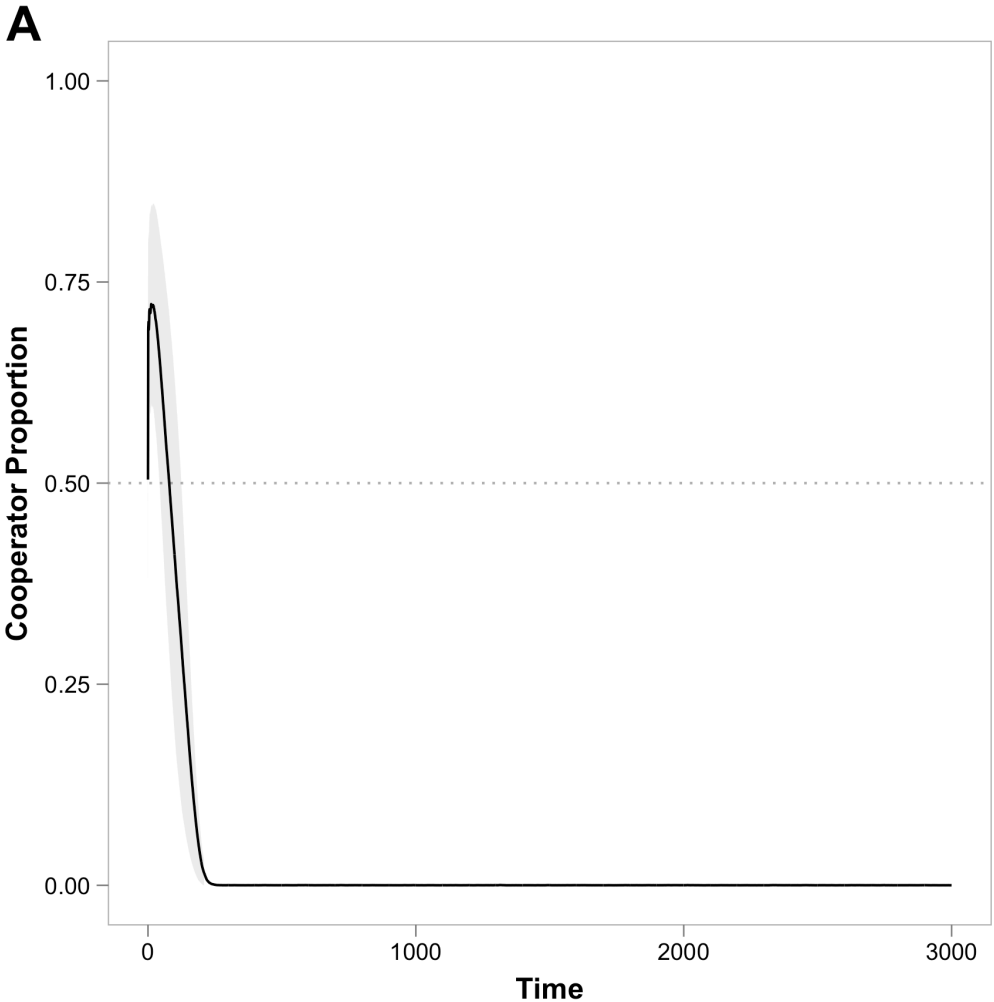


Figure 1: Proportion of cooperators over time when there are no opportunities for non-social adaptation



297 **Figure 1B**

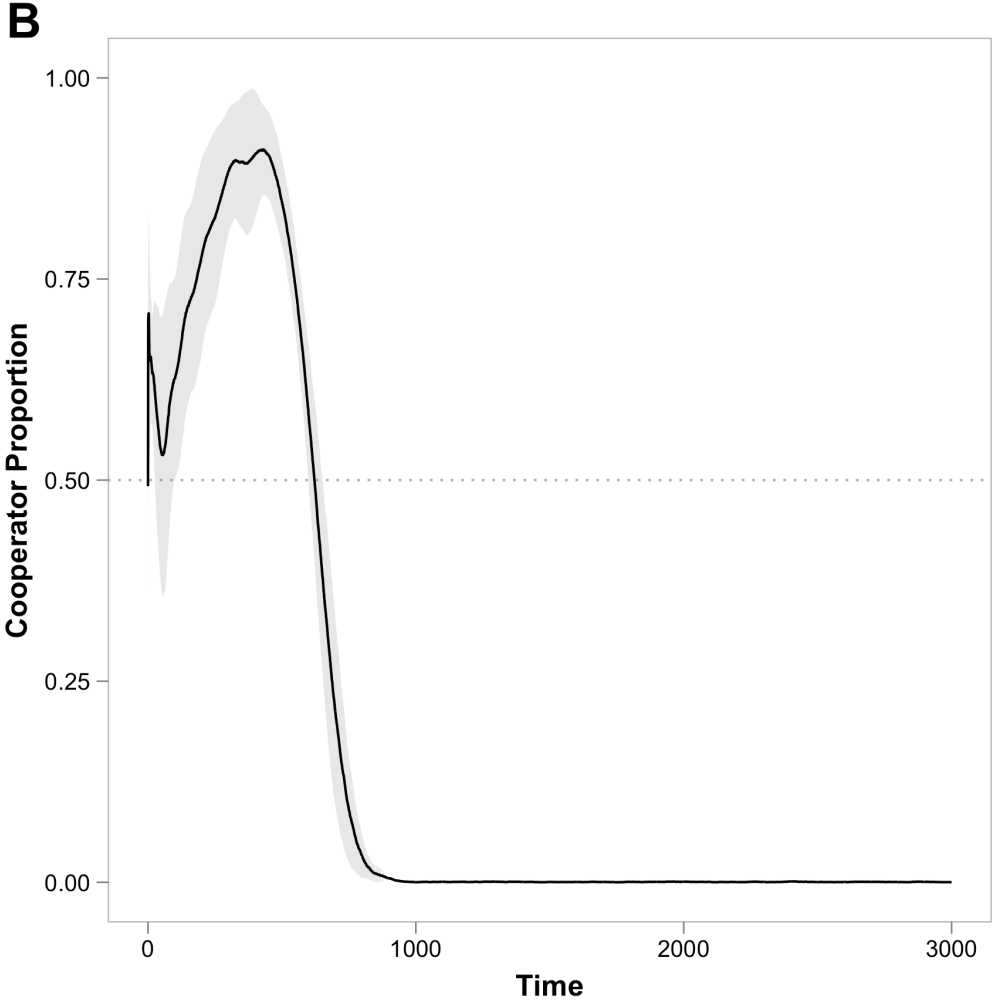


Figure 2: Proportion of cooperators over time with non-social adaptation (GNH)

298 **Figure 1C**

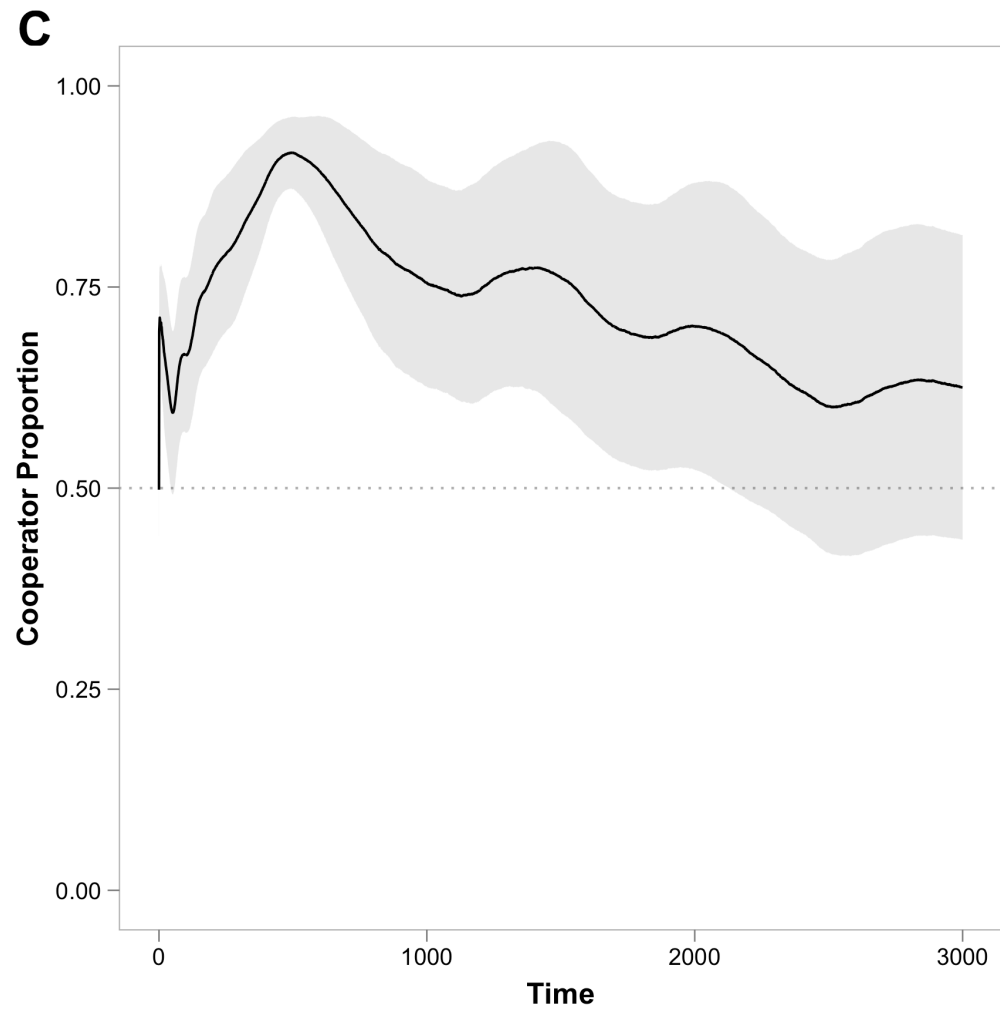


Figure 3: Proportion of cooperators over time with non-social adaptation and selective feedbacks

299 **Figure 2**

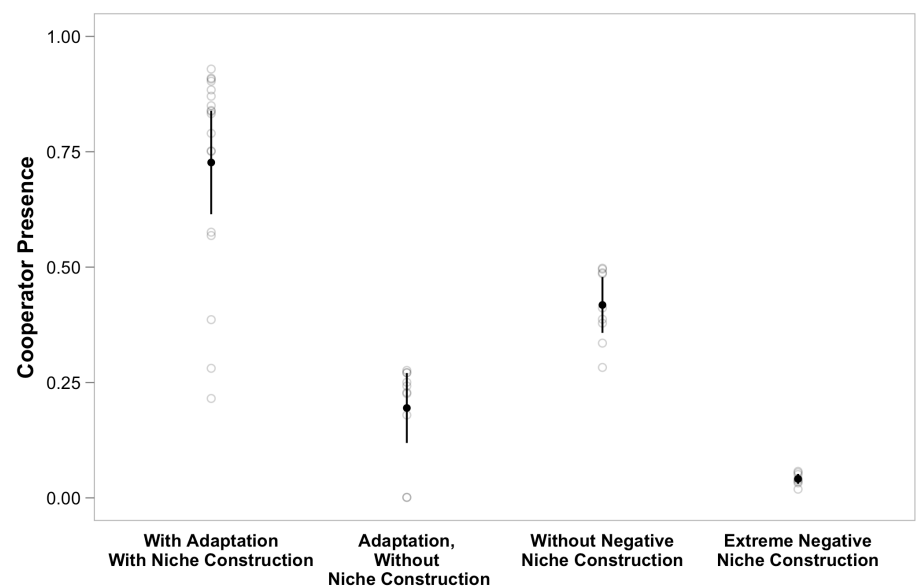


Figure 4: Cooperator Presence TODO

300 **Figure 3**

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

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

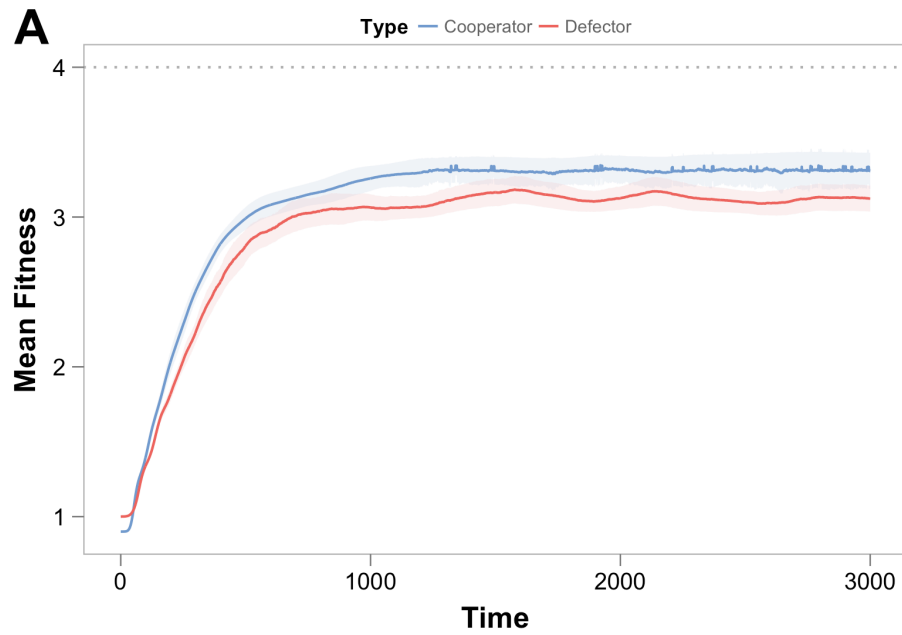


Figure 5: Grand mean Fitness of cooperators and defectors TODO

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

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

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

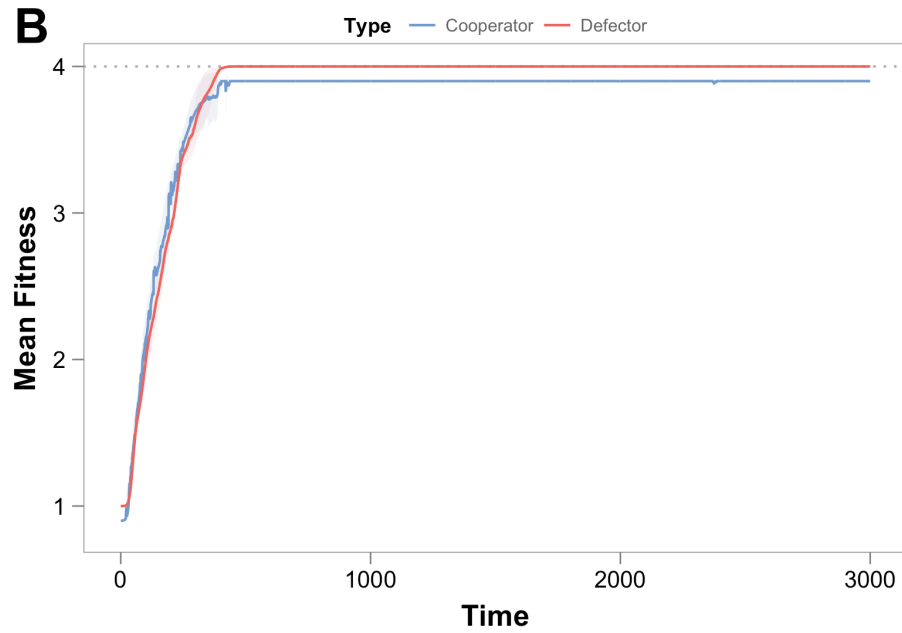


Figure 6: Grand mean Fitness of cooperators and defectors, double delta, no epsilon TODO

307 **Figure 4**

308 Cooperators invade from single population

309 **Figure 5**

310 Defectors are kept at bay

311 **Figure 6**

312 **Figure 6A - Effect of Migration Rate ( $m$ )**

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

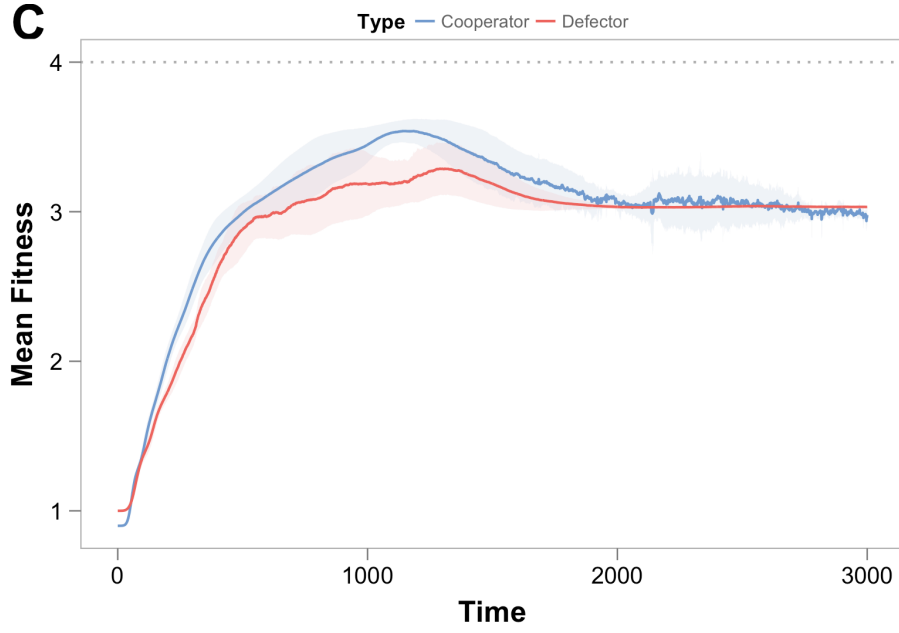


Figure 7: Grand mean Fitness of cooperators and defectors, no negative niche construction TODO

## 314 Tables

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          |
| $\delta$   | Fitness benefit, nonzero alleles    | 0.3        |
| $c$        | Production cost                     | 0.1        |
| $\epsilon$ | Fitness benefit, sequential alleles | 0.00015    |
| $z$        | Baseline fitness                    | 1          |

| Parameter | Description                             | Base Value |
|-----------|-----------------------------------------|------------|
| $S_{min}$ | Minimum population size                 | 800        |
| $S_{max}$ | Maximum population size                 | 2000       |
| $\mu_a$   | Mutation rate (adaptation)              | $10^{-5}$  |
| $\mu_c$   | Mutation rate (cooperation)             | $10^{-5}$  |
| $m$       | Migration rate                          | 0.05       |
| $p_0$     | Initial cooperator proportion           | 0.5        |
| $\mu_t$   | Mutation rate (tolerance to new stress) | $10^{-5}$  |
| $T$       | Number of simulation cycles             | 1000       |
| $d$       | Population dilution factor              | 0.1        |

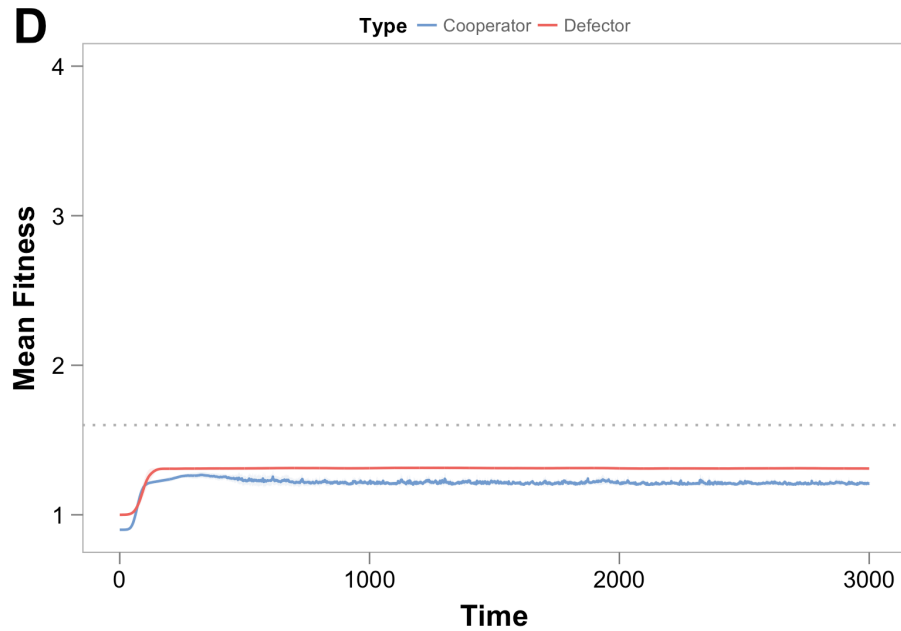


Figure 8: Grand mean Fitness of cooperators and defectors, extreme negative niche construction TODO

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