

TODO title

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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 examine whether the changes in selection that arise as organisms modify their environment can create opportunities that allow cooperators to be maintained by hitchhiking. We expand upon the model presented in Hankshaw and Kerr (2015), by allowing populations to alter their local environment based on the the presence of different non-social adaptations. This niche construction creates feedback that increasingly favors the adaptations present in each population. We first examine how the intensity of these feedbacks affects the hitchhiking process. Because the production of public goods increases population density, populations containing cooperators will exert a greater influence on their environment. As a result, these environments will be more quickly brought to states where fitness is higher.

As populations construct unique niches, they potentially decrease the threat

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

77 Finally, we demonstrate how *negative* niche construction, where populations
78 change their environment in ways that reduce fitness, can further support
79 cooperation. Even though the niche construction process creates selective
80 feedbacks, we would expect the magnitude of these feedbacks to decrease as
81 populations evolve. Once individuals can no longer gain adaptations that
82 compensate for the costs of cooperation, they are then outcompeted by non-
83 cooperators. However if populations construct their environment in a way
84 which decreases fitness, cooperation can still hitchhike when this change also
85 creates the opportunity to gain compensatory adaptations.

86 **Materials and Methods**

87 We build upon the model described in Hankshaw and Kerr (2015), in which co-
88 operators and defectors compete and evolve in a spatially-structured metapop-

99 ulation of populations. Each of these populations grows to carrying capacity,
 90 mutates, and migrates to neighboring patches. During this process, popula-
 91 tions adapt to their local environments. In our extended model, we allow
 92 populations to modify their local environment, and these modifications feed
 93 back to affect selection.

94 Model Description

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

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

110 Organisms also influence their environment, which, in turn, influences selec-
 111 tion. We model this as a form of frequency dependent selection. Specifically,
 112 the selective value of adaptive allele a at locus l increases with the number
 113 of individuals in the population that have allele $a - 1$ at locus $l - 1$ (note
 114 that we treat both adaptive loci and allelic states as circular, so the allelic
 115 state at locus 1 is affected by locus L , and allele 1 is best preceded by allele
 116 a_{max}). The slope of this increase is ϵ , which specifies the intensity of niche con-
 117 struction. As a consequence of this form of frequency dependence, genotypes
 118 with sequentially-increasing allelic states will tend to evolve. Because muta-
 119 tions are random, as described later, each population will evolve sequences
 120 that start with different allelic states. These different sequences represent the
 121 unique niches constructed by populations. Under this model, the fitness of an
 122 individual with genotype g in population P is:

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

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

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

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:

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

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). π_i therefore reflects that an individual's ability to persist is proportional to its fitness relative to others'.

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

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

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

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

159 Metapopulations are initiated in a state that follows an environmental change.
 160 First, populations are seeded at all patches with cooperator proportion p_0 and
 161 grown to density $S(p_0)$. An environmental challenge is then introduced, which
 162 subjects the population to a bottleneck. For each individual, the probability

163 of survival is μ_t , which represents the likelihood that a mutation occurs that
 164 confers tolerance. Survivors are chosen by binomial sampling. Because indi-
 165 viduals have not yet adapted to this new environment, the allelic state of each
 166 individual’s genotype is set to 0 at each adaptive locus ($\forall i \in P, l \in \{1, \dots, L\} :$
 167 $a_{\gamma(i),l} = 0$). Following initialization, simulations are run for T cycles, where
 168 each discrete cycle consists of growth, mutation, and migration. At the end
 169 of each cycle, populations are thinned to allow for growth in the next cycle.
 170 The individuals that remain are chosen by binomial sampling, where each
 171 individual persists with probability d , regardless of allelic state.

172 **Source Code and Software Environment**

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

177 **Results**

178 **Niche construction prolongs cooperator survival**

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

180 **Negative Niche construction helps**

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

182 **NC Prevents/Limits Defector invasion**

183 **NC Enables Cooperator Spread by “exporting” environ-** 184 **ment**

185 **Discussion**

- 186 • summary of results
- 187 • similarities/differences from previous work
 - 188 – Schwilk and Kerr (2002)
 - 189 – 10.1073/pnas.0812644106
- 190 • public goods as niche construction
- 191 • future QS or other environmental sensing
- 192 • Facultative cooperation
 - 193 – Rodrigues (2012)
 - 194 – Dumas and Kümmerli (2010)
 - 195 – Kümmerli and Brown (2010)
 - 196 – Darch/Diggle
 - 197 – QS?

198 – Environmental Sensing? - (Koestler and Waters, 2014, Bernier et
199 al. (2011))

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

203 Niche construction and selective feedbacks Niche construction and other social
204 interactions

205 **Public Goods**

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

208 By their very nature, public goods benefit populations by making their environ-
209 ment more hospitable. For example, bacteria produce extracellular products
210 that find soluble iron (Griffin *et al.*, 2004), digest large proteins (Diggle *et al.*,
211 2007; Darch *et al.*, 2012), and reduce the risk of predation (Cosson *et al.*, 2002),
212 among many others (West *et al.*, 2007a). While many studies have explored
213 how the environment affects the evolution of cooperative behaviors, relatively
214 few have examined how those behaviors affect the environment and the result-
215 ing change in evolutionary trajectories. Lehmann (2007) demonstrated analyti-
216 cally that when niche construction act benefits future generations, cooperation
217 is favored due to reduced competition among kin. When rate-benefitting and
218 yield-benefitting altruistic acts co-evolve, Van Dyken and Wade (2012) showed

219 that “reciprocal niche construction”, where the selective feedbacks produced
 220 by one act benefitted the other, can lead to increased selection for both traits.
 221 While these studies have focused on the niche constructing effects of cooper-
 222 ation, we instead focus our attention here on how niche construction enables
 223 cooperators to escape defection by hitchhiking along with non-social traits.

224 **Primacy/Recency**

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

236 **Cooperative Niche Construction**

237 While our focus for this work has been on the eco-evolutionary feedbacks cre-
 238 ated by non-social traits, it would also be interesting to explore how this system
 239 is affected by the timescale at which carrying capacity at a given patch is in-

240 creased by public goods. In natural settings, a multitude of factors including
 241 protein durability (Brown, 2007; Kümmerli and Brown, 2010), diffusion (Al-
 242 lison, 2005; Driscoll and Pepper, 2010), and resource availability (Zhang and
 243 Rainey, 2013; Ghoul *et al.*, 2014) influence both the rate and the degree to
 244 which public goods alter the environment (and thereby selection). Lehmann
 245 (2007) demonstrated that a cooperative, niche constructing behavior can be fa-
 246 vored when it only affected selection for future generations, thus reducing the
 247 potential for competition among contemporary kin. The evolutionary inertia
 248 that this creates, however, may ultimately work against cooperators. When
 249 public good accumulates in the environment, cooperators must reduce their in-
 250 vestment in production to remain competitive (Kümmerli and Brown, 2010).
 251 TODO: wrap up. Facultative cooperation requires sensing.

252 **Host-Symbiont**

253 In many instances of cooperation, the environment is itself a biological entity,
 254 which can produce additional evolutionary feedbacks. As the host population
 255 changes, so too will selection on their symbiont populations. Here, evolution-
 256 ary outcomes depend greatly on the degree of shared interest between the host
 257 and symbiont. For example, the cooperative production of virulence factors by
 258 the human pathogen *P. aeruginosa* in lung infections is harmful to those with
 259 cystic fibrosis (Harrison, 2007). Conversely, cooperative light production by *A.*
 260 *fischeri* is vital for the survival of its host, the Hawaiian bobtail squid (Ruby,
 261 1996). It was recently argued that incorporating the effects of niche construc-

tion 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.

Acknowledgments

- TODO: Organizers?
- TODO: lab comments

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278 **Figures**

279 **Figure 1**

280 **Figure 1A**

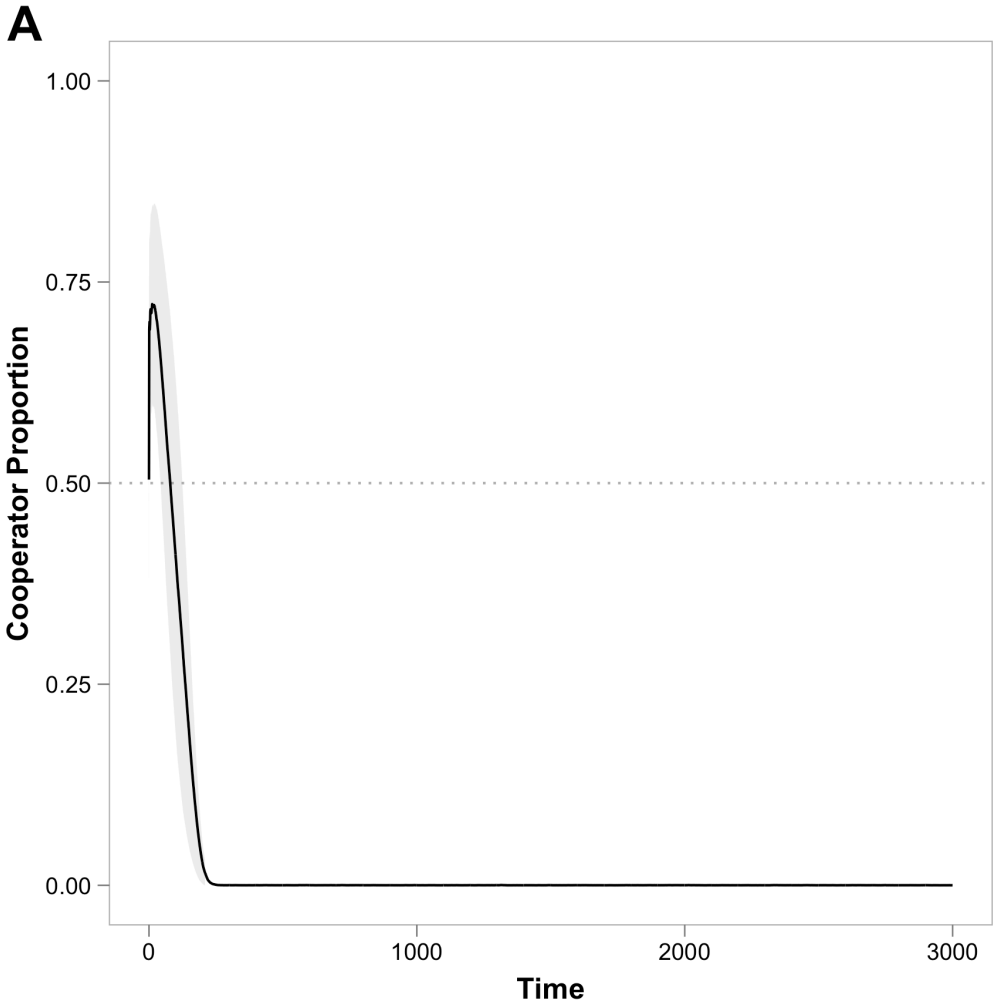


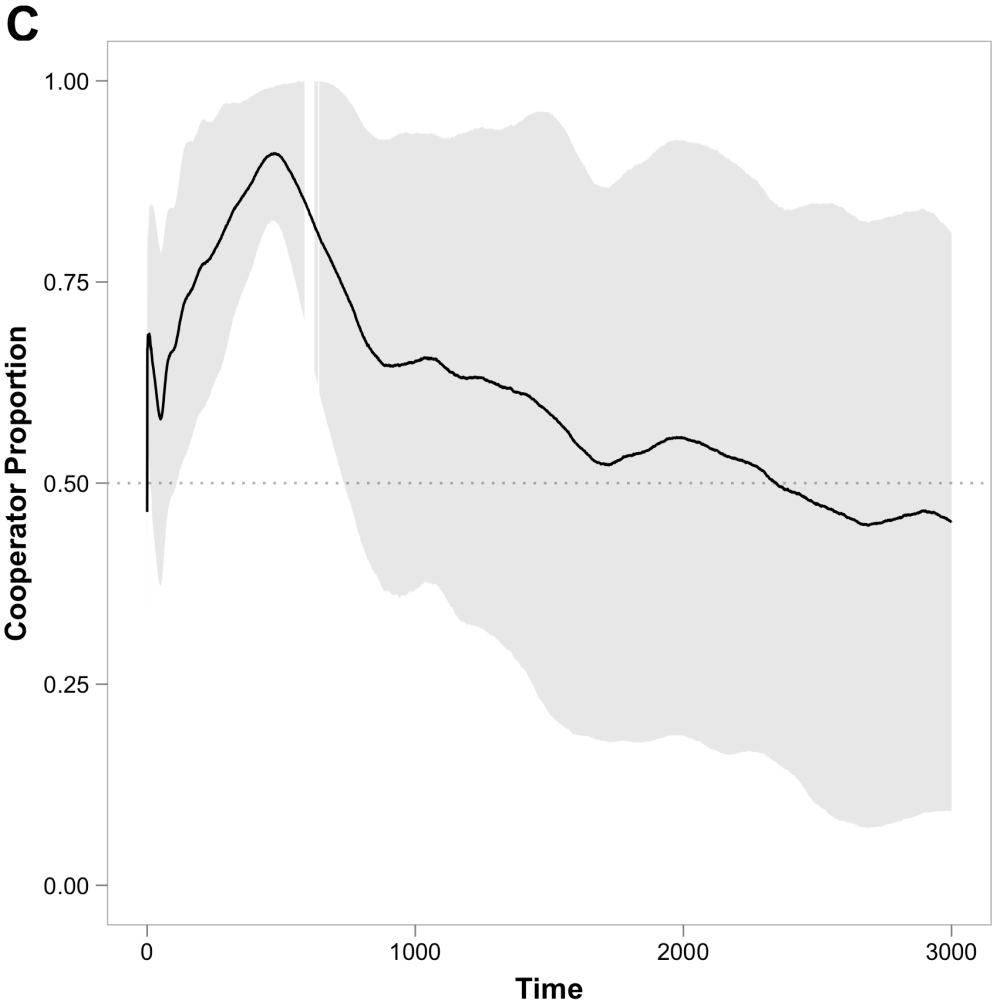
Figure 1: Proportion of cooperators over time when there are no opportunities for non-social adaptation

281 **Figure 1B**

282 Proportion of cooperators over time with non-social adaptation

283 **Figure 1C**

284 Proportion of cooperators over time with non-social adaptation and niche con-



285 struction

286 **Figure 2**

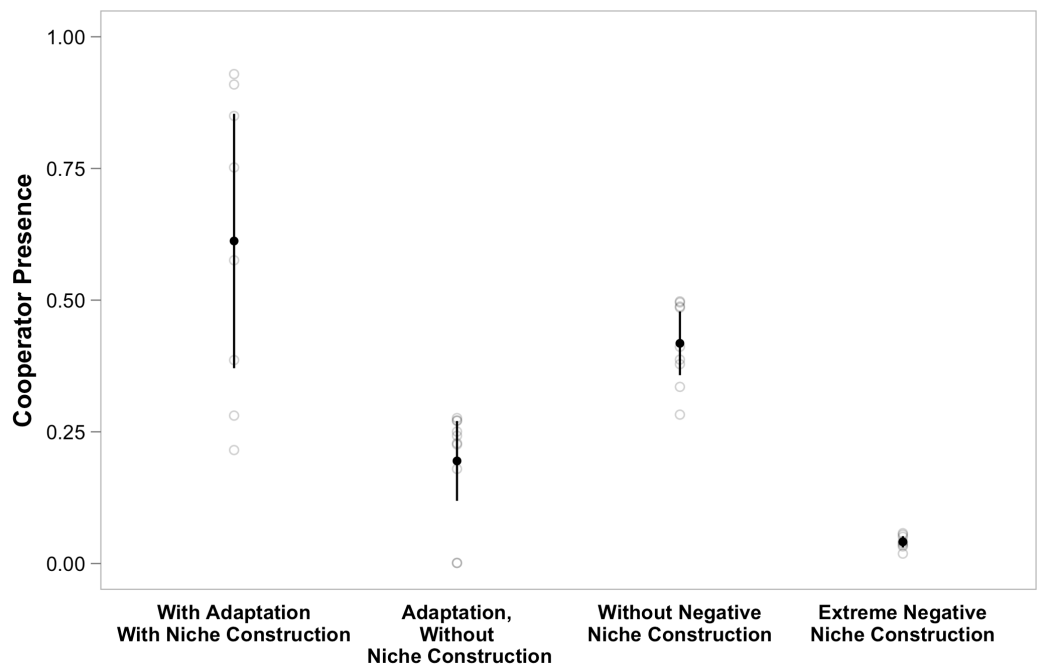


Figure 2: Cooperator Presence TODO

287 **Figure 3**

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

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

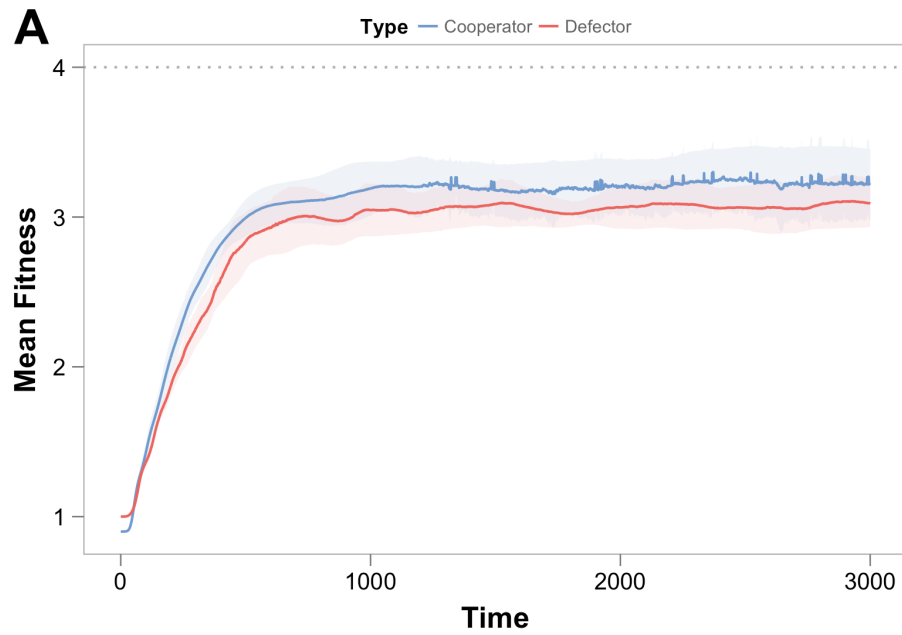


Figure 3: Grand mean Fitness of cooperators and defectors TODO

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

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

292 **Figure 3D - Fitness with extreme negative niche construction ($L=1$,
293 $A=6$)**

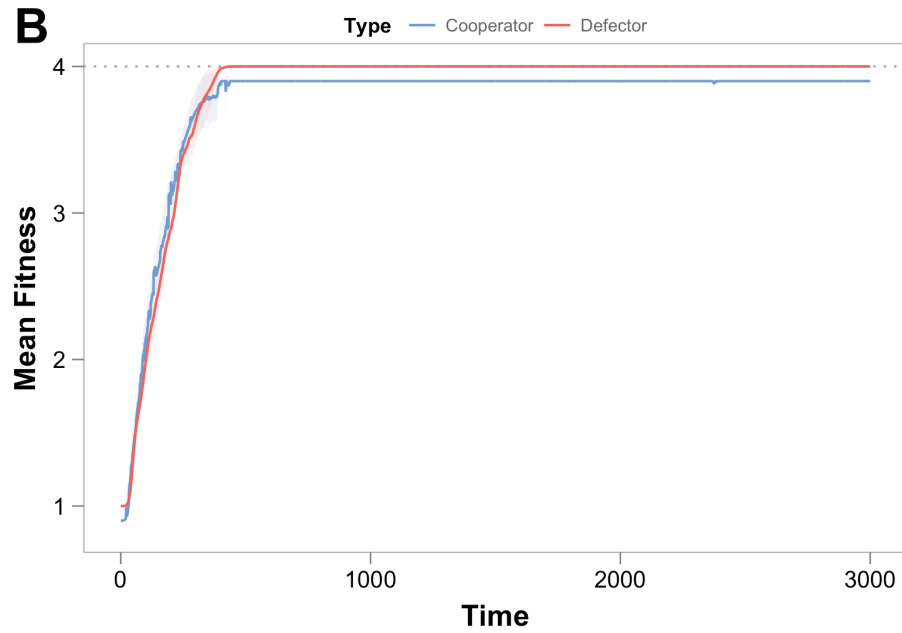


Figure 4: Grand mean Fitness of cooperators and defectors, double delta, no epsilon TODO

Figure 4

Cooperators invade from single population

Figure 5

Defectors are kept at bay

Figure 6

Figure 6A - Effect of Migration Rate (m)

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

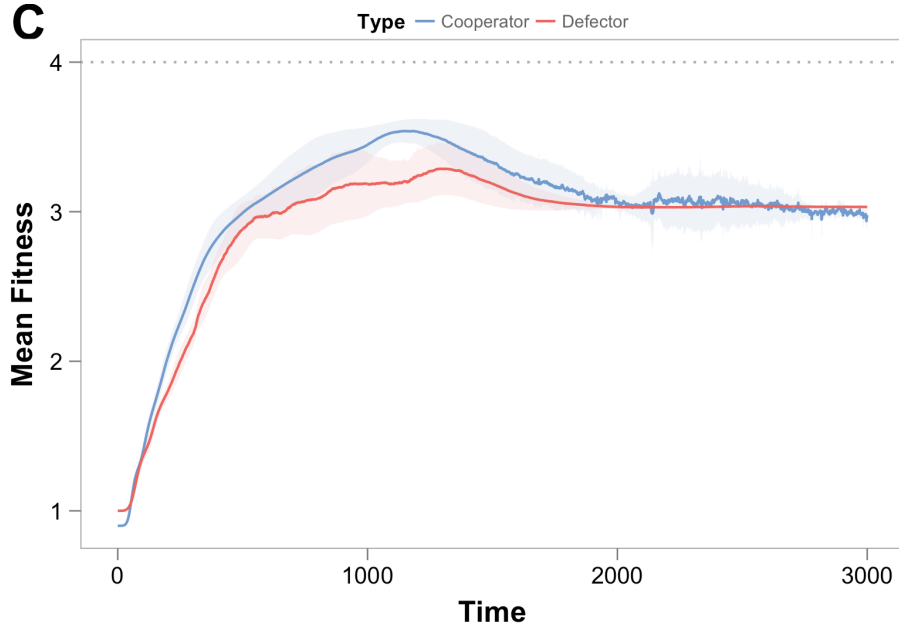


Figure 5: Grand mean Fitness of cooperators and defectors, no negative niche construction TODO

301 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
δ	Fitness benefit, nonzero alleles	0.3
c	Production cost	0.1
ϵ	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
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 stress)	10^{-5}
T	Number of simulation cycles	1000
d	Population dilution factor	0.1

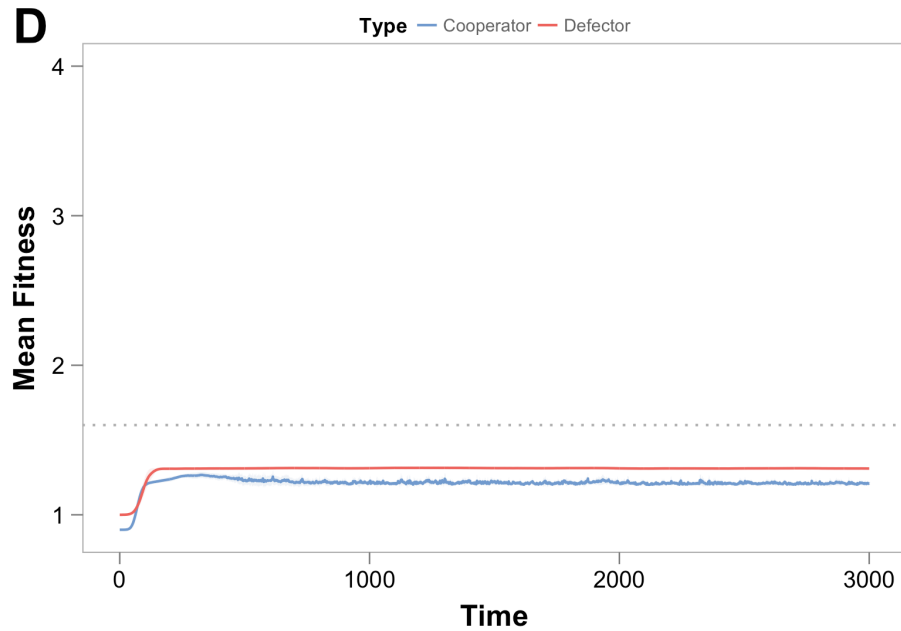


Figure 6: Grand mean Fitness of cooperators and defectors, extreme negative niche construction TODO

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