

# Negative Niche Construction Favors the Evolution of Cooperation

**Abstract**

TODO

## Introduction

Cooperative behaviors are common across all branches of the tree of life. Insects divide labor within their colonies, plants and soil bacteria exchange essential nutrients, birds care for others' young, and the trillions of cells in the human body 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.

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 these cases, the alleles may provide private benefits that are completely inde-  
 28 pendent from the public benefits of cooperation. In an asexual population of  
 29 cooperators and defectors, this sets the stage for an “adaptive race” in which  
 30 both types vie for the first highly beneficial adaptation (Waite and Shou, 2012;  
 31 Morgan *et al.*, 2012). The tragedy of the commons can be deferred if a coop-  
 32 erator, 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. This advantage is reminiscent of Sissy Han-  
 36 kshaw, a fictional character in Tom Robbins’ *Even Cowgirls Get the Blues*,  
 37 whose oversized thumbs—which were otherwise an impairment—made her a  
 38 prolific hitchhiker. Similarly, cooperation is costly, but it increases local pop-  
 39 ulation density. As a result, cooperators are more likely to acquire beneficial

40 mutations. By hitchhiking along with these adaptations, cooperation can then  
41 rise in abundance. Nevertheless, this advantage is fleeting. As soon as the  
42 opportunities for adaptation are exhausted, cooperators are once again at a  
43 selective disadvantage against equally-adapted defectors that arise via muta-  
44 tion. However, Hammarlund et al. (2015) demonstrated that cooperation can  
45 be maintained indefinitely when frequent environmental changes produce a  
46 steady stream of new adaptive opportunities. Although organisms typically  
47 find themselves in dynamic environments, the nature and frequency of these  
48 changes might not ensure long-term cooperator survival.

49 Importantly, however, organisms do more than simply experience changing  
50 environments passively. Through their activities, their interactions with oth-  
51 ers, and even their deaths, organisms constantly modify their environment.  
52 These changes can produce evolutionary feedback loops in which environmen-  
53 tal change alters selection, which, in turn, alters the distribution of types and  
54 their corresponding influence on the environment (Odling-Smee *et al.*, 2003).  
55 The nature of this feedback can have dramatic evolutionary consequences. One  
56 critical distinction is whether the constructing type or some other type is most  
57 adapted in the resulting environment. Under positive niche construction, se-  
58 lection favors the constructor, and evolution stagnates. Under negative niche  
59 construction, selection favors a type other than the constructor. In this latter  
60 case, populations find themselves continually chasing beneficial mutations as  
61 their adaptive landscape perpetually shifts.

62 Here, we show that the selective feedbacks that result from niche construction  
63 can maintain cooperation indefinitely. We find that it is specifically negative

64 niche construction that is responsible for this result because of the adaptive  
65 opportunities that it produces. Furthermore, we show that the rate at which  
66 niche construction occurs is also crucial. These results indicate that coopera-  
67 tors can ensure their survival when they play an active role in the evolutionary  
68 process.

## 69 **Methods**

70 Building upon Hammarlund et al. (2015), we develop an individual-based  
71 model in which cooperators and defectors evolve and compete in a population  
72 of subpopulations (i.e., a metapopulation). Through mutations, individuals  
73 gain adaptations to their environment, which increase reproductive fitness,  
74 and allow those lineages to rise in abundance. Migration among neighboring  
75 subpopulations allows more successful lineages to spread.

76 In our expanded model, subpopulations additionally modify their local envi-  
77 ronment. As this process occurs, environmental changes feed back to affect  
78 selection. We explore how niche construction affects this process of adaptation  
79 and whether cooperation can be maintained because of selective feedbacks.

## 80 **Model Description**

### 81 **Individual Genotypes and Adaptation**

82 Each individual has a haploid genome with  $L + 1$  loci (see [Table 1](#) for model  
83 parameters and their values). Different alleles at each locus are represented by

84 different integers. A binary allele at the first locus (here, locus zero) determines  
 85 whether that individual is a cooperator (1), which carries fitness cost  $c$ , or a  
 86 defector (0). Cooperation is independent from adaptation to the environment.  
 87 The remaining  $L$  loci are *adaptive loci*, and are each occupied by 0 or a value  
 88 from the set  $\{1, 2, \dots, A\}$ . Allele 0 represents a lack of adaptation, while  
 89 a non-zero allele represents one of the  $A$  possible adaptations at that locus.  
 90 These non-zero alleles signify adaptations to the external environment that  
 91 are not affected by other individuals or the local niche. Adaptations confer  
 92 a fitness benefit  $\delta$ , regardless of which non-zero allele is present. We assume  
 93  $\delta > c$ , which allows a minimally adapted cooperator to recoup the cost of  
 94 cooperation and gain a fitness advantage.

## 95 Niche Construction and Selective Feedbacks

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

100 Niche construction takes the form of density dependent selection, and indi-  
 101 viduals evolve to better match their niche by a second form of adaptation.  
 102 Specifically, the selective value of adaptive allele  $a$  at locus  $l$  increases with  
 103 the number of individuals in the subpopulation that have allele  $a - 1$  at locus  
 104  $l - 1$ . As a consequence, genotypes with sequentially increasing allelic states  
 105 will tend to evolve. We treat both adaptive loci and allelic states as “circular”:

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

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

111 Here,  $\text{mod}_X(x)$  is the integer remainder when dividing  $x$  by  $X$ . The selective  
 112 value of adaptive allele  $a$  at locus  $l$  is increased by  $\epsilon$  for each individual in the  
 113 subpopulation that has allele  $\beta(a, A)$  at locus  $\beta(l, L)$ . Thus,  $\epsilon$  specifies the  
 114 intensity of niche construction.

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

$$W_g = z - \underbrace{ca_{g,0}}_{\text{cost of cooperation}} + \underbrace{\delta \sum_{l=1}^L I(a_{g,l})}_{\text{adaptation to external environment}} + \underbrace{\epsilon \sum_{l=1}^L n(\beta(a_{g,l}, A), \beta(l, L))}_{\text{adaptation to constructed environment}} \quad (2)$$

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

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

Thus, an individual's fitness is determined both by adaptations to the external environment ( $\delta$ ) and adaptations to its constructed environment ( $\epsilon$ ). **Figure 1** illustrates the effects of these two components.

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

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

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

During growth, individuals compete through differential reproduction. Each individual's probability of success is determined by its fitness. The composition of a subpopulation with size  $P$  and cooperator proportion  $p$  after growth is multinomial with parameters  $S(p)$  and  $\{\pi_1, \pi_2, \dots, \pi_P\}$ , where:

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

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

## 135 **Mutation**

136 For simplicity, we apply mutations after growth. Mutations occur indepen-  
137 dently at each locus and cause an allelic state change. At the binary coopera-  
138 tion locus, mutations occur at rate  $\mu_c$ . These mutations flip the allelic state,  
139 causing cooperators to become defectors and vice versa. Mutations occur at  
140 rate  $\mu_a$  at each adaptive locus. These mutations replace the existing allele  
141 with a random selection from the set  $\{0\} \cup \{1, 2, \dots, A\}$ .

## 142 **Migration**

143 Populations are composed by  $N^2$  patches arranged as an  $N \times N$  lattice, where  
144 each patch can support a subpopulation. After mutation, individuals emigrate  
145 to an adjacent patch with probability  $m$ . During each migration event, a  
146 single destination patch is randomly chosen with uniform probability from  
147 each source patch's Moore neighborhood, which is composed of the nearest 8  
148 patches on the lattice. Because the population lattice has boundaries, patches  
149 located on the periphery have smaller neighborhoods.

## 150 **Population Initialization and Simulation**

151 At the beginning of each simulation, subpopulations are seeded at all patches  
152 with cooperator proportion  $p_0$  and grown to density  $S(p_0)$ . An environmental  
153 challenge is then introduced, which subjects all subpopulations to a bottleneck.  
154 For each individual, the probability of survival is  $\mu_t$ , which represents the  
155 likelihood that tolerance arises via mutation. Because individuals have not yet



156 adapted to this new environment, the allelic state of each individual's genotype  
157 is 0 at each adaptive locus. Following initialization, simulations are run for  $T$   
158 cycles, where each discrete cycle consists of subpopulation growth, mutation,  
159 migration, and dilution. Dilution thins the population to support growth in  
160 the next cycle. Each individual remains with probability  $d$ , regardless of allelic  
161 state.

## 162 Simulation Source Code and Software Dependencies

163 The simulation software and configurations for the experiments reported are  
164 available online.<sup>1</sup> Simulations used Python 3.4, NumPy 1.9.1, Pandas 0.15.2  
165 (McKinney, 2010), and NetworkX 1.9.1 (Hagberg *et al.*, 2008). Data analy-  
166 ses were performed with R 3.1.3 (R Core Team, 2015). Reported confidence  
167 intervals were estimated by bootstrapping with 1000 resamples.

## 168 Results

169 Using the model described in the previous section, we perform simulations  
170 that follow the evolution of cooperation in a population consisting of subpopu-  
171 lations that are connected by spatially-limited migration. Individuals compete  
172 in these subpopulations by gaining a limited number of adaptations that con-  
173 fer fitness benefits. While cooperation does not directly affect the selective  
174 value of these adaptations, cooperation can have indirect effects on the adap-

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<sup>1</sup>These materials will be made public at the time of publication, and a reference will be placed here.

tive process. Specifically, cooperation increases subpopulation density. As a  
 result, larger subpopulations of cooperators experience more mutational op-  
 portunities to gain adaptations. Cooperation can hitchhike along with these  
 adaptations, which compensate for the cost of cooperation. During this pro-  
 cess, subpopulations 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 elim-  
 inated in competition with defectors ([Figure 2A](#)). Despite an initial lift in  
 cooperator abundance due to increased productivity, the cost of cooperation  
 becomes disadvantageous as migration mixes the initially isolated subpopula-  
 tions. When populations can adapt to the external environment ( $L = 5$ ), but  
 niche construction is absent ( $\epsilon = 0$ ), cooperators are maintained transiently  
 ([Figure 2B](#)). Here, larger cooperator subpopulations can more quickly adapt  
 to their external environment as before. As previously described by Hammar-  
 lund et al. (2015), however, cooperation is subsequently lost once populations  
 become fully adapted to their environment. Once this has occurred, isogenic  
 defectors (i.e., defectors with identical adaptive loci) arise via mutation and  
 displace cooperation due to their selective advantage. However, when niche  
 construction creates selective feedbacks, cooperation persists in over 2/3 of the

197 replicate populations (Figure 2C). We see in Figure 3A that despite oscillations,  
198 cooperation is maintained at high levels in these populations.

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

201 In the model, both adaptation and niche construction contribute to an indi-  
202 vidual's fitness. To determine whether cooperation is maintained solely due to  
203 the larger selective values that result from the contributions of niche construc-  
204 tion ( $\epsilon$ ), we performed simulations in which these contributions were removed  
205 ( $\epsilon = 0$ ), and we instead increased the fitness benefits conferred by adapta-  
206 tion to the external, non-constructed environment ( $\delta = 0.6$ ). In doing so, we  
207 conservatively estimate the selective effects of niche construction by supple-  
208 menting the selective benefits of adaptations to the external environment by  
209 the maximum possible selective benefit that results from niche construction.  
210 We find that simply increasing selective values does not enable cooperators to  
211 persist (Figure 3B). Niche construction therefore plays an important role here.

## 212 **Negative Niche Construction is Critical to Cooperator** 213 **Persistence**

214 Negative niche construction can occur in our model due to the selection for  
215 sequentially-increasing allelic states and the circular arrangement of these al-  
216 leles. This occurs when the number of adaptive alleles ( $A$ ) does not divide

217 evenly into the number of adaptive loci ( $L$ ). In such a case, any sequence of  
 218 integers on the circular genome will always contain a break in the sequence;  
 219 that is, one locus with an allele that is not one less than the allele at the  
 220 next locus (see [Figure 1](#)). Given this unavoidable mismatch, any type that  
 221 has fixed will always favor selection for a new type. However, if this negative  
 222 niche construction is removed (by setting  $L = 5$ ,  $A = 5$ ), cooperators are again  
 223 driven extinct after an initial lift in abundance ([Figure 3C](#)).

## 224 **Selective Feedbacks Limit Defector Invasion**

225 The adaptation resulting from selective feedbacks can limit invasion by de-  
 226 fectors, which arise either through immigration from neighboring patches or  
 227 through mutation from a cooperator ancestor. The challenge is particularly  
 228 threatening, as they are equally adapted, yet do not incur the cost of coopera-  
 229 tion. When isogenic defectors are introduced at a single patch in the center of  
 230 an  $11 \times 11$  population of cooperator subpopulations, they quickly spread if no  
 231 mutations are allowed ([Figure 4A](#)). However, when resident cooperators can  
 232 adapt (mutations occur at adaptive loci), cooperators evade defector invasion  
 233 in over half of the replicate populations ([Figure 4B](#)). [Figure 5](#) depicts one such  
 234 instance where cooperators gained an adaptation that stopped and eliminated  
 235 invading defectors. We further highlight this process in [Figure 4C](#), where an  
 236 adapted cooperator can rapidly invade a population of defectors.

## 237 The Rate of Niche Construction Matters

238 **TODO:** Sorry, results coming soon!

## 239 Discussion

240 Despite their negative effects, deleterious traits can rise in abundance due to  
241 genetic linkage with other traits that are strongly favored by selection (May-  
242 nard Smith and Haigh, 1974). In a process termed the “Hankshaw effect”,  
243 Hammarlund et al. (2015) recently demonstrated that cooperation can pro-  
244 long its existence by increasing the likelihood of hitchhiking with a beneficial  
245 trait. While this process does favor cooperation in the short term, it eventually  
246 reaches a dead end; when the opportunities for adaptation are exhausted, and  
247 cooperators can no longer hitchhike, they face extinction. In this work, we  
248 have considered whether niche construction might serve to perpetually gener-  
249 ate new adaptive opportunities, and thus favor cooperation indefinitely.

250 When niche construction occurs, cooperation can indeed persist (Figure 2C).  
251 In our model, niche construction introduces additional selective effects that  
252 could influence the evolutionary process, leading to a more pronounced Han-  
253 kshaw effect. However, simply raising the selective benefits provided by adap-  
254 tations does not prolong cooperation (Figure 3B), which indicates that niche  
255 construction and the selective feedbacks that it produces play a crucial role.

256 Further, we find that it is specifically negative niche construction that main-  
257 tains cooperation (Figure 3C). Here we observe another facet of the Hankshaw

258 effect: because populations of cooperators are larger, they are better able to  
 259 respond to the adaptive opportunities that result from negative niche construc-  
 260 tion. Without adaptive opportunities, adaptation eventually grinds to a halt.  
 261 Once this occurs, cooperators face the threat of invasion by defectors that arise  
 262 de novo through mutation. Since these defectors are equally adapted but do  
 263 not bear the cost of cooperation, they quickly drive cooperators to extinction.  
 264 Because every type constructs an environment in which a different type is  
 265 more fit, negative niche construction creates continual adaptive opportunities.  
 266 These opportunities can allow cooperators to resist invasion by defectors, even  
 267 when defectors are equally adapted (Figure 4B). It is these recurring cycles  
 268 of invasion and adaptation that underlie the oscillations in cooperator popula-  
 269 tions that we see in Figure 3A. When stochastic mutations do not confer these  
 270 adaptations, defectors invade, and the cycle is broken.

#### 271 **TODO: the rate of niche construction is crucial**

272 In our model, cooperation and niche construction are orthogonal, which al-  
 273 lows us to focus on hitchhiking. However, the form of cooperation used in  
 274 this model could itself be seen as a niche constructing behavior. Explicitly  
 275 modeling this cooperative behavior, which is akin to the production of pub-  
 276 lic goods, would likely yield additional insights into the relationship between  
 277 cooperation and niche construction. For example, previous work has shown  
 278 that niche construction can favor deleterious alleles (Laland *et al.*, 1996, 1999).  
 279 Cooperation, especially in competition against equally-adapted defectors, can  
 280 be considered deleterious, so introducing selective feedbacks from cooperation  
 281 could further bolster cooperation. Van Dyken and Wade (2012) showed that

282 when two cooperative behaviors co-evolve and niche construction feedbacks  
283 benefit the other type, niche construction can increasingly favor these traits,  
284 which were otherwise disfavored when alone. Arguably, this can be viewed  
285 as another instance of hitchhiking: the maladaptive form of cooperation is  
286 maintained by association with the adaptive form. However, negative niche  
287 construction then reverses these roles and perpetuates the cycle.

288 By their very nature, public goods benefit populations by making their envi-  
289 ronment more hospitable (West *et al.*, 2007a). For example, bacteria produce  
290 a host of extracellular products that scavenge soluble iron (Griffin *et al.*, 2004),  
291 digest large proteins (Diggle *et al.*, 2007; Darch *et al.*, 2012), and reduce the  
292 risk of predation (Cosson *et al.*, 2002). While many studies have focused on  
293 how the environment affects the evolution of cooperative behaviors such as  
294 the production of these public goods, relatively few have examined how the  
295 resulting selective feedbacks influence evolution as public goods modify the  
296 environment. In these instances, environmental changes are likely to occur  
297 on different timescales than reproduction. These differences can have pro-  
298 found effects. For example, a multitude of factors including protein durabil-  
299 ity (Brown and Taddei, 2007; Kümmerli and Brown, 2010), diffusion (Allison,  
300 2005; Driscoll and Pepper, 2010), and resource availability (Zhang and Rainey,  
301 2013; Ghoul *et al.*, 2014) influence both the rate and the degree to which public  
302 goods alter the environment. Lehmann (2007) demonstrated that cooperative,  
303 niche constructing behaviors can be favored when they affect selection for  
304 future generations. When this occurs, conflict among contemporary kin is re-  
305 duced. The evolutionary inertia that this creates, however, may ultimately

306 work against cooperators. When public goods accumulate in the environment,  
307 cooperators must decrease production to remain competitive (Kümmerli and  
308 Brown, 2010; Dumas and Kümmerli, 2012). This favors cooperation that oc-  
309 curs facultatively, perhaps by sensing the abiotic (Bernier *et al.*, 2011; Koestler  
310 and Waters, 2014) or biotic environment (Brown and Johnstone, 2001; Darch  
311 *et al.*, 2012).

312 In many instances where cooperation occurs, the environment is itself a biolog-  
313 ical entity, which can introduce additional evolutionary feedbacks. As the host  
314 population changes, so too does selection on their symbiont populations. Here,  
315 evolutionary outcomes depend greatly on the degree of shared interest between  
316 the host and symbiont. For example, the cooperative production of virulence  
317 factors by the human pathogen *P. aeruginosa* in lung infections is harmful to  
318 hosts with cystic fibrosis (Harrison, 2007). Conversely, cooperative light pro-  
319 duction by *A. fischeri* is vital for the survival of its host, the Hawaiian bobtail  
320 squid (Ruby, 1996). It was recently argued that incorporating the effects of  
321 niche construction is critical for improving our understanding of viral evolu-  
322 tion (Hamblin *et al.*, 2014) and evolution in co-infecting parasites (Hafer and  
323 Milinski, 2015). Incorporating host dynamics, co-evolution, and the feedbacks  
324 that they produce into models is likely to be equally important for gaining  
325 an understanding of how cooperative behaviors evolve in these host-symbiont  
326 settings.

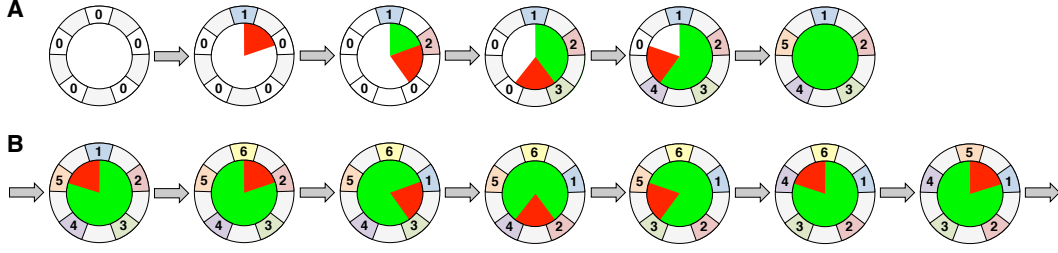


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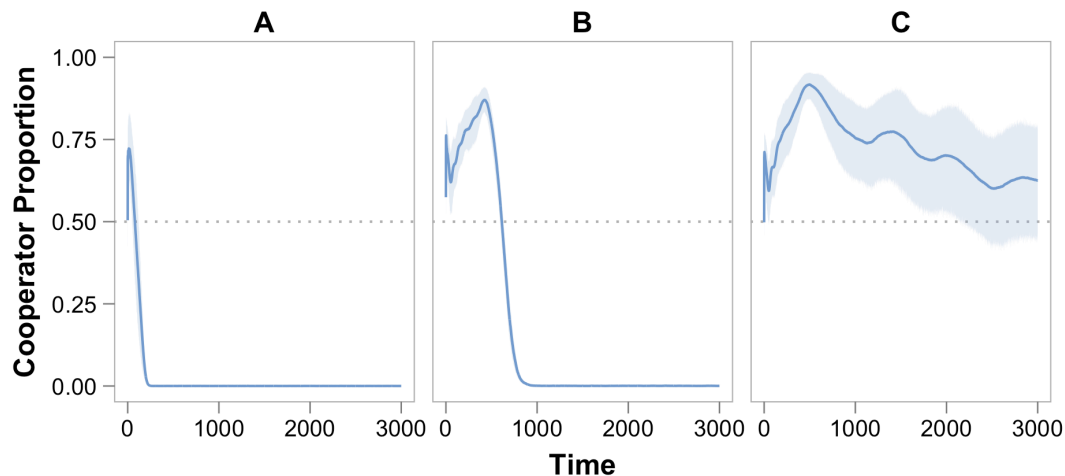
334 **Figures**

335 **Figure 1**



**Figure 1: Adaptation to External and Constructed Environments.** (A) We start with the case with five loci ( $L = 5$ ) and five non-zero alleles ( $A = 5$ ). All simulations are initialized with a non-adapted genotype with allele 0 at every locus—the genotype on the far left. Random mutation will introduce a non-zero allele, which is expected to increase in frequency. For simplicity, we assume that allele 1 arises at the first locus (in the “12 o’clock” position). The rest of this schematic focuses on niche construction. Every non-zero allele at any locus influences selection at the next locus in the clockwise direction. There is a “mismatch” in this genotype (highlighted by the red sector) because the niche constructed by allele 1 at the first locus favors allele 2 (not 0) at its immediate clockwise neighbor (the second locus). Once the appropriate allele arises, it will be selected. In this case, the genotype  $[1,2,0,0,0]$  receives an epsilon effect in addition to the extra delta. The “match” at the first and second locus is highlighted as a green sector. However, now there is a new mismatch (between the second and third locus), which a new round of mutation and selection corrects, and so on. The green sector grows as the red sector ticks clockwise. Importantly, because  $A$  divides evenly into  $L$ , this genotype can evolve into a perfectly reinforcing sequence  $[1,2,3,4,5]$ , which enjoys an maximal epsilon increment of fitness of due to its niche construction. (B) The case of negative niche construction is illustrated for the case of five loci ( $L = 5$ ) and six non-zero alleles ( $A = 6$ ). Here we start with a population fixed for the genotype on the far left  $[1,2,3,4,5]$ . There is a single mismatch in this genotype (highlighted by the red sector) because the niche constructed by allele 5 favors allele 6 (not 1) at its immediate clockwise neighbor. If the fitter mutant  $[6,2,3,4,5]$  arises (see next genotype to the right), it will fix. (We note that the strength of selection will drop as its frequency increases). However, now there is a new mismatch in the genotype (highlighted again with a red sector). Thus, we see that correcting one mismatch generates a new mismatch. Thus, this system will never escape its mismatches—the red sector just clicks clockwise around the genome. Indeed, after six (or  $A$ ) rounds of mismatch correction/generation, we have ended back where we started with the original genotype turned clockwise by one locus. Here, the adaptation to previous niche construction generates further niche construction that leads to novel adaptation.

336 **Figure 2**



**Figure 2: 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. **(C)** Niche construction enables cooperation to be maintained indefinitely. In the majority of populations (13/18), cooperation remained the dominant strategy. Individual populations are shown in Figure 3A.

337 **Figure 3**

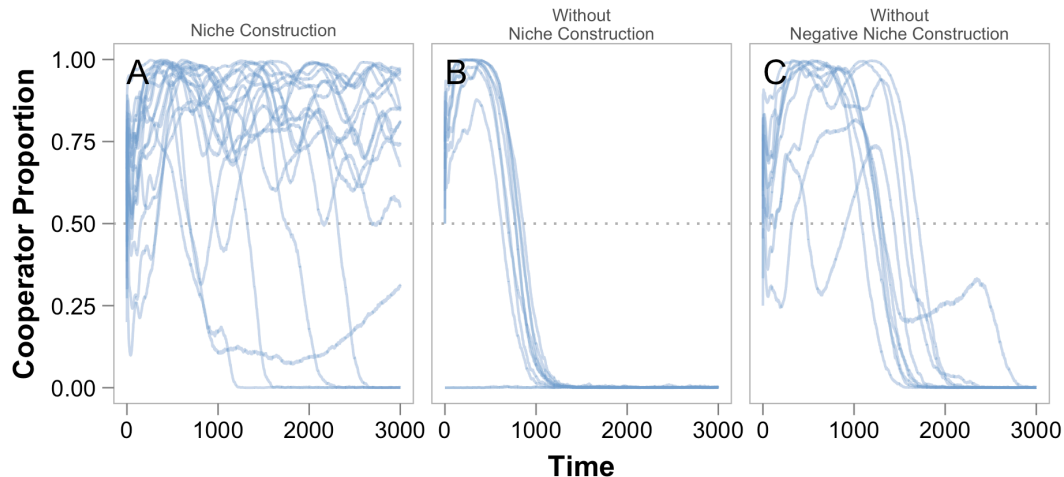
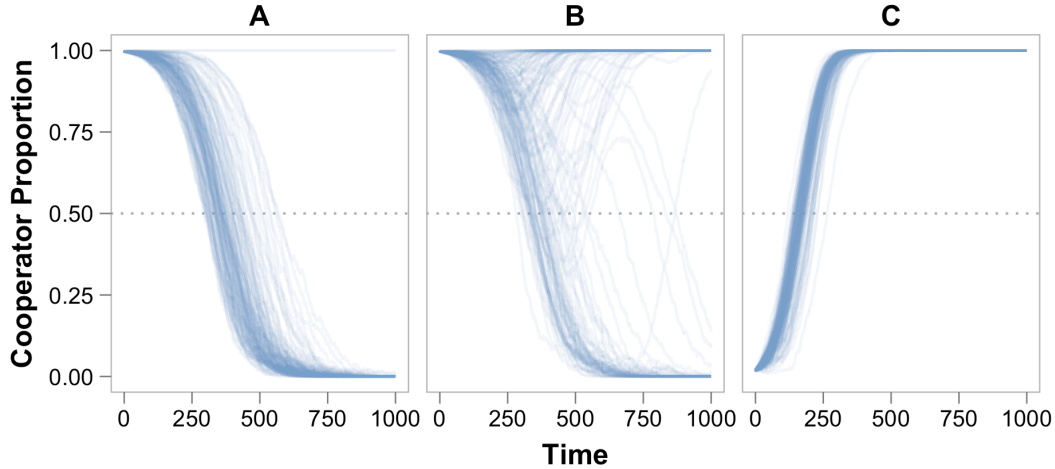


Figure 3: **Niche Construction and the Evolution of Cooperation.** The proportion of cooperators present in each replicate population is shown for the duration of simulations. **(A)** Despite some oscillations, niche construction enables cooperation to be maintained indefinitely in 14 of 18 populations. **(B)** When niche construction is removed and the fitness benefit of adaptation is increased to compensate ( $\epsilon = 0$ ,  $\delta = 0.6$ ), adapted defectors arise and drive cooperators to extinction. **(C)** Without negative niche construction, cooperation is not maintained ( $A = 5$ ).

**Figure 4**

**Figure 4: Niche Construction and Invasion.** Curves trace the proportion of cooperators present in the population for the duration of 160 replicate simulations ( $T = 1000$ ). These experiments examine whether a rare cooperator or defector strategy can invade when initiated at a single patch in the center of the population lattice ( $N^2 = 121$ ). Unless otherwise noted, mutations ( $\mu_a = 0, \mu_c = 0$ ) are disabled in these ecological simulations to highlight the dynamics of invasion. The results from simulations where this limitation is removed are shown in Figure S1. **(A)** When cooperators and defectors are isogenic (i.e., both types have stress alleles [1,2,3,4,5]) and mutation 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 isogenic defectors. Here, cooperation persisted in the majority of populations ( $\mu_a = 0.00005$ , the base mutation rate). **(C)** We demonstrate that adaptations such as these can enable an cooperator (stress alleles [6,2,3,4,5], see Figure 1) to displace a population of defectors when defectors cannot arise or adapt via mutation.

339 **Figure 5**

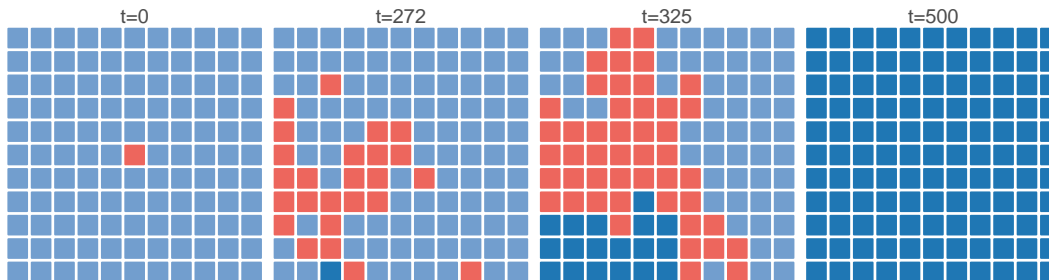


Figure 5: **Defector Invasion Stopped by Cooperator Adaptation.** Here we depict the distribution of dominant types among populations over time for one representative simulation in which isogenic defectors arise. For clarity, mutations occurred at the adaptive loci, but not at the cooperation locus ( $\mu_c = 0$ ) during this ecological simulation. A time  $t = 0$  (leftmost panel), a single matched defector population (red) is placed among cooperator populations (light blue). Because these defectors do not bear the costs of cooperation, they spread ( $t = 272$ , second panel). However, cooperators in a single population gain an adaptation that give them a fitness advantage over defectors (dark blue, lower left). At  $t = 325$  (third panel), defectors continue to invade cooperator populations. However, the adapted cooperator type, which can invade both defector populations and ancestral cooperator populations, can spread more quickly due to its greater fitness. Eventually, this strategy spreads and fixes in all populations (rightmost panel) until this strategy itself is replaced by the next adaptation.

340 **Figure 6**

341 **TODO** Yep. Almost ready.



<sup>342</sup> **Supplemental Figure 1**

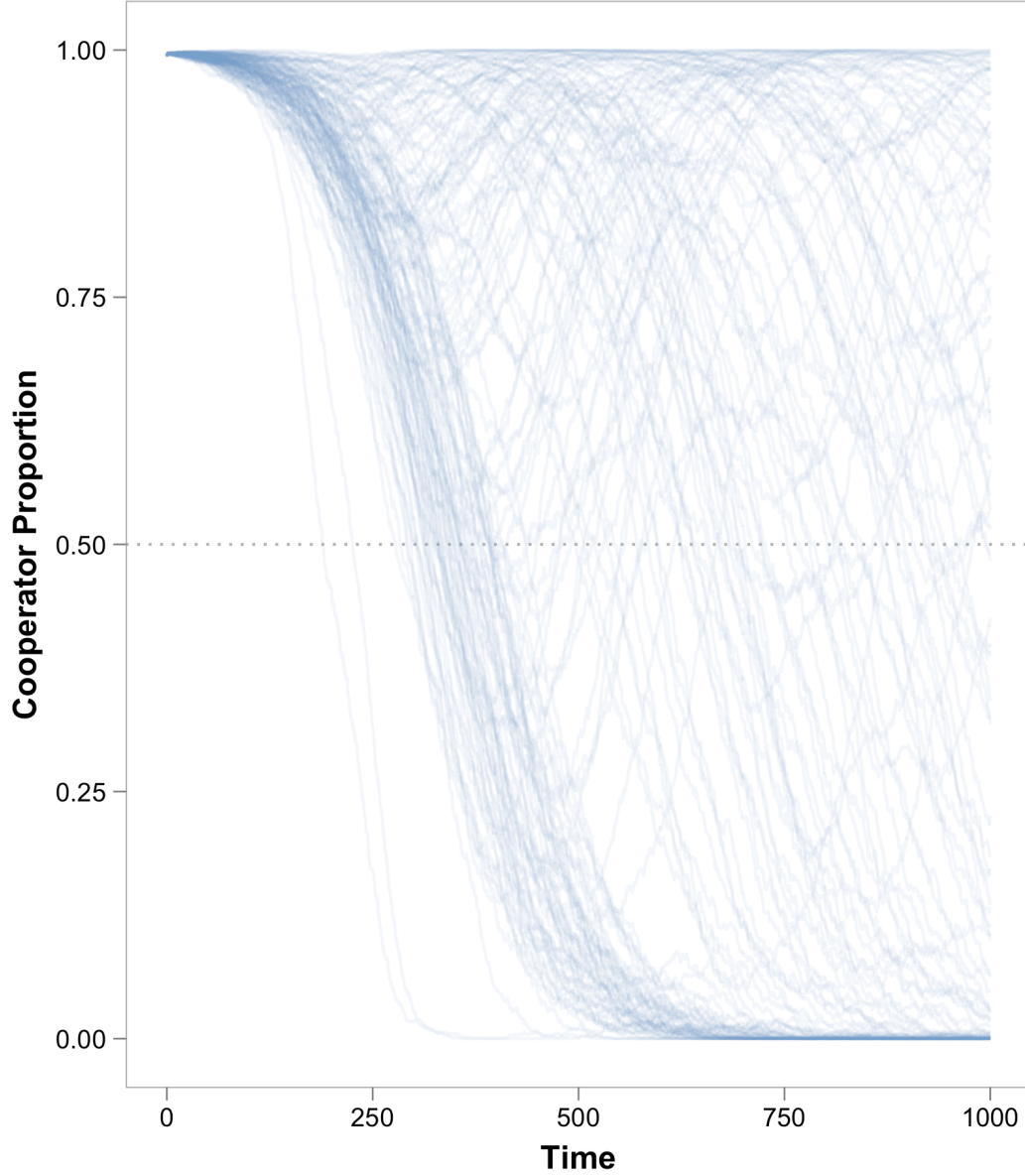


Figure S1: **Defector Invasion with Mutations.** With mutations occurring both at the adaptive loci and the cooperation locus ( $\mu_a = \mu_c = 0.00005$ ), cooperation remains the dominant strategy in 58 replicate simulations. Curves trace the proportion of cooperators present in the population for the duration of 160 replicate simulations ( $T = 1000$ )

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 subpopulation size	800
$S_{max}$	Maximum subpopulation size	2000
$\mu_a$	Mutation rate (adaptation)	$10^{-5}$
$\mu_c$	Mutation rate (cooperation)	$10^{-5}$
$N^2$	Number of patches	625
$m$	Migration rate	0.05
$p_0$	Initial cooperator proportion	0.5
$\mu_t$	Mutation rate (tolerance to new environment)	$10^{-5}$
$T$	Number of simulation cycles	3000
$d$	Subpopulation dilution factor	0.1

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