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

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). 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 adapted

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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 populations produce more emigrants, these populations will exert a stronger in-

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fluence 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 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 $\{1, 2, \ldots, A\}$, where A is the number of alleles conferring a selective benefit. Specifically, the presence of any 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

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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.

Organisms also influence their environment, which, in turn, influences selection.
We model this as a form of density 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 at the previous locus. For the remainder of this section, this
circularity is represented by the function below, which gives the integer below
x in the set $\{1, 2, \ldots, X\}$.

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

Here, $\text{mod}_Y(y)$ 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 $\beta(a, A)$ 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:

$$W_g = z + \delta \sum_{l=1}^{L} I(a_{g,l}) + \epsilon \sum_{l=1}^{L} n(\beta(a_{g,l}, A), \beta(l, L)) - c a_{g,L+1} \tag{2}$$

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

$$I(a) = \begin{cases} 1 & \text{if } a \in \{1, 2, \ldots, A\} \\ 0 & \text{otherwise} \end{cases} \tag{3}$$

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.

Cooperation allows the population to reach greater density. 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:

$$S(p) = S_{min} + p(S_{max} - S_{min}) \tag{4}$$

The function $S(p)$ reflects the benefit of cooperation. During growth, individuals compete for inclusion in the resulting population. The composition of a population with size P and cooperator proportion p after growth is multinomial with parameters and $S(p)$ and $\{\pi_1, \pi_2, \ldots, \pi_P\}$, where:

$$\pi_i = \frac{W_{\gamma(i)}}{\sum_{j=1}^{P} W_{\gamma(j)}} \tag{5}$$

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Here, $W_{\gamma(i)}$ is the fitness of an individual i with genotype $\gamma(i)$ (see Equation 2). 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 $\{0\} \cup \{1, 2, \ldots, A\}$. 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.

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 population growth, mutation, and migration. At the end of each cycle, popu-

lations 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. 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). Confidence intervals were estimated by bootstrapping with 1000 resamples.

Results

We follow the evolution of cooperation in a metapopulation consisting of populations connected by spatially-limited migration. Individuals in these populations can gain a limited number of adaptations that confer selective benefits. While the allele at an individual's cooperation locus does not directly affect the value of alleles at adaptive loci, cooperation can have indirect effects on the process of adaptation. Specifically, because cooperation increases population density, isolated cooperators experience more mutational opportunities to gain adaptations. Cooperation can hitchhike along with these adaptations, which compensate for the cost of cooperation. Additionally, populations alter their environment. Here, we explore how niche construction can favor the evolution

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of cooperation. Our simulation environment is defined by the parameter values listed in Table 1. Unless otherwise noted, 10 replicate simulations were performed for each experiment. We quantify cooperator success using the area under the cooperator proportion curve. This measure of cooperator presence increases as cooperators rise in abundance or remain in the population longer.

Niche Construction Maintains Cooperation

Without any 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. When there are opportunities for adaptation ($L = 5$) but no niche construction ($\epsilon = 0$), cooperators are maintained transiently (Figure 1B). Here, the additional mutational opportunities provided by their larger sizes allows cooperator populations to more quickly adapt to their environment. As previously described by Hammarlund et al. (2015), however, cooperation is subsequently lost as *adapted* defector populations arise via mutation. When niche construction ins incorporated, cooperation persists (Figure 1C).

Fitness Increases Alone do not Support Persisting Cooperation

In our model, niche construction introduces additional selective benefits. To determine how these selective effects influence evolutionary outcomes, we per-

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formed simulations in which the selective effects of niche construction were removed ($\epsilon = 0$), and we instead increased the fitness benefits conferred by adaptation ($\delta = 0.6$). Here, we are consevative by lifting the selective value of exogenous adaptation by the maximum value possible from niche construction.

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.

Negative Niche Construction is Critical to Cooperator Persistence

Negative niche construction 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 adaptive alleles (A), then it is not possible for the population to be fixed for a genotype that is perfectly adapted to the constructed environment. Technically (in terms of the model) this is because the equality:

$$\beta(a_{g,l}, A) = a_{g,\beta(l,L)}$$

cannot simultaneously hold for all l.

For example, consider genotype $(1, 2)$ when $L = 2$ and $A = 3$. Here, allelic

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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 relative to allelic state 3 at locus 1. Yet, fixation for genotype $(3, 2)$ does not solve the problem, because a mutant $(3, 1)$ is fitter, and so on.

We first focus on the effects of positive niche construction by removing the allelic conflict that leads to negative niche construction ($L = 5$, $A = 5$). 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).

Positive niche construction is important to cooperator persistence

To determine how negative niche construction influences the evolution of co-operation, we maximize the allelic conflict ($L = 1$, $A = 6$). Here, selection 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).

NC Enables Cooperator Spread

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

NC Prevents Defector Invasion

Figure 5

How Cooperation 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 4). 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 does favor 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

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extinction. In this work, we have considered whether niche construction can maintain cooperation indefinitely.

We demonstrate that when niche construction occurs, cooperation can indeed persist (Figure 1C). But what aspects of niche construction produce this result? 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. As with the Hankshaw effect, adaption eventually slows, allowing defectors to outcompete cooperators (Figure 3C). While it does not 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.

When successful, we observe that populations do not reach the maximum possible fitness (Figure 3A). Although cooperation is the focus of this study, it can be seen as deleterious. Previous work has shown that niche construction can favor deleterious alleles (Laland *et al.*, 1996, 1999). Similarly here, cooperation is maintained in the presence of niche construction, but lost otherwise (Figure 2). Van Dyken and Wade (2012) showed that when two cooperative behaviors co-evolve and niche construction feedbacks benefit the other type,

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niche construction can increasingly favor these traits, which were otherwise disfavored when alone.

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.

In our model, the environmental state was implicitly modeled, and depended solely on the current state of the population. In natural settings, however, the timescales at which environments are modified and reproduction are likely to be decoupled. For example, 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. These factors are likely to influence evolutionary trajectories (Laland *et al.*, 1996). 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 re-

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main competitive (Kümmerli and Brown, 2010; Dumas and Kümmerli, 2012). Cooperation that occurs facultatively, perhaps by sensing the abiotic (Bernier *et al.*, 2011; Koestler and Waters, 2014) or biotic environment (Brown and Johnstone, 2001; Darch *et al.*, 2012), are likely to be favored in these environments.

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?
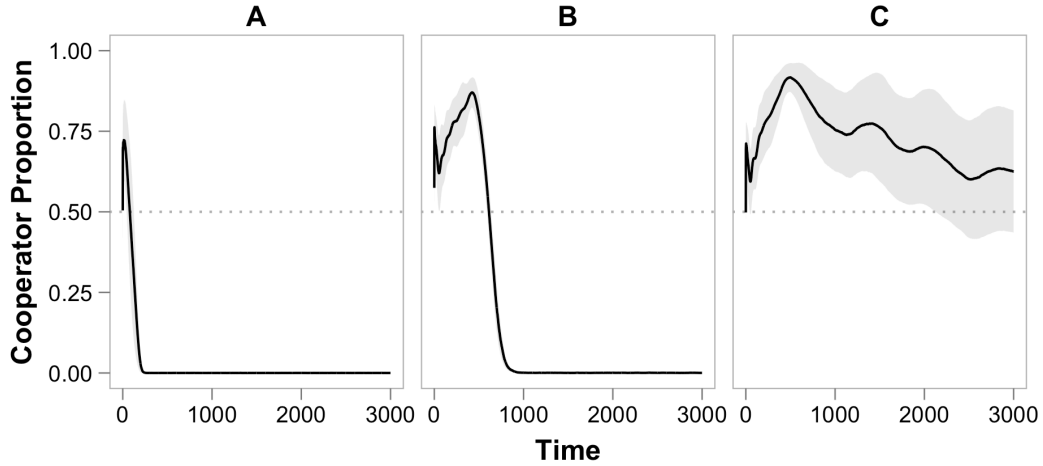- TODO: lab comments

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320 # Figures

321 ## Figure 1

Figure 1: **Adaptation, niche construction, and the evolution of cooperation.** 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 allow cooperation to be the dominant phenotype in 13 of 18 replicate populations.
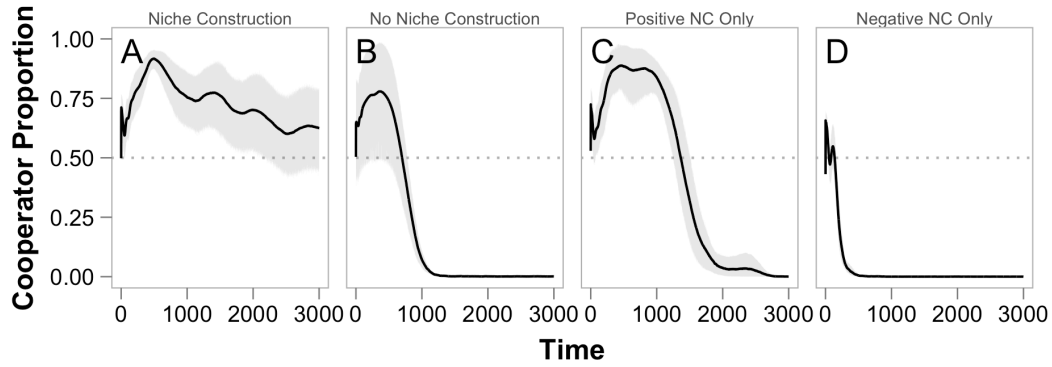
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Figure 2

Figure 2: **Evolutionary Processes and their Effect on Cooperator Presence.** (**A**) In our model, adaptations allow cooperation to hitchhike. This effect is transient, which limits cooperator presence. (**B**) In the presence of niche construction (positive and negative), cooperator presence is significantly increased. (**C**) When incorporating the potential benefits that it provides, but removing the selective feedback produced by niche construction, cooperator presence is unaffected. (**D**) Positive niche construction increases cooperator proportion, but not to the levels seen in B. (**E**) Negative niche construction alone does not account for the increase in cooperator presence. In these box plots, whiskers show range of data within 1.5 IQR.
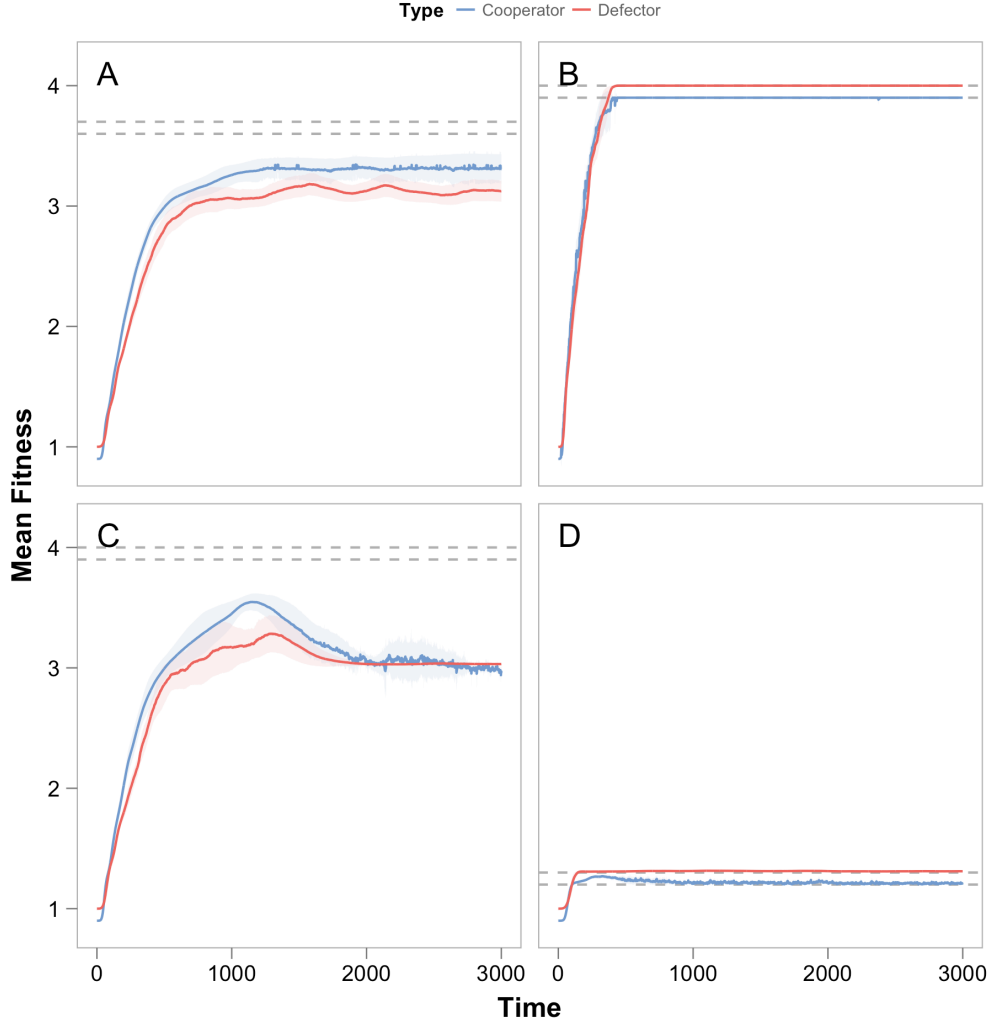
Figure 3

Figure 3: **Fitness Effects of Mutation Accumulation by Cooperators and Defectors.** Lines indicate the grand mean of cooperator (blue) and defector (red) fitness among replicate populations, while shaded areas indicate 95% confidence intervals. Upper and lower dotted lines indicate the maximum fitness values achievable by defectors and cooperators, respectively. (**A**) In the presence of niche construction, cooperators persist in the population by maintaining a greater mean fitness. (**B**) When selective values are increased ($\delta = 0.6$), populations rapidly adapt. In the absence of niche construction ($\epsilon = 0$), defectors eventually become equally adapted and surpass cooperators. At this point, cooperators are driven from the population due to the cost of cooperation. (**C**) With the effects of niche construction removed ($\epsilon = 0$), positive niche construction prolongs the time when cooperators are at an advantage over defectors. Once again, however, defectors eventually become equally adapted, leading to the loss of cooperation. (**D**) Without positive niche construction or further adaptive opportunities ($L = 1$, $a_{max} = 6$) cooperators do not benefit from niche construction.

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Figure 4

Cooperators invade defector population. Fully adapted but mismatched. Negative NC.

Figure 5

Defectors invade cooperator population. Fully adapted and matched. Role of Export.

Figure 6

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

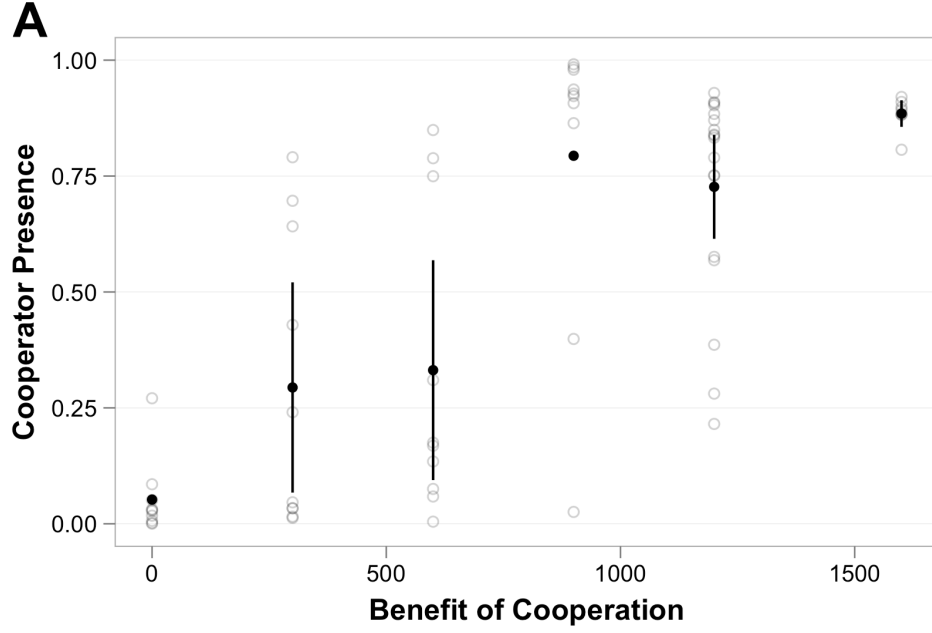**Figure 6B - Effect of Migration Rate (m)**

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Figure 4: **Cooperator Presence as a Function of Population Size and Migration Rate.** Cooperator presence for each replicate population is shown as an open circle. The mean among these replicates is represented by a filled circle, and bars indicate 95% confidence intervals. (**A**) Cooperator presence increases proportional to increases in population size. Here, the benefit of cooperation (S_{max}) is varied (the density-dependent fitness effects of niche construction are adjusted accordingly in the model parameter ϵ). (**B**) Cooperator presence decreases with migration rate (m). When migration is low, cooperators can not export their niche, which limits expansion. When migration is high, the defectors immigrate into populations more quickly than cooperators can adapt.
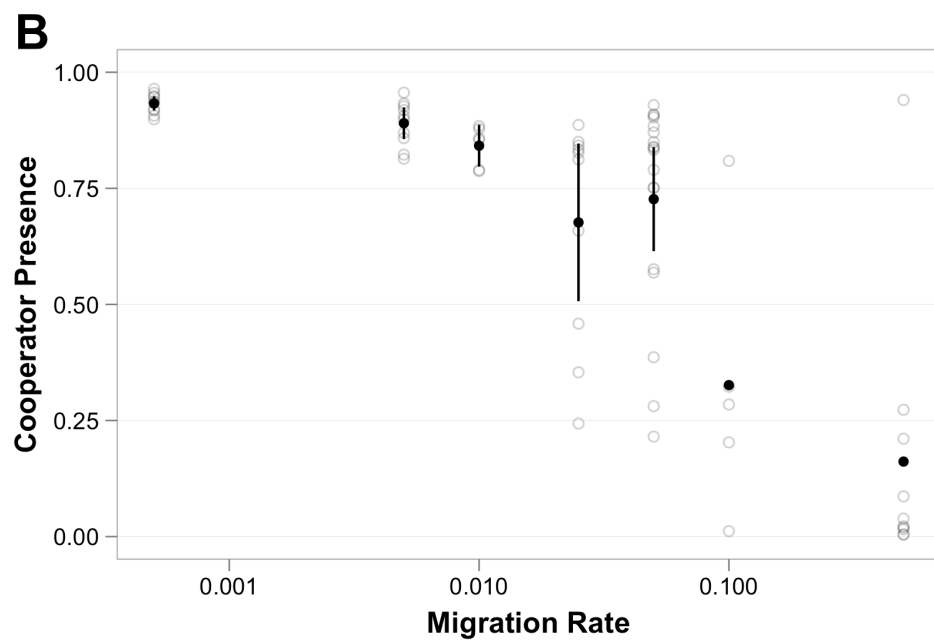
Figure 5: Will share caption with 6A

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	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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