

# 1 A Combination of Positive and Negative Niche 2 Construction Favors the Evolution of 3 Cooperation

4  
5 **Abstract**

6 TODO

## 7 **Introduction**

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

17 Several factors can prevent this *tragedy of the commons* (Hamilton, 1964;  
18 Hardin, 1968; Nowak, 2006; West *et al.*, 2007b). One important factor in-  
19 volves non-random social interaction, in which cooperators benefit more from  
20 the cooperative act than defectors. This can occur when cooperators are clus-  
21 tered together in spatially-structured populations (Fletcher and Doebeli, 2009;  
22 Nadell *et al.*, 2010; Kuzdzal-Fick *et al.*, 2011) or when cooperators use com-  
23 munication (Brown and Johnstone, 2001; Darch *et al.*, 2012) or other cues  
24 (Sinervo *et al.*, 2006; Gardner and West, 2010; Veelders *et al.*, 2010) to coop-  
25 erate conditionally with kin. Cooperation can also be bolstered by pleiotropic  
26 connections to personal benefits (Foster *et al.*, 2004; Dandekar *et al.*, 2012)  
27 or association with alleles encoding self-benefitting traits (Asfahl *et al.*, 2015).  
28 In the latter case, the alleles may provide private benefits that are completely  
29 independent from the public benefits of cooperation. In a mixed population of  
30 cooperators and defectors, this sets the stage for an “adaptive race” in which  
31 both types vie for the first highly beneficial adaptation (Waite and Shou, 2012;  
32 Morgan *et al.*, 2012). The tragedy of the commons can be deferred if a coop-  
33 erator, by chance, wins the adaptive race.

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

41 lective disadvantage against adapted defectors. However, Hammarlund et al.  
42 (2015) demonstrated that cooperation can be maintained indefinitely when  
43 frequent environmental changes produce a steady stream of adaptive opportu-  
44 nities. Although organisms typically find themselves in dynamic environments,  
45 the nature and frequency of these changes might not ensure long-term cooper-  
46 ator survival.

47 Importantly, this environmental influence is not a completely passive process.  
48 Through their activities, their interactions with others, and even through their  
49 deaths, organisms constantly modify their environment. These changes can  
50 produce evolutionary feedback loops in which environmental change alters  
51 selection, which, in turn, alters the distribution of phenotypes and their cor-  
52 responding influence on the environment (Odling-Smee *et al.*, 2003). Because  
53 of these feedback loops, populations may find themselves continually chasing  
54 beneficial mutations as their adaptive landscape shifts beneath them.

55 Here, we explore whether the selective feedbacks that arise during niche con-  
56 struction can maintain cooperation indefinitely. We expand the model pre-  
57 sented by Hammarlund et al. (2015) to allow populations to modify their  
58 local environments in ways that affect their fitness. We first use this model to  
59 address whether niche construction can prolong the Hangar effect, allowing co-  
60 operation to continue hitchhiking as populations continually adapt. We then  
61 focus on how niche construction influences outcomes when cooperator popula-  
62 tions encounter populations of defectors, either through migration or through  
63 mutations that inevitably produce defectors that share the same adaptations.  
64 Finally, the niche construction process can increase diversity (???). We ex-

65 plore whether this diversity helps or hinders cooperation.

## 66 **Methods**

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

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

## 78 **Model Description**

### 79 **Individual Genotypes and Adaptation**

80 Each individual in a population has a genotype, which is an ordered list of  $L+1$   
81 integers, or *loci* (see [Table 1](#) for model parameters and their values). Different  
82 values at these loci represent different alleles. A binary allele at locus  $L + 1$   
83 determines whether that individual is a defector (0) or a cooperator (1), which

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

### 93 **Niche Construction and Selective Feedbacks**

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

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

106 the next locus. This circularity is represented by the function  $\beta(x, X)$ , which  
 107 gives the integer that follows an arbitrary value  $x$  in the set  $\{1, 2, \dots, X\}$ :

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

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

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

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

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

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

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

118 Because mutations occur randomly (see below), each population will evolve  
 119 different consecutive sequences. These different sequences represent the unique

120 niches constructed by populations.

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

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

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

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

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

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

## 134 **Mutation**

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

## 143 **Migration**

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

## 151 **Metapopulation Initialization and Simulation**

152 Metapopulations are initiated in a state that follows an environmental change,  
153 which leaves most patches empty. First, populations are seeded at all patches  
154 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 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 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

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

175 the value of alleles at adaptive loci, cooperation can have indirect effects on the  
 176 process of adaptation. Specifically, because cooperation increases population  
 177 density, isolated cooperators experience more mutational opportunities to gain  
 178 adaptations. Cooperation can hitchhike along with these adaptations, which  
 179 compensate for the cost of cooperation. Additionally, populations alter their  
 180 environment. Here, we explore how niche construction can favor the evolution  
 181 of cooperation. Our simulation environment is defined by the parameter val-  
 182 ues listed in [Table 1](#). Unless otherwise noted, 10 replicate simulations were  
 183 performed for each experiment. We quantify cooperator success using the area  
 184 under the cooperator proportion curve. This measure of cooperator presence  
 185 increases as cooperators rise in abundance or remain in the population longer.

## 186 **Niche Construction Maintains Cooperation**

187 Without any opportunity for adaptation ( $L = 0$ ), cooperators are swiftly elim-  
 188 inated in competition with defectors (Figure 1A). Despite an initial lift due  
 189 to increased productivity, the cost of cooperation becomes disadvantageous as  
 190 migration mixes the initially isolated populations. When there are opportun-  
 191 ties for adaptation ( $L = 5$ ) but no niche construction ( $\epsilon = 0$ ), cooperators are  
 192 maintained transiently (Figure 1B). Here, the additional mutational oppor-  
 193 tunities provided by their larger sizes allows cooperator populations to more  
 194 quickly adapt to their environment. As previously described by Hammarlund  
 195 et al. (2015), however, cooperation is subsequently lost as *adapted* defector  
 196 populations arise via mutation. When niche construction is incorporated,

197 cooperation persists (Figure 1C).

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

200 In our model, niche construction introduces additional selective benefits. To  
201 determine how these selective effects influence evolutionary outcomes, we per-  
202 formed simulations in which the selective effects of niche construction were  
203 removed ( $\epsilon = 0$ ), and we instead increased the fitness benefits conferred by  
204 adaptation ( $\delta = 0.6$ ). Here, we are conservative by lifting the selective value of  
205 exogenous adaptation by the maximum value possible from niche construction.

206 We find that higher selective values do not provide a significant increase in  
207 cooperator presence (Figure 2B). As shown in Figure 3, cooperators gain adap-  
208 tations more quickly than defectors, which provides a fitness advantage. How-  
209 ever, the cost of cooperation puts defectors at an advantage once these popu-  
210 lations become fully adapted.

## 211 **Negative Niche Construction is Critical to Cooperator** 212 **Persistence**

213 Negative niche construction occurs in our model due to selection for  
214 sequentially-increasing allelic states and the circular arrangement of these  
215 alleles. When the genome length ( $L$ ) is not evenly divided by the number  
216 of adaptive alleles ( $A$ ), then it is not possible for the population to be fixed

217 for a genotype that is perfectly adapted to the constructed environment.  
 218 Technically (in terms of the model) this is because the equality:

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

219 cannot simultaneously hold for all  $l$ .

220 For example, consider genotype  $(1, 2)$  when  $L = 2$  and  $A = 3$ . Here, allelic  
 221 state 2 at locus 2 will be be beneficial, because it follows allelic state 1 at  
 222 locus 1. However, due to the circular effects, allelic state 1 at locus 1 will be  
 223 deleterious relative to allelic state 3 at locus 1. Yet, fixation for genotype  $(3, 2)$   
 224 does not solve the problem, because a mutant  $(3, 1)$  is fitter, and so on.

225 We first focus on the effects of positive niche construction by removing the  
 226 allelic conflict that leads to negative niche construction ( $L = 5$ ,  $A = 5$ ). In  
 227 the absence of this conflict, cooperator presence is significantly increased (Fig-  
 228 ure 2C). Within these environments, we find that positive niche construction  
 229 prolongs the fitness advantage that cooperators have over defectors (Figure  
 230 3C).

## 231 **Positive niche construction is important to cooperator** 232 **persistence**

233 To determine how negative niche construction influences the evolution of co-  
 234 operation, we maximize the allelic conflict ( $L = 1$ ,  $A = 6$ ). Here, selection for  
 235 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 ( $S_{max}$ , see Equation 4). Figure 6A shows the result of these simulations. (TODO description of results)

To address how migration affects the evolutionary process in this system, we vary the rate at which migration occurs ( $m$ ). As seen in Figure 6B, cooperation decreases as migration rate increases. This is likely because migration defines the spatial structuring in this system. As migration increases, the population becomes more like a well-mixed system, where defectors are better able to exploit the benefits of cooperation (Griffin *et al.*, 2004; Kümmerli *et al.*, 2009).

# Discussion

255 Despite their negative effects, deleterious traits can rise in abundance due to  
256 genetic linkage with other traits that are strongly favored by selection (May-  
257 nard Smith and Haigh, 1974). In a process termed the “Hankshaw effect”,  
258 Hammarlund et al. (2015) recently demonstrated that cooperative behaviors  
259 can prolong their existence by actively increasing their likelihood of hitchhik-  
260 ing with a beneficial trait. While this process does favor cooperation in the  
261 short term, it eventually reaches a dead end. When the opportunities for  
262 adaptation are exhausted, and cooperators can no longer hitchhike, they face  
263 extinction. In this work, we have considered whether niche construction can  
264 maintain cooperation indefinitely.

265 We demonstrate that when niche construction occurs, cooperation can indeed  
266 persist (Figure 1C). But what aspects of niche construction produce this re-  
267 sult? In our model, niche construction introduces additional selective effects  
268 that could influence the evolutionary process. However, simply raising the  
269 selective benefits provided by adaptations does not significantly increase co-  
270 operator presence (Figure 2B), and indicates that niche construction plays an  
271 important role. Although cooperators benefit greatly from positive niche con-  
272 struction, it does not fully explain our results (Figure 2C). Indeed, despite an  
273 initial increase in abundance, cooperators are eventually driven to extinction  
274 when environmental change produces only positive fitness effects. As with the  
275 Hankshaw effect, adaption eventually slows, allowing defectors to outcompete  
276 cooperators (Figure 3C). While it does not benefit cooperation when alone  
277 (Figure 3E), negative niche construction acts to prevent this stasis. Combined,  
278 we find that both positive and negative niche construction are required to main

279 cooperation.

280 When successful, we observe that populations do not reach the maximum pos-  
281 sible fitness (Figure 3A). Although cooperation is the focus of this study, it  
282 can be seen as deleterious. Previous work has shown that niche construction  
283 can favor deleterious alleles (Laland *et al.*, 1996, 1999). Similarly here, coop-  
284 eration is maintained in the presence of niche construction, but lost otherwise.  
285 Van Dyken and Wade (2012) showed that when two cooperative behaviors  
286 co-evolve and niche construction feedbacks benefit the other type, niche con-  
287 struction can increasingly favor these traits, which were otherwise disfavored  
288 when alone.

289 By their very nature, public goods benefit populations by making their envi-  
290 ronment more hospitable (West *et al.*, 2007a). For example, bacteria produce  
291 a host of extracellular products that find soluble iron (Griffin *et al.*, 2004),  
292 digest large proteins (Diggle *et al.*, 2007; Darch *et al.*, 2012), and reduce the  
293 risk of predation (Cosson *et al.*, 2002). While many studies have explored how  
294 the environment affects the evolution of cooperative behaviors such as these,  
295 relatively few have examined how those behaviors affect the environment and  
296 how the resulting feedbacks influence evolutionary trajectories.

297 In our model, the environmental state was implicitly modeled, and depended  
298 solely on the current state of the population. In natural settings, however, the  
299 timescales at which environments are modified and reproduction are likely to  
300 be decoupled. For example, a multitude of factors including protein durabil-  
301 ity (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*



326 *al.*, 2014) and evolution in co-infecting parasites (Hafer and Milinski, 2015).  
327 Incorporating host dynamics, co-evolution, and the feedbacks that they pro-  
328 duce into models is likely to be equally important for gaining an understanding  
329 of how cooperative behaviors evolve in these host-symbiont settings.

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## 337 Figures

338 **Figure 1**

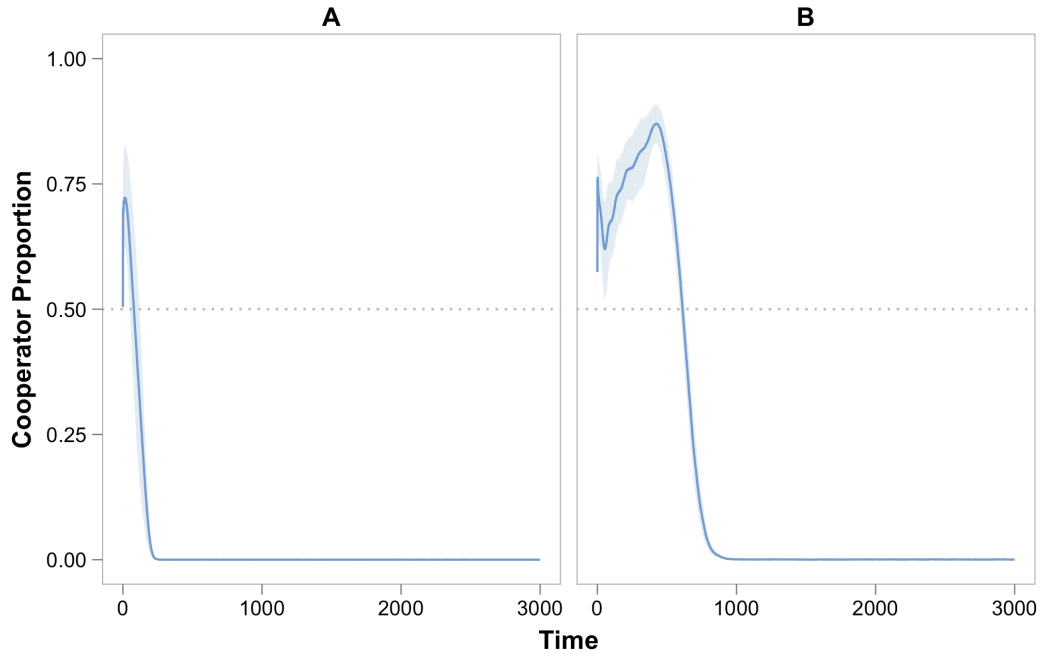


Figure 1: **Adaptation, Hitchhiking, and the Evolution of Cooperation.** The proportion of cooperators present in the population is shown for the duration of simulations. Curves show the average among replicate populations, and shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter 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.

339 **Figure 2**

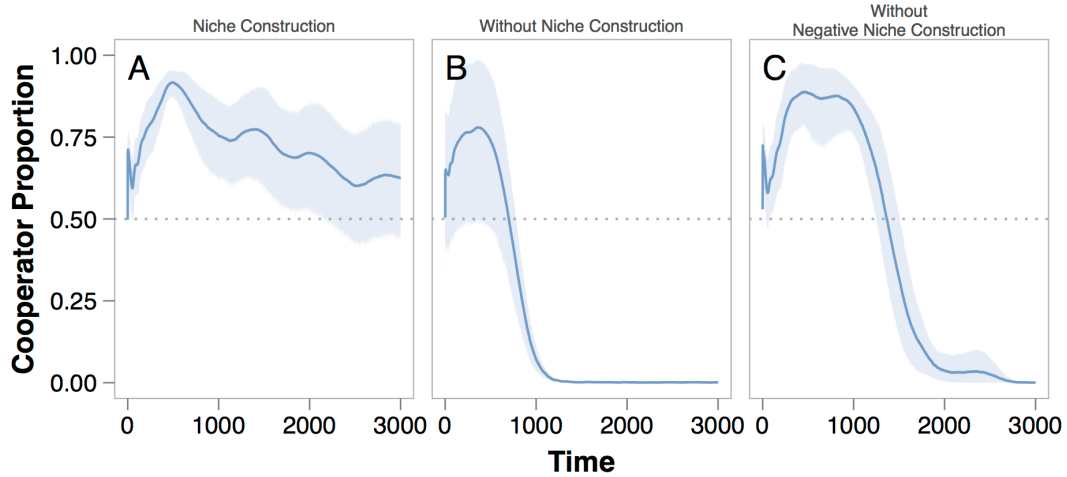


Figure 2: **Niche Construction and the Evolution of Cooperation.** The proportion of cooperators present in the population is shown for the duration of simulations. Curves show the average among replicate populations, and shaded areas indicate 95% confidence intervals. **(A)** Niche construction enables 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.

340 **Figure 3**

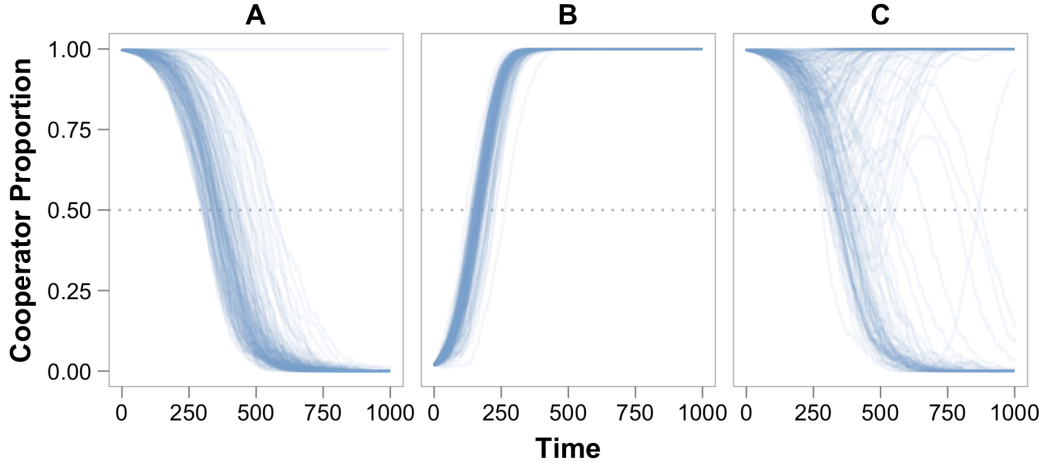


Figure 3: **Niche Construction and Invasion.** Curves trace the proportion of cooperators present in the population for the duration of 160 replicate simulations. These experiments examine whether a strategy initiated at a single population in the center of the metapopulation lattice ( $N^2 = 121$ ) can invade. Unless otherwise noted, we disable mutations ( $\mu_a = 0, \mu_c = 0$ ) to focus on how invasion depends on particular combinations of genotypes. **(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 and density dependence enable an adapted cooperator (genotype [1,2,3,4,6]) to invade a population of defectors. **(C)** These same adaptive opportunities can allow cooperators to resist invasion by initially-matching defectors, which arise via mutation and remain a constant threat. Here, cooperation persisted in 91 populations ( $\mu_a = 0.00005$ , the base mutation rate).

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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