A Combination of Positive and Negative Niche Construction Favors the Evolution of Cooperation

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.

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 and Doebeli, 2009; Nadell *et al.*, 2010; Kuzdzal-Fick *et al.*, 2011) or when cooperators 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).

Hankshaw and Kerr (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, Hankshaw and Kerr (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 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 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.

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.

Materials and Methods

We build upon the model described in Hankshaw and Kerr (2015), in which co-operators 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.

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

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

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

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

Where $\bmod_Y(y)$ 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 ϵ, 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:

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

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

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

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 π_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 μ_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 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:

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

where $H_a(g,\ g')$ and $H_c(g,\ g')$ are the Hamming distances between genotypes g and g' at the cooperation locus and adaptive loci, respectively. The Hamming distance is the number of loci at which allelic states differ (Hamming, 1950).

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

Metapopulations are initiated in a state that follows an environmental change. First, populations are seeded at all patches with cooperator proportion p_0 and grown to density $S(p_0)$. An environmental challenge is then introduced, which subjects the population to a bottleneck. For each individual, the probability of survival is μ_t, which represents the likelihood that a mutation occurs that confers tolerance. Survivors are chosen by binomial sampling. Because individuals have not yet adapted to this new environment, the allelic state of each individual's genotype is set to 0 at each adaptive locus. Following initialization, simulations are run for T cycles, where each discrete cycle consists of growth, mutation, and migration. At the end of each cycle, populations are thinned to allow for growth in the next cycle. The individuals that remain are chosen by binomial sampling, where each individual persists with probability d, regardless of allelic state.

Source Code and Software Environment

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).

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 Hankshaw and Kerr (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 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 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

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}, 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 environment more hospitable. For example, bacteria produce extracellular products that find soluble iron (Griffin *et al.*, 2004), digest large proteins (Diggle *et al.*, 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 bahviors, 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 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 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 availability (Zhang and Rainey, 2013; Ghoul *et al.*, 2014) influence both the rate and the degree to which public goods alter the environment (and thereby selection). Lehmann (2007) demonstrated that a cooperative, niche constructing behavior can be favored when it only affected selection for future generations, thus reducing the potential for competition among contemporary kin. The evolutionary inertia that this creates, however, may ultimately work against cooperators. When public good accumulates in the environment, cooperators must reduce their investment in production to remain competitive (Kümmerli and Brown, 2010).

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.

Acknowledgments

- TODO: Organizers?
- TODO: lab comments

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Figures

Figure 1

Figure 1A

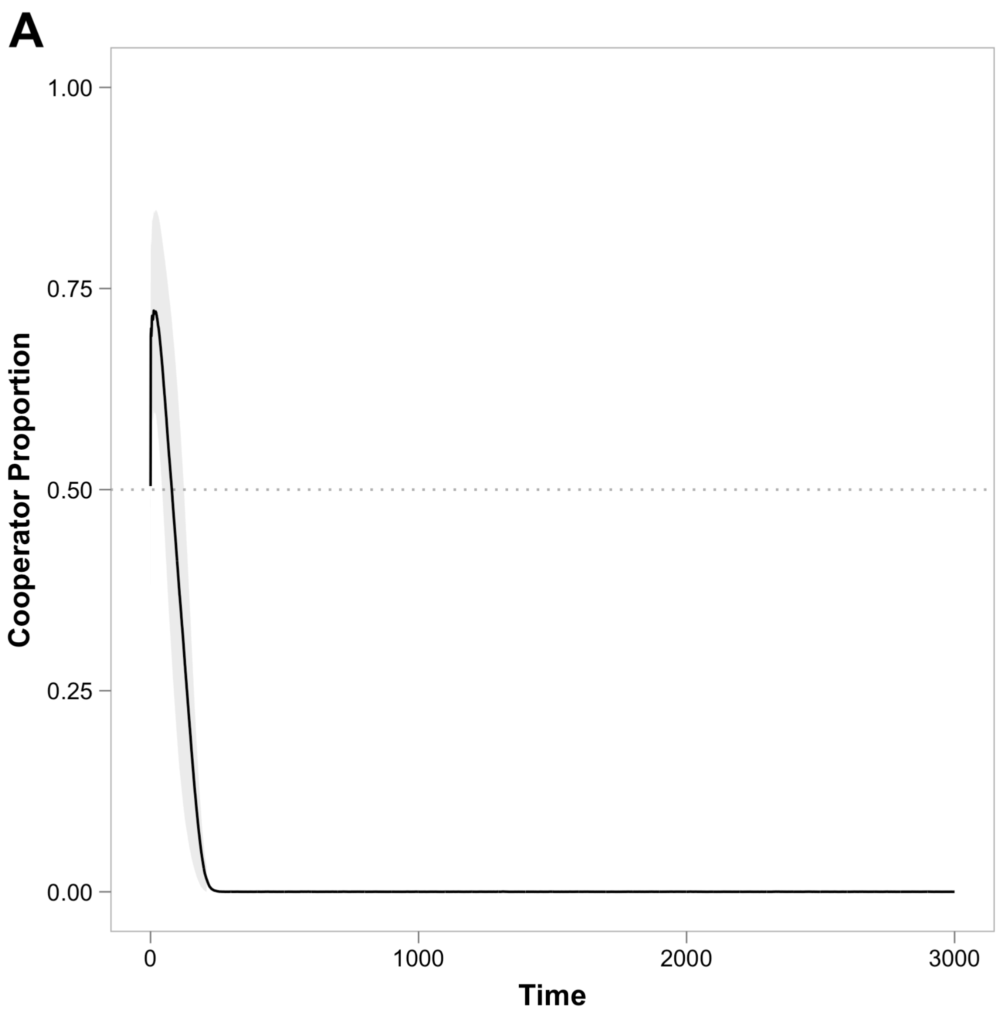

Figure 1: Proportion of cooperators over time when there are no opportunities for non-social adaptation

Figure 1B

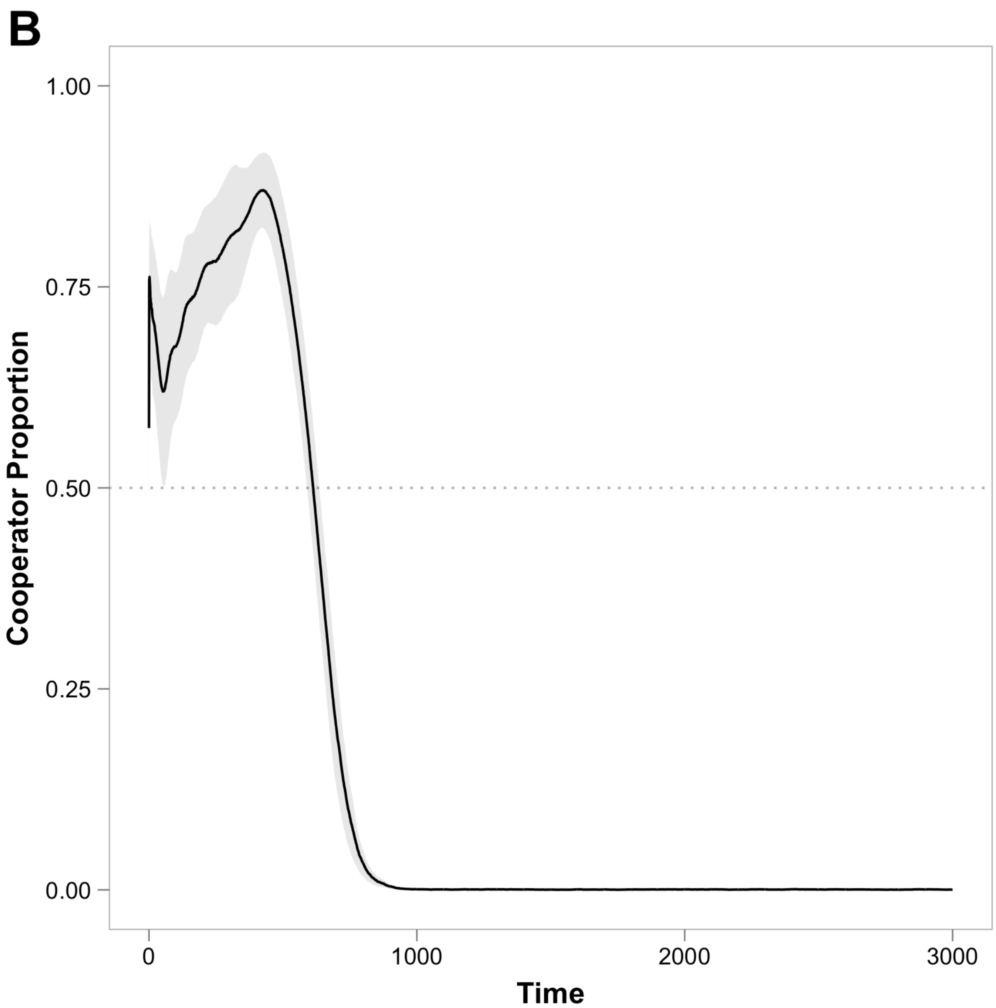

Figure 2: Proportion of cooperators over time with non-social adaptation (GNH)

Figure 1C

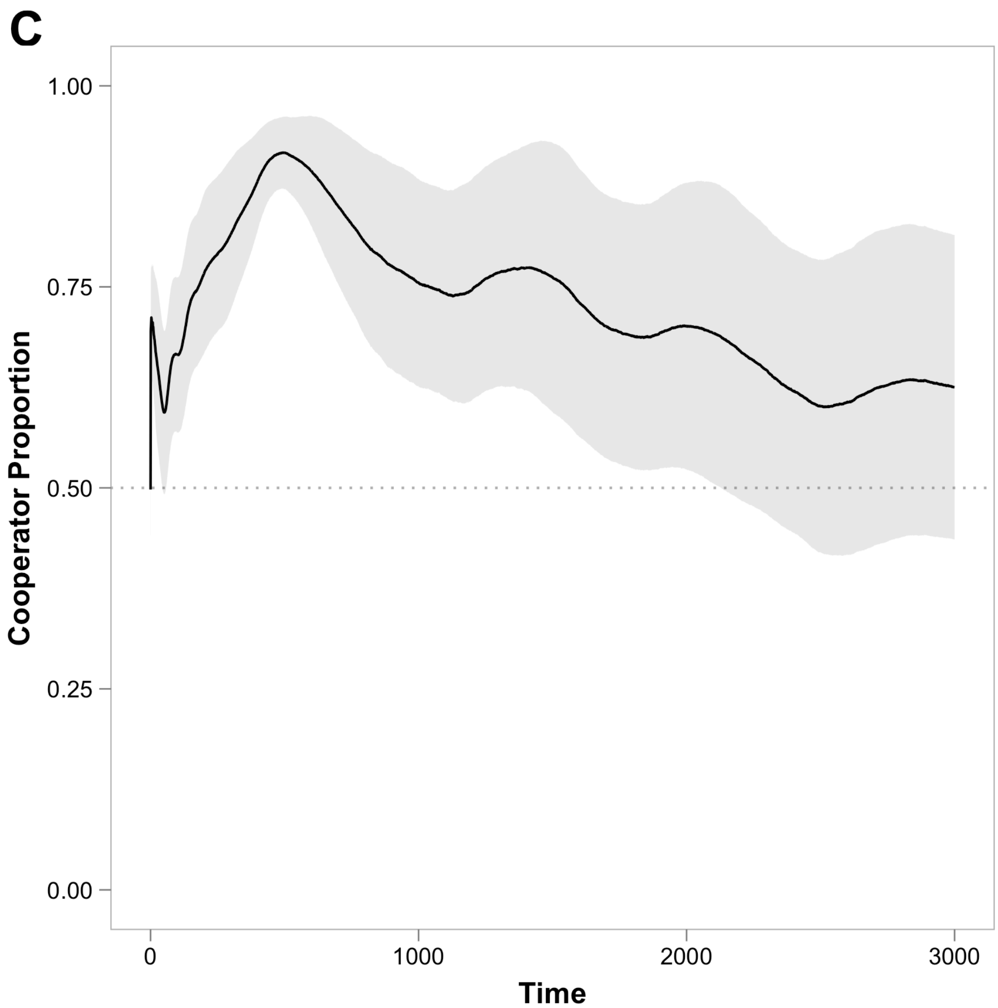

Figure 3: Proportion of cooperators over time with non-social adaptation and selective feedbacks

Figure 1X

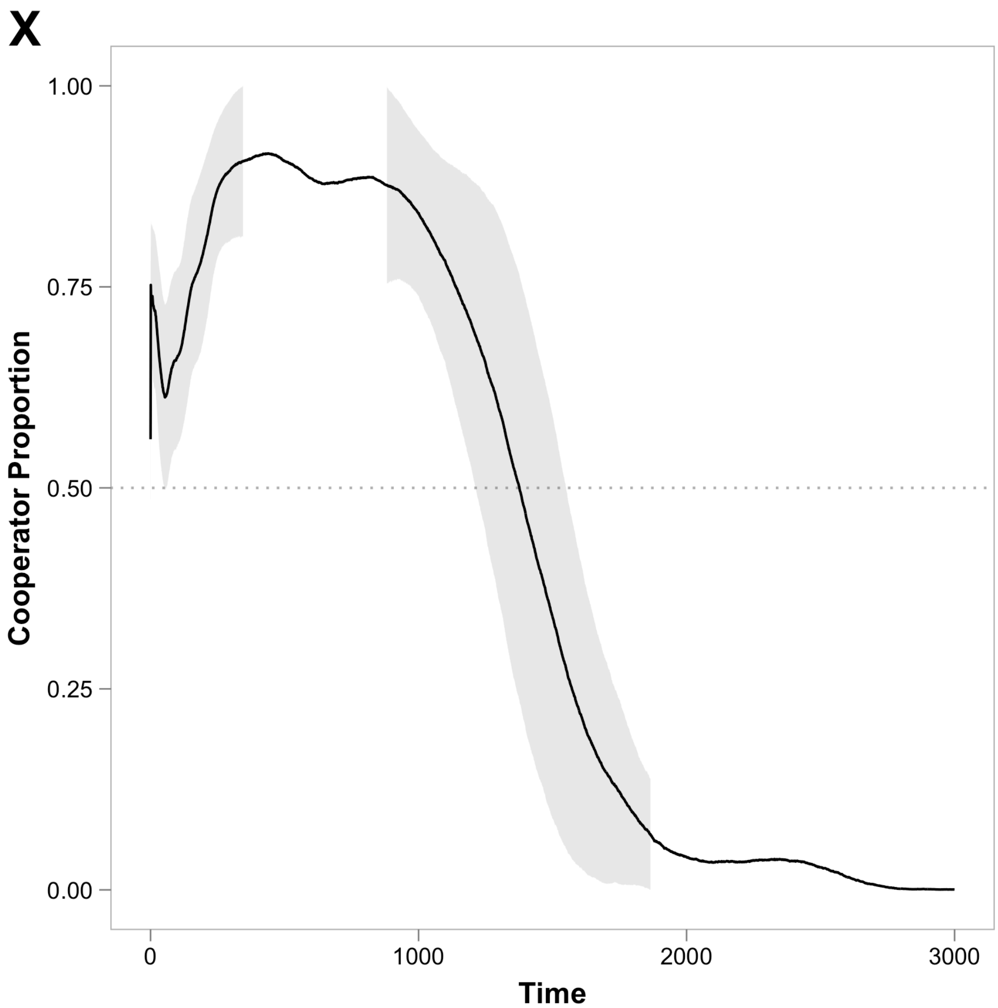

Figure 4: Proportion of cooperators over time without negative niche construction

394 **Figure 2**

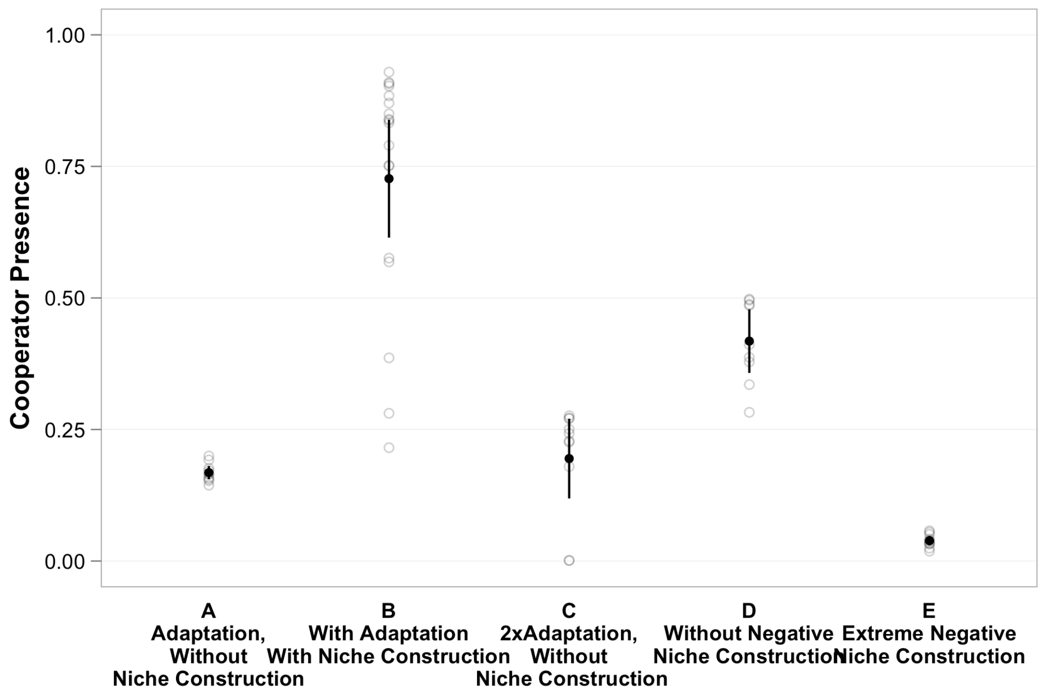

Figure 5: Cooperator Presence TODO

Figure 3

Mean fitness over time for the treatments shown in Figure 2

Figure 3A - Fitness for base case: niche construction

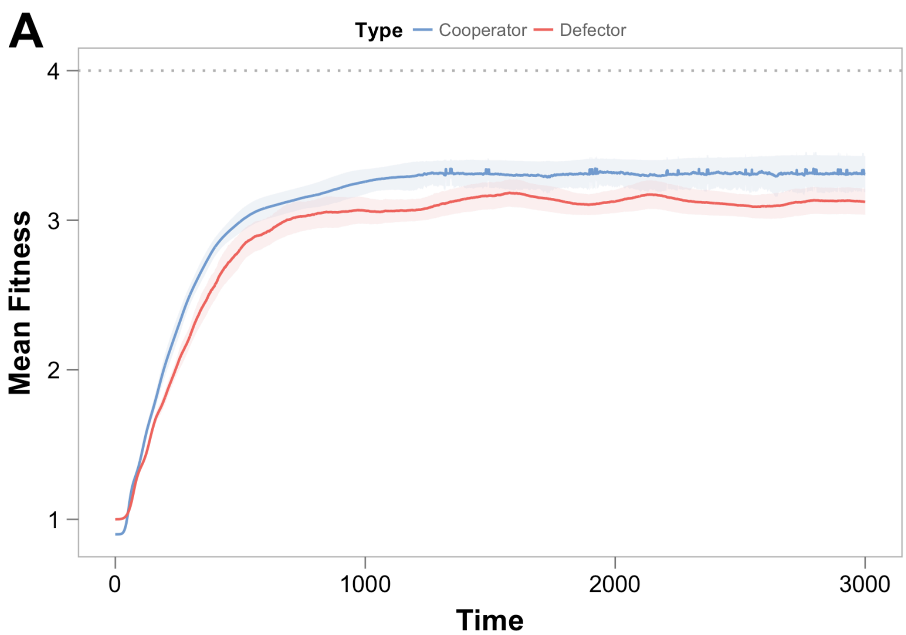

Figure 6: Grand mean Fitness of cooperators and defectors TODO

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

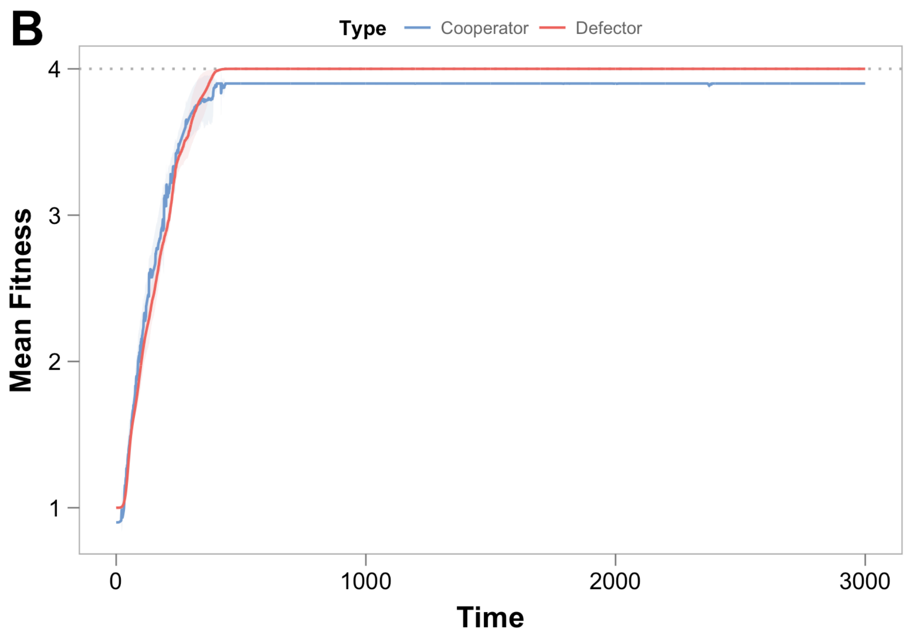

Figure 7: Grand mean Fitness of cooperators and defectors, double delta, no epsilon TODO

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

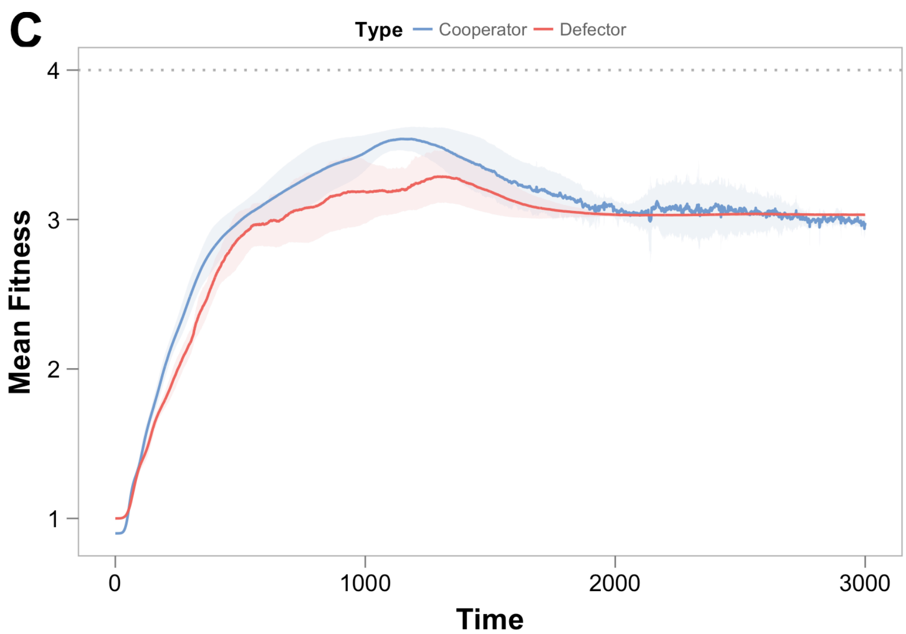

Figure 8: Grand mean Fitness of cooperators and defectors, no negative niche construction TODO

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

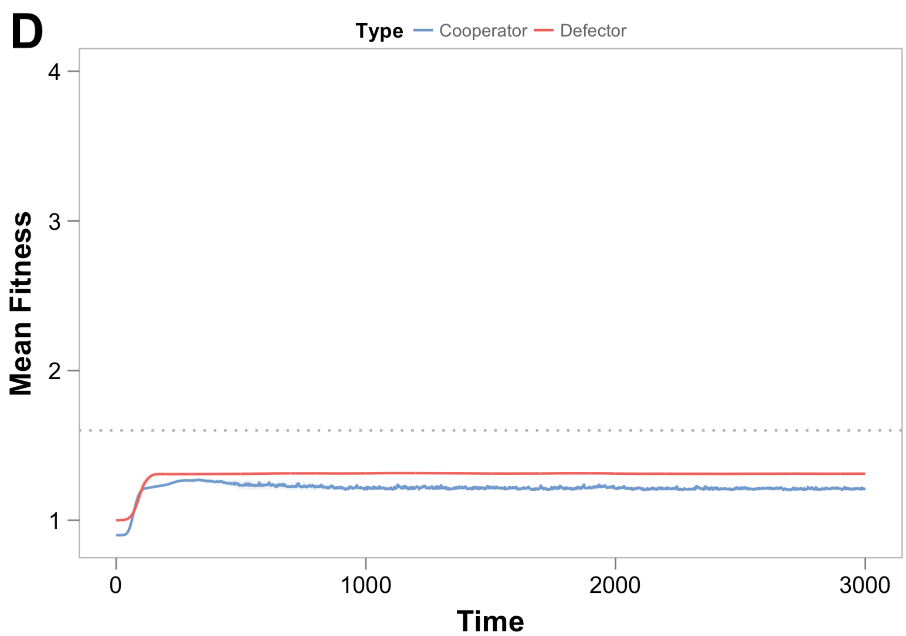

Figure 9: Grand mean Fitness of cooperators and defectors, extreme negative niche construction TODO

Figure 4

Cooperators invade from single population

Figure 5

Defectors are kept at bay

Figure 6

Figure 6A - Effect of Public Good Benefit (Smax-Smin)

Figure 6B - Effect of Migration Rate (m)

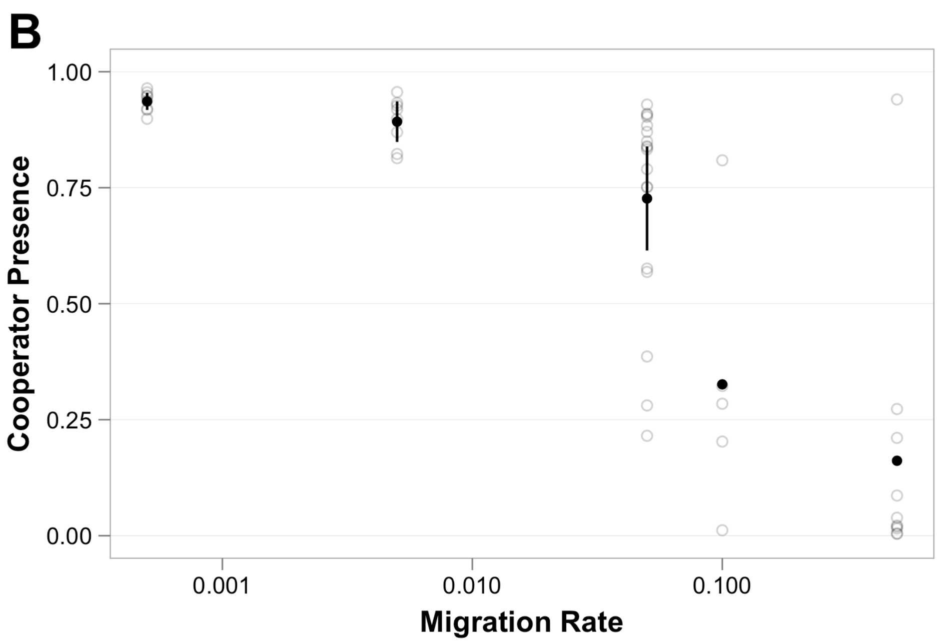

Figure 10: TODO Cooperator Presence for different migration rates

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
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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