

1 Negative Niche Construction Favors the  
2 Evolution of Cooperation

3  
4 **Abstract**

5 TODO

6 **Introduction**

7 Cooperative behaviors are common across all branches of the tree of life. In-  
8 sects divide labor within their colonies, plants and soil bacteria exchange es-  
9 sential nutrients, birds care for others' young, and the trillions of cells in the  
10 human body coordinate to provide vital functions. Each instance of cooper-  
11 ation presents an evolutionary challenge: How can individuals that sacrifice  
12 their own well-being to help others avoid subversion by those that do not? Over  
13 time, we would expect these *defectors* to rise in abundance at the expense of  
14 others, eventually driving cooperators—and perhaps the entire population—to  
15 extinction.

16 Several factors can prevent this *tragedy of the commons* (Hamilton, 1964;  
 17 Nowak, 2006; West *et al.*, 2007b). One such factor involves non-random so-  
 18 cial interaction, in which cooperators benefit more from the cooperative act  
 19 than defectors. This can occur when cooperators are clustered together in  
 20 spatially-structured populations (Fletcher and Doebeli, 2009; Nadell *et al.*,  
 21 2010; Kuzdzal-Fick *et al.*, 2011) or when cooperators use communication  
 22 (Brown and Johnstone, 2001; Darch *et al.*, 2012) or other cues (Sinervo *et*  
 23 *al.*, 2006; Gardner and West, 2010; Veelders *et al.*, 2010) to cooperate condi-  
 24 tionally with kin. Cooperation can also be bolstered by pleiotropic connections  
 25 to personal benefits (Foster *et al.*, 2004; Dandekar *et al.*, 2012) or through as-  
 26 sociation with alleles encoding self-benefitting traits (Asfahl *et al.*, 2015). In  
 27 the latter case, the alleles may provide private benefits that are completely  
 28 independent from the public benefits of cooperation. In an asexual popula-  
 29 tion of cooperators and defectors, this sets the stage for an “adaptive race” in  
 30 which both types vie for the first highly beneficial adaptation (Waite and Shou,  
 31 2012; Morgan *et al.*, 2012). The tragedy of the commons can be deferred if a  
 32 cooperator, by chance, wins the adaptive race.

33 Hammarlund et al. (2015) recently demonstrated that in spatially-structured  
 34 populations, the “Hankshaw effect” can give cooperators a substantial leg up  
 35 on defectors in an adaptive race. When cooperation increases local population  
 36 density, the likelihood of acquiring beneficial mutations is also increased. The  
 37 cooperative trait can rise in abundance by hitchhiking along with these adap-  
 38 tations. Nevertheless, this advantage is fleeting. As soon as the opportunities  
 39 for adaptation are exhausted, cooperators are once again at a selective disad-

40 vantage against equally-adapted defectors that arise via mutation. However,  
41 Hammarlund et al. (2015) demonstrated that cooperation can be maintained  
42 indefinitely when frequent environmental changes produce a steady stream of  
43 new adaptive opportunities. Although organisms typically find themselves in  
44 dynamic environments, the nature and frequency of these changes might not  
45 ensure long-term cooperator survival.

46 Importantly, however, organisms do not simply play passive roles in environ-  
47 mental change and in evolution. Through their activities, their interactions  
48 with others, and even their deaths, organisms constantly modify their envi-  
49 ronment. These changes can produce evolutionary feedback loops in which  
50 environmental change alters selection, which, in turn, alters the distribution  
51 of phenotypes and their corresponding influence on the environment (Odling-  
52 Smee *et al.*, 2003). Because of these feedback loops, populations may find  
53 themselves continually chasing beneficial mutations as their adaptive land-  
54 scape perpetually shifts beneath them.

55 Here, we explore whether the selective feedbacks that result from niche con-  
56 struction can prolong cooperation. We build upon the model presented by  
57 Hammarlund et al. (2015) to allow populations to modify their local environ-  
58 ments in ways that affect fitness. We first use this model to address whether  
59 niche construction can extend the Hankshaw effect, allowing cooperation to  
60 keep hitchhiking as populations continually adapt. We then focus on how  
61 niche construction influences outcomes when isolated cooperator populations  
62 encounter populations of defectors, either through migration or through mu-  
63 tations that inevitably produce defectors that share the same adaptations.

64 Finally, niche construction has frequently been shown to increase diversity  
65 (???). We explore whether this diversity helps or hinders the evolution of  
66 cooperation.

## 67 **Methods**

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

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

## 79 **Model Description**

### 80 **Individual Genotypes and Adaptation**

81 Each individual in a population has a genotype, which is an ordered list of  $L+1$   
82 integers, or *loci* (see [Table 1](#) for model parameters and their values). Different

83 values at these loci represent different alleles. A binary allele at locus  $L + 1$   
 84 determines whether that individual is a cooperator (1), which carries fitness  
 85 cost  $c$ , or a defector (0). Cooperation is independent from adaptation to the  
 86 environment. The first  $L$  loci are *adaptive loci*, and are each occupied by 0 or  
 87 an integer from the set  $\{1, 2, \dots, A\}$ . Allele 0 represents a lack of adaptation,  
 88 while a non-zero allele represents one of the  $A$  possible adaptations at that  
 89 locus. Adaptations confer a fitness benefit  $\delta$ , regardless of which non-zero allele  
 90 is present. We choose  $\delta > c$ , which allows a minimally adapted cooperator to  
 91 recoup the cost of cooperation and gain a fitness advantage. The benefits that  
 92 these adaptations engender are purely endogenous, and are not affected by the  
 93 other individuals or the state of the environment.

## 94 **Niche Construction and Selective Feedbacks**

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

99 We use a form of density dependent selection to favors individuals that better  
 100 match their niche. Specifically, the selective value of adaptive allele  $a$  at locus  
 101  $l$  increases with the number of individuals in the population that have allele  
 102  $a + 1$  at locus  $l + 1$ . As a consequence, genotypes with sequentially increasing  
 103 allelic states will tend to evolve. We treat both adaptive loci and allelic states  
 104 as “circular”: the selective value of an allele at locus  $L$  is affected by the allelic

105 composition of the population at locus 1. Similarly, the selective value of allele  
 106  $A$  at any locus increases with the number of individuals carrying allele 1 at  
 107 the next locus. This circularity is represented by the function  $\beta(x, X)$ , which  
 108 gives the integer that follows an arbitrary value  $x$  in the set  $\{1, 2, \dots, X\}$ :

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

109 Here,  $\text{mod}_X(x)$  is the integer remainder when dividing  $x$  by  $X$ . Thus, the  
 110 selective value of adaptive allele  $a$  at locus  $l$  increases with the number of  
 111 individuals that have allele  $\beta(a, A)$  at locus  $\beta(l, L)$ . The slope of this increase  
 112 is  $\epsilon$ , which specifies the intensity of niche construction.

113 Consider a genotype  $g$  with the allelic state at locus  $l$  given by  $a_{g,l}$ ; the fitness  
 114 of an individual with this genotype is defined as:

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

115 where  $z$  is a baseline fitness and  $I(a)$  indicates whether a given adaptive allele  
 116 is non-zero:

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

117 Thus, an individual's fitness is determined both endogenously by adaptation  
 118 ( $\delta$ ) and exogenously by its niche ( $\epsilon$ ).

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

## 122 **Population Growth and the Benefit of Cooperation**

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

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

128 During growth, individuals compete for inclusion in the resulting population.  
 129 Each individual's probability of success is determined by its fitness. The com-  
 130 position of a population with size  $P$  and cooperator proportion  $p$  after growth  
 131 is multinomial with parameters and  $S(p)$  and  $\{\pi_1, \pi_2, \dots, \pi_P\}$ , where:

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

132 Here,  $W_{\gamma(i)}$  is the fitness of an individual  $i$  with genotype  $\gamma(i)$  (see Equation 2).  
 133 The value  $\pi_i$  represents an individual's reproductive fitness relative to others  
 134 in the population.

## 135 **Mutation**

136 For simplicity, we apply mutations after population growth. Mutations occur  
137 independently at each locus and cause an allelic state change. At each adaptive  
138 locus, mutations occur at rate  $\mu_a$ . These mutations replace the existing allele  
139 with a random selection from the set  $\{0\} \cup \{1, 2, \dots, A\}$ . Note that this allows  
140 for the possibility of an allele replacing itself, thus slightly reducing the effective  
141 mutation rate. At the binary cooperation locus, mutations occur at rate  $\mu_c$ .  
142 These mutations flip the allelic state, causing cooperators to become defectors  
143 and vice versa.

## 144 **Migration**

145 Our simulated environment consists of  $N^2$  patches arranged as an  $N \times N$   
146 lattice, where each patch can support a population. After mutation, individ-  
147 uals emigrate to an adjacent patch at rate  $m$ . During each migration event,  
148 a single destination patch is randomly chosen with uniform probability from  
149 each source patch's Moore neighborhood, which is composed of the nearest  
150 8 patches on the lattice. Because the metapopulation lattice has boundaries,  
151 patches located on an edge have smaller neighborhoods.

## 152 **Metapopulation Initialization and Simulation**

153 Metapopulations are initiated in a state that follows an environmental change,  
154 which leaves most patches empty. First, populations are seeded at all patches  
155 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  $\mu_t$ , which represents the likelihood that tolerance arises via mutation. Because individuals have not yet adapted to this new environment, the allelic state of each individual's genotype is 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, populations are thinned to allow for growth in the next cycle. 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, 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 fit-

ness 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](#).

## **Cooperation Persists with Niche Construction**

Without any opportunity for adaptation ( $L = 0$ ), 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 opportunities for adaptation ( $L = 5$ ) but no niche construction ( $\epsilon = 0$ ), cooperators are maintained transiently ([Figure 1B](#)). 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 repli-

198 cate populations (Figure 2A).

## 199 **Fitness Increases Alone do not Support Persisting Coop-** 200 **eration**

201 In the model, both adaptation and niche construction contribute to an individ-  
202 ual's fitness. To determine whether cooperation is maintained solely because  
203 to the larger selective values, we performed simulations in which the selective  
204 contributions of niche construction were removed ( $\epsilon = 0$ ), and we instead in-  
205 creased the fitness benefits conferred by adaptation ( $\delta = 0.6$ ). In doing so, we  
206 conservatively represent the selective effects of niche construction, as fitness  
207 benefits of this magnitude would only be given for sequential allelic states that  
208 are fixed in full populations. We find that simply increasing selective values  
209 does not allow cooperators to persist (Figure 2B).

## 210 **Negative Niche Construction is Critical to Cooperator** 211 **Persistence**

212 Negative niche construction can occur in our model due to the selection for  
213 sequentially-increasing allelic states and the circular arrangement of these al-  
214 leles. When this occurs, adaptations at one locus reduce the selective effects  
215 at another locus, and thus negatively affect fitness. This occurs when when  
216 the genome length ( $L$ ) is not evenly divided by the number of adaptive alleles  
217 ( $A$ ), which makes it impossible to evolve sequentially increasing allelic states.

218 When negative niche construction is removed ( $L = 5$ ,  $A = 5$ ), cooperators are  
219 again driven to extinction after an initial lift in abundance (Figure 2C).

## 220 **Selective Feedbacks Limit Defector Invasion**

221 The adaptation resulting from selective feedbacks can limit invasion by de-  
222 fectors, which arise either through immigration from neighboring patches or  
223 through mutation from a cooperator ancestor. The latter pose a particularly  
224 challenging threat, as they are equally adapted, yet do not incur the cost of  
225 cooperation. When homologous defectors (i.e., defectors with identical stress  
226 loci) are introduced as a single population in the center of an  $11 \times 11$  metapop-  
227 ulation of cooperators, they quickly spread (Figure 3A). However, when res-  
228 ident cooperators can adapt and respond to defector invasion, the situation  
229 improves dramatically, allowing cooperation to evade defector invasion in 91  
230 of 160 replicate populations (Figure 3B). Figure 4 depicts one such instance  
231 where cooperators gained an adaptation that stopped and eliminated invading  
232 defectors. We further highlight this process in Figure 3C, where an adapted  
233 cooperator genotype can rapidly invade a population of defectors.

## 234 **Diversity Hampers the Evolution of Cooperation**

235 TODO: defector can invade a diverse population of cooperators, while adapta-  
236 tion 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). 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), and indicates that niche construction plays an important role.

We find that cooperator success is due to negative niche construction. 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). Here we observe another facet of the Hawkshaw 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 envi-

283 ronment more hospitable (West *et al.*, 2007a). For example, bacteria produce  
 284 a host of extracellular products that scavenge soluble iron (Griffin *et al.*, 2004),  
 285 digest large proteins (Diggle *et al.*, 2007; Darch *et al.*, 2012), and reduce the  
 286 risk of predation (Cosson *et al.*, 2002). While many studies have explored  
 287 how the environment affects the evolution of cooperative behaviors such as  
 288 the production of these public goods, relatively few have examined how the  
 289 resulting selective feedbacks influence evolution as public goods modify the  
 290 environment. In these instances, the timescale at which the environment is  
 291 likely to be decoupled from the timescale at which reproduction occurs. These  
 292 differences can have profound effects. For example, a multitude of factors in-  
 293 cluding protein durability (Brown and Taddei, 2007; Kümmerli and Brown,  
 294 2010), diffusion (Allison, 2005; Driscoll and Pepper, 2010), and resource avail-  
 295 ability (Zhang and Rainey, 2013; Ghoul *et al.*, 2014) influence both the rate  
 296 and the degree to which public goods alter the environment. Lehmann (2007)  
 297 demonstrated that cooperative, niche constructing behaviors can be favored  
 298 when they affect selection for future generations. When this occurs, conflict  
 299 among contemporary kin is reduced. The evolutionary inertia that this cre-  
 300 ates, however, may ultimately work against cooperators. When public good  
 301 accumulates in the environment, cooperators must decrease production to re-  
 302 main competitive (Kümmerli and Brown, 2010; Dumas and Kümmerli, 2012).  
 303 This favors cooperation that occurs facultatively, perhaps by sensing the abi-  
 304 otic (Bernier *et al.*, 2011; Koestler and Waters, 2014) or biotic environment  
 305 (Brown and Johnstone, 2001; Darch *et al.*, 2012).

306 In many instances of cooperation, the environment is itself a biological entity,

307 which can produce additional evolutionary feedbacks. As the host population  
308 changes, so too does selection on their symbiont populations. Here, evolution-  
309 ary outcomes depend greatly on the degree of shared interest between the host  
310 and symbiont. For example, the cooperative production of virulence factors by  
311 the human pathogen *P. aeruginosa* in lung infections is harmful to those with  
312 cystic fibrosis (Harrison, 2007). Conversely, cooperative light production by *A.*  
313 *fischeri* is vital for the survival of its host, the Hawaiian bobtail squid (Ruby,  
314 1996). It was recently argued that incorporating the effects of niche construc-  
315 tion is critical for improving our understanding of viral evolution (Hamblin *et*  
316 *al.*, 2014) and evolution in co-infecting parasites (Hafer and Milinski, 2015).  
317 Incorporating host dynamics, co-evolution, and the feedbacks that they pro-  
318 duce into models is likely to be equally important for gaining an understanding  
319 of how cooperative behaviors evolve in these host-symbiont settings.

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## 327 Figures

328 **Figure 1**

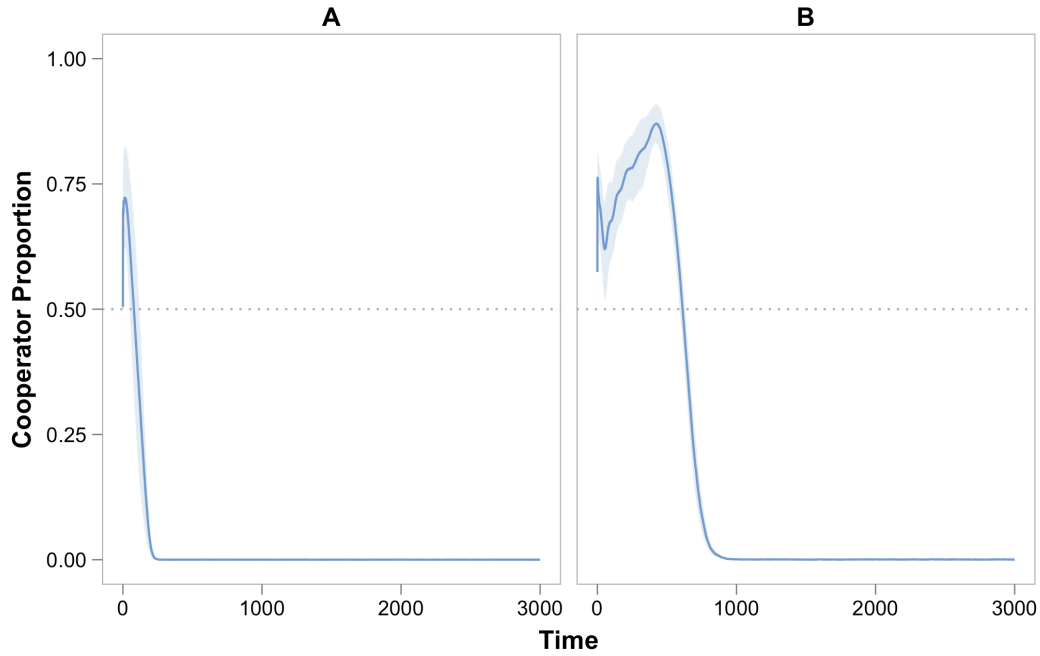
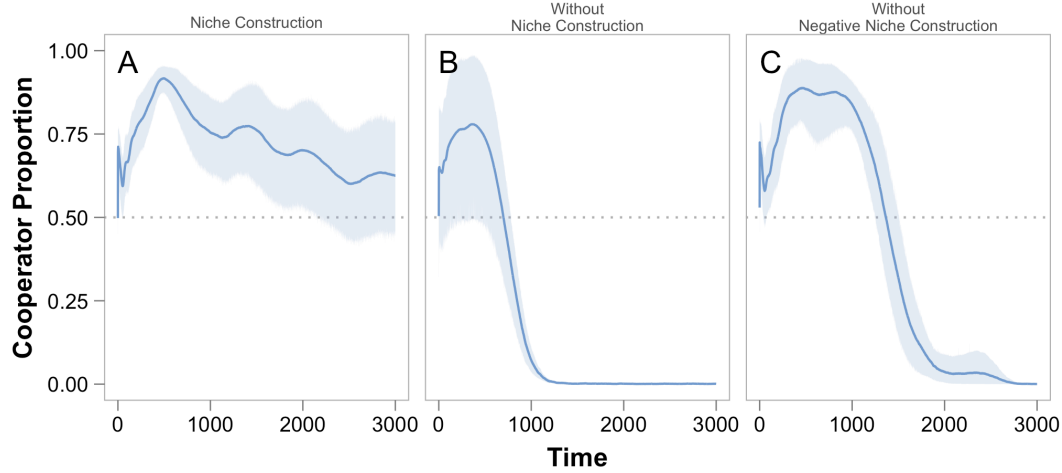


Figure 1: **Adaptation, Hitchhiking, and the Evolution of Cooperation.** The proportion of cooperators present in the population is shown for the duration of simulations. Curves show the average among replicate populations, and shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter values are listed in [Table 1](#). **(A)** Without any opportunity to adapt ( $L$ , 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 ( $\epsilon$ , the intensity of niche construction, is zero), cooperation hitchhikes along with adaptations, allowing cooperators to temporarily rise in abundance before eventually going extinct.

329 **Figure 2**



**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, cooperation remained as the dominant strategy. **(B)** When niche construction is removed and the fitness benefit of adaptation is increased as compensation ( $\epsilon = 0$ ,  $\delta = 0.6$ ), adapted defectors arise and drive cooperators to extinction. **(C)** Without negative niche construction, cooperation is not maintained ( $A = 5$ ). Here again, cooperators are at a selective disadvantage against equally-adapted defectors.

330 **Figure 3**

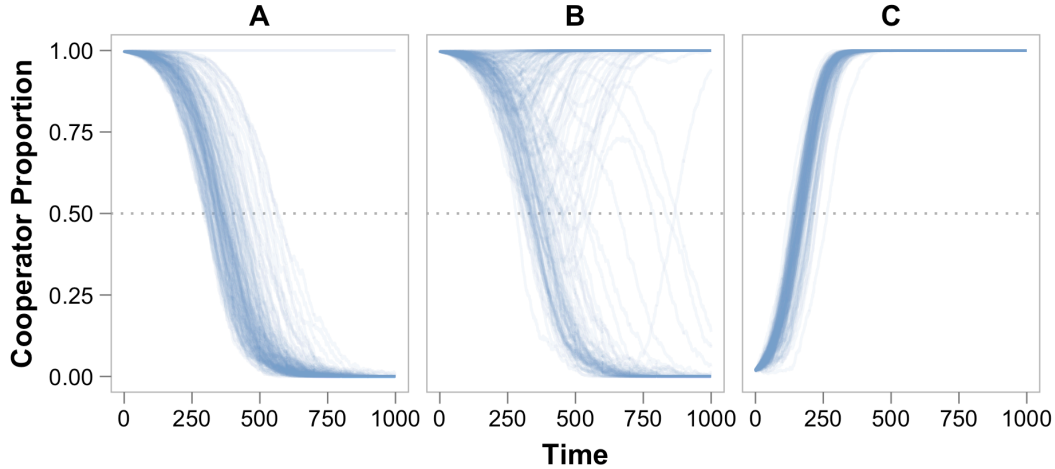


Figure 3: **Niche Construction and Invasion.** Curves trace the proportion of cooperators present in the population for the duration of 160 replicate simulations. These experiments examine whether a cooperator or defector strategy can invade when initiated at a single population in the center of the metapopulation lattice ( $N^2 = 121$ ). Unless otherwise noted, we disable mutations ( $\mu_a = 0, \mu_c = 0$ ) 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 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 can allow cooperators to resist invasion by initially-matching defectors. Here, cooperation persisted in the majority of populations ( $\mu_a = 0.00005$ , 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 can not arise or adapt via mutation.

331 **Figure 4**

332 TODO: snapshots of cooperators adapting to thwart defector invasion

333 **Figure 5**

334 TODO: A: defector invading diverse C popuation, B: Adapted cooperators can  
335 not spread to resist defector invasion.

Table 1: Model parameters and their value

Parameter	Description	Base Value
$L$	Number of adaptive loci	5
$c$	Fitness cost of cooperation	0.1
$A$	Number of alleles	6
$\delta$	Fitness benefit, nonzero alleles	0.3
$\epsilon$	Fitness benefit, sequential alleles	0.00015
$z$	Baseline fitness	1
$S_{min}$	Minimum population size	800
$S_{max}$	Maximum population size	2000
$\mu_a$	Mutation rate (adaptation)	$10^{-5}$
$\mu_c$	Mutation rate (cooperation)	$10^{-5}$
$N^2$	Number of metapopulation sites	625
$m$	Migration rate	0.05
$p_0$	Initial cooperator proportion	0.5
$\mu_t$	Mutation rate (tolerance to new environment)	$10^{-5}$
$d$	Population dilution factor	0.1
$T$	Number of simulation cycles	1000

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