

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

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

55 In this work, we demonstrate how cooperation can be maintained indefinitely
56 by niche construction. We expand upon the model presented in Hankshaw and
57 Kerr (2015) to allow populations to alter their local environment. As environ-
58 ments change, so too does selection. This creates an eco-evolutionary feedback
59 whereby selection is dependent on current genotypes, and the composition of
60 genotypes is dependent on selection. Niche construction can be positive or neg-
61 ative, depending on whether the environmental change increases or decreases
62 the fitness of the niche-constructing individual. Although niche construction
63 occurs independently of cooperation in our model, the increase in density that
64 results from cooperation has a profound effect on how populations evolve in
65 the presence of selective feedbacks. First, these populations exert greater in-
66 fluence on their environments, which better enables them to benefit from posi-

67 tive niche construction. And as environments change, either through negative
68 niche construction or external influences, these larger populations can adapt
69 more quickly. We show that it is the combination of these factors that allows
70 cooperation to persist.

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

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

83 Finally, we demonstrate how *negative* niche construction, where populations
84 change their environment in ways that reduce fitness, can further support
85 cooperation. Even though the niche construction process creates selective
86 feedbacks, we would expect the magnitude of these feedbacks to decrease as
87 populations evolve. Once individuals can no longer gain adaptations that
88 compensate for the costs of cooperation, they are then outcompeted by non-

89 cooperators. However if populations construct their environment in a way
90 which decreases fitness, cooperation can still hitchhike when this change also
91 creates the opportunity to gain compensatory adaptations.

92 **Materials and Methods**

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

100 **Model Description**

101 Our simulated environment consists of N^2 patches arranged as an $N \times N$
102 lattice (see [Table 1](#) for model parameters and their values), where each patch
103 can support a population. Each individual in a population has a genotype,
104 which is an ordered list of $L + 1$ integers (loci). The first L loci are *adaptive*
105 *loci*, and are each occupied by 0 or an integer from the set $A \equiv \{1, 2, \dots, a_{max}\}$,
106 where a_{max} is the number of alleles conferring a selective benefit. Specifically,
107 the presence of a non-zero allele at any of these loci represents an adaptation
108 that confers fitness benefit δ . A binary allele at locus $L + 1$ determines whether

109 or not that individual is a cooperator. Individuals with allelic state 1 at this
 110 locus are cooperators, carrying a cost c , while individuals with allelic state 0
 111 are defectors. When $\delta \geq c$, a minimally adapted cooperator recoups the cost
 112 of cooperation. Equation 1 defines function $n(a, l)$, which gives the number
 113 of individuals in the population with allelic state a at locus l . $I_x(y)$ indicates
 114 whether the allelic state y matches allelic state x (1) or not (0), and $\gamma(i)$ is
 115 the genotype of individual i .

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

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

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

126 Where $\text{mod}_Y(y)$ is the integer remainder after dividing y by Y . Thus, the

127 value of adaptive allele a at locus l increases with the number of individuals
 128 that have allele $\beta(a, a_{max})$ at locus $\beta(l, L)$. The slope of this increase is ϵ ,
 129 which specifies the intensity of niche construction. Consider a genotype g with
 130 allelic state at locus l given by $a_{g,l}$; its fitness is defined as:

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

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

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

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

138 Cooperators produce a public good that is equally accessible to all members
 139 of the population. This public good increases the carrying capacity at that
 140 patch, allowing the population to reach greater density. This benefit increases
 141 linearly with the proportion of cooperators. Thus, if p is the proportion of
 142 cooperators in a population at the beginning of a growth cycle, then that
 143 population reaches the following size during the growth phase:

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

144 The function $S(p)$ reflects the benefit of public good production. A population
 145 composed entirely of defectors reaches size S_{min} , while one composed entirely
 146 of cooperators reaches size S_{max} (with $S_{max} \geq S_{min}$). During growth, indi-
 147 viduals compete for inclusion in the resulting population. The composition of
 148 population P with cooperator proportion p after growth is multinomial with
 149 parameters and $S(p)$ and $\{\pi_1, \pi_2, \dots, \pi_{|P|}\}$, where:

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

150 Here, $W_{\gamma(i)}$ is the fitness of an individual i with genotype $\gamma(i)$ (see Equation
 151 3). The value π_i therefore reflects an individual's relative reproductive fitness.
 152 For simplicity, we apply mutations after population growth. Mutations occur
 153 independently at each locus and cause the allelic state to change. Mutations
 154 occur at each adaptive locus at rate μ_a , in which a new allele is chosen at
 155 random from the set $\{0\} \cup A$. At the binary cooperation locus, mutations
 156 occur at rate μ_c . These mutations flip the allelic state, causing cooperators to
 157 become defectors and vice versa. Therefore, the probability that genotype g
 158 mutates into genotype g' is given by:

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

159 where $H_a(g, g')$ and $H_c(g, g')$ are the Hamming distances between genotypes g
 160 and g' at the cooperation locus and adaptive loci, respectively. The Hamming
 161 distance is the number of loci at which allelic states differ (Hamming, 1950).
 162 After mutation, individuals emigrate to an adjacent patch at rate m . The
 163 destination patch is randomly chosen with uniform probability from the source
 164 patch's Moore neighborhood, which is composed of the nearest 8 patches on the
 165 lattice. Because the metapopulation lattice has boundaries, patches located
 166 on an edge have smaller neighborhoods.
 167 Metapopulations are initiated in a state that follows an environmental change.
 168 First, populations are seeded at all patches with cooperator proportion p_0 and
 169 grown to density $S(p_0)$. An environmental challenge is then introduced, which
 170 subjects the population to a bottleneck. For each individual, the probability
 171 of survival is μ_t , which represents the likelihood that a mutation occurs that
 172 confers tolerance. Survivors are chosen by binomial sampling. Because indi-
 173 viduals have not yet adapted to this new environment, the allelic state of each
 174 individual's genotype is set to 0 at each adaptive locus. Following initializa-
 175 tion, simulations are run for T cycles, where each discrete cycle consists of
 176 growth, mutation, and migration. At the end of each cycle, populations are
 177 thinned to allow for growth in the next cycle. The individuals that remain are
 178 chosen by binomial sampling, where each individual persists with probability
 179 d , regardless of allelic state.

180 **Source Code and Software Environment**

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

185 **Results**

186 **Niche Construction Maintains Cooperation**

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

195 **Not Just Because of Additional Fitness from Epsilon** 196 **(TODO title)**

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

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

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

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

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

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

265 NC Enables Cooperator Spread

266 Figure 4

267 NC Prevents Defector Invasion

268 Figure 5

269 How Public Good Fuels all of this

270 Figure 6 A: effect of S_{\max} - S_{\min} , B: effect of migration rate

271 Discussion

- 272 • summary of results
- 273 • similarities/differences from previous work
 - 274 – Schwilk and Kerr (2002)
 - 275 – 10.1073/pnas.0812644106
- 276 • negative/positive NC
 - 277 – laland1996evolutionary
- 278 • public goods as niche construction
- 279 • future QS or other environmental sensing
- 280 • Facultative cooperation
 - 281 – Rodrigues (2012)
 - 282 – Dumas and Kümmerli (2010)
 - 283 – Kümmerli and Brown (2010)
 - 284 – Darch/Diggle

- 285 – QS?
- 286 – Environmental Sensing? - (Koestler and Waters, 2014, Bernier et
- 287 al. (2011))
- 288 • Negative Niche construction as a stragegy? - would those that create this
- 289 constant pressure (L=5, A=6) do better than those that do not (L=5,
- 290 A=5)?

291 Niche construction and selective feedbacks Niche construction and other social
 292 interactions

293 **Public Goods**

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

296 By their very nature, public goods benefit populations by making their environ-
 297 ment more hospitable. For example, bacteria produce extracellular products
 298 that find soluble iron (Griffin *et al.*, 2004), digest large proteins (Diggle *et al.*,
 299 2007; Darch *et al.*, 2012), and reduce the risk of predation (Cosson *et al.*, 2002),
 300 among many others (West *et al.*, 2007a). While many studies have explored
 301 how the environment affects the evolution of cooperative bahviors, relatively
 302 few have examined how those behaviors affect the environment and the result-
 303 ing change in evolutionary trajectories. Lehmann (2007) demonstrated analyti-
 304 cally that when niche construction act benefits future generations, cooperation
 305 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. While these studies have focused on the niche constructing effects of cooperation, we instead focus our attention here on how niche construction enables 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 3, 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

327 system is affected by the timescale at which carrying capacity at a given patch
328 is increased by public goods. In natural settings, a multitude of factors in-
329 cluding protein durability (Brown and Taddei, 2007; Kümmerli and Brown,
330 2010), diffusion (Allison, 2005; Driscoll and Pepper, 2010), and resource avail-
331 ability (Zhang and Rainey, 2013; Ghoul *et al.*, 2014) influence both the rate
332 and the degree to which public goods alter the environment (and thereby selec-
333 tion). Lehmann (2007) demonstrated that a cooperative, niche constructing
334 behavior can be favored when it only affected selection for future generations,
335 thus reducing the potential for competition among contemporary kin. The
336 evolutionary inertia that this creates, however, may ultimately work against
337 cooperators. When public good accumulates in the environment, cooperators
338 must reduce their investment in production to remain competitive (Kümmerli
339 and Brown, 2010).

340 TODO: wrap up. Facultative cooperation requires sensing.

341 **Host-Symbiont**

342 In many instances of cooperation, the environment is itself a biological entity,
343 which can produce additional evolutionary feedbacks. As the host population
344 changes, so too will selection on their symbiont populations. Here, evolution-
345 ary outcomes depend greatly on the degree of shared interest between the host
346 and symbiont. For example, the cooperative production of virulence factors by
347 the human pathogen *P. aeruginosa* in lung infections is harmful to those with
348 cystic fibrosis (Harrison, 2007). Conversely, cooperative light production by *A.*

349 *fischeri* is vital for the survival of its host, the Hawaiian bobtail squid (Ruby,
350 1996). It was recently argued that incorporating the effects of niche construc-
351 tion is critical for improving our understanding of viral evolution (Hamblin *et*
352 *al.*, 2014) and evolution in co-infecting parasites (Hafer and Milinski, 2015).
353 Incorporating host dynamics, co-evolution, and the feedbacks that they pro-
354 duce into models is likely to be equally important for gaining an understanding
355 of how cooperative behaviors evolve in these host-symbiont settings.

356 Acknowledgments

- 357 • TODO: Organizers?
- 358 • TODO: lab comments

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367 **Figures**

368 **Figure 1**

369 **Figure 1A**

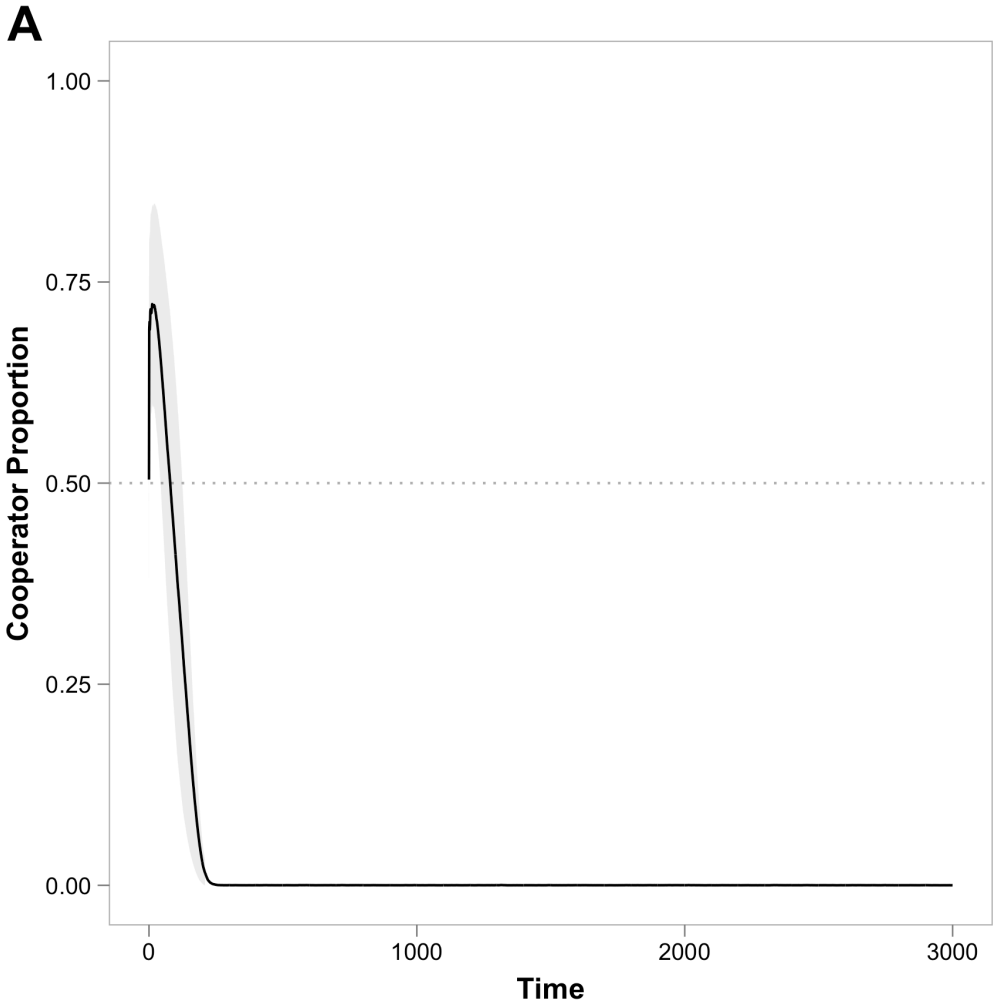


Figure 1: Proportion of cooperators over time when there are no opportunities for non-social adaptation

370 **Figure 1B**

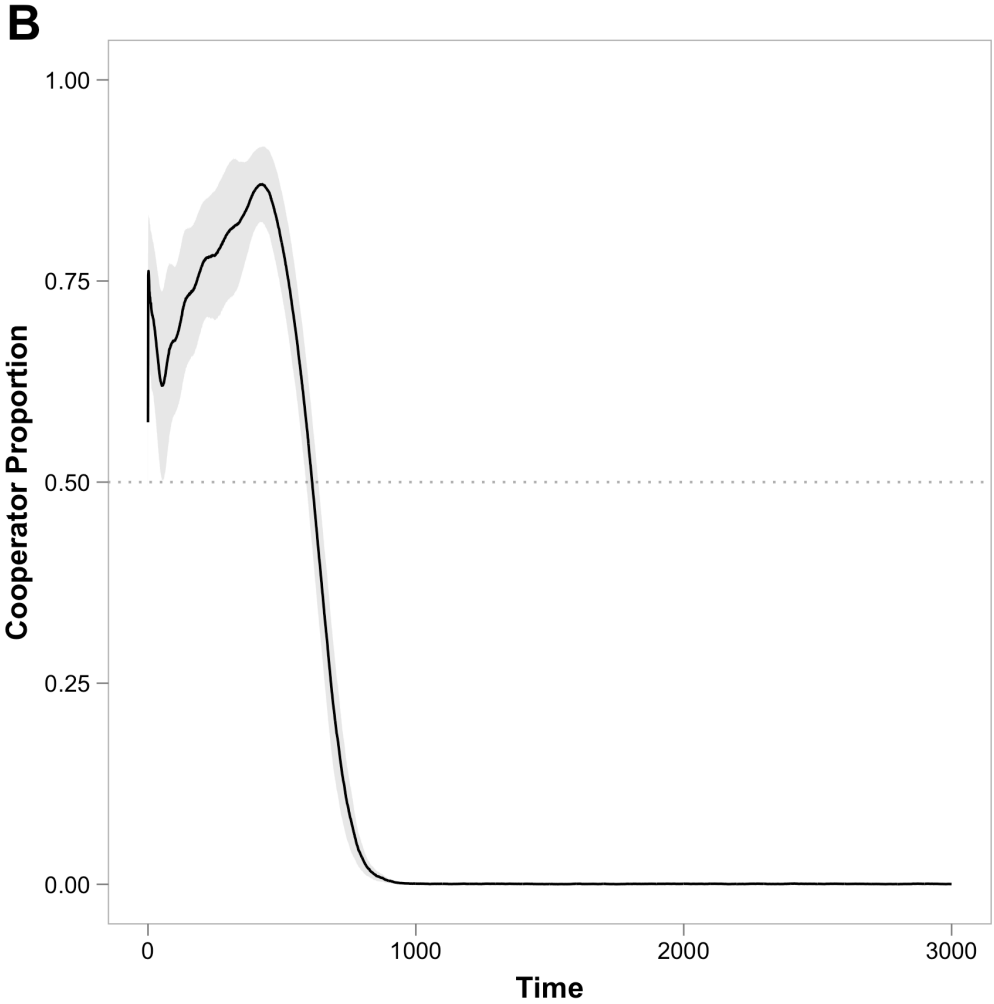


Figure 2: Proportion of cooperators over time with non-social adaptation (GNH)

371 **Figure 1C**

372 **Figure 1X**

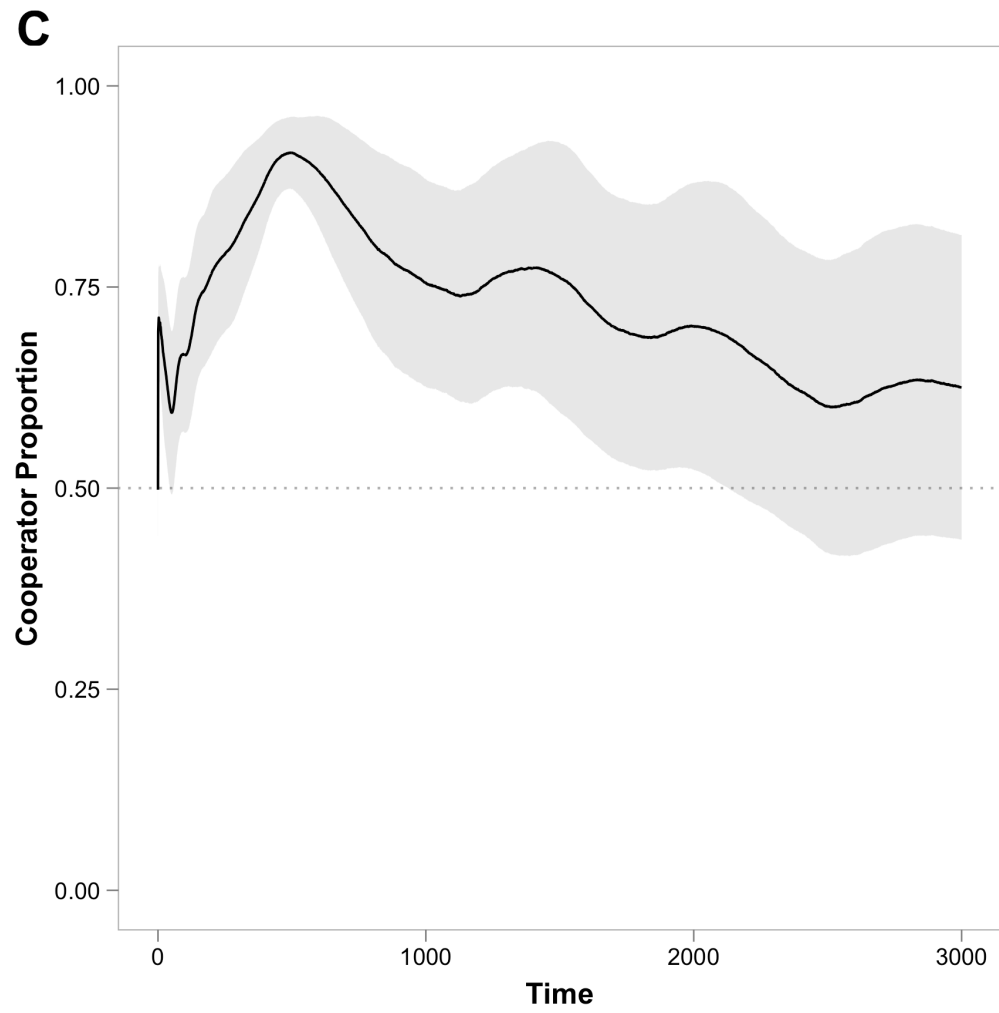


Figure 3: Proportion of cooperators over time with non-social adaptation and selective feedbacks

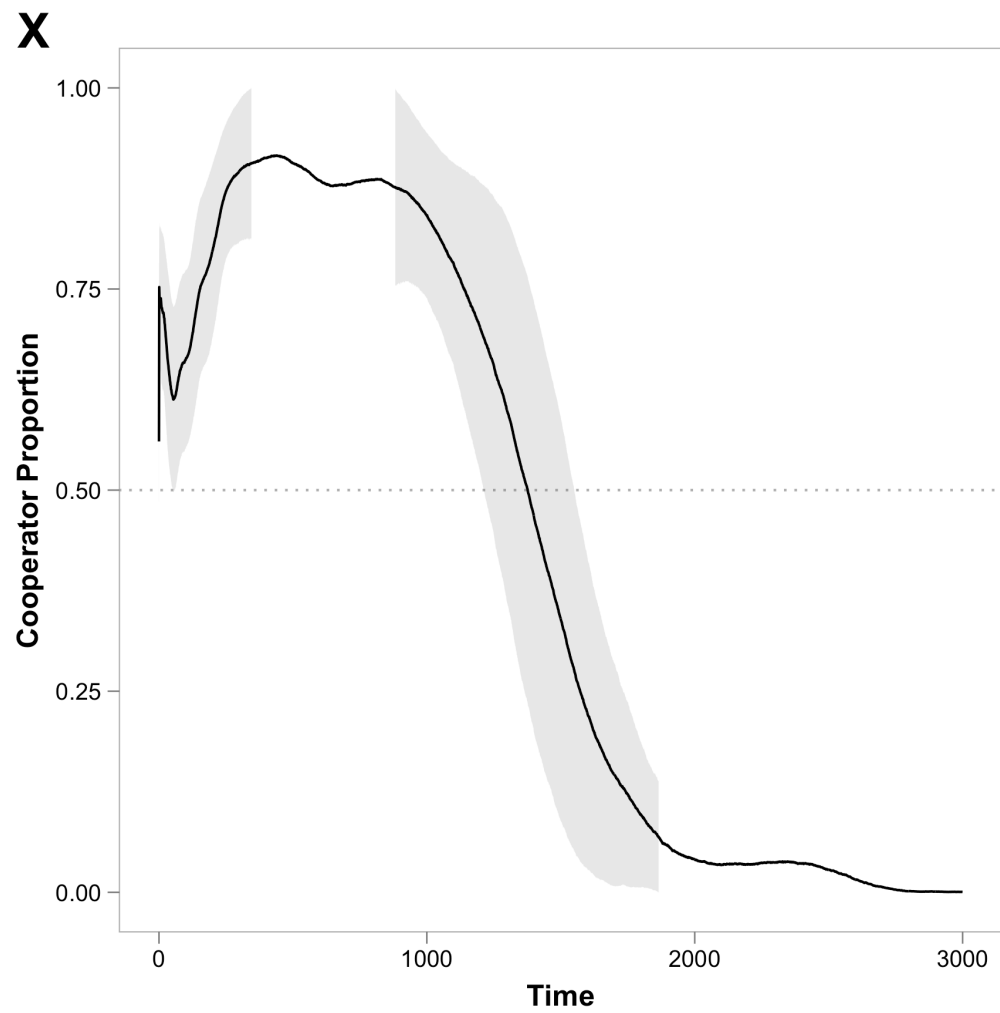


Figure 4: Proportion of cooperators over time without negative niche construction

373 **Figure 2**

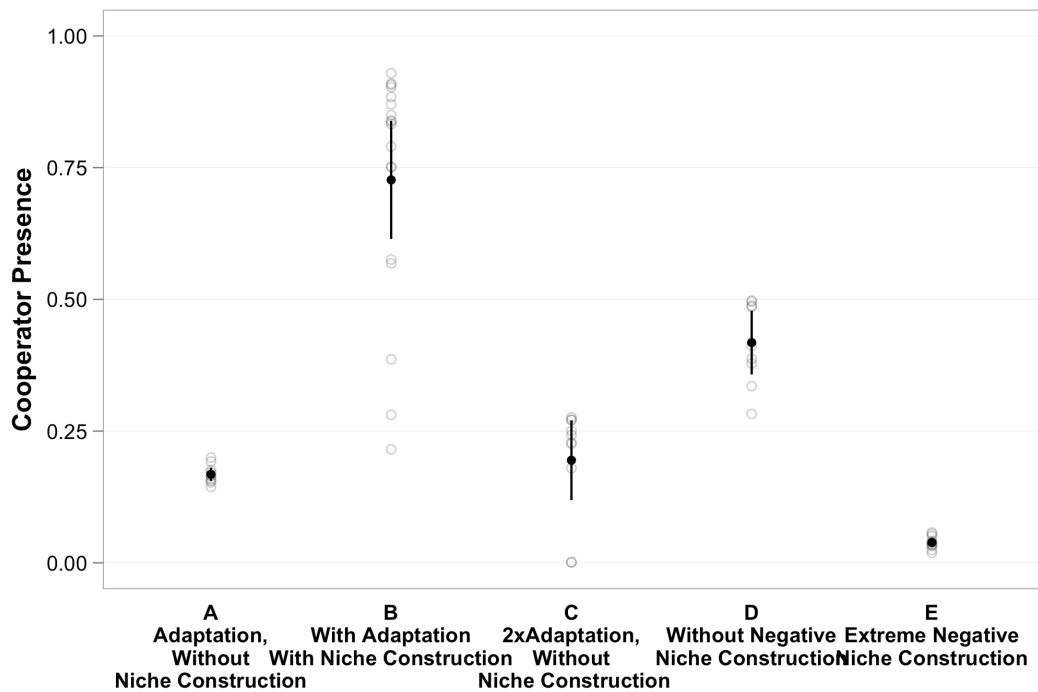


Figure 5: Cooperator Presence TODO

374 **Figure 3**

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

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

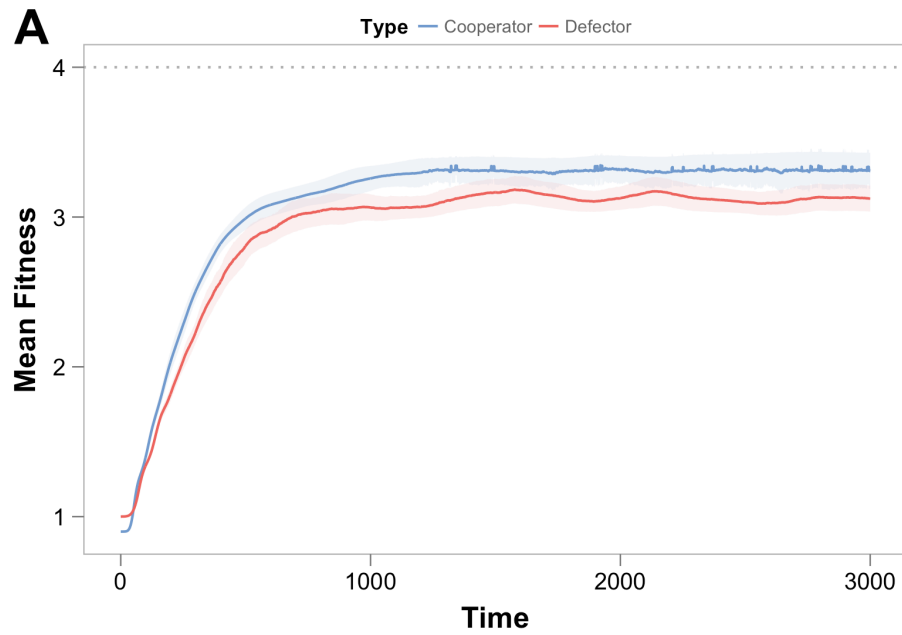


Figure 6: Grand mean Fitness of cooperators and defectors TODO

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

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

379 **Figure 3D - Fitness with extreme negative niche construction ($L=1$,
380 $A=6$)**

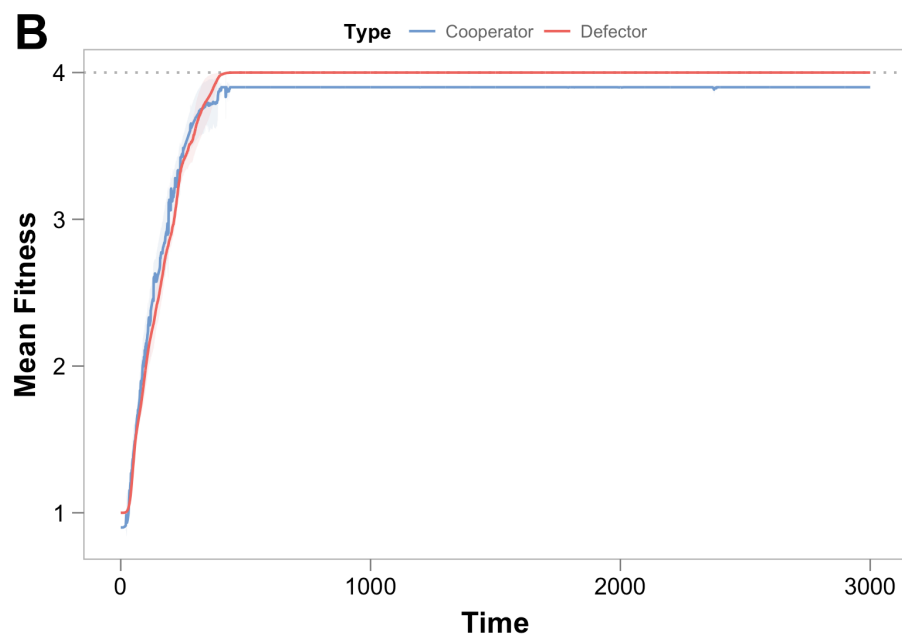


Figure 7: Grand mean Fitness of cooperators and defectors, double delta, no epsilon TODO

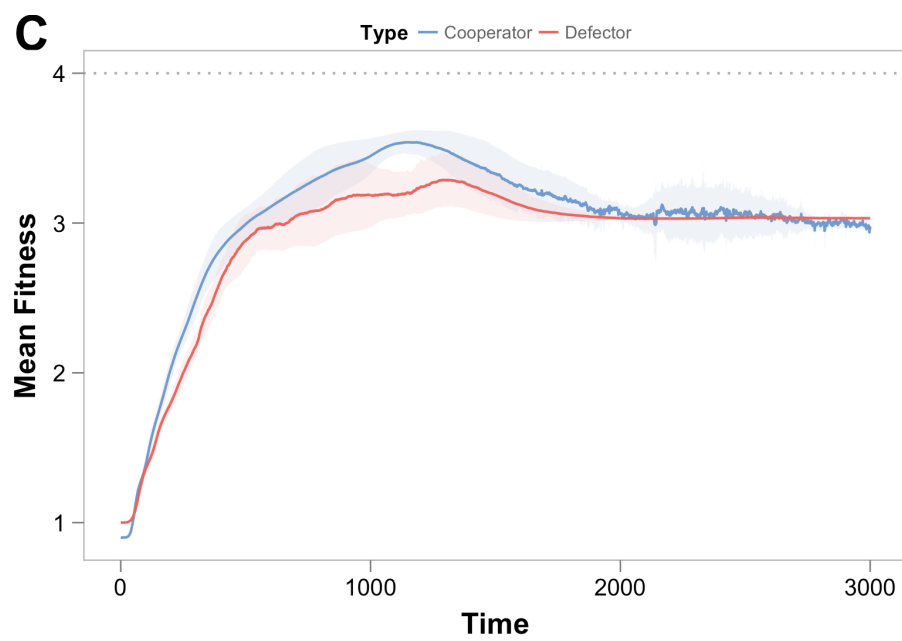


Figure 8: Grand mean Fitness of cooperators and defectors, no negative niche construction TODO

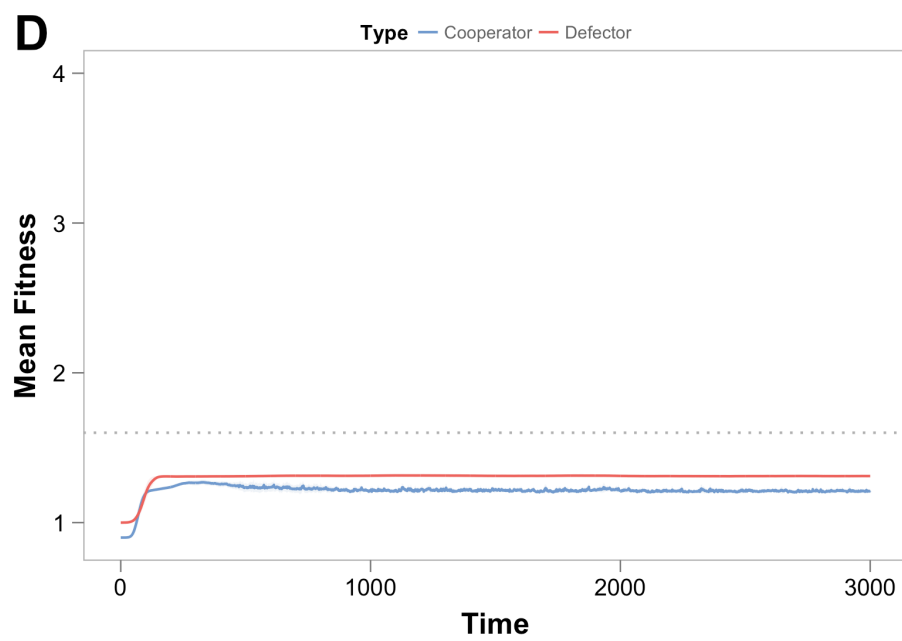


Figure 9: Grand mean Fitness of cooperators and defectors, extreme negative niche construction TODO

381 **Figure 4**

382 Cooperators invade from single population

383 **Figure 5**

384 Defectors are kept at bay

385 **Figure 6**

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

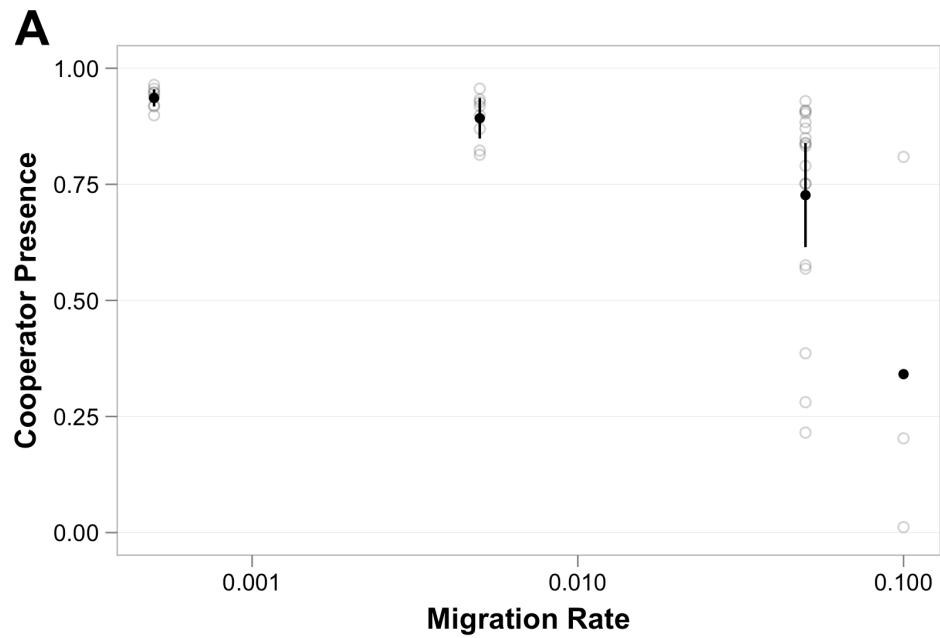


Figure 10: TODO Cooperator Presence for different migration rates

387 **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_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

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