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

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 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 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 develop an individual-based model in which populations of cooperators and defectors evolve and compete in a spatially-structured metapopulation (a collection of populations). Through mutations, individuals gain adaptations to their environment, which increase reproductive fitness, and allow those lineages to rise in abundance. Migration among neighboring populations allows more successful lineages to spread.

We expand upon the model described by Hammarlund et al. (2015) to allow populations to modify their local environment. As this process occurs, environmental changes feed back to affect selection. We perform simulations using this model to explore how niche construction affects this adaptation process and whether selective feedbacks allow cooperation to be maintained.

## Model Description

### Individual Genotypes and Adaptation

Each individual in a population has a genotype, which is an ordered list of integers, or *loci* (see [Table 1](#tables) for model parameters and their values). Different values at these loci represent different alleles. A binary allele at locus determines whether that individual is a defector () or a cooperator (), which carries fitness cost . Cooperation is independent from adaptation to the environment. The first loci are *adaptive loci*, and are each occupied by or an integer from the set . Allele represents a lack of adaptation, while a non-zero allele represents one of the possible adaptations at that locus. The presence of any of these adaptations confers a fitness benefit . We choose , which allows a minimally adapted cooperator to recoup the cost of cooperation and gain a fitness advantage. The benefits that these adaptations engender are purely endogenous, and are not affected by the other individuals or the state of the environment.

### Niche Construction and Selective Feedbacks

Individual fitness is also affected by the current state of the local environment. Here, we represent the “niche” implicitly based on the allelic states present in the population. As allelic states change, populations alter their environment in different ways, creating a unique niche.

We use a form of density dependent selection to favors individuals that better match their niche. Specifically, the selective value of adaptive allele at locus increases with the number of individuals in the population that have allele at locus . As a consequence, genotypes with sequentially increasing allelic states will tend to evolve. We treat both adaptive loci and allelic states as “circular”, so the selective value of an allele at locus is affected by the allelic composition of the population at locus 1. Similarly, the selective value of allele at any locus increases with the number of individuals carrying allele at the next locus. This circularity is represented by the function , which gives the integer that follows an arbitrary value in the set :

$$ \beta(x, X) = \bmod\_{X}(x) + 1 \qquad (1)$$

Here, $\bmod\_{X}(x)$ is the integer remainder when dividing by . Thus, the selective value of adaptive allele at locus increases with the number of individuals that have allele at locus . The slope of this increase is , which specifies the intensity of niche construction.

Consider a genotype with the allelic state at locus given by ; the fitness of an individual with this genotype is defined as:

where is a baseline fitness and indicates whether a given adaptive allele is non-zero:

Thus, an individual’s fitness is determined both endogenously by adaptation () and exogenously by its niche ().

Because mutations occur randomly (see below), each population will evolve different consecutive sequences. These different sequences represent the unique niches constructed by populations.

### Population Growth and the Benefit of Cooperation

Cooperation benefits a population by allowing it to reach greater density. This benefit affects all individuals equally and accumulates linearly with the proportion of cooperators in the population. If is the proportion of cooperators in a population at the beginning of a growth cycle, then that population reaches the following size:

During growth, individuals compete for inclusion in the resulting population. Each individual’s probability of success is determined by its fitness. The composition of a population with size and cooperator proportion after growth is multinomial with parameters and and , where:

Here, is the fitness of an individual with genotype (see Equation 2). The value represents an individual’s reproductive fitness relative to others in the population.

### Mutation

For simplicity, we apply mutations after population growth. Mutations occur independently at each locus and cause an allelic state change. At each adaptive locus, mutations occur at rate . These mutations replace the existing allele with a random selection from the set . Note that this allows for the possibility of an allele replacing itself, thus slightly reducing the effective mutation rate. At the binary cooperation locus, mutations occur at rate . These mutations flip the allelic state, causing cooperators to become defectors and vice versa.

### Migration

Our simulated environment consists of patches arranged as an lattice, where each patch can support a population. After mutation, individuals emigrate to an adjacent patch at rate . During each migration event, a single destination patch is randomly chosen with uniform probability from each 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.

### Metapopulation Initialization and Simulation

Metapopulations are initiated in a state that follows an environmental change, which leaves most patches empty. First, populations are seeded at all patches with cooperator proportion and grown to density . An environmental challenge is then introduced, which subjects the population to a bottleneck. For each individual, the probability of survival is , which represents the likelihood that a mutation occurs that confers tolerance. Because individuals have not yet adapted to this new environment, the allelic state of each individual’s genotype is at each adaptive locus. Following initialization, simulations are run for cycles, where each discrete cycle consists of population growth, mutation, and migration. At the end of each cycle, populations are thinned to allow for growth in the next cycle. Each individual persists with probability , 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, 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). Reported 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 of cooperation. Our simulation environment is defined by the parameter values listed in [Table 1](#tables). 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 (), cooperators are swiftly eliminated in competition with defectors (Figure 1A). Despite an initial lift due to increased productivity, the cost of cooperation becomes disadvantageous as migration mixes the initially isolated populations. When there are opportunties for adaptation () but no niche construction (), 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 performed simulations in which the selective effects of niche construction were removed (), and we instead increased the fitness benefits conferred by adaptation (. 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 2B). 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 () is not evenly divided by the number of adaptive alleles (), 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:

cannot simultaneously hold for all .

For example, consider genotype when and . 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 relative to allelic state 3 at locus 1. Yet, fixation for genotype does not solve the problem, because a mutant 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 (, ). In the absence of this conflict, cooperator presence is significantly increased (Figure 2C). 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 cooperation, we maximize the allelic conflict (, ). Here, selection for increasing allelic states among the adaptive 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 2D).

## 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 (, 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 (). 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 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 2B), 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 2C). 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. Van Dyken and Wade (2012) showed that when two cooperative behaviors co-evolve and niche construction feedbacks benefit the other type, 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 remain 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.

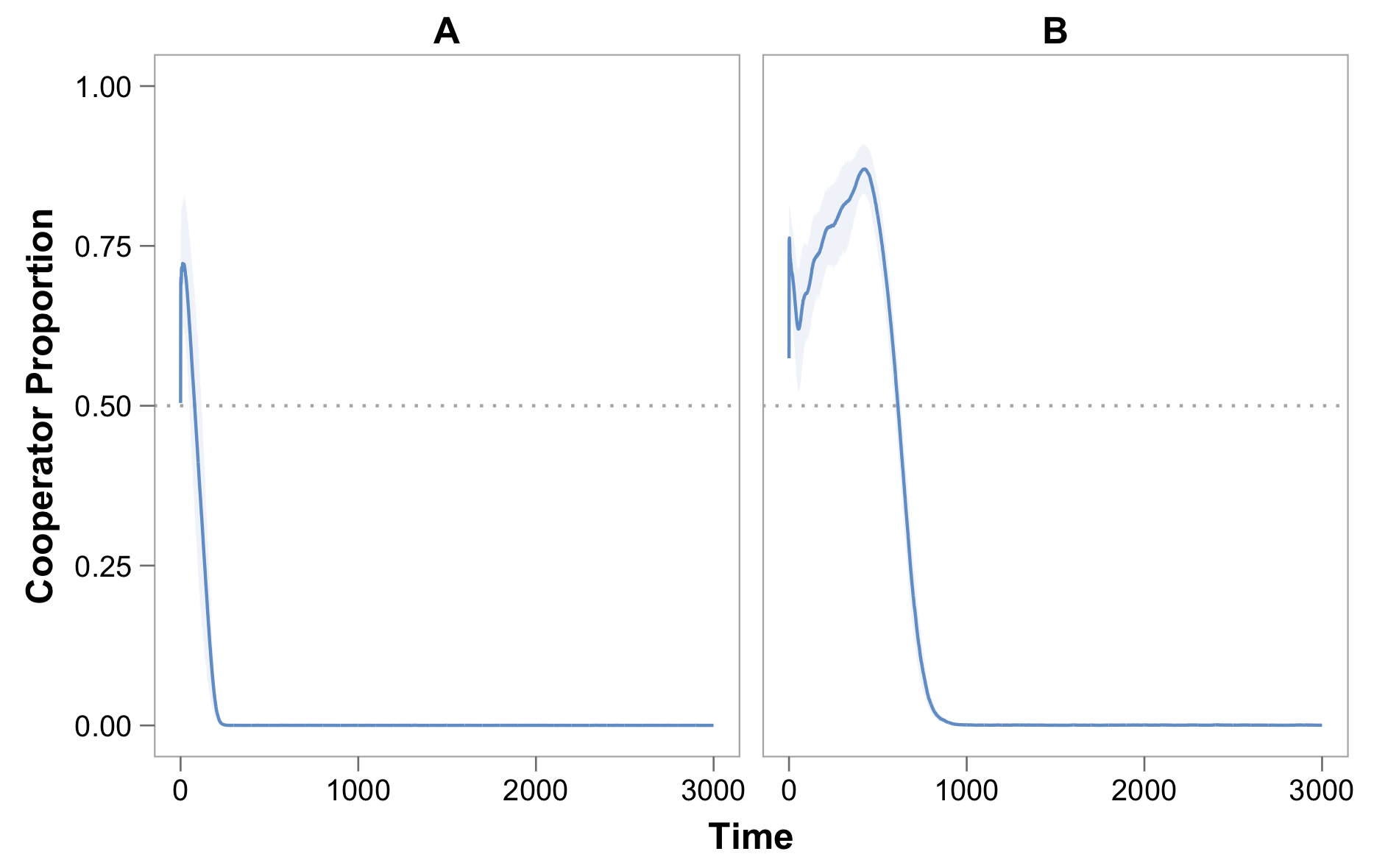
In many instances of cooperation, the environment is itself a biological entity, which can produce additional evolutionary feedbacks. As the host population changes, so too will selection on their symbiont populations. Here, evolutionary outcomes depend greatly on the degree of shared interest between 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.

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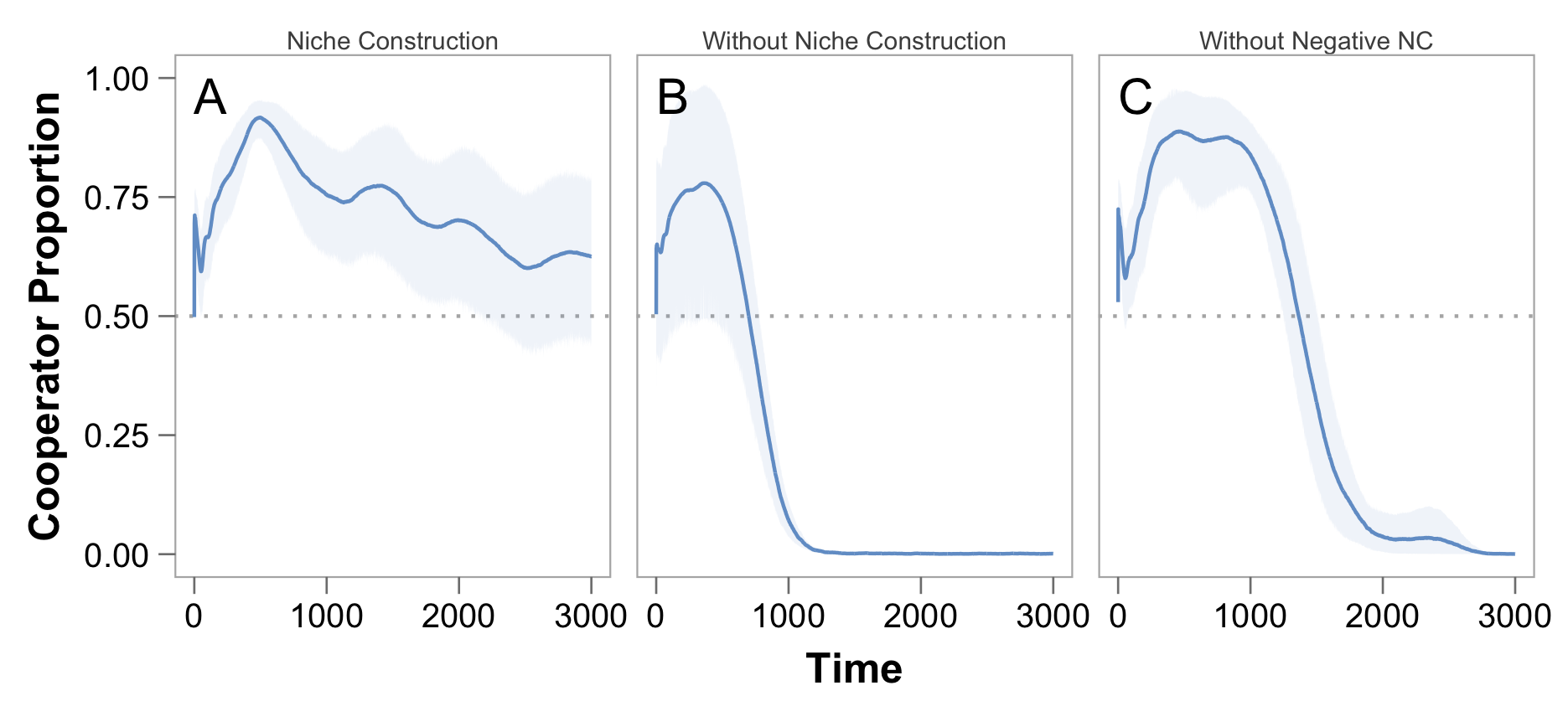
# Figures

## Figure 1



**Adaptation, Hitchhiking, and the evolution of cooperation.** The proportion of cooperators present in the population is shown for the duration of simulations. Curves show the average among replicates, and shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter values are listed in [Table 1](#tables). (**A**) When there is no opportunity for adaptation (, the number of adaptive loci, is zero), cooperation is quickly lost. (**B**) When adaptation can occur (), but populations do not alter their environment (, the intensity of niche construction, is zero), cooperation hitchhikes along with adaptions, allowing cooperators to temporarily rise in abundance before eventually going extinct.

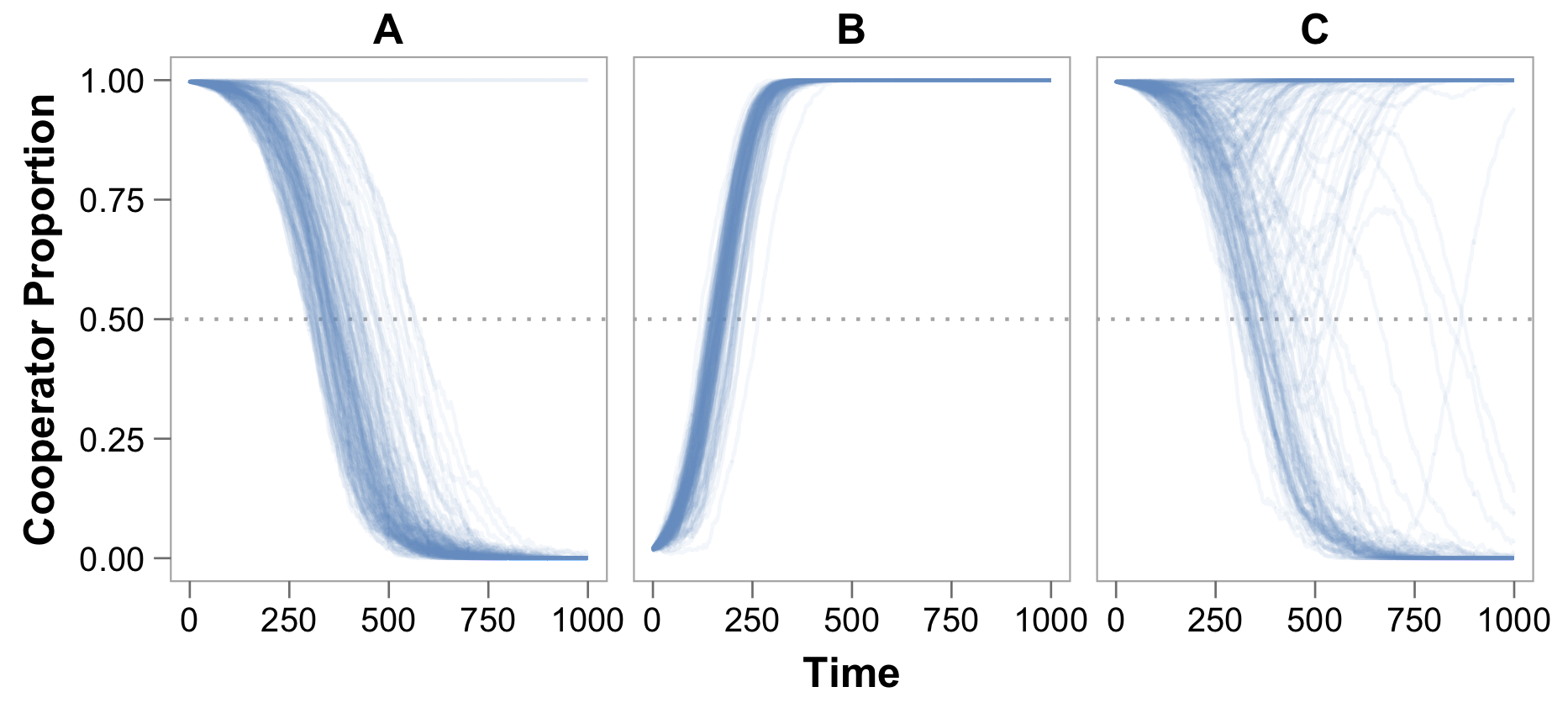
## Figure 2



**Niche Construction and the Evolution of Cooperation.** The proportion of cooperators present in the population is shown for the duration of simulations. Curves show the average among replicates, and shaded areas indicate 95% confidence intervals. (**A**) Niche construction enables cooperation to be maintained indefinitely. In the majority of populations, cooperation remained as the dominant strategy. (**B**) When niche construction is removed () and the fitness benefit of adaptation is increased as compensation (), cooperation is quickly lost when adapted defectors arise. (**C**) Without negative niche construction, cooperation is not maintained (). Here again, cooperation is driven to extinction by equally-adapted defectors.

## Figure 3

# TODO switch B and C?



**Niche Construction and Invasion.** Curves trace the proportion of cooperators present in the population for the duration of 160 replicate simulations. In these experiments, we examined whether a strategy initiated at a single population in the center of the metapopulation lattice () can invade. Unless otherwise noted, we disable mutations () to focus on how invasion depends on particular combinations of genotypes. (**A**) When cooperators and defectors are matched (i.e., genotypes ) and adaptation can not occur, defectors quickly drive cooperators to extinction due to the cost of cooperation. Defectors were stochastically eliminated in 2 replicate populations. (**B**) However, the adaptive opportunities produced by negative niche construction and density dependence can enable an adapted cooperator (genotype ) to invade a population of defectors. (**C**) These same adaptive opportunities can allow cooperators to resist invasion by matching defectors, which arise via mutation and remain a constant threat. Here, cooperation persisted in 91 populations ().

## Figure 4

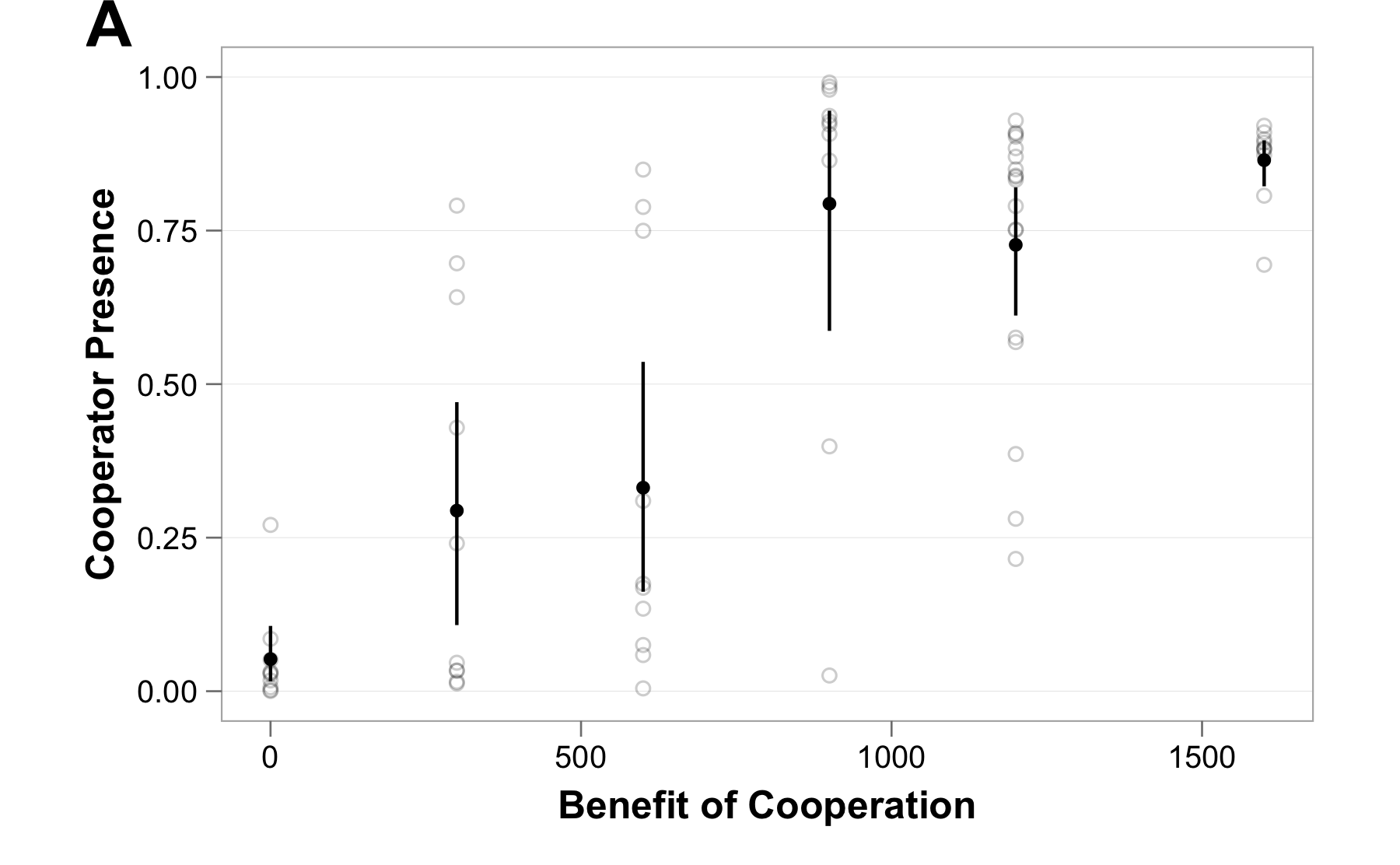
Cooperators invade defector population. Fully adapted but mismatched. Negative NC.

## Figure 5

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

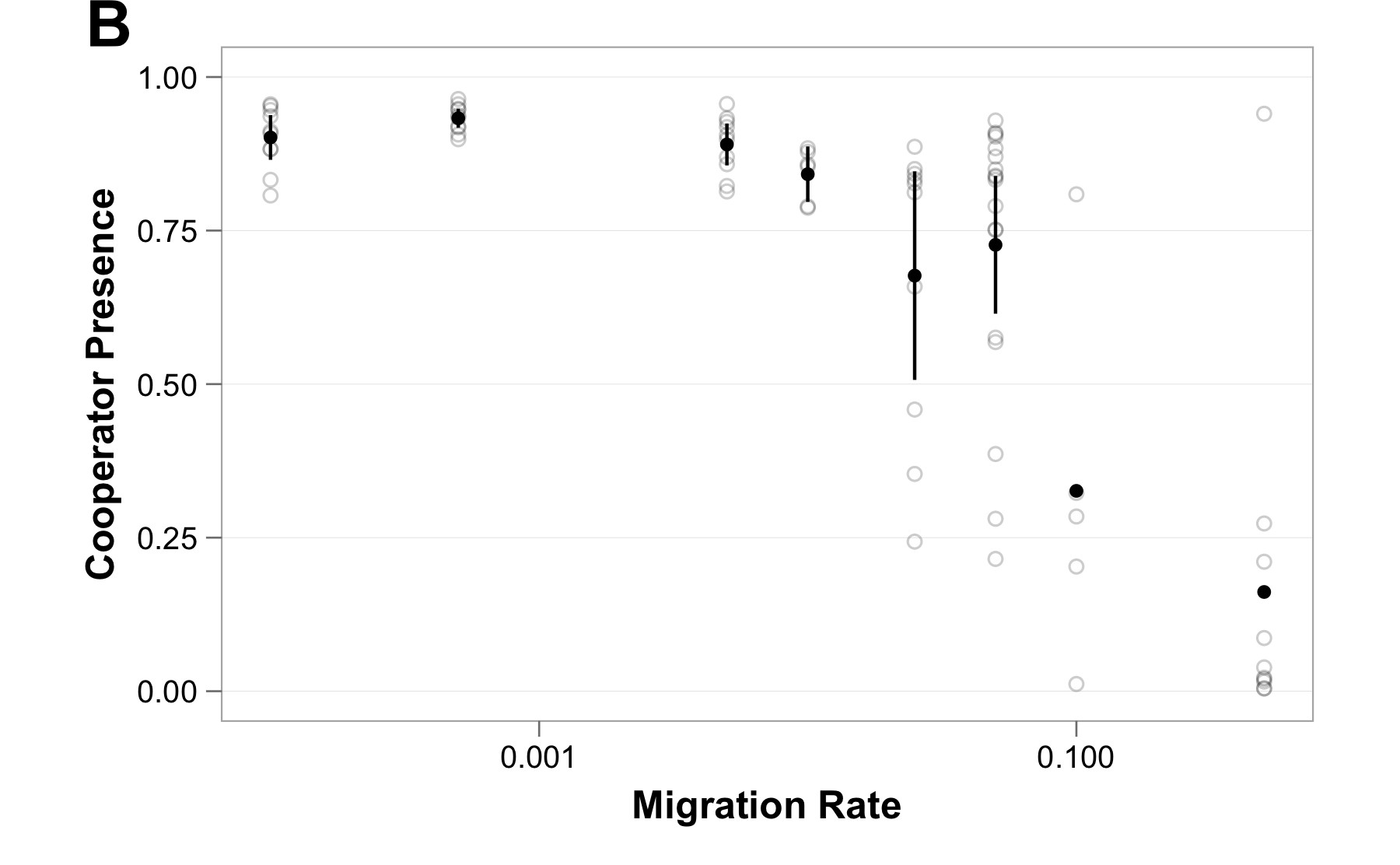
## Figure 6

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



**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 () is varied (the density-dependent fitness effects of niche construction are adjusted accordingly in the model parameter ). (**B**) Cooperator presence decreases with migration rate (). 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 6B - Effect of Migration Rate (m)



Will share caption with 6A

# Tables

Model parameters and their value

|  |  |  |
| --- | --- | --- |
| Parameter | Description | Base Value |
|  | Number of adaptive loci | 5 |
|  | Fitness cost of cooperation | 0.1 |
|  | Number of alleles | 6 |
|  | Fitness benefit, nonzero alleles | 0.3 |
|  | Fitness benefit, sequential alleles | 0.00015 |
|  | Baseline fitness | 1 |
|  | Minimum population size | 800 |
|  | Maximum population size | 2000 |
|  | Mutation rate (adaptation) |  |
|  | Mutation rate (cooperation) |  |
|  | Number of metapopulation sites | 625 |
|  | Migration rate | 0.05 |
|  | Initial cooperator proportion | 0.5 |
|  | Mutation rate (tolerance to new environment) |  |
|  | Population dilution factor | 0.1 |
|  | Number of simulation cycles | 1000 |

# References

Allison, S.D. 2005. Cheaters, diffusion and nutrients constrain decomposition by microbial enzymes in spatially structured environments. *Ecology Letters*, **8**: 626–635.

Asfahl, K.L., Walsh, J., Gilbert, K. and Schuster, M. 2015. Non-social adaptation defers a tragedy of the commons in Pseudomonas aeruginosa quorum sensing. *The ISME Journal*, doi: [10.1038/ismej.2014.259](http://dx.doi.org/10.1038/ismej.2014.259).

Bernier, S.P., Ha, D.-G., Khan, W., Merritt, J.H.M. and O’Toole, G.A. 2011. Modulation of Pseudomonas aeruginosa surface-associated group behaviors by individual amino acids through c-di-GMP signaling. *Research in Microbiology*, **162**: 680–688.

Brown, S.P. and Johnstone, R.A. 2001. Cooperation in the dark: Signalling and collective action in quorum-sensing bacteria. *Proceedings of the Royal Society of London B: Biological Sciences*, **268**: 961–965.

Brown, S.P. and Taddei, F. 2007. The durability of public goods changes the dynamics and nature of social dilemmas. *PLoS ONE*, **2**: e593. Public Library of Science.

Cosson, P., Zulianello, L., Join-Lambert, O., Faurisson, F., Gebbie, L. and Benghezal, M.*et al.* 2002. Pseudomonas aeruginosa virulence analyzed in a Dictyostelium discoideum host system. *Journal of Bacteriology*, **184**: 3027–3033.

Dandekar, A.A., Chugani, S. and Greenberg, E.P. 2012. Bacterial quorum sensing and metabolic incentives to cooperate. *Science*, **338**: 264–266.

Darch, S.E., West, S.A., Winzer, K. and Diggle, S.P. 2012. Density-dependent fitness benefits in quorum-sensing bacterial populations. *Proceedings of the National Academy of Sciences*, **109**: 8259–8263.

Diggle, S.P., Griffin, A.S., Campbell, G.S. and West, S.A. 2007. Cooperation and conflict in quorum-sensing bacterial populations. *Nature*, **450**: 411–414.

Driscoll, W.W. and Pepper, J.W. 2010. Theory for the evolution of diffusible external goods. *Evolution*, **64**: 2682–2687.

Dumas, Z. and Kümmerli, R. 2012. Cost of cooperation rules selection for cheats in bacterial metapopulations. *Journal of Evolutionary Biology*, **25**: 473–484.

Fletcher, J.A. and Doebeli, M. 2009. A simple and general explanation for the evolution of altruism. *Proceedings of the Royal Society B: Biological Sciences*, **276**: 13–19.

Foster, K., Shaulsky, G., Strassmann, J., Queller, D. and Thompson, C. 2004. Pleiotropy as a mechanism to stabilize cooperation. *Nature*, **431**: 693–696. Nature Publishing Group.

Gardner, A. and West, S.A. 2010. Greenbeards. *Evolution*, **64**: 25–38.

Ghoul, M., West, S.A., Diggle, S.P. and Griffin, A.S. 2014. An experimental test of whether cheating is context dependent. *Journal of Evolutionary Biology*, **27**: 551–556.

Griffin, A.S., West, S.A. and Buckling, A. 2004. Cooperation and competition in pathogenic bacteria. *Nature*, **430**: 1024–1027.

Hafer, N. and Milinski, M. 2015. When parasites disagree: Evidence for parasite-induced sabotage of host manipulation. *Evolution*, doi: [10.1111/evo.12612](http://dx.doi.org/10.1111/evo.12612).

Hagberg, A.A., Schult, D.A. and Swart, P.J. 2008. Exploring network structure, dynamics, and function using NetworkX. In: *Proceedings of the 7th Python in Science Conference (SciPy2008)*, pp. 11–15.

Hamblin, S.R., White, P.A. and Tanaka, M.M. 2014. Viral niche construction alters hosts and ecosystems at multiple scales. *Trends in Ecology & Evolution*, **29**: 594–599.

Hamilton, W.D. 1964. The genetical evolution of social behaviour I & II. *Journal of Theoretical Biology*, **7**: 1–52.

Hammarlund, S.P., Connelly, B.D., Dickinson, K.J. and Kerr, B. 2015. The evolution of cooperation by the Hankshaw effect. *bioRxiv*, doi: [10.1101/016667](http://dx.doi.org/10.1101/016667). Cold Spring Harbor Labs Journals.

Hardin, G. 1968. The tragedy of the commons. *Science*, **162**: 1243–1248.

Harrison, F. 2007. Microbial ecology of the cystic fibrosis lung. *Microbiology*, **153**: 917–923.

Koestler, B.J. and Waters, C.M. 2014. Bile acids and bicarbonate inversely regulate intracellular cyclic di-GMP in Vibrio cholerae. *Infection and Immunity*, **82**: 3002–3014.

Kuzdzal-Fick, J.J., Fox, S.A., Strassmann, J.E. and Queller, D.C. 2011. High relatedness is necessary and sufficient to maintain multicellularity in Dictyostelium. *Science*, **334**: 1548–1551.

Kümmerli, R. and Brown, S.P. 2010. Molecular and regulatory properties of a public good shape the evolution of cooperation. *Proceedings of the National Academy of Sciences*, **107**: 18921–18926.

Kümmerli, R., Griffin, A.S., West, S.A., Buckling, A. and Harrison, F. 2009. Viscous medium promotes cooperation in the pathogenic bacterium Pseudomonas aeruginosa. *Proceedings of the Royal Society of London B: Biological Sciences*, **282**.

Laland, K.N., Odling-Smee, F.J. and Feldman, M.W. 1999. Evolutionary consequences of niche construction and their implications for ecology. *Proceedings of the National Academy of Sciences*, **96**: 10242–10247.

Laland, K.N., Odling-Smee, F.J. and Feldman, M.W. 1996. The evolutionary consequences of niche construction: A theoretical investigation using two-locus theory. *Journal of Evolutionary Biology*, **9**: 293–316.

Lehmann, L. 2007. The evolution of trans-generational altruism: Kin selection meets niche construction. *Journal of Evolutionary Biology*, **20**: 181–189. Blackwell Publishing Ltd.

Maynard Smith, J. and Haigh, J. 1974. The hitch-hiking effect of a favourable gene. *Genetics Research*, **23**: 23–35.

McKinney, W. 2010. Data structures for statistical computing in Python. In: *Proceedings of the 9th Python in Science Conference* (S. van der Walt and J. Millman, eds), pp. 51–56.

Morgan, A.D., Quigley, B.J.Z., Brown, S.P. and Buckling, A. 2012. Selection on non-social traits limits the invasion of social cheats. *Ecology Letters*, **15**: 841–846.

Nadell, C.D., Foster, K.R. and Xavier, J.B. 2010. Emergence of spatial structure in cell groups and the evolution of cooperation. *PLoS Computational Biology*, **6**: e1000716.

Nowak, M.A. 2006. Five rules for the evolution of cooperation. *Science*, **314**: 1560–1563.

R Core Team. 2015. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Ruby, E.G. 1996. Lessons from a cooperative, bacterial-animal association: The Vibrio fischeri–Euprymna scolopes light organ symbiosis. *Annual Review of Microbiology*, **50**: 591–624.

Sinervo, B., Chaine, A., Clobert, J., Calsbeek, R., Hazard, L. and Lancaster, L.*et al.* 2006. Self-recognition, color signals, and cycles of greenbeard mutualism and altruism. *Proceedings of the National Academy of Sciences*, **103**: 7372–7377.

Van Dyken, J.D. and Wade, M.J. 2012. Origins of altruism diversity II: Runaway coevolution of altruistic strategies via “reciprocal niche construction”. *Evolution*, **66**: 2498–2513.

Veelders, M., Brückner, S., Ott, D., Unverzagt, C., Mösch, H.-U. and Essen, L.-O. 2010. Structural basis of flocculin-mediated social behavior in yeast. *Proceedings of the National Academy of Sciences*, **107**: 22511–22516.

Waite, A.J. and Shou, W. 2012. Adaptation to a new environment allows cooperators to purge cheaters stochastically. *Proceedings of the National Academy of Sciences*, **109**: 19079–19086.

West, S.A., Diggle, S.P., Buckling, A., Gardner, A. and Griffin, A.S. 2007a. The social lives of microbes. *Annual Review of Ecology, Evolution, and Systematics*, **38**: 53–77.

West, S.A., Griffin, A.S. and Gardner, A. 2007b. Evolutionary explanations for cooperation. *Current Biology*, **17**: R661–R672.

Zhang, X.-X. and Rainey, P.B. 2013. Exploring the sociobiology of pyoverdin-producing Pseudomonas. *Evolution*, **67**: 3161–3174.