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

TODO

Abstract

TODO

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. One important factor involves non-random social interaction, in which cooperators benefit more from the cooperative act than defectors. 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. Cooperation can also be bolstered by pleiotropic connections to personal benefits (Foster *et al.*, 2004; Dandekar *et al.*, 2012) or alleles encoding self-benefitting traits (Asfahl *et al.*, 2015). In the latter case, the alleles may provide (private) benefits that are completely independent from the (public) benefits of cooperation. In a population of both cooperators and defectors, this sets the stage for an "adaptive race" in which both types vie for the first highly beneficial adaptation (Waite and Shou, 2012; Morgan *et al.*, 2012). The tragedy of the commons can be deferred if a cooperator, by chance, wins the adaptive race.

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, cooperation 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 explore whether 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, which creates an eco-evolutionary feedback whereby selection is dependent on the genotypes present in the population, 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. We investigate whether these selective feedbacks can act as a continual source of adaptive opportunities for cooperators.

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. Additionally, as environments change, either through negative niche construction or external influences, these larger populations can adapt more quickly. Finally, because large

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populations produce more emigrants, these populations will exert a stronger influence on neighboring populations, effectively exporting their niche. Because of these potential benefits, we also focus our attention on how population size and migration rate influence evolutionary outcomes in these environments.

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.

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

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85 that confers fitness benefit δ. A binary allele at locus $L+1$ determines whether

86 or not that individual is a cooperator. Individuals with allelic state 1 at this

87 locus are cooperators, carrying a cost c, while individuals with allelic state 0

88 are defectors. When $\delta \geq c$, a minimally adapted cooperator recoups the cost

89 of cooperation. Equation 1 defines function $n(a, l)$, which gives the number

90 of individuals in the population with allelic state a at locus l. $I_x(y)$ indicates

91 whether the allelic state y matches allelic state x (1) or not (0), and $\gamma(i)$ is

92 the genotype of individual i.

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

93 Organisms also influence their environment, which, in turn, influences selec-

94 tion. We model this as a form of density dependent selection. Specifically,

95 the selective value of adaptive allele a at locus l increases with the number

96 of individuals in the population that have allele $a - 1$ at locus $l - 1$. We

97 treat both adaptive loci and allelic states as "circular", so the allelic state

98 at locus 1 is affected by the allelic composition of the population at locus L,

99 and the selective value of allele 1 at any locus increases with the number of

100 individuals carrying allele a_{max} at the previous locus. To make this circularity

101 mathematically crisp, we define a function giving the integer below x in the

102 set $\{1, 2, \ldots, X\}$

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

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$_{103}$ Where $\mathrm{mod}_Y(y)$ is the integer remainder after dividing y by Y. Thus, the

$_{104}$ value of adaptive allele a at locus l increases with the number of individuals

$_{105}$ that have allele $\beta(a, a_{max})$ at locus $\beta(l, L)$. The slope of this increase is ϵ,

$_{106}$ which specifies the intensity of niche construction. Consider a genotype g with

$_{107}$ allelic state at locus l given by $a_{g,l}$; its fitness is defined as:

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

$_{108}$ where z is a baseline fitness, and $I_A(a)$ indicates whether an adaptive allele is

$_{109}$ non-zero:

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

$_{110}$ As a consequence of this form of density dependent selection, genotypes with

$_{111}$ sequentially increasing allelic states will tend to evolve. Because mutations

$_{112}$ are random (see below), each population will evolve different consecutive se-

$_{113}$ quences. These different sequences represent the unique niches constructed by

$_{114}$ populations.

$_{115}$ Cooperators produce a public good that is equally accessible to all members

$_{116}$ of the population. This public good increases the carrying capacity at that

$_{117}$ patch, allowing the population to reach greater density. This benefit increases

$_{118}$ linearly with the proportion of cooperators. Thus, if p is the proportion of

$_{119}$ cooperators in a population at the beginning of a growth cycle, then that

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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:

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

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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

We use the model described earlier to follow the evolution of cooperation in a metapopulation of populations that are connected by spatially-limited migration. Individuals in these populations gain a limited number of adaptations that confer selective benefits. Adaptation is independent of cooperation. However, because cooperation increases population density, these populations have more mutational opportunities to gain adaptations. Cooperation can hitchhike along with these adaptations, which compensate for the cost of public good production. During this process, individuals also alter their environment based on the genotypes present in the population. This niche construction process can be either positive or negative, depending on its effects on fitness. Here, we explore how niche construction can favor the evolution of cooperation. Our simulation environment is defined by the parameter values listed in Table 1.

Niche Construction Maintains Cooperation

Without the opportunity for adaptation ($L = 0$), cooperators are swiftly eliminated in competition with defectors (Figure 1). Despite an initial lift due to increased productivity, the cost of cooperation becomes disadvantageous as migration mixes the initially isolated populations. With adaptive opportunities ($L = 5$, $\epsilon = 0$), cooperators are maintained transiently (Figure 1B). Here, the additional mutational abilities provided by their larger sizes allows cooperator populations to more quickly adapt to their environment. As previously described by Hammarlund et al. (2015), however, this advantage diminishes as defector populations become equally adapted, and cooperators are outcompeted. When populations affect their environment and these changes feed back on selection, we find that cooperation can persist, perhaps indefinitely (Figure 1C, 3A). In these environments, cooperators maintain higher fitness than cooperators, which enables survival (Figure 3A).

Fitness Increases do not Support Cooperation

In our model, niche construction provides additional selective benefits. To determine how these selective effects contribute to our results, we performed simulations in which the selective effects of niche construction were removed ($\epsilon = 0$). As compensation, we increased the fitness benefits conferred by adaptation ($\delta = 0.6$). Here, the selective effects of niche construction are exaggerated, as a fitness benefit of 0.3 (our increase in δ) is the maximum value possible (see 3). To quantify cooperator success and permit comparison, we

use the area under the cooperator proportion curve. This measure of *cooperator presence* increases as cooperators rise in abundance or remain in the population longer.

We find that higher selective values do not provide a significant increase in cooperator presence (Figure 2, column C). As shown in Figure 3, cooperators gain adaptations more quickly than defectors, which provides a fitness advantage. However, the cost of cooperation puts defectors at an advantage once these populations become fully adapted.

Positive Niche Construction Prolongs Cooperation but is not Sufficient

We first focus on the effects of positive niche construction by removing the allelic conflict that leads to negative niche construction ($L = 5$, $a_{max} = 5$). In the absence of this conflict, cooperator presence is significantly increased (Figure 2, column D). Within these environments, we find that positive niche construction prolongs the fitness advantage that cooperators have over defectors (Figure 3C). Nevertheless, cooperators are eventually driven to extinction once defectors gain the fitness advantage.

Negative Niche Construction is not Sufficient

To determine how negative niche construction influences the evolution of cooperation, we maximize the allelic conflict ($L = 1$, $a_{max} = 6$). However, selection

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for increasing allelic states among the stress loci means that any allelic state will not be greater than at the previous allele (itself), and thus there will always be opportunity for adaptation. Despite this constant opportunity, niche construction does not increase cooperator presence (Figure 2, column E). Here, defectors rapidly gain the fitness advantage.

NC Enables Cooperator Spread

Figure 4 - if not, could be why thinning is a must.

NC Prevents Defector Invasion

Figure 5

How Public Good Fuels all of this

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

Despite their negative effects, deleterious traits can rise in abundance due to genetic linkage with other traits that are strongly favored by selection (Maynard Smith and Haigh, 1974). In a process termed the "Hankshaw effect", Hammarlund et al. (2015) recently demonstrated that cooperative behaviors can prolong their existence by actively increasing their likelihood of hitchhiking with a beneficial trait. While this process favors cooperation in the short term, it eventually reaches a dead end. When the opportunities for adaptation are exhausted and cooperators can no longer hitchhike, they face extinction. In this work, we have considered whether niche construction can maintain cooperation indefinitely.

Our results reveal that with niche construction, cooperation can indeed persist (Figure 1C). But what it is it about this process that maintains cooperation? In our model, niche construction introduces additional selective effects that could influence the evolutionary process. However, simply raising the selective benefits provided by adaptations does not significantly increase cooperator presence (Figure 2, columns C and A), and indicates that niche construction plays an important role. Although cooperators benefit greatly from positive niche construction, it does not fully explain our results (Figure 2 D). Indeed, despite an initial increase in abundance, cooperators are eventually driven to extinction when environmental change produces only positive fitness effects (Figure 1D). As with the "Hankshaw effect", adaption eventually slows, allowing defectors to outcompete cooperators (Figure 3C). While it does not

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benefit cooperation when alone (Figure 3E), negative niche construction acts to prevent this stasis. Combined, we find that both positive and negative niche construction are required to main cooperation.

This work further demonstrates that niche

Previously, Van Dyken and Wade (2012) showed that

By their very nature, public goods benefit populations by making their environment more hospitable (West *et al.*, 2007a). For example, bacteria produce a host of 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). While many studies have explored how the environment affects the evolution of cooperative behaviors such as these, relatively few have examined how those behaviors affect the environment and how the resulting feedbacks influence evolutionary trajectories. Lehmann (2007) demonstrated analytically that when niche construction 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.

TODO: 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

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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.

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.

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- 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

Primacy/Recency

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.

Acknowledgments

- TODO: Organizers?
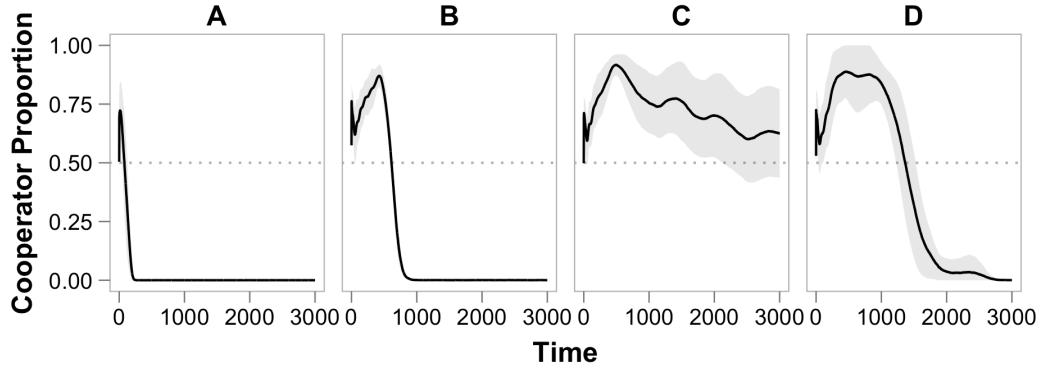
- TODO: lab comments

Figures

Figure 1

Figure 1: **Adaptation, niche construction, and the evolution of co-operation.** Curves show the average cooperator proportion among replicate populations, while shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter values used are listed in Table 1. (**A**) When there is no opportunity for adaptation (L, the number of adaptive loci, is zero), cooperation is quickly lost. (**B**) When adaptation can occur ($L = 5$), but populations do not alter their environment (ϵ, the intensity of niche construction, is zero), cooperators temporarily rise in abundance before eventually going extinct. (**C**) Selective feedbacks from niche construction allows cooperation to be maintained in 13 of 18 replicate populations. (**D**) While it does contribute to success, positive niche construction alone does not maintain cooperation ($A = 5$).

Figure 2

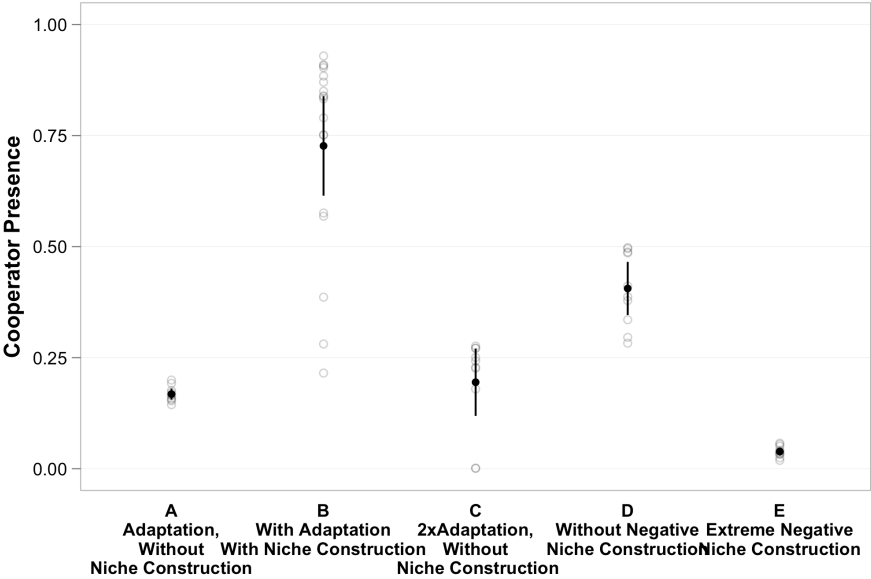Figure 2: Cooperator Presence TODO

Figure 3

Mean fitness over time for the treatments shown in Figure 2

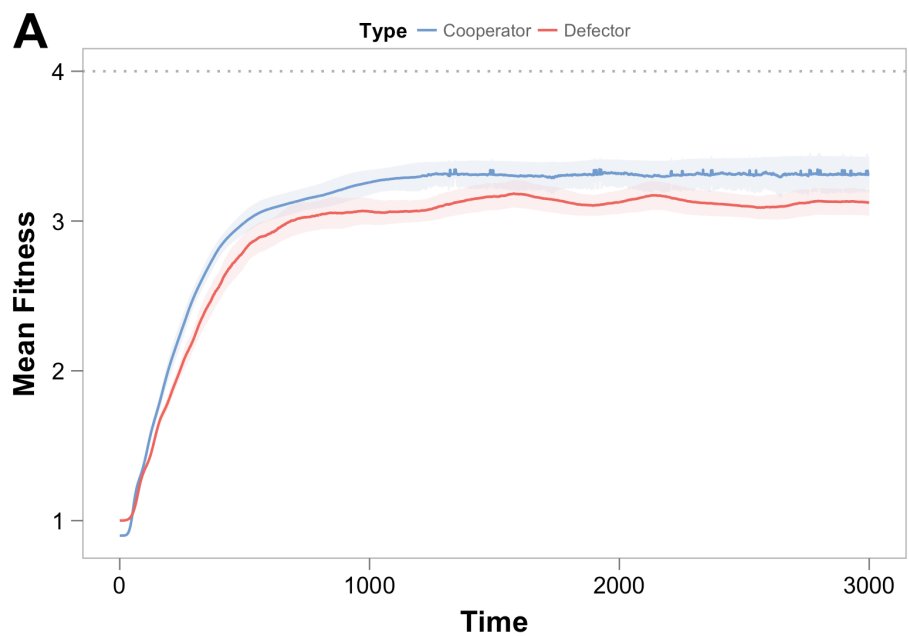## Figure 3A - Fitness for base case: niche construction

Figure 3: Grand mean Fitness of cooperators and defectors TODO
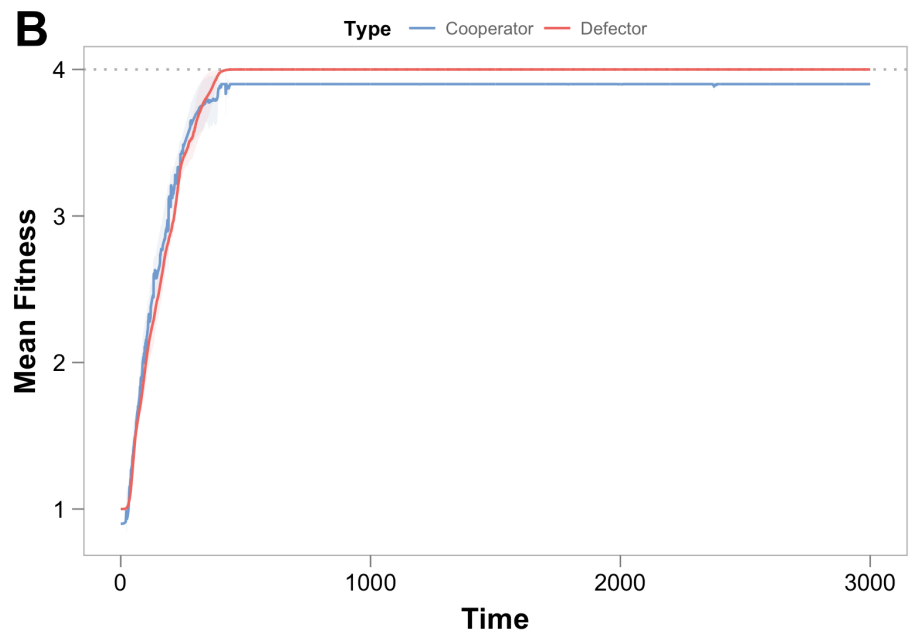
Figure 3B - Fitness with double delta, no epsilon

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

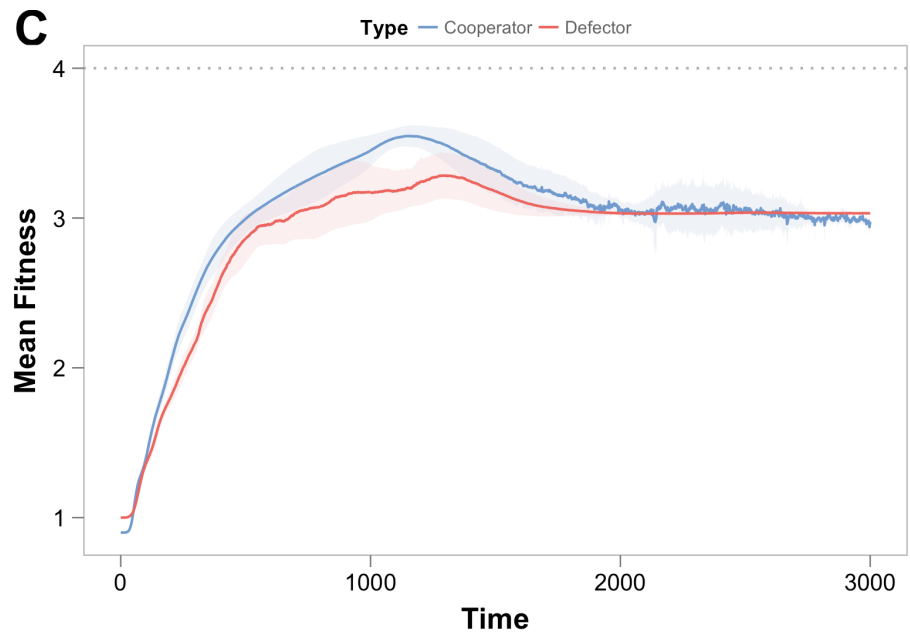**Figure 3C - Fitness with no negative niche construction (L=5, A=5)**

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

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

A=6)
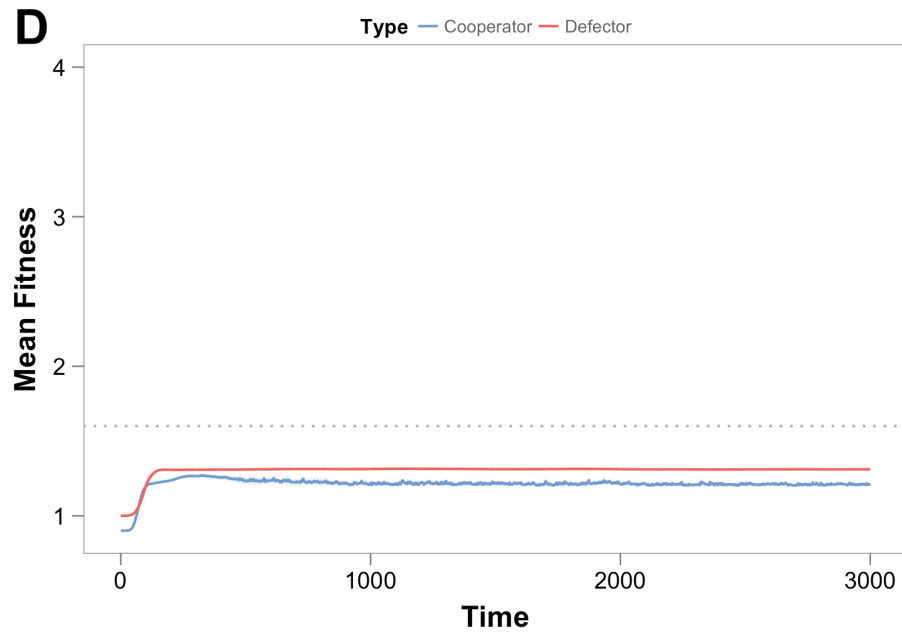

Figure 6: Grand mean Fitness of cooperators and defectors, extreme negative niche construction TODO

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)
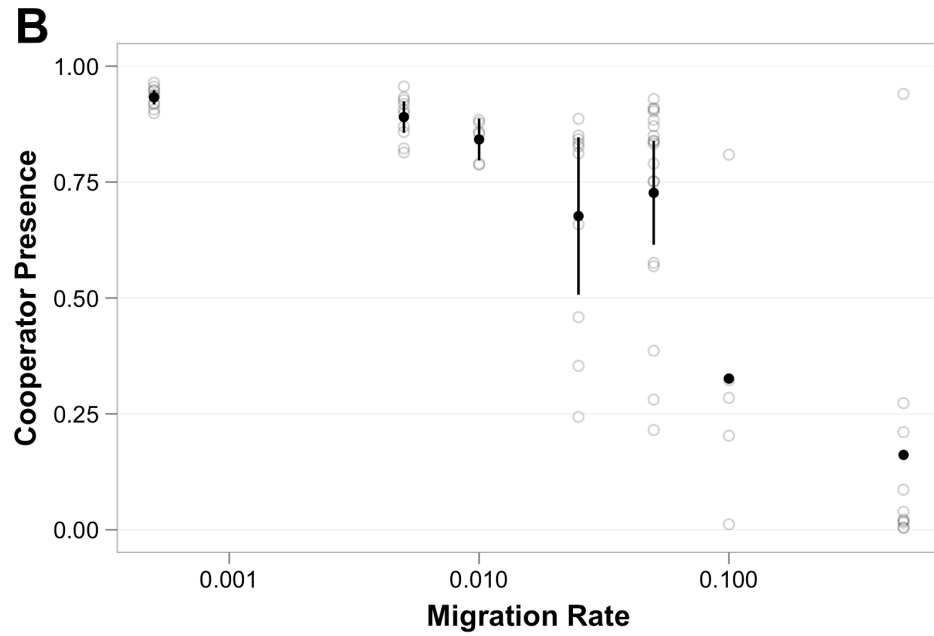
Figure 6B - Effect of Migration Rate (m)

Figure 7: 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 environment)	10^{-5}
T	Number of simulation cycles	1000
d	Population dilution factor	0.1

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