

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 better

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

71 **Description of positive NC effects**

72 Include S_{\max} 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 δ . 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 ϵ , 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). π_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 μ_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 μ_c . These mutations flip the allelic state, causing cooperators to become defectors and vice versa. Therefore, the probability that genotype g mutates into genotype g' is given by:

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

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 μ_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 Maintains Cooperation

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

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

In our model, an individual's fitness is the product of two processes. First, mutations can engender environmental adaptations, which are represented by non-zero alleles. These adaptations create the transient lift in cooperation seen in Figure 1B. The second process that contributes to fitness is niche construction. Selection favors individuals with sequentially-increasing alleles. Because larger populations will have a greater effect on their environment, this benefit is density dependent. In our experiments, this positive niche construction contributed equally to fitness when all individuals shared the same allele in a population at maximum carrying capacity. To determine whether cooperation was maintained simply due to the higher selective values made possible by this second source of fitness, we compared our results against the results of experiments in which the ordering of alleles did not matter, and the fitness benefit provided by adaptation was doubled ($\epsilon = 0$, $\delta = 0.6$). That this doubling is an over estimate of the magnitude of fitness contributions that arise from niche construction, since these values would only occur in populations at maximum carrying capacity, which does not occur in the presence of defectors. Nevertheless, Figure 2 shows that higher selective values have little effect (columns A and C) and do not explain the maintenance of cooperation that we observe when niche construction occurs (column B).

Although we have seen that maximum fitness does not substantially effect the maintenance of cooperation, perhaps the rate at which fitness accumulates in

cooperator and defector populations matters. When we compare the accumulation of fitness via adaptation in the presence of niche construction (Figure 3A) against simulations in which selective values are doubled (Figure 3B), two features emerge. In both scenarios, cooperators gain adaptations more quickly than defectors due to their size. When niche construction is not present, cooperator 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 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.

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

(TODO: explain why defector fitness doesn't reach 4 (density dependent fitness)) maybe better in figure caption?)

To further explore the influence of negative niche construction, we performed experiments in which the positive effects of niche construction were removed. Here, individuals had a single adaptive locus that was constantly in conflict ($L = 1$, $a_{max} = 6$). As seen in Figures 2 (column E) and 3D, the constant source of adaptation that is provided by negative niche construction is not sufficient to maintain cooperation via hitchhiking, and cooperators are quickly purged

271 from the population. This provides further evidence that feedbacks from both
272 positive and negative niche construction are required for cooperation to persist.

273 **NC Enables Cooperator Spread**

274 Figure 4

275 **NC Prevents Defector Invasion**

276 Figure 5

277 **How Public Good Fuels all of this**

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

279 **Discussion**

- 280 • summary of results
- 281 • similarities/differences from previous work
 - 282 – Schwilk and Kerr (2002)
 - 283 – [10.1073/pnas.0812644106](https://doi.org/10.1073/pnas.0812644106)
- 284 • negative/positive NC
 - 285 – laland1996evolutionary
- 286 • public goods as niche construction

- 287 • future QS or other environmental sensing
- 288 • Facultative cooperation
 - 289 – Rodrigues (2012)
 - 290 – Dumas and Kümmerli (2010)
 - 291 – Kümmerli and Brown (2010)
 - 292 – Darch/Diggle
 - 293 – QS?
 - 294 – Environmental Sensing? - (Koestler and Waters, 2014, Bernier et
 - 295 al. (2011))
- 296 • Negative Niche construction as a strategy? - would those that create this
- 297 constant pressure (L=5, A=6) do better than those that do not (L=5,
- 298 A=5)?

299 Niche construction and selective feedbacks Niche construction and other social
 300 interactions

301 **Public Goods**

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

304 By their very nature, public goods benefit populations by making their environ-
 305 ment more hospitable. For example, bacteria produce extracellular products
 306 that find soluble iron (Griffin *et al.*, 2004), digest large proteins (Diggle *et al.*,
 307 2007; Darch *et al.*, 2012), and reduce the risk of predation (Cosson *et al.*, 2002),

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

330 by defectors, cooperator populations will also be less effective at exporting
331 their niche.

332 **Cooperative Niche Construction**

333 While our focus for this work has been on the eco-evolutionary feedbacks cre-
334 ated by non-social traits, it would also be interesting to explore how this system
335 is affected by the timescale at which carrying capacity at a given patch is in-
336 creased by public goods. In natural settings, a multitude of factors including
337 protein durability (Brown, 2007; Kümmerli and Brown, 2010), diffusion (Al-
338 lison, 2005; Driscoll and Pepper, 2010), and resource availability (Zhang and
339 Rainey, 2013; Ghoul *et al.*, 2014) influence both the rate and the degree to
340 which public goods alter the environment (and thereby selection). Lehmann
341 (2007) demonstrated that a cooperative, niche constructing behavior can be fa-
342 vored when it only affected selection for future generations, thus reducing the
343 potential for competition among contemporary kin. The evolutionary inertia
344 that this creates, however, may ultimately work against cooperators. When
345 public good accumulates in the environment, cooperators must reduce their in-
346 vestment in production to remain competitive (Kümmerli and Brown, 2010).

347 TODO: wrap up. Facultative cooperation requires sensing.

348 **Host-Symbiont**

349 In many instances of cooperation, the environment is itself a biological entity,
350 which can produce additional evolutionary feedbacks. As the host population

351 changes, so too will selection on their symbiont populations. Here, evolution-
352 ary outcomes depend greatly on the degree of shared interest between the host
353 and symbiont. For example, the cooperative production of virulence factors by
354 the human pathogen *P. aeruginosa* in lung infections is harmful to those with
355 cystic fibrosis (Harrison, 2007). Conversely, cooperative light production by *A.*
356 *fischeri* is vital for the survival of its host, the Hawaiian bobtail squid (Ruby,
357 1996). It was recently argued that incorporating the effects of niche construc-
358 tion is critical for improving our understanding of viral evolution (Hamblin *et*
359 *al.*, 2014) and evolution in co-infecting parasites (Hafer and Milinski, 2015).
360 Incorporating host dynamics, co-evolution, and the feedbacks that they pro-
361 duce into models is likely to be equally important for gaining an understanding
362 of how cooperative behaviors evolve in these host-symbiont settings.

363 Acknowledgments

- 364 • TODO: Organizers?
- 365 • TODO: lab comments

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370 sions or recommendations expressed in this material are those of the authors
371 and do not necessarily reflect the views of the National Science Foundation.

³⁷² Computational resources were provided by an award from Google (to BDC
³⁷³ and BK).

374 Figures

375 Figure 1

376 Figure 1A

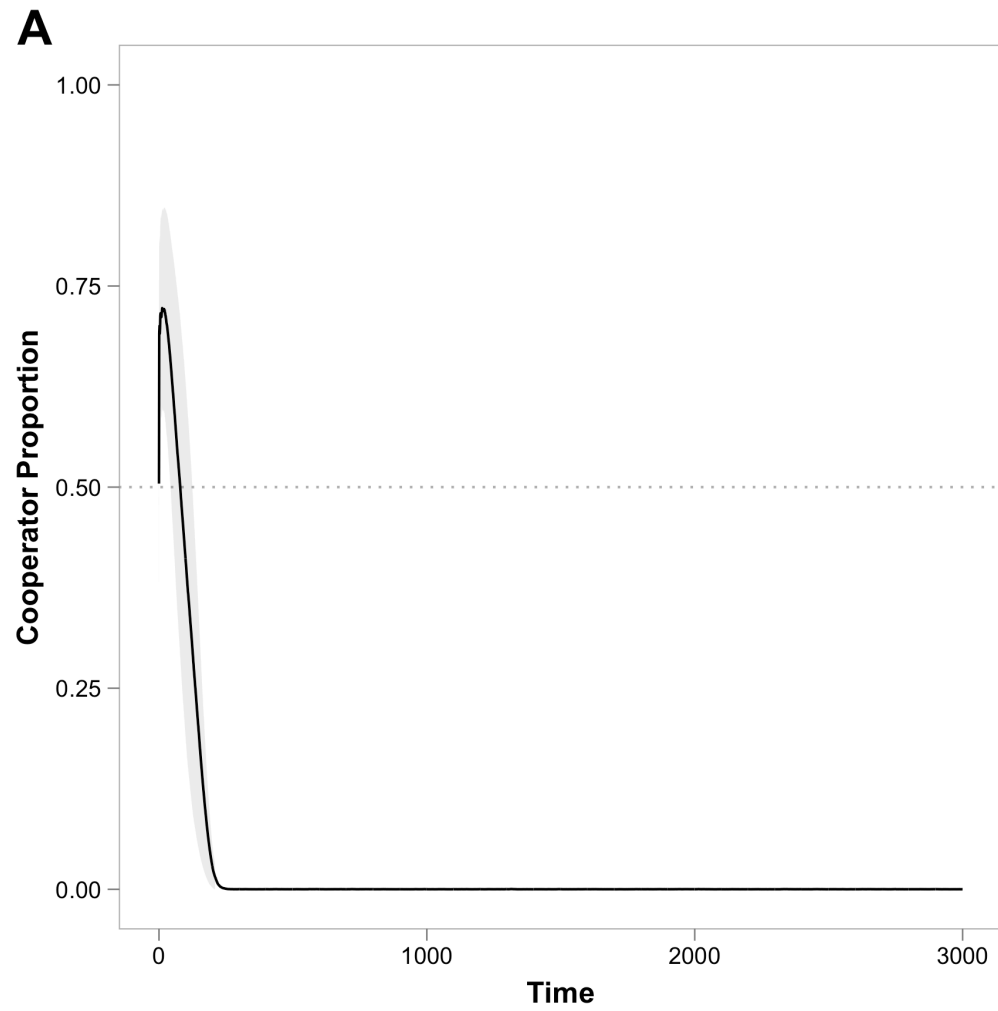


Figure 1: Proportion of cooperators over time when there are no opportunities for non-social adaptation

377 **Figure 1B**

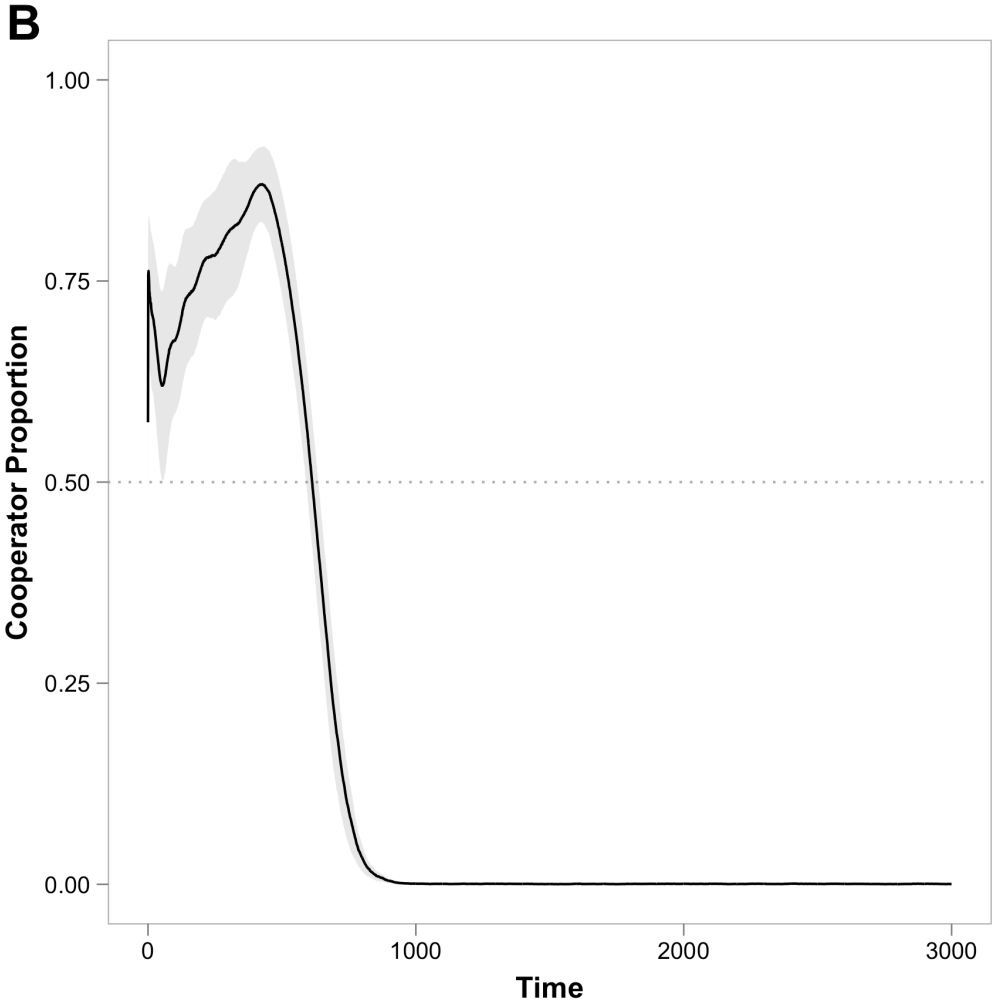


Figure 2: Proportion of cooperators over time with non-social adaptation (GNH)

378 **Figure 1C**

379 **Figure 1X**

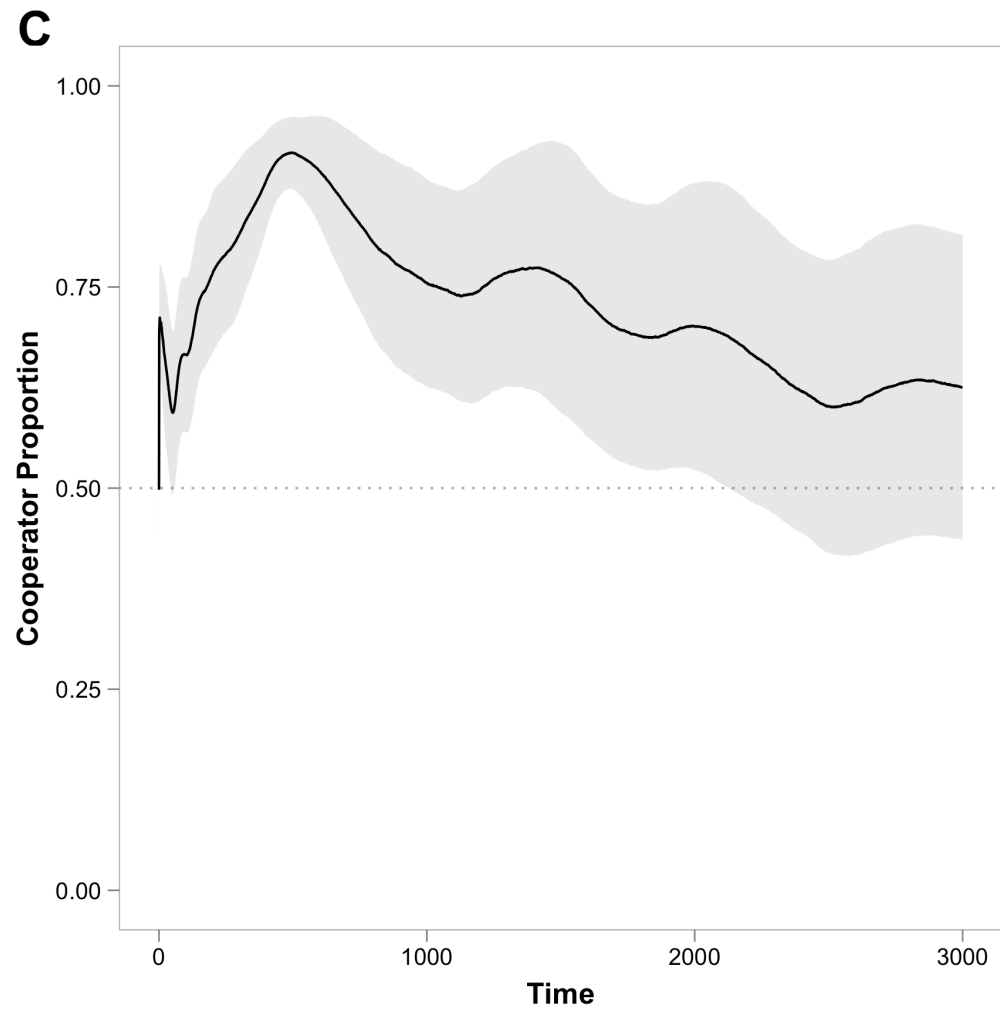


Figure 3: Proportion of cooperators over time with non-social adaptation and selective feedbacks

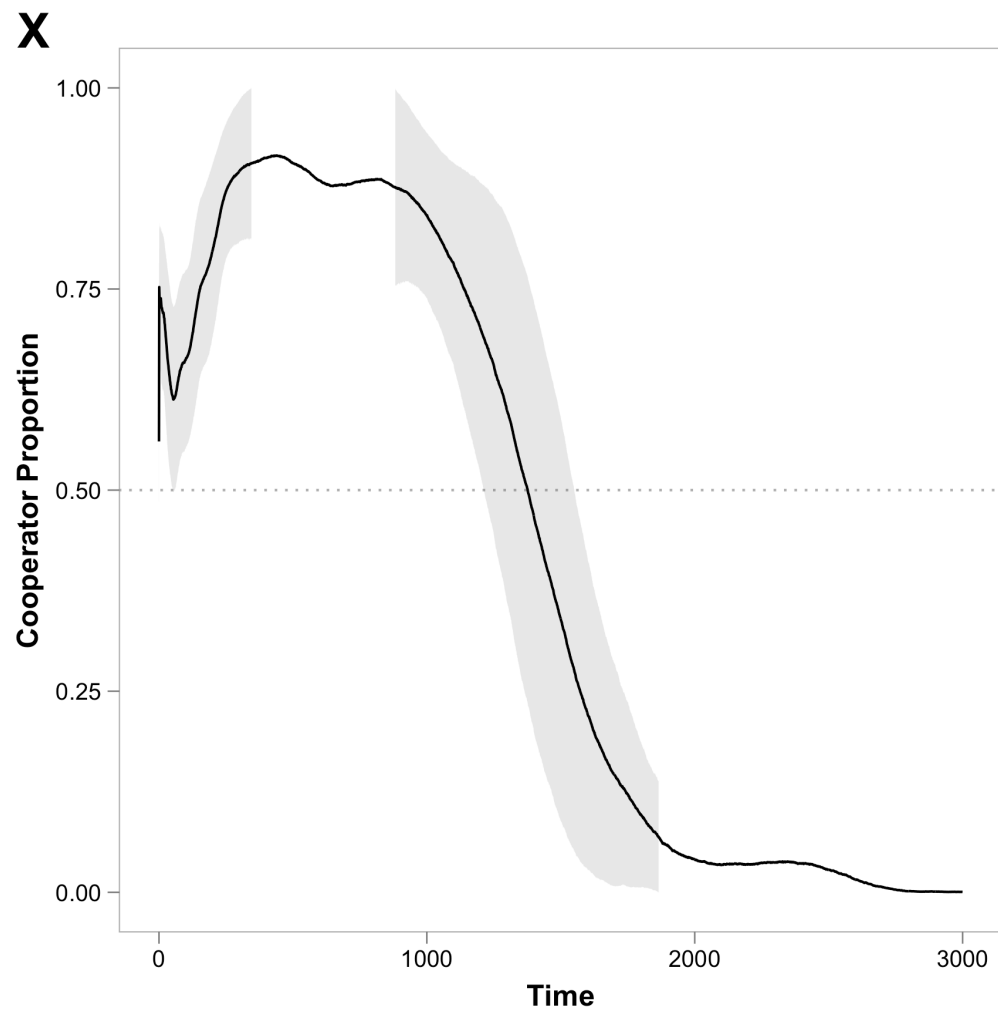


Figure 4: Proportion of cooperators over time without negative niche construction

380 **Figure 2**

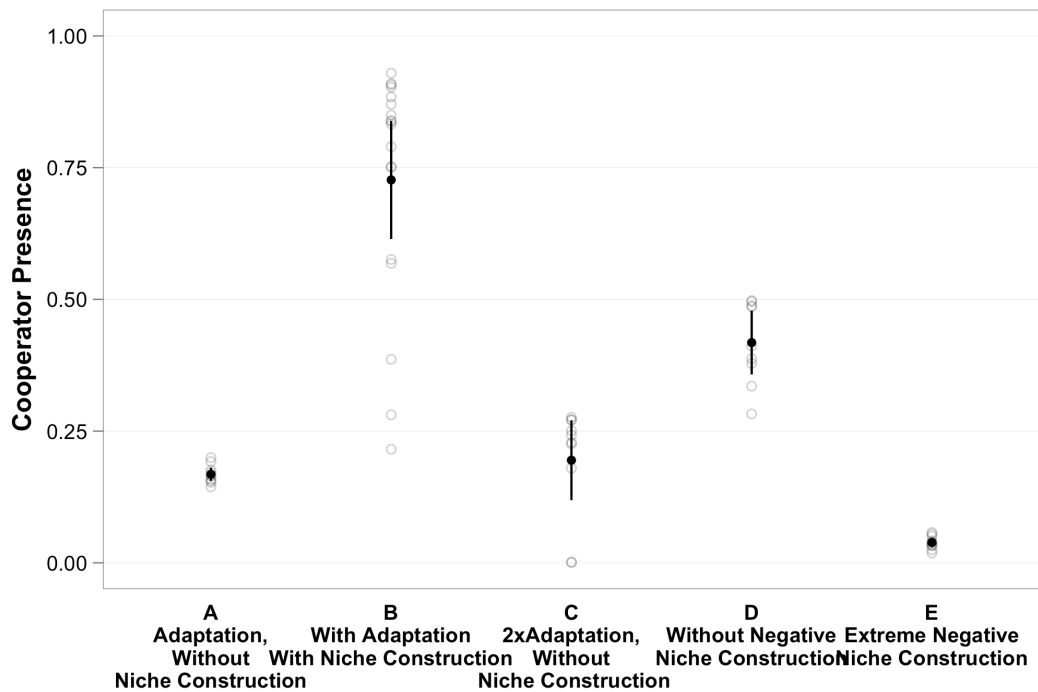


Figure 5: Cooperator Presence TODO

381 **Figure 3**

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

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

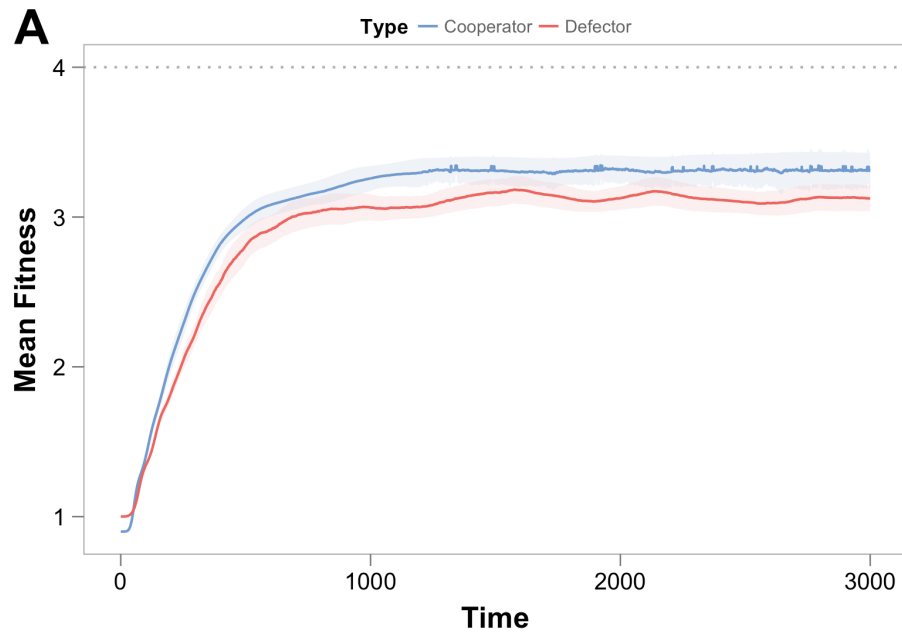


Figure 6: Grand mean Fitness of cooperators and defectors TODO

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

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

386 **Figure 3D - Fitness with extreme negative niche construction ($L=1$,
387 $A=6$)**

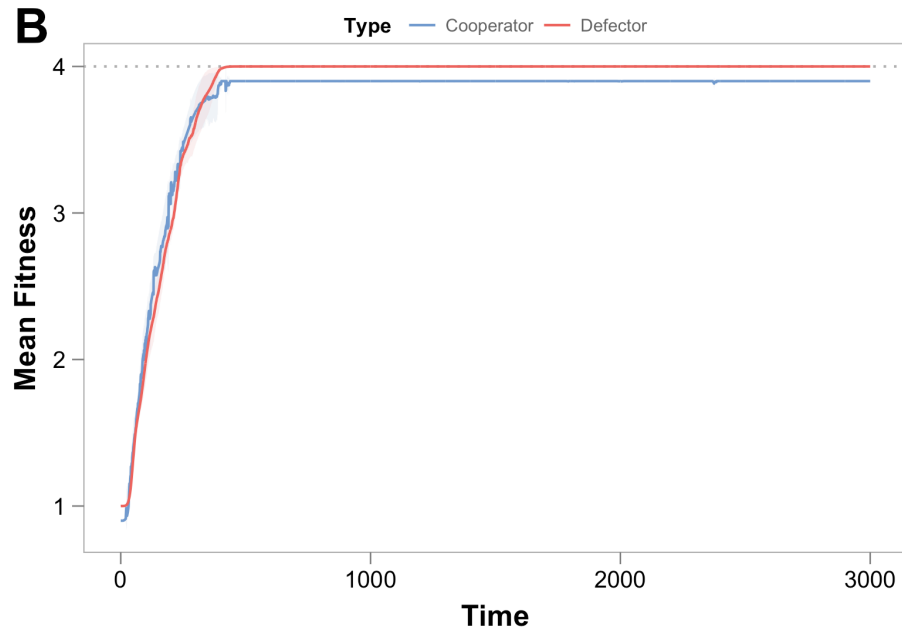


Figure 7: Grand mean Fitness of cooperators and defectors, double delta, no epsilon TODO

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 ($S_{\max}-S_{\min}$)

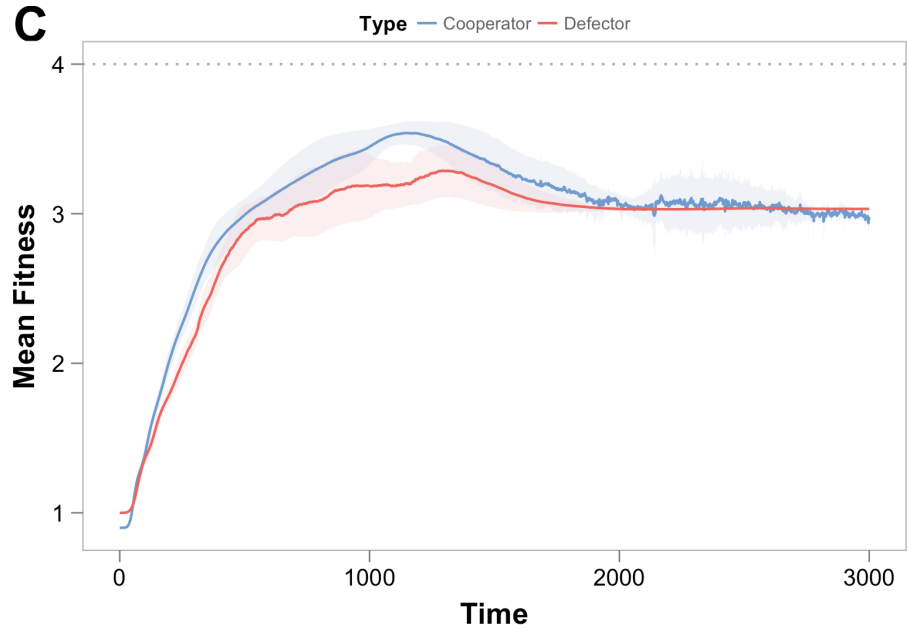


Figure 8: Grand mean Fitness of cooperators and defectors, no negative niche construction TODO

395 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

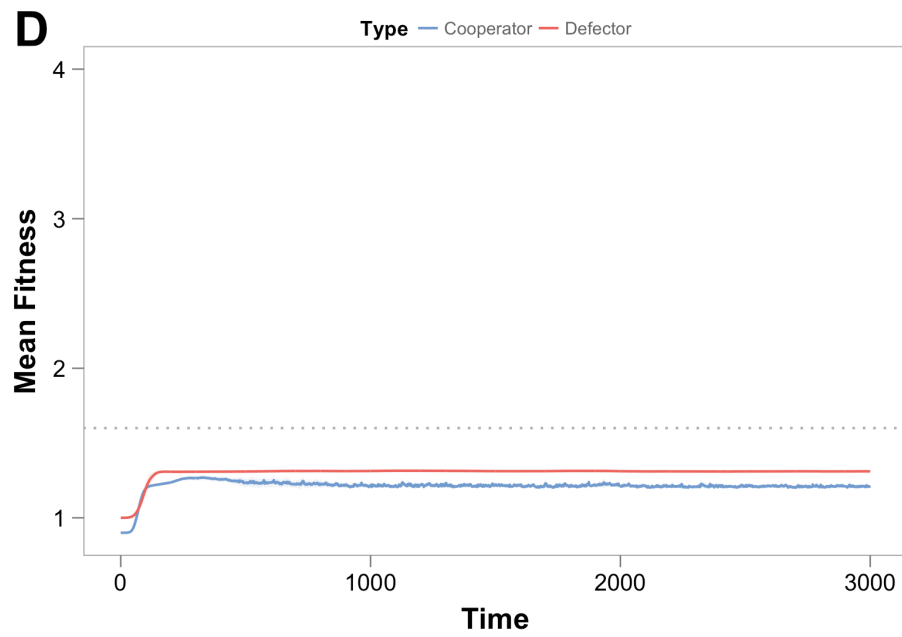


Figure 9: Grand mean Fitness of cooperators and defectors, extreme negative niche construction TODO

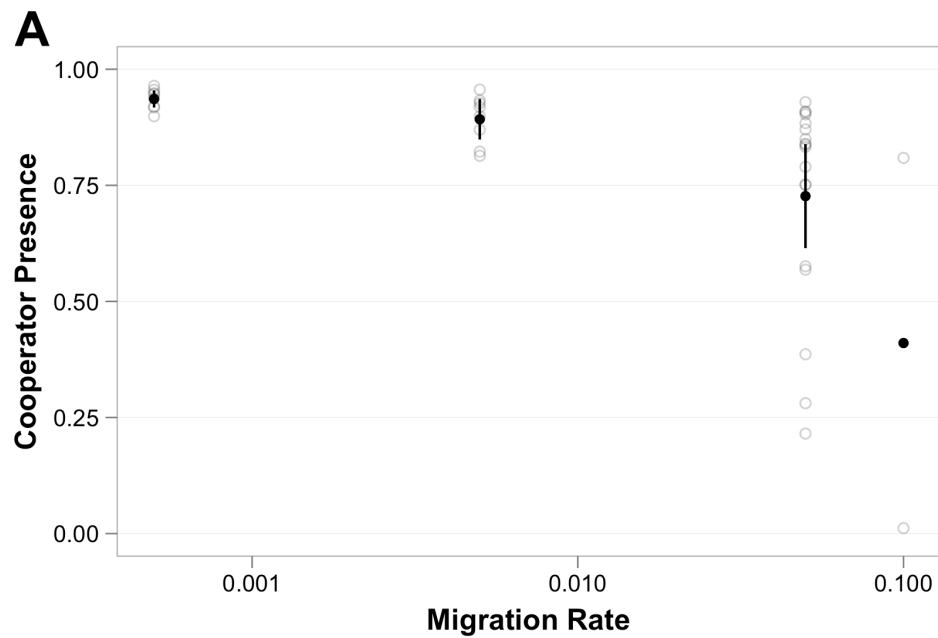


Figure 10: TODO Cooperator Presence for different migration rates

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