

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-

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

Model Description

Our simulated environment consists of N^2 patches arranged as an $N \times N$ lattice (see [Table 1](#) for model parameters and their values), where each patch supports a population of zero or more individuals. Each individual in the population has a genotype, which is an ordered list of $L + 1$ integers (loci). The first L loci are *adaptive loci*, and are each occupied by a 0 or an integer from the set $A = \{1, \dots, a_{max}\}$, where a_{max} is the number of potential alleles. At each of these loci, the presence of a non-zero allele represents an adaptation to the environment that confers fitness benefit δ . A binary allele at locus $L + 1$ determines whether or not that individual is a cooperator. Individuals with allelic state 1 at this locus are cooperators, carrying a cost c , while individuals with allelic state 0 are defectors. When $\delta \geq c$, an adapted cooperator recoups the cost of cooperation.

Organisms also influence their environment, which can feed back to influence selection. We model this as a form of frequency dependent selection. Specifically, the selective value of adaptive allele a at locus l increases with the number of individuals in the population that have allele $a - 1$ at locus $l - 1$

111 (note that we treat both adaptive loci and allelic states as circular, so the
 112 allelic state at locus 1 is affected by locus L , and allele 1 is best preceded by
 113 allele a_{max}). The slope of this increase is ϵ , which specifies the intensity of
 114 niche construction. As a consequence of this form of frequency dependence,
 115 genotypes with sequentially-increasing allelic states will tend to evolve. Be-
 116 cause mutations are random, as described later, each population will evolve
 117 sequences that start with different allelic states. These different sequences rep-
 118 resent the unique niches constructed by populations. Under this model, the
 119 fitness of an individual with genotype g in population P is:

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

120 where z is a baseline fitness, $a_{g,l}$ represents the allelic state of genotype g at
 121 locus l , L is the number of adaptive loci, and c is the cost of the cooperative
 122 allele. The function I_A indicates whether allelic state y is in A (i.e., it is non-
 123 zero). The function $n(a, l)$ gives the number of individuals in the population
 124 with allelic state a at the locus l (Equation 2), and *the function* $\beta(x, x_{max})$
 125 gives the value below some value x in the circular set $\{1, \dots, x_{max}\}$ (Equation
 126 3).

$$n(a, l) = \sum_{i \in P} I_{a_{g,l}}(a_{\gamma(i),l}) \quad (2)$$

127 Here, $I_x(y)$ indicates whether the allelic state y matches allelic state x (1) or
 128 not (0), and $\gamma(j)$ is the genotype of individual j .

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

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, $\gamma(i)$ is the genotype of individual i , and $W_{\gamma(i)}$ is its fitness (see Equation 1). π_i therefore reflects that an individual's ability to persist is proportional to its fitness relative to others'.

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

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

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

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

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

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

174 **Source Code and Software Environment**

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

179 **Results**

180 **Niche construction prolongs cooperator survival**

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

182 **Negative Niche construction helps**

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

184 **NC Prevents/Limits Defector invasion**

185 **NC Enables Cooperator Spread by “exporting” environ-** 186 **ment**

187 **Discussion**

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

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

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

205 Niche construction and selective feedbacks Niche construction and other social
206 interactions

207 **Public Goods**

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

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

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

226 **Primacy/Recency**

227 In our model, alterations to the environment were immediately echoed by
228 changes in selection. However, decoupling the timescales on which these pro-
229 cesses occur can have substantial effects (Laland *et al.*, 1996). By integrating
230 past allelic states into Equation 1, we can begin to explore how the cumulative
231 effects of niche construction affect the creation of non-social adaptive oppor-
232 tunities and the benefits that they offer cooperation. Here, how these past
233 allelic states are integrated will play an important role. For example, when
234 the effects of earlier generations are weighted more heavily, the influence of
235 migration may be diminished. While this will reduce the threat of emigration
236 by defectors, cooperator populations will also be less effective at exporting
237 their niche.

238 **Cooperative Niche Construction**

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

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

254 **Host-Symbiont**

255 In many instances of cooperation, the environment is itself a biological entity,
 256 which can produce additional evolutionary feedbacks. As the host population
 257 changes, so too will selection on their symbiont populations. Here, evolution-
 258 ary outcomes depend greatly on the degree of shared interest between the host
 259 and symbiont. For example, the cooperative production of virulence factors by
 260 the human pathogen *P. aeruginosa* in lung infections is harmful to those with
 261 cystic fibrosis (Harrison, 2007). Conversely, cooperative light production by *A.*
 262 *fischeri* is vital for the survival of its host, the Hawaiian bobtail squid (Ruby,
 263 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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280 **Figures**

281 **Figure 1**

282 **Figure 1A**

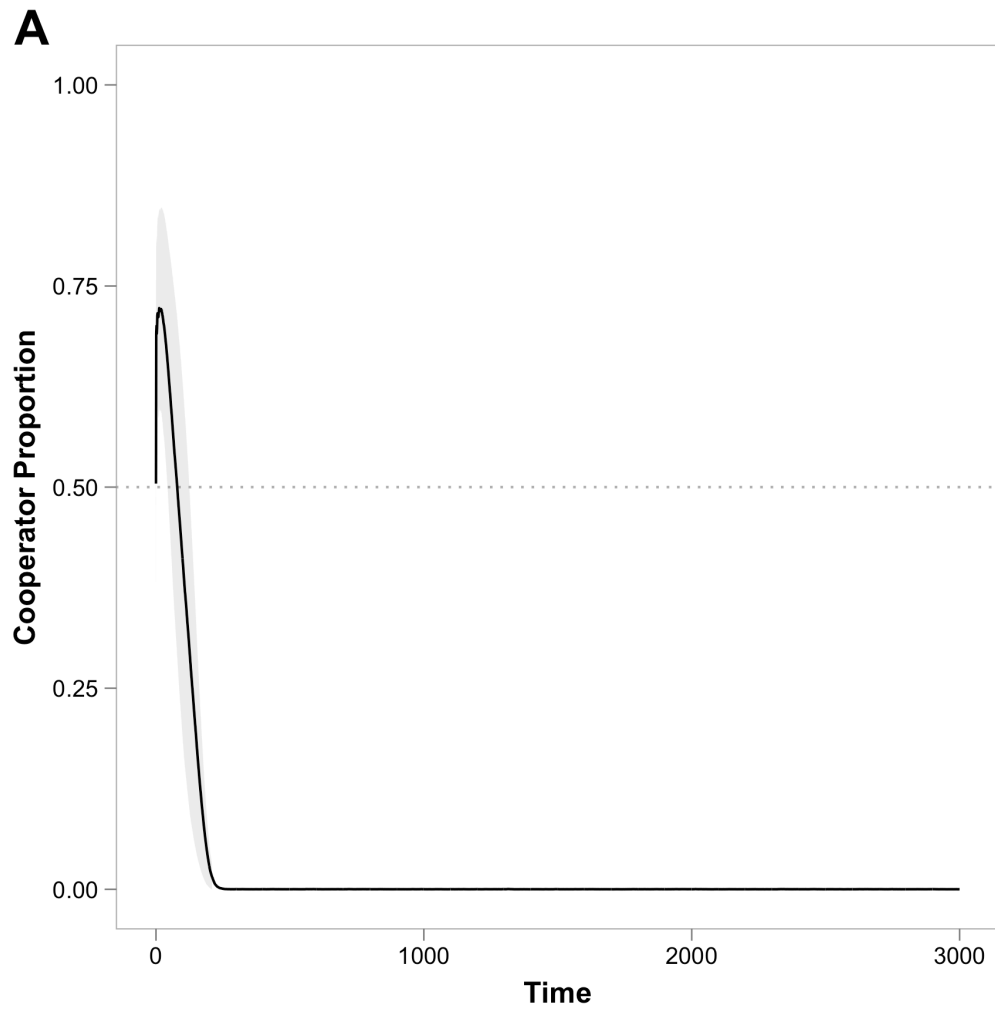


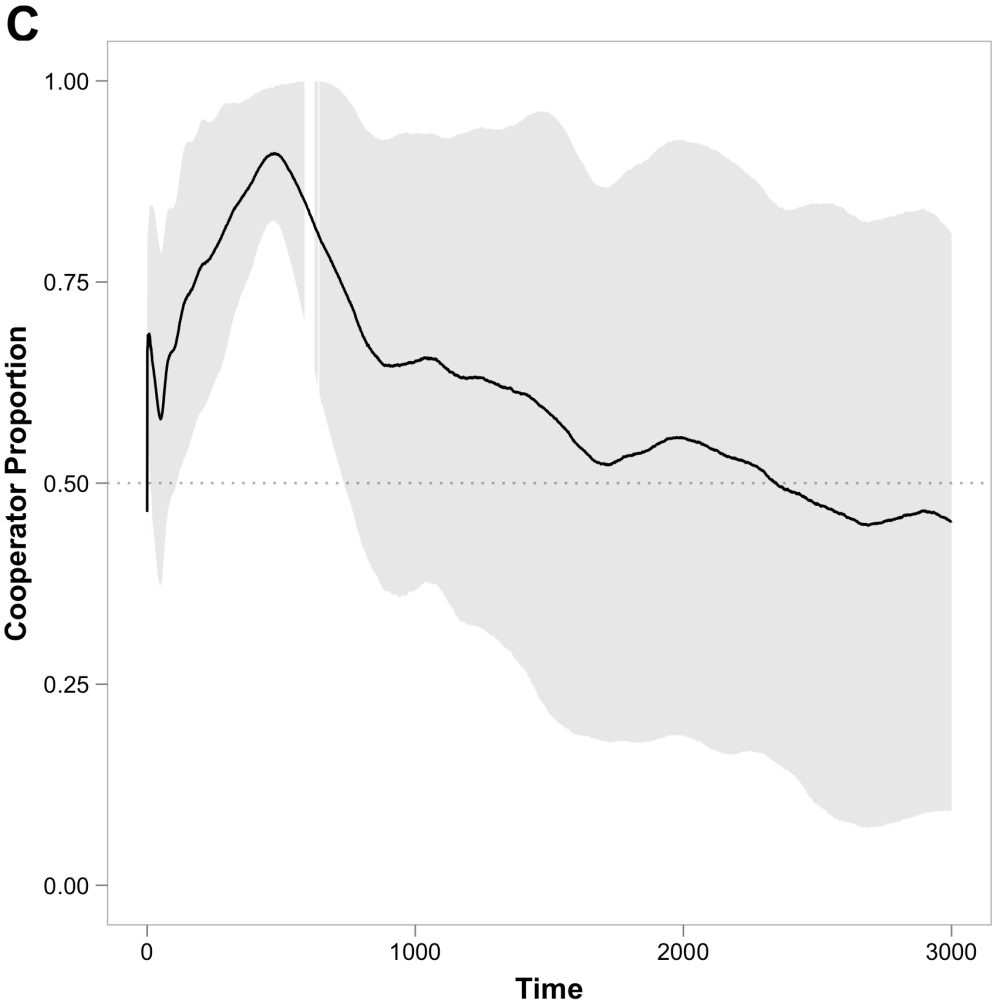
Figure 1: Proportion of cooperators over time when there are no opportunities for non-social adaptation

283 **Figure 1B**

284 Proportion of cooperators over time with non-social adaptation

285 **Figure 1C**

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



287 struction

288 **Figure 2**

289 Plot showing integral for baseline values, double adaptive benefit (no NC,
 290 epsilon=0), no negative NC (L=5, A=5), Extreme negative niche construction
 291 (L=1, A=6)

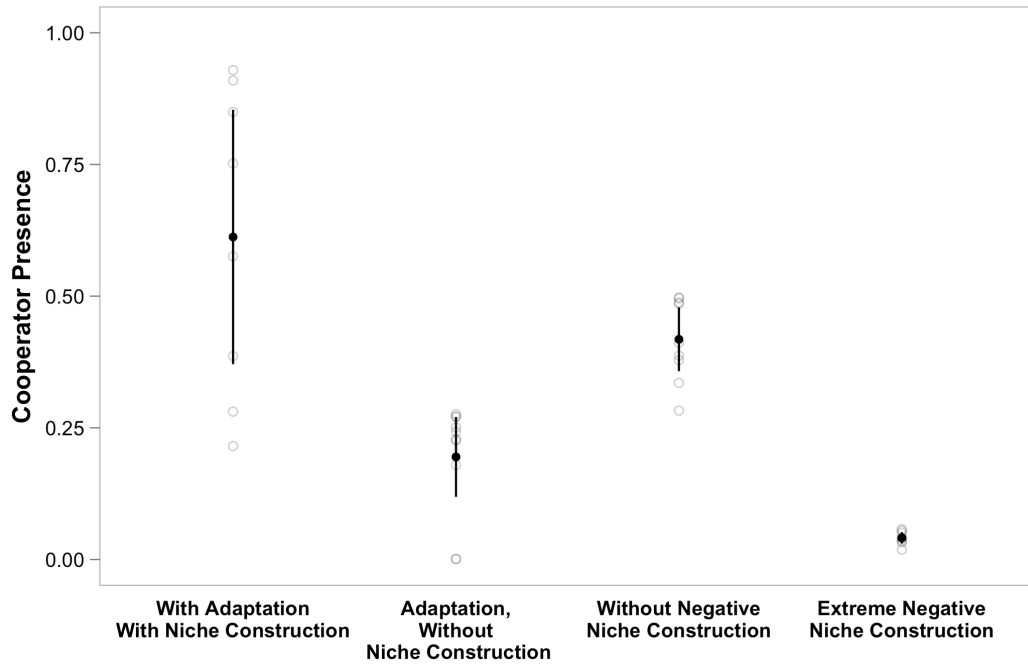


Figure 2: Cooperator Presence

292 **Figure 3**

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

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

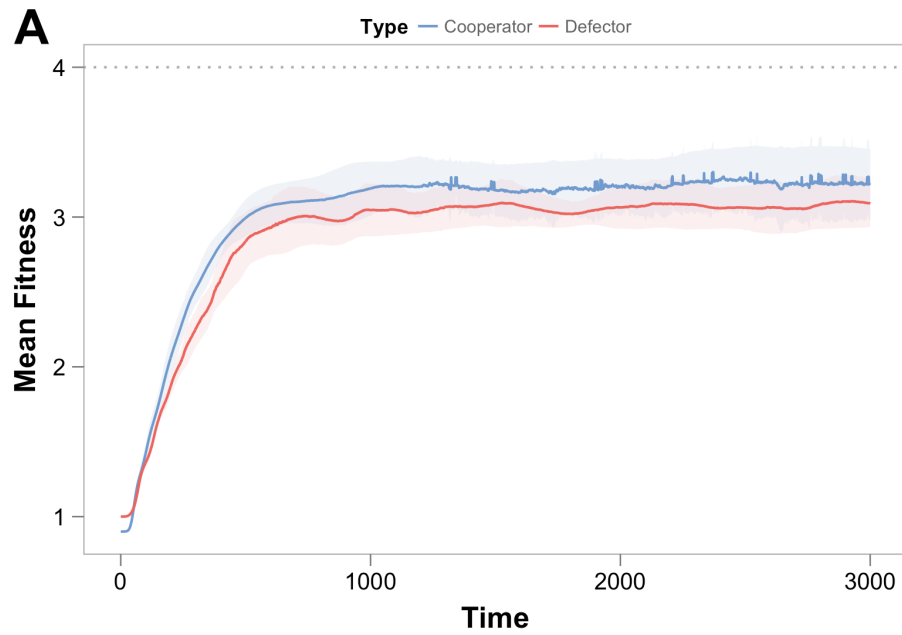


Figure 3: Grand mean Fitness of cooperators and defectors

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

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

297 **Figure 3D - Fitness with extreme negative niche construction ($L=1$,
298 $A=6$)**

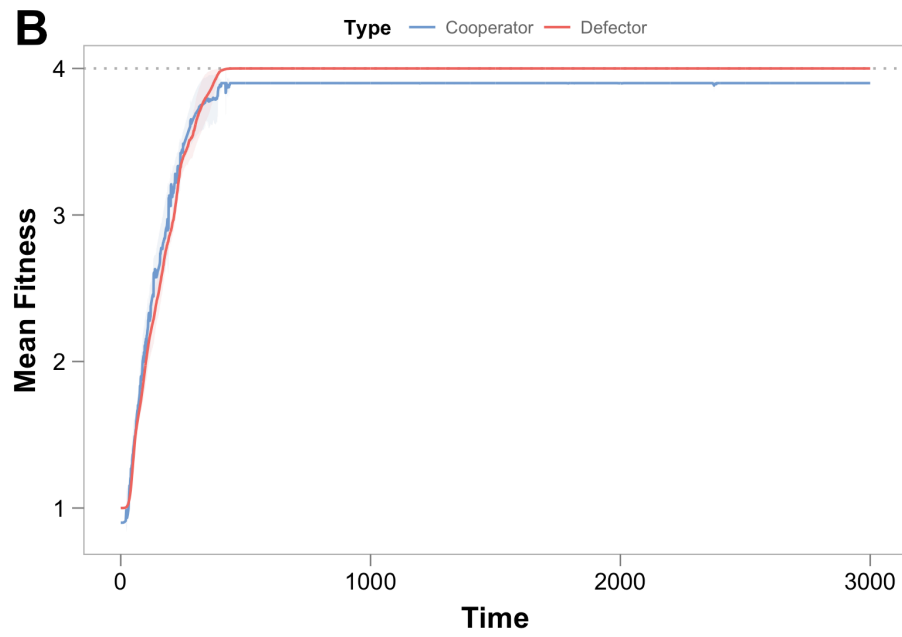


Figure 4: Grand mean Fitness of cooperators and defectors, double delta, no epsilon

299 **Figure 4**

300 Cooperators invade from single population

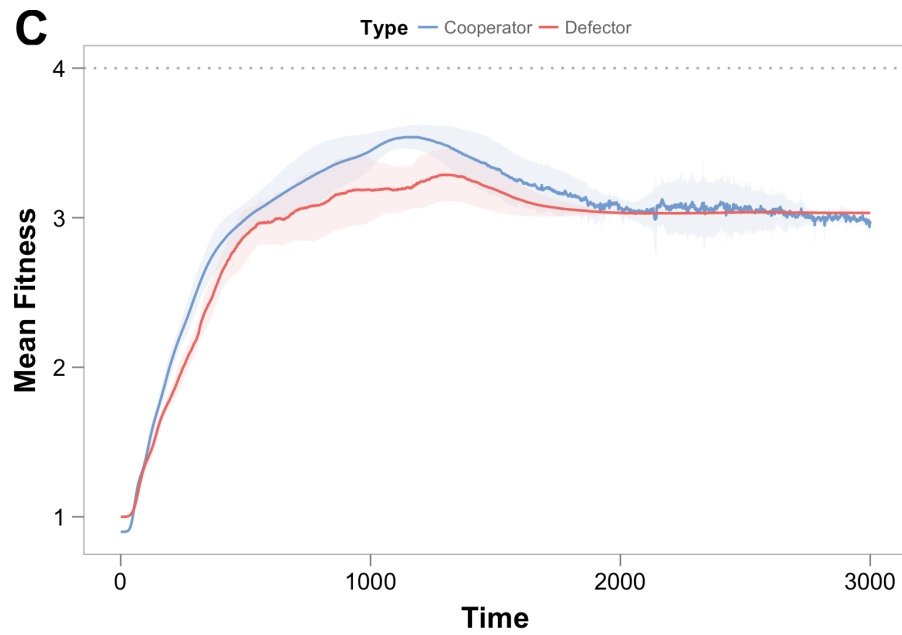


Figure 5: Grand mean Fitness of cooperators and defectors, no negative niche construction

301 **Figure 5**

302 Defectors are kept at bay

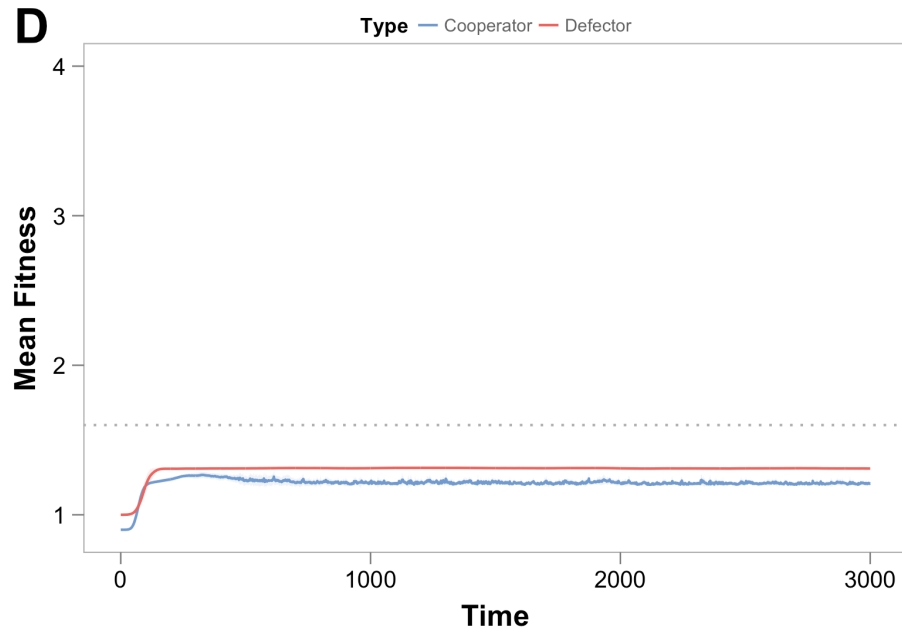


Figure 6: Grand mean Fitness of cooperators and defectors, extreme negative niche construction

303 **Figure 6**

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

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

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_c	Mutation rate (cooperation)	10^{-5}
μ_a	Mutation rate (adaptation)	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

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