# A Combination of Positive and Negative Niche

## Construction Favors the Evolution of

# Cooperation

TODO

5 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.

#### 22 Introduction

Cooperative behaviors are common across all branches of the tree of life. Insects divide labor within their colonies, plants and soil bacteria exchange essential nutrients, birds care for others' young, and the trillions of cells in the human body restrain their growth and coordinate to provide vital functions. Each instance of cooperation presents an evolutionary challenge: How can individuals that sacrifice their own well-being to help others avoid subversion by those that do not? Over time, we would expect these defectors to rise in abundance at the expense of others, eventually driving cooperators—and perhaps the entire population—to extinction. Several factors can prevent this tragedy of the commons (Hamilton, 1964; Hardin, 1968; Nowak, 2006; West et al., 2007b). For example, cooperators must benefit more from the cooperative act than others. This can occur when cooperators are clustered together in spatially structured populations (Fletcher 35 and Doebeli, 2009; Nadell et al., 2010; Kuzdzal-Fick et al., 2011) or when co-36 operators use communication (Brown and Johnstone, 2001; Darch et al., 2012) or other cues (Sinervo et al., 2006; Gardner and West, 2010; Veelders et al., 2010) to cooperate conditionally with kin. Interestingly, cooperation can also be bolstered by genetic linkage with self-benefitting traits (Foster et al., 2004;

Dandekar et al., 2012; Asfahl et al., 2015), setting the stage for an "adaptive race" in which cooperators and defectors vie for the first highly-beneficial adaptation (Waite and Shou, 2012; Morgan et al., 2012). Hammarlund et al. (2015) recently showed that in spatially structured populations, cooperators can gain a substantial leg up on defectors in an adaptive race. Specifically, cooperative behavior increases local population density, thus increasing the likelihood of acquiring beneficial 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, Hammarlund et al. (2015) demonstrated that cooperation can be maintained indefinitely when frequent environmental changes produce a steady stream of 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 persistence.

In this work, we demonstrate how cooperation can be maintained indefinitely by niche construction. We expand upon the model presented in Hammarlund et al. (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 dependent on current genotypes, and the composition of genotypes is dependent on selection. Niche construction can be 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 cooperation 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 enables them to benefit from positive niche construction. And as environments change, either through negative
niche construction or external influences, these larger populations can adapt
more quickly. We show that it is the combination of these factors that allows
cooperation to persist.

#### 73 Stuff to be cut/integrated above

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

Finally, we demonstrate how *negative* niche construction, where populations change their environment in ways that reduce fitness, can further support

cooperation. Even though the niche construction process creates selective feedbacks, we would expect the magnitude of these feedbacks to decrease as populations evolve. Once individuals can no longer gain adaptations that compensate for the costs of cooperation, they are then outcompeted by non-cooperators. However if populations construct their environment in a way which decreases fitness, cooperation can still hitchhike when this change also creates the opportunity to gain compensatory adaptations.

#### $_{ ext{\tiny 94}}$ Materials and Methods

We build upon the model described in Hammarlund et al. (2015), in which cooperators and defectors compete and evolve in a metapopulation (a collection
of populations). Individuals in each of the populations reproduce, mutate, and
migrate to neighboring populations. Importantly, adaptation that is independent of cooperation can occur. In our model here, we further allow populations
to modify their local environment, and these modifications feed back to affect
selection.

### 102 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 can support a population. Each individual in a 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 0 or an integer from the set  $A \equiv \{1, 2, \dots, a_{max}\},\$ 107 where  $a_{max}$  is the number of alleles conferring a selective benefit. Specifically, 108 the presence of a non-zero allele at any of these loci represents an adaptation 109 that confers fitness benefit  $\delta$ . A binary allele at locus L+1 determines whether 110 or not that individual is a cooperator. Individuals with allelic state 1 at this 111 locus are cooperators, carrying a cost c, while individuals with allelic state 0 112 are defectors. When  $\delta \geq c$ , a minimally adapted cooperator recoups the cost 113 of cooperation. Equation 1 defines function n(a, l), which gives the number 114 of individuals in the population with allelic state a at locus l.  $I_x(y)$  indicates 115 whether the allelic state y matches allelic state x (1) or not (0), and  $\gamma(i)$  is 116 the genotype of individual i. 117

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

Organisms also influence their environment, which, in turn, influences selection. We model this as a form of frequency dependent selection. Specifically, 119 the selective value of adaptive allele a at locus l increases with the number 120 of individuals in the population that have allele a-1 at locus l-1. We 121 treat both adaptive loci and allelic states as "circular", so the allelic state 122 at locus 1 is affected by the allelic composition of the population at locus L, 123 and the selective value of allele 1 at any locus increases with the number of 124 individuals carrying allele  $a_{max}$  at the previous locus. To make this circularity 125 mathematically crisp, we define a function giving the integer below x in the 126 set  $\{1, 2, \dots, X\}$ 

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

Where  $\operatorname{mod}_Y(y)$  is the integer remainder after dividing y by Y. Thus, the value of adaptive allele a at locus l increases with the number of individuals that have allele  $\beta(a, a_{max})$  at locus  $\beta(l, L)$ . The slope of this increase is  $\epsilon$ , which specifies the intensity of niche construction. Consider a genotype g with allelic state at locus l given by  $a_{g,l}$ ; its fitness is defined as:

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

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

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

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

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:

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

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  $\{\pi_1, \pi_2, \ldots, \pi_{|P|}\}$ , where:

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

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

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

where  $H_a(g, g')$  and  $H_c(g, g')$  are the Hamming distances between genotypes gand g' at the cooperation locus and adaptive loci, respectively. The Hamming 162 distance is the number of loci at which allelic states differ (Hamming, 1950). 163 After mutation, individuals emigrate to an adjacent patch at rate m. The 164 destination patch is randomly chosen with uniform probability from the source 165 patch's Moore neighborhood, which is composed of the nearest 8 patches on the 166 lattice. Because the metapopulation lattice has boundaries, patches located 167 on an edge have smaller neighborhoods. 168 Metapopulations are initiated in a state that follows an environmental change. 169 First, populations are seeded at all patches with cooperator proportion  $p_0$  and 170 grown to density  $S(p_0)$ . An environmental challenge is then introduced, which 171 subjects the population to a bottleneck. For each individual, the probability 172 of survival is  $\mu_t$ , which represents the likelihood that a mutation occurs that 173 confers tolerance. Survivors are chosen by binomial sampling. Because indi-174 viduals have not yet adapted to this new environment, the allelic state of each 175 individual's genotype is set to 0 at each adaptive locus. Following initializa-176 tion, simulations are run for T cycles, where each discrete cycle consists of 177 growth, mutation, and migration. At the end of each cycle, populations are 178 thinned to allow for growth in the next cycle. The individuals that remain are 179 chosen by binomial sampling, where each individual persists with probability 180

d, regardless of allelic state.

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#### Source Code and Software Environment

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

### 187 Results

#### Niche Construction Maintains Cooperation

Despite being able to form larger populations, cooperators are swiftly eliminated in competition with defectors, despite spatial structuring in the metapopulation (Figure 1A). As demonstrated by Hammarlund et al. (2015), cooperators are temporarily bolstered by the ability to hitchhike along with non-social adaptations (Figure 1B). As shown in Figure 1C, we find that niche hiking can prolong cooperation, perhaps indefinitely (see Table 1 for model parameters).

(TODO describe the oscillations). We now explore this process further to 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 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 construc-202 tion. Selection favors individuals with sequentially-increasing alleles. Because 203 larger populations will have a greater effect on their environment, this bene-204 fit is density dependent. In our experiments, this positive niche construction 205 contributed equally to fitness when all individuals shared the same allele in a population at maximum carrying capacity. To determine whether cooperation 207 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 exper-209 iments in which the ordering of alleles did not matter, and the fitness benefit 210 provided by adaptation was doubled ( $\epsilon = 0, \delta = 0.6$ ). That this doubling is an 211 over estimate of the magnitude of fitness contributions that arise from niche 212 construction, since these values would only occur in populations at maximum 213 carrying capacity, which does not occur in the presence of defectors. Never-214 theless, Figure 2 shows that higher selective values have little effect (columns 215 A and C) and do not explain the maintenance of cooperation that we observe 216 when niche construction occurs (column B). 217 Although we have seen that maximum fitness does not substantially effect the 218 maintenance of cooperation, perhaps the rate at which fitness accumulates in 219 cooperator and defector populations matters. When we compare the accumu-220 lation 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, co-

operator fitness is eventually surpassed by that of defectors (Figure 3B). As described by Hammarlund et al. (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.

<sup>229</sup> 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 max-233 imum fitness. One major contributor to this is the density dependence of 234 the benefit provided by niche construction. Because defectors remain present 235 (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 arrange-239 ment of these alleles. When the genome length (L) is not evenly divided by 240 the number of non-zero alleles  $(a_{max})$ , a conflict arises when the allelic state at 241 locus 1 is not 1 larger than the allelic state at locus L. For example, consider 242 genotype (1,2) when L=2 and  $a_{max}=3$ . Here, allelic state 2 at locus 2 will 243 be be beneficial, because it follows allelic state 1 at locus 1. However, due to 244 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=5,248  $a_{max} = 5$ ). Figure 2 shows that although positive niche construction still led 249 to an increase in cooperation (column D), these populations were not able to 250 maintain the same level of cooperation seen in the presence of negative niche 251 construction (column B). We find that because this lack of conflict allows populations to reach a fully-adapted state, cooperators once again acquire 253 these adaptations more quickly but are eventually driven from the population (Figures 3C and 1X). These results indicate that both positive and negative 255 niche construction is required to maintain cooperation. 256

<sup>257</sup> (TODO: explain why defector fitness doesn't reach 4 (density de-<sup>258</sup> pendent 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 from the population. This offers further evidence that feedbacks from both positive and negative niche construction are required for cooperation to persist.

#### NC Enables Cooperator Spread

Figure 4

#### NC Prevents Defector Invasion

Figure 5

#### 272 How Public Good Fuels all of this

The production of public goods has played a central role in all of the results that
we have presented. By enabling populations to reach larger sizes, these public
goods have effectively increased the rate of evolution for these populations. As
a result, larger populations are able to gain adaptations more quickly, both in
response to their environment and the environmental changes brought about
by niche construction. Additionally, these larger populations more effectively
"export" their niche. As more individuals migrate to neighboring patches, these
emigrants exert greater selective pressure. Here, we examine how population
size and migration rate influence these processes.

To directly explore how the increase in population size affects evolutionary outcomes, we vary the maximum size that a population can reach  $(S_{max}, \text{ see})$  Equation 5). Figure 6A shows the result of these simulations. (**TODO** description of results)

To address how migration affects the evolutionary process in this system, we vary the rate at which migration occurs (m). As seen in Figure 6B, cooperation

- decreases as migration rate increases. This is likely because migration defines
  the spatial structuring in this system. As migration increases, the population
  becomes more like a well-mixed system, where defectors are better able to
  exploit the benefits of cooperation (Griffin et al., 2004; Kümmerli et al., 2009).

  # Discussion
- summary of results
- similarities/differences from previous work
- Schwilk and Kerr (2002)
- -10.1073/pnas.0812644106
- negative/positive NC
- laland1996evolutionary
- public goods as niche construction
- future QS or other environmental sensing
- Facultative cooperation
- Rodrigues (2012)
- Dumas and Kümmerli (2010)
- Kümmerli and Brown (2010)
- Darch/Diggle
- QS?
- Environmental Sensing? (Koestler and Waters, 2014, Bernier et al. (2011))

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

Niche construction and selective feedbacks Niche construction and other social interactions

#### Public Goods

TODO: merge this in with the "Cooperative Niche Construction" section

TEST

By their very nature, public goods benefit populations by making their environ-317 ment more hospitable. For example, bacteria produce extracellular products 318 that find soluble iron (Griffin et al., 2004), digest large proteins (Diggle et al., 319 2007; Darch et al., 2012), and reduce the risk of predation (Cosson et al., 2002), 320 among many others (West et al., 2007a). While many studies have explored 321 how the environment affects the evolution of cooperative bahviors, relatively 322 few have examined how those behaviors affect the environment and the result-323 ing change in evolutionary trajectories. Lehmann (2007) demonstrated analyti-324 cally 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.

### 333 Primacy/Recency

In our model, alterations to the environment were immediately echoed by 334 changes in selection. However, decoupling the timescales on which these pro-335 cesses occur can have substantial effects (Laland et al., 1996). By integrating 336 past allelic states into Equation 3, we can begin to explore how the cumulative 337 effects of niche construction affect the creation of non-social adaptive opportunities and the benefits that they offer cooperation. Here, how these past 339 allelic states are integrated will play an important role. For example, when 340 the effects of earlier generations are weighted more heavily, the influence of 341 migration may be diminished. While this will reduce the threat of emigration 342 by defectors, cooperator populations will also be less effective at exporting their niche.

#### Cooperative Niche Construction

While our focus for this work has been on the eco-evolutionary feedbacks created by non-social traits, it would also be interesting to explore how this system is affected by the timescale at which carrying capacity at a given patch is increased by public goods. In natural settings, a multitude of factors including protein durability (Brown and Taddei, 2007; Kümmerli and Brown,

2010), diffusion (Allison, 2005; Driscoll and Pepper, 2010), and resource avail-351 ability (Zhang and Rainey, 2013; Ghoul et al., 2014) influence both the rate 352 and the degree to which public goods after the environment (and thereby selec-353 tion). Lehmann (2007) demonstrated that a cooperative, niche constructing 354 behavior can be favored when it only affected selection for future generations, 355 thus reducing the potential for competition among contemporary kin. The evolutionary inertia that this creates, however, may ultimately work against 357 cooperators. When public good accumulates in the environment, cooperators must reduce their investment in production to remain competitive (Kümmerli and Brown, 2010). 360

TODO: wrap up. Facultative cooperation requires sensing.

## Host-Symbiont

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

al., 2014) and evolution in co-infecting parasites (Hafer and Milinski, 2015).

Incorporating host dynamics, co-evolution, and the feedbacks that they produce into models is likely to be equally important for gaining an understanding of how cooperative behaviors evolve in these host-symbiont settings.

## 377 Acknowledgments

• TODO: Organizers?

379

• TODO: lab comments

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and BK).

# Figures

- Figure 1
- Figure 1A

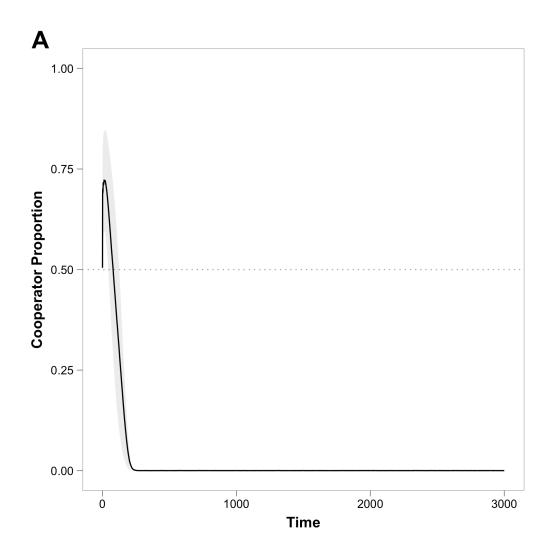


Figure 1: Proportion of cooperators over time when there are no opportunities for non-social adaptation

### Figure 1B

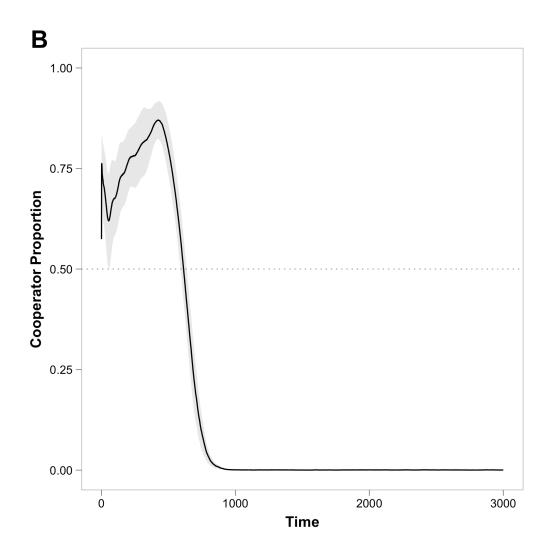


Figure 2: Proportion of cooperators over time with non-social adaptation (GNH)  $\,$ 

### Figure 1C

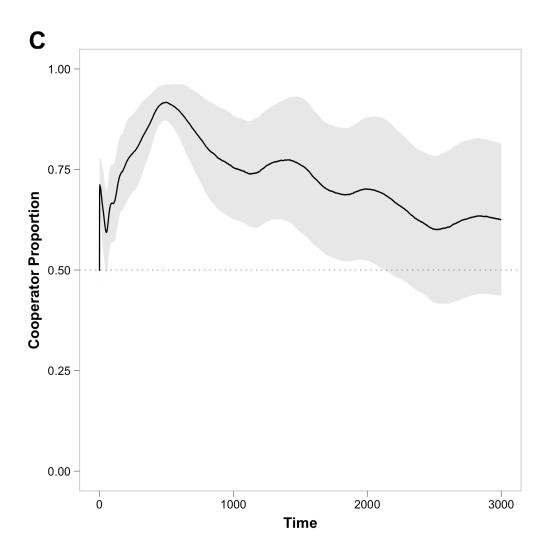


Figure 3: Proportion of cooperators over time with non-social adaptation and selective feedbacks  ${\bf r}$ 

### Figure 1X

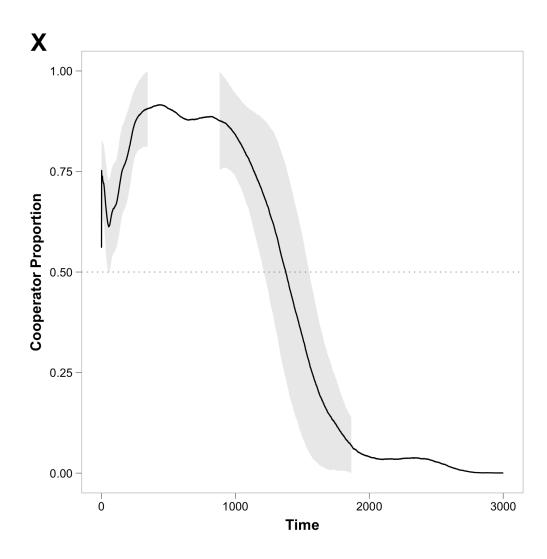


Figure 4: Proportion of cooperators over time without negative niche construction

## Figure 2

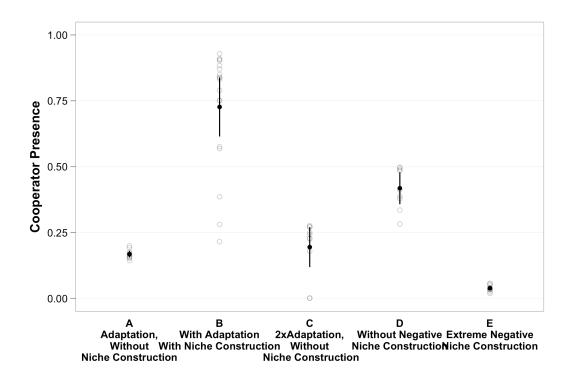


Figure 5: Cooperator Presence TODO

## Figure 3

 $^{396}$  Mean fitness over time for the treatments shown in Figure 2

### <sup>397</sup> Figure 3A - Fitness for base case: niche construction

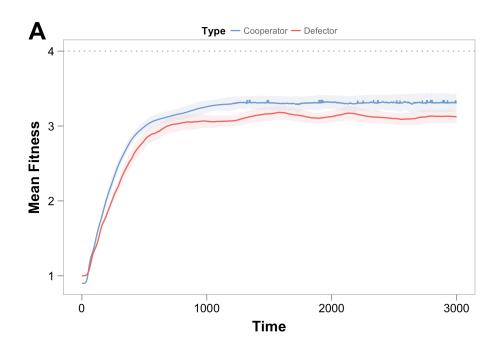


Figure 6: Grand mean Fitness of cooperators and defectors TODO

#### Figure 3B - Fitness with double delta, no epsilon

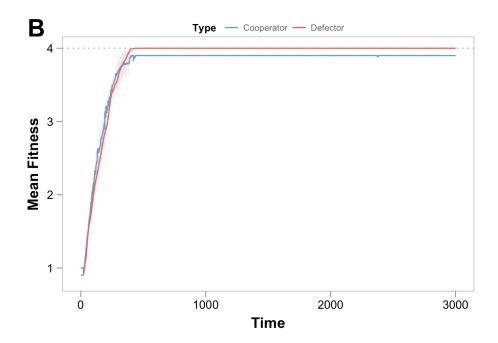


Figure 7: Grand mean Fitness of cooperators and defectors, double delta, no epsilon  $\operatorname{TODO}$ 

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

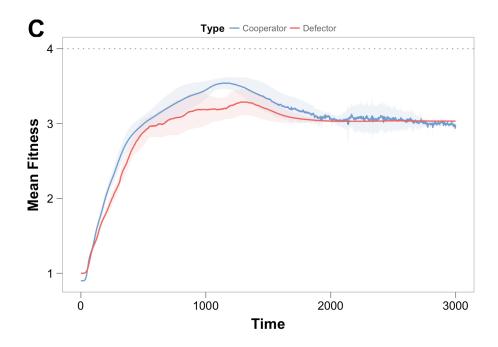


Figure 8: Grand mean Fitness of cooperators and defectors, no negative niche construction  $\operatorname{TODO}$ 

 $_{\mbox{\tiny 400}}$  Figure 3D - Fitness with extreme negative niche construction (L=1,  $_{\mbox{\tiny 401}}$  A=6)

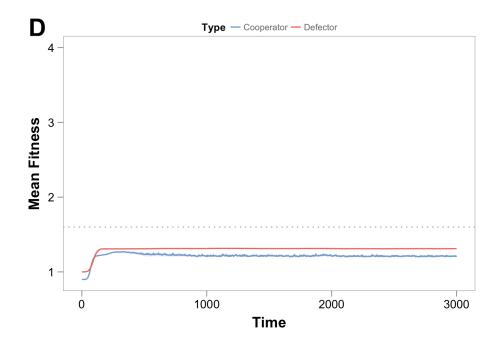


Figure 9: Grand mean Fitness of cooperators and defectors, extreme negative niche construction  ${\it TODO}$ 

- Figure 4
- 403 Cooperators invade from single population
- Figure 5
- 405 Defectors are kept at bay
- Figure 6
- Figure 6A Effect of Public Good Benefit (Smax-Smin)
- <sup>408</sup> Figure 6B Effect of Migration Rate (m)

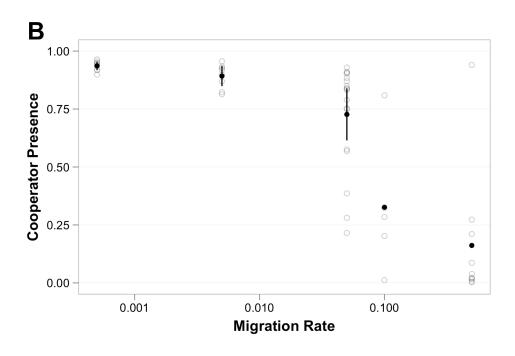


Figure 10: TODO Cooperator Presence for different migration rates

# 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
$\epsilon$	Fitness benefit, sequential alleles	0.00015
z	Baseline fitness	1
$S_{min}$	Minimum population size	800
$S_{max}$	Maximum population size	2000
$\mu_a$	Mutation rate (adaptation)	$10^{-5}$
$\mu_c$	Mutation rate (cooperation)	$10^{-5}$
m	Migration rate	0.05
$p_0$	Initial cooperator proportion	0.5
$\mu_t$	Mutation rate (tolerance to new stress)	$10^{-5}$
T	Number of simulation cycles	1000
d	Population dilution factor	0.1

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