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 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; Nowak, 2006; West *et al.*, 2007b). One such 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 through association with alleles encoding self-benefitting traits (Asfahl *et al.*, 2015). In these cases, the alleles may provide private benefits that are completely independent from the public benefits of cooperation. In an asexual population of 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 demonstrated that in spatially-structured populations, the “Hankshaw effect” can give cooperators a substantial leg up on defectors in an adaptive race. When cooperation increases local population density, the likelihood of acquiring beneficial mutations is also increased. The cooperative trait can rise in abundance by hitchhiking along with these adaptations. Nevertheless, this advantage is fleeting. As soon as the opportunities for adaptation are exhausted, cooperators are once again at a selective disadvantage against equally-adapted defectors that arise via mutation. However, Hammarlund et al. (2015) demonstrated that cooperation can be maintained indefinitely when frequent environmental changes produce a steady stream of new adaptive opportunities. Although organisms typically find themselves in dynamic environments, the nature and frequency of these changes might not ensure long-term cooperator survival.

Importantly, however, organisms do not simply play passive roles in environmental change and in evolution. Through their activities, their interactions with others, and even their death, organisms constantly modify their environment. These changes can produce evolutionary feedback loops in which environmental change alters selection, which, in turn, alters the distribution of phenotypes and their corresponding influence on the environment (Odling-Smee *et al.*, 2003). Because of these feedback loops, populations may find themselves continually chasing beneficial mutations as their adaptive landscape perpetually shifts beneath them.

Here, we explore whether the selective feedbacks that result from niche construction can prolong cooperation. We build upon the model presented by Hammarlund et al. (2015) to allow populations to modify their local environments in ways that affect fitness. We first use this model to address whether niche construction can extend the Hankshaw effect, allowing cooperation to continue to hitchhike as populations continually adapt. We then focus on how niche construction influences outcomes when isolated cooperator populations encounter populations of defectors, either through migration or through mutations that inevitably produce defectors that share the same adaptations. Finally, niche construction has frequently been shown to increase diversity (**???**). We explore whether this diversity helps or hinders the evolution of cooperation.

# 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 cooperator (), which carries fitness cost , or a defector (). 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. Adaptations confer a fitness benefit , regardless of which non-zero allele is present. 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 favor 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”: 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 . The selective value of adaptive allele at locus is increased by for each individual in the population that has allele at locus . Thus, 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 , 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 the periphery 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 all populations to a bottleneck. For each individual, the probability of survival is , which represents the likelihood that tolerance to the new environmental conditions arises via mutation. 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

Using the model described in the previous section, we perform simulations that follow the evolution of cooperation in a metapopulation consisting of populations connected by spatially-limited migration. Individuals compete in these populations by gaining a limited number of adaptations that confer fitness benefits. While cooperation does not directly affect the selective value of these adaptations, cooperation can have indirect effects on the adaptive process. Specifically, cooperation increases population density. As a result, larger populations of cooperators experience more mutational opportunities to gain adaptations. Cooperation can hitchhike along with these adaptations, which compensate for the cost of cooperation. During this process, populations alter their local environments, which, in turn, influences selection. Here, we explore how niche construction affects the evolution of cooperation in the simulation environment defined by the parameter values listed in [Table 1](#tables).

## Cooperation Persists with Niche Construction

Without any opportunity for adaptation (), cooperators are swiftly eliminated in competition with defectors ([Figure 1A](#fig1)). Despite an initial lift in cooperator abundance due to increased productivity, the cost of cooperation becomes disadvantageous as migration mixes the initially isolated populations. When there are opportunities for adaptation () but no niche construction (), cooperators are maintained transiently ([Figure 1B](#fig1)). Here, larger cooperator populations can more quickly adapt to their environment. As previously described by Hammarlund et al. (2015), however, cooperation is subsequently lost once populations become fully adapted to their environment. Once this has occurred, adapted defectors that arise via mutation at the cooperation locus have a selective advantage and drive cooperators from the population. However, when niche construction creates selective feedbacks, cooperation persists in 13 of 18 replicate populations ([Figure 2A](#fig2)).

## Fitness Increases Alone do not Support Persisting Cooperation

In the model, both adaptation and niche construction contribute to an individual’s fitness. To determine whether cooperation is maintained solely due to the larger selective values that result from the contributions of niche construction (), we performed simulations in which these contributions were removed (), and we instead increased the fitness benefits conferred by adaptation (. In doing so, we conservatively mimic the selective effects of niche construction, as fitness benefits of this magnitude would only be given for sequential allelic states that are fixed in full populations. We find that simply increasing selective values does not allow cooperators to persist ([Figure 2B](#fig2)).

## Negative Niche Construction is Critical to Cooperator Persistence

Negative niche construction can occur in our model due to the selection for sequentially-increasing allelic states and the circular arrangement of these alleles. When this occurs, adaptations at one locus reduce the selective effects at another locus, and thus negatively affect fitness. This occurs when when the genome length () is not evenly divided by the number of adaptive alleles (), which makes it impossible to evolve sequentially increasing allelic states. This allelic conflict exists with our base parameter values ([Table 1](#tables)), where and . Here, a mutation that produces genotype is beneficial in a population where has fixed, as a 6 at the last locus precedes the 1 at the first locus. However, once fixes, genotype will be favored, and so on. When we remove negative niche construction (, ), cooperators are again driven to extinction after an initial lift in abundance ([Figure 2C](#fig2)). Here we observe that because niche construction presents additional opportunities for hitchhiking, the Hankshaw effect extends the initial lift in cooperation. However, once a genotype with sequential allelic states fixes, cooperation…

## Selective Feedbacks Limit Defector Invasion

The adaptation resulting from selective feedbacks can limit invasion by defectors, which arise either through immigration from neighboring patches or through mutation from a cooperator ancestor. The challenge is particularly threatening, as they are equally adapted, yet do not incur the cost of cooperation. When homologous defectors (i.e., defectors with identical adaptive loci) are introduced as a single population in the center of an metapopulation of cooperators, they quickly spread ([Figure 3A](#fig3)). However, when resident cooperators can adapt and respond to defector invasion, the situation improves dramatically, allowing cooperation to evade defector invasion in 91 of 160 replicate simulations (57%; [Figure 3B](#fig3)). [Figure 4](#fig4) depicts one such instance where cooperators gained an adaptation that stopped and eliminated invading defectors. We further highlight this process in [Figure 3C](#fig3), where an adapted cooperator genotype can rapidly invade a population of defectors.

## Diversity Hampers the Evolution of Cooperation

TODO: defector can invade a diverse population of cooperators, while adaptation to a matching defector can’t spread to stop invasion.

# 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.

When niche construction occurs, cooperation can indeed persist ([Figure 2A](#fig2)). In our model, niche construction introduces additional selective effects that could influence the evolutionary process, leading to a more pronounced Hankshaw effect. However, simply raising the selective benefits provided by adaptations does not prolong cooperation ([Figure 2B](#fig2)), and indicates that niche construction plays an important role.

We find that cooperator success is due to niche construction. Further, we find that it is specifically negative niche construction that maintains cooperation ([Figure 2C](#fig2)). Without adaptive opportunities, adaptation eventually slows. Once this occurs, cooperators face the threat of invasion by defectors that arise de novo through mutation. Since these defectors are equally adapted but do not bear the cost of cooperation, they are favored by selection, and quickly drive cooperators to extinction. By reducing fitness, negative niche construction creates adaptive opportunities. These opportunities can allow cooperators to resist invasion by defectors, even when defectors are equally adapted ([Figure 3B](#fig3)). Here we observe another facet of the Hankshaw effect: because populations of cooperators are larger, they are better able to respond to the adaptive opportunities that result from negative niche construction.

TODO: diversity results TODO: references about diversity

In our model, cooperation and niche construction are orthogonal, which allows us to focus on hitchhiking. However, the form of cooperation used in this model could itself be seen as a niche constructing behavior. Explicitly modeling this cooperative behavior, which is akin to the production of public goods, would likely yield additional insights into the relationship between cooperation and niche construction. For example, previous work has shown that niche construction can favor deleterious alleles (Laland *et al.*, 1996, 1999). Cooperation, especially in competition against equally-adapted defectors, can be considered deleterious, so introducing selective feedbacks from cooperation could further bolster cooperation. 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. Arguably, this can be viewed as another instance of hitchhiking: the maladaptive form of cooperation is maintained by association with the adaptive form. However, negative niche construction then reverses these roles and perpetuates the cycle.

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 scavage 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 the production of these public goods, relatively few have examined how the resulting selective feedbacks influence evolution as public goods modify the environment. In these instances, environmental changes are likely to occur on different timescales than reproduction. These differences can have profound effects. 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. Lehmann (2007) demonstrated that cooperative, niche constructing behaviors can be favored when they affect selection for future generations. When this occurs, conflict among contemporary kin is reduced. The evolutionary inertia that this creates, however, may ultimately work against cooperators. When public goods accumulate in the environment, cooperators must decrease production to remain competitive (Kümmerli and Brown, 2010; Dumas and Kümmerli, 2012). This favors 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).

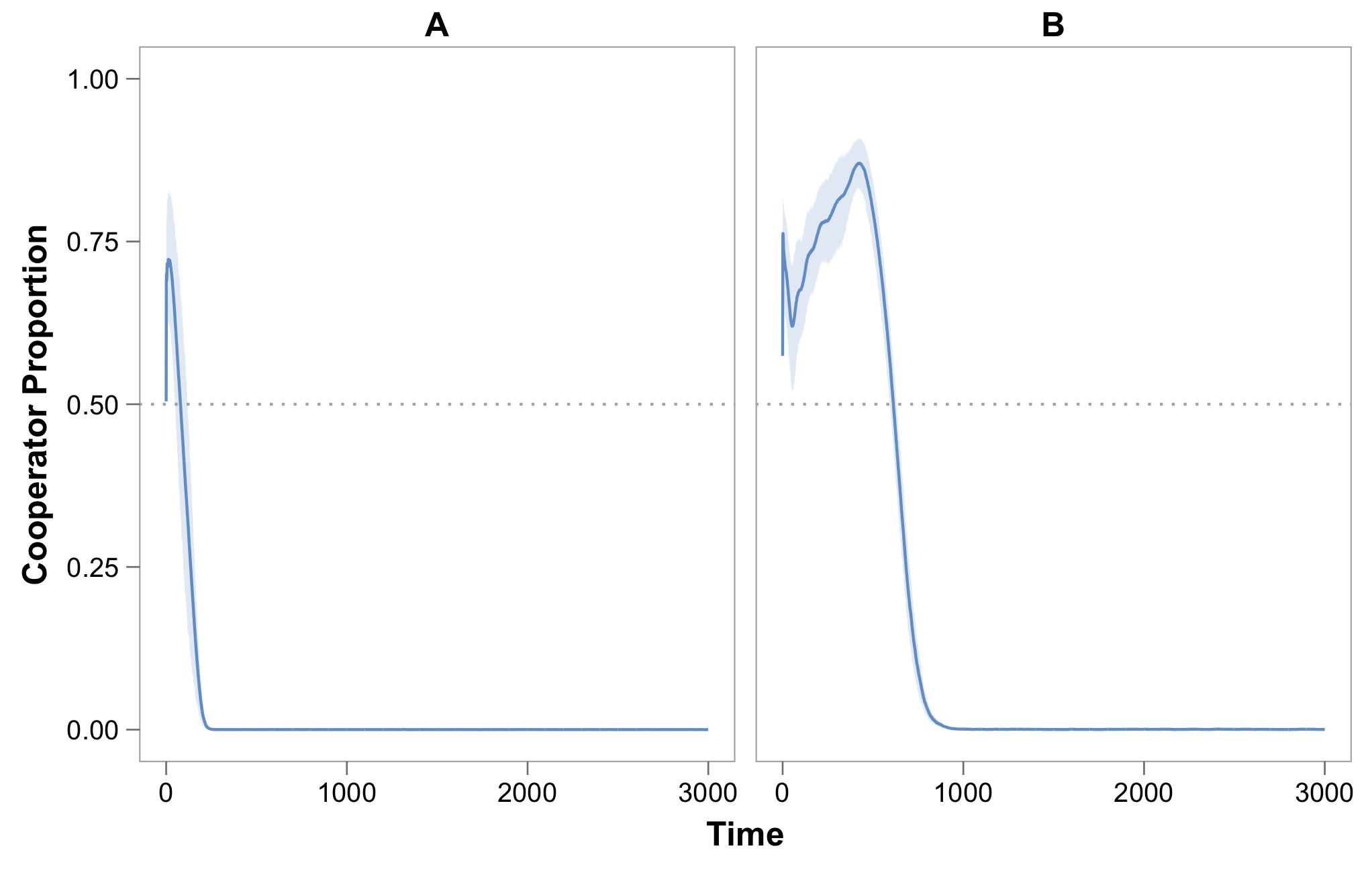
In many instances of cooperation, the environment is itself a biological entity, which can produce additional evolutionary feedbacks. As the host population changes, so too does selection on their symbiont populations. Here, evolutionary outcomes depend greatly on the degree of shared interest between the host and symbiont. For example, the cooperative production of virulence factors by the human pathogen *P. aeruginosa* in lung infections is harmful to hosts 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

We thank Anuraag Pakanati for assistance with simulations. This material is based upon work supported by the National Science Foundation Postdoctoral Research Fellowship in Biology under Grant No. DBI-1309318 (to BDC) and under Cooperative Agreement No. DBI-0939454 (BEACON STC). Computational resources were provided by an award from Google (to BDC and BK).

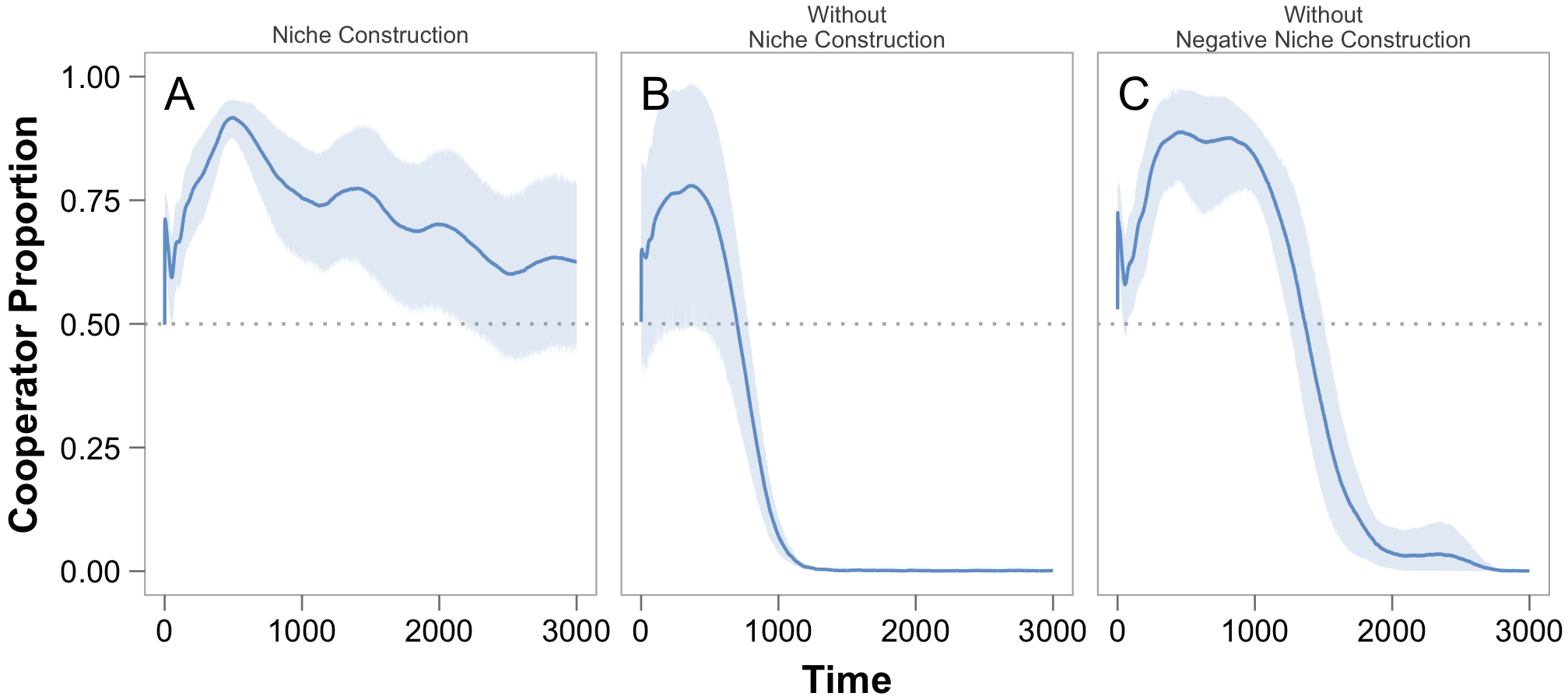
# Figures

## 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 replicate populations, and shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter values are listed in [Table 1](#tables). (**A**) Without any opportunity to adapt (, 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 replicate populations, and shaded areas indicate 95% confidence intervals. (**A**) Niche construction enables cooperation to be maintained indefinitely. In the majority of populations (13/18), cooperation remained the dominant strategy. (**B**) When niche construction is removed and the fitness benefit of adaptation is increased as compensation (, ), adapted defectors arise and drive cooperators to extinction. (**C**) Without negative niche construction, cooperation is not maintained (). Here again, cooperators are at a selective disadvantage against equally-adapted defectors that arise via mutation.

## Figure 3



**Niche Construction and Invasion.** Curves trace the proportion of cooperators present in the population for the duration of 160 replicate simulations (). These experiments examine whether a rare cooperator or defector strategy can invade when initiated at a single population in the center of the metapopulation lattice (). Unless otherwise noted, mutations () are disabled in these ecological simulations to focus on the dynamics of invasion. This limitation is removed in the results shown in Figure SX. (**A**) When cooperators and defectors are matched (i.e., genotypes [1,2,3,4,5]) and adaptation cannot occur, rare defectors quickly invade and 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 can allow cooperators to resist invasion by initially-matching defectors. Here, cooperation persisted in the majority of populations (, the base mutation rate). (**C**) Here we demonstrate that these adaptations can enable an adapted cooperator (genotype [1,2,3,4,*6*]) to displace a population of defectors when defectors cannot arise or adapt via mutation.

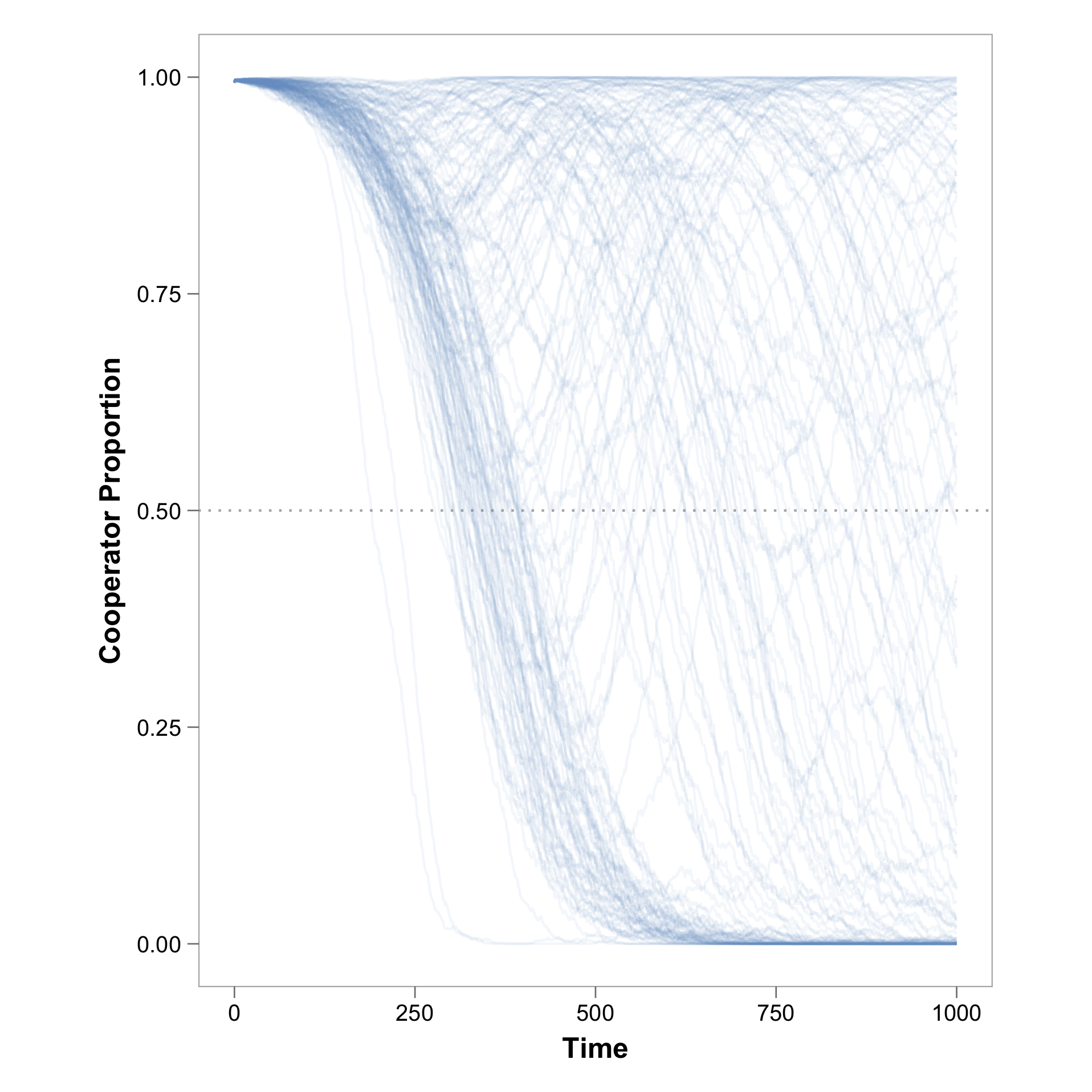
## Figure 4

TODO: snapshots of cooperators adapting to thwart defector invasion

## Figure 5

TODO: A: defector invading diverse C population, B: Adapted cooperators cannot spread to resist defector invasion.

## Supplemental Figure 1



**Defector Invasion with Mutations.** With mutations occurring both at the adaptive loci and the cooperation locus (), cooperation remains the dominant strategy in 58 replicate simulations. Curves trace the proportion of cooperators present in the population for the duration of 160 replicate simulations ()

# 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 | 3000 |

# 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.

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.

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.

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.

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.

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.

Odling-Smee, F.J., Laland, K.N. and Feldman, M.W. 2003. *Niche construction: The neglected process in evolution*. Princeton University Press.

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.