

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 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. 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 more than simply experience changing
47 environments passively. Through their activities, their interactions with oth-
48 ers, and even their death, organisms constantly modify their environment.
49 These changes can produce evolutionary feedback loops in which environmen-
50 tal change alters selection, which, in turn, alters the distribution of pheno-
51 types and their corresponding influence on the environment (Odling-Smee *et*
52 *al.*, 2003). Because of these feedback loops, populations may find themselves
53 continually chasing beneficial mutations as their adaptive landscape perpetu-
54 ally 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 Hawkshaw effect, allowing cooperation to
60 continue to hitchhike as populations continually adapt. We then focus on
61 how niche construction influences outcomes when isolated 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, niche construction has frequently been shown to increase diversity
65 (???). We explore whether this diversity helps or hinders the evolution of
66 cooperation.

67 We find that niche construction can promote and sustain cooperation indef-
68 initely. However, the niche construction must have a negative component.
69 Furthermore, we show that the level of diversity promoted by this negative
70 feedback must be sufficiently low to favor the evolution of cooperation.

71 **Methods**

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

78 In our expanded model, populations modify their local environment. As this
79 process occurs, environmental changes feed back to affect selection. We per-
80 form simulations using this model to explore how niche construction affects
81 this adaptation process and whether selective feedbacks allow cooperation to
82 be maintained.

83 **Model Description**

84 **Individual Genotypes and Adaptation**

85 Each individual has a haploid genome with $L+1$ loci (see [Table 1](#) for model
86 parameters and their values). Different alleles at each locus are represented
87 by different integers. A binary allele at locus $L + 1$ determines whether that
88 individual is a cooperator (1), which carries fitness cost c , or a defector (0).
89 Cooperation is independent from adaptation to the environment. The first
90 L loci are *adaptive loci*, and are each occupied by 0 or a value from the set
91 $\{1, 2, \dots, A\}$. Allele 0 represents a lack of adaptation, while a non-zero allele
92 represents one of the A possible adaptations at that locus. Adaptations confer
93 a fitness benefit δ , regardless of which non-zero allele is present. We assume
94 $\delta > c$, which allows a minimally adapted cooperator to recoup the cost of
95 cooperation and gain a fitness advantage. The benefits that these adaptations
96 engender are purely exogenous, and are not affected by the other individuals
97 or the state of the environment.

98 **Niche Construction and Selective Feedbacks**

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

103 We use a form of density dependent selection to favor individuals that better

104 match their niche. Specifically, the selective value of adaptive allele a at locus
105 l increases with the number of individuals in the population that have allele
106 $a + 1$ at locus $l + 1$. As a consequence, genotypes with sequentially increasing
107 allelic states will tend to evolve. We treat both adaptive loci and allelic states
108 as “circular”: the selective value of an allele at locus L is affected by the allelic
109 composition of the population at locus 1. Similarly, the selective value of allele
110 A at any locus increases with the number of individuals carrying allele 1 at
111 the next locus. This circularity is represented by the function $\beta(x, X)$, which
112 gives the integer that follows an arbitrary value x in the set $\{1, 2, \dots, X\}$:

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

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

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

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

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

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

121 Thus, an individual's fitness is determined both exogenously by adaptation (δ)
 122 and endogenously by its niche (ϵ).

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

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

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

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

132 During population growth, individuals compete through differential reproduc-
 133 tion. Each individual's probability of success is determined by its fitness. The
 134 composition of a population with size P and cooperator proportion p after
 135 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 π_i represents an individual's reproductive fitness relative to others in the population.

Mutation

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

Migration

Metapopulations are composed by N^2 patches arranged as an $N \times N$ lattice, where each patch can support a population. After mutation, individuals emigrate to an adjacent patch with probability m . During each migration event, a single destination patch is randomly chosen with uniform probability from each source patch's Moore neighborhood, which is composed of the nearest

154 8 patches on the lattice. Because the metapopulation lattice has boundaries,
155 patches located on the periphery have smaller neighborhoods.

156 **Metapopulation Initialization and Simulation**

157 At the beginning of each simulation, populations are seeded at all patches
158 with cooperator proportion p_0 and grown to density $S(p_0)$. An environmental
159 challenge is then introduced, which subjects all populations to a bottleneck.
160 For each individual, the probability of survival is μ_t , which represents the
161 likelihood that tolerance arises via mutation. Because individuals have not yet
162 adapted to this new environment, the allelic state of each individual's genotype
163 is 0 at each adaptive locus. Following initialization, simulations are run for
164 T cycles, where each discrete cycle consists of population growth, mutation,
165 migration, and thinning. Thinning allows for growth in the next cycle. Each
166 individual remains with probability d , regardless of allelic state.

167 **Simulation Source Code and Software Dependencies**

168 The simulation software and configurations for the experiments reported are
169 available online.¹ Simulations used Python 3.4, NumPy 1.9.1, Pandas 0.15.2
170 (McKinney, 2010), and NetworkX 1.9.1 (Hagberg *et al.*, 2008). Data analy-
171 ses were performed with R 3.1.3 (R Core Team, 2015). Reported confidence
172 intervals were estimated by bootstrapping with 1000 resamples.

¹To be made public at the time of publication

Results

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

Cooperation Persists with Niche Construction

Without any opportunity for adaptation ($L = 0$), cooperators are swiftly eliminated 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 populations. When there are opportunities for adaptation ($L = 5$) but no niche construction ($\epsilon = 0$), cooperators are maintained transiently ([Figure 2B](#)). Here, larger cooperator populations can more quickly adapt to their environment as before.

195 As previously described by Hammarlund et al. (2015), however, cooperation
196 is subsequently lost once populations become fully adapted to their environ-
197 ment. Once this has occurred, adapted defectors that arise via mutation at the
198 cooperation locus have a selective advantage and displace cooperators. How-
199 ever, when niche construction creates selective feedbacks, cooperation persists
200 in over 2/3 of the replicate populations (Figure 3A).

201 **Fitness Increases Alone do not Support Persisting Coop-** 202 **eration**

203 In the model, both adaptation and niche construction contribute to an indi-
204 vidual's fitness. To determine whether cooperation is maintained solely due to
205 the larger selective values that result from the contributions of niche construc-
206 tion (ϵ), we performed simulations in which these contributions were removed
207 ($\epsilon = 0$), and we instead increased the fitness benefits conferred by adaptation
208 ($\delta = 0.6$). In doing so, we conservatively estimate the selective effects of niche
209 construction, as fitness benefits of this magnitude would only be given for se-
210 quential allelic states that are fixed in full populations. We find that simply
211 increasing selective values does not allow cooperators to persist (Figure 3B).
212 Niche construction therefore plays an important role here.

213 Negative Niche Construction is Critical to Cooperator 214 Persistence

215 Negative niche construction can occur in our model due to the selection for
216 sequentially-increasing allelic states and the circular arrangement of these alle-
217 les. This occurs when the number of adaptive alleles (A) does not divide evenly
218 into the number of adaptive loci (L). In such a case, any sequence of integers
219 on the circular genome will always contain a break in the sequence; that is,
220 one locus with an allele that is not one less than the allele at the next locus
221 (see [Figure 1](#)). Given this unavoidable mismatch, any genotype that has fixed
222 will always favor selection for a new genotype (see Figure). However, if this
223 negative niche construction is removed (by setting $L = 5$, $A = 5$), cooperators
224 are again driven extinct after an initial lift in abundance ([Figure 3C](#)).

225 Selective Feedbacks Limit Defector Invasion

226 The adaptation resulting from selective feedbacks can limit invasion by de-
227 fectors, which arise either through immigration from neighboring patches or
228 through mutation from a cooperator ancestor. The challenge is particularly
229 threatening, as they are equally adapted, yet do not incur the cost of coopera-
230 tion. When homologous defectors (i.e., defectors with identical adaptive loci)
231 are introduced as a single population in the center of an 11×11 metapopula-
232 tion of cooperators, they quickly spread if no mutations are allowed ([Figure](#)
233 [4A](#)). However, when resident cooperators can adapt (mutations occur at adap-
234 tive loci), cooperators evade defector invasion in over half of the replicate

235 metapopulations (Figure 4B). Figure 5 depicts one such instance where coop-
236 erators gained an adaptation that stopped and eliminated invading defectors.
237 We further highlight this process in Figure 4C, where an adapted cooperator
238 genotype can rapidly invade a population of defectors.

239 Diversity Hampers the Evolution of Cooperation

240 TODO: defector can invade a diverse population of cooperators, while adapta-
241 tion to a matching defector can't spread to stop invasion.

242 Discussion

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

254 When niche construction occurs, cooperation can indeed persist (Figure 3A). 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 3B), and indicates that niche construction plays an important role.

We find that cooperator success is due to niche construction. Further, we find that it is specifically negative niche construction that maintains cooperation (Figure 3C). Without adaptive opportunities, adaptation eventually grinds to a halt. 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. Because every genotype constructs an environment in which a different genotype is more fit, negative niche construction creates continual adaptive opportunities. These opportunities can allow cooperators to resist invasion by defectors, even when defectors are equally adapted (Figure 4B). Here we observe another facet of the Hankshaw effect: because populations of cooperators are larger, they are better able to respond to the adaptive opportunities that result from negative niche construction.

TODO: diversity results TODO: references about diversity

In our model, cooperation and niche construction are orthogonal, which allows us to focus on hitchhiking. However, the form of cooperation used in this model could itself be seen as a niche constructing behavior. Explicitly modeling this cooperative behavior, which is akin to the production of pub-

278 lic goods, would likely yield additional insights into the relationship between
279 cooperation and niche construction. For example, previous work has shown
280 that niche construction can favor deleterious alleles (Laland *et al.*, 1996, 1999).
281 Cooperation, especially in competition against equally-adapted defectors, can
282 be considered deleterious, so introducing selective feedbacks from cooperation
283 could further bolster cooperation. Van Dyken and Wade (2012) showed that
284 when two cooperative behaviors co-evolve and niche construction feedbacks
285 benefit the other type, niche construction can increasingly favor these traits,
286 which were otherwise disfavored when alone. Arguably, this can be viewed
287 as another instance of hitchhiking: the maladaptive form of cooperation is
288 maintained by association with the adaptive form. However, negative niche
289 construction then reverses these roles and perpetuates the cycle.

290 By their very nature, public goods benefit populations by making their envi-
291 ronment more hospitable (West *et al.*, 2007a). For example, bacteria produce
292 a host of extracellular products that scavenge soluble iron (Griffin *et al.*, 2004),
293 digest large proteins (Diggle *et al.*, 2007; Darch *et al.*, 2012), and reduce the
294 risk of predation (Cosson *et al.*, 2002). While many studies have explored
295 how the environment affects the evolution of cooperative behaviors such as
296 the production of these public goods, relatively few have examined how the
297 resulting selective feedbacks influence evolution as public goods modify the
298 environment. In these instances, environmental changes are likely to occur
299 on different timescales than reproduction. These differences can have pro-
300 found effects. 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. Lehmann (2007) demonstrated that cooperative, niche constructing behaviors can be favored when they affect selection for future generations. When this occurs, conflict among contemporary kin is reduced. The evolutionary inertia that this creates, however, may ultimately work against cooperators. When public goods accumulate in the environment, cooperators must decrease production to remain competitive (Kümmerli and Brown, 2010; Dumas and Kümmerli, 2012). This favors cooperation that occurs facultatively, perhaps by sensing the abiotic (Bernier *et al.*, 2011; Koestler and Waters, 2014) or biotic environment (Brown and Johnstone, 2001; Darch *et al.*, 2012).

In many instances of cooperation, the environment is itself a biological entity, which can produce additional evolutionary feedbacks. As the host population changes, so too does selection on their symbiont populations. Here, evolutionary outcomes depend greatly on the degree of shared interest between the host and symbiont. For example, the cooperative production of virulence factors by the human pathogen *P. aeruginosa* in lung infections is harmful to hosts with cystic fibrosis (Harrison, 2007). Conversely, cooperative light production by *A. fischeri* is vital for the survival of its host, the Hawaiian bobtail squid (Ruby, 1996). It was recently argued that incorporating the effects of niche construction is critical for improving our understanding of viral evolution (Hamblin *et al.*, 2014) and evolution in co-infecting parasites (Hafer and Milinski, 2015). Incorporating host dynamics, co-evolution, and the feedbacks that they pro-

326 duce into models is likely to be equally important for gaining an understanding
327 of how cooperative behaviors evolve in these host-symbiont settings.

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335 Figures

336 Figure 1

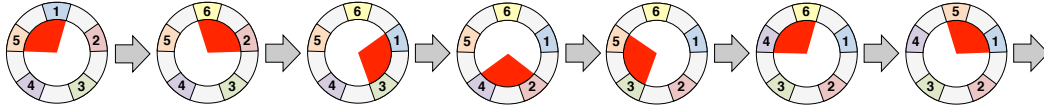


Figure 1: Negative niche construction is illustrated for the case of five adaptive loci ($L = 5$) and six alleles ($A = 6$). The adaptive loci are wrapped into a circle, where niche construction at each locus influences selection at the next locus in the clockwise direction. Suppose we start with a population fixed for the genotype on the far left, $[1, 2, 3, 4, 5]$. There is a mismatch in this genotype (highlighted by the red arc), 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 arc). Thus, we see that correcting one mismatch generates a new mismatch. Thus, this system will never escape these mismatches—the red arc just moves 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.

337 **Figure 2**

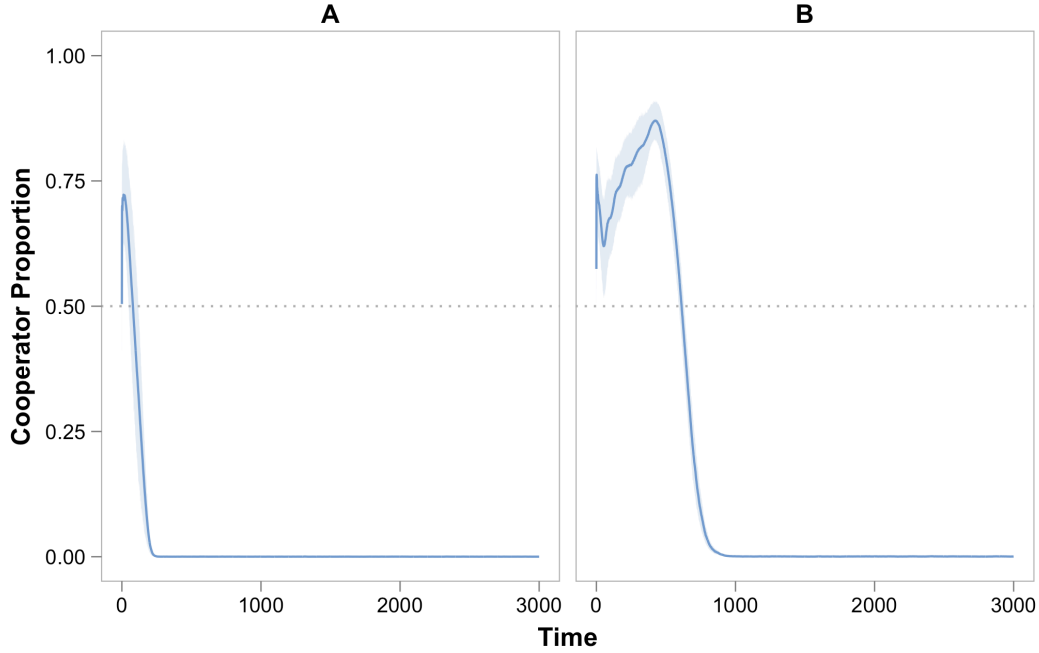


Figure 2: Adaptation, Hitchhiking, and the Evolution of Cooperation. The proportion of cooperators present in the population is shown for the duration of simulations. Curves show the average among replicate populations, and shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter 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 (ϵ , the intensity of niche construction, is zero), cooperation hitchhikes along with adaptations, allowing cooperators to temporarily rise in abundance before eventually going extinct.

338 **Figure 3**

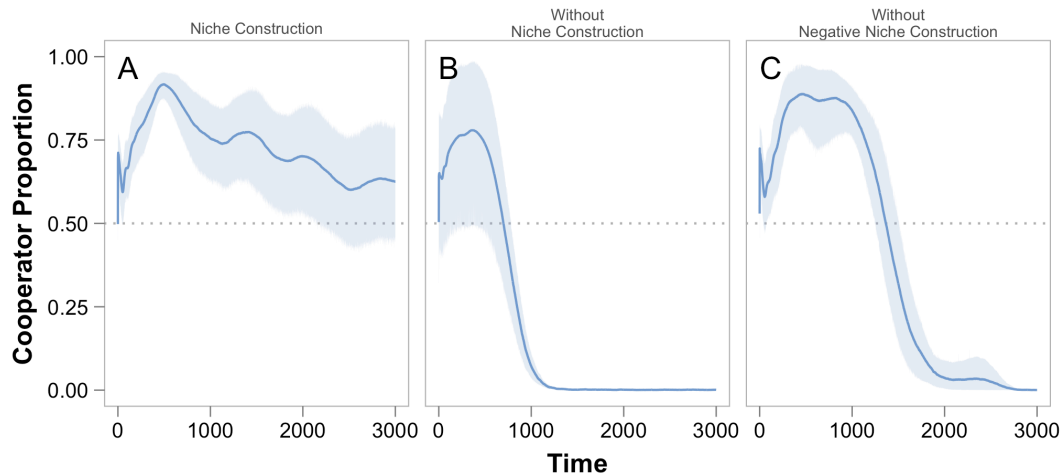


Figure 3: Niche Construction and the Evolution of Cooperation. The proportion of cooperators present in the population is shown for the duration of simulations. Curves show the average among replicate populations, and shaded areas indicate 95% confidence intervals. **(A)** Niche construction enables cooperation to be maintained indefinitely. In the majority of populations (13/18), cooperation remained the dominant strategy. **(B)** When niche construction is removed and the fitness benefit of adaptation is increased to compensate ($\epsilon = 0$, $\delta = 0.6$), adapted defectors arise and drive cooperators to extinction. **(C)** Without negative niche construction, cooperation is not maintained ($A = 5$).

339 **Figure 4**

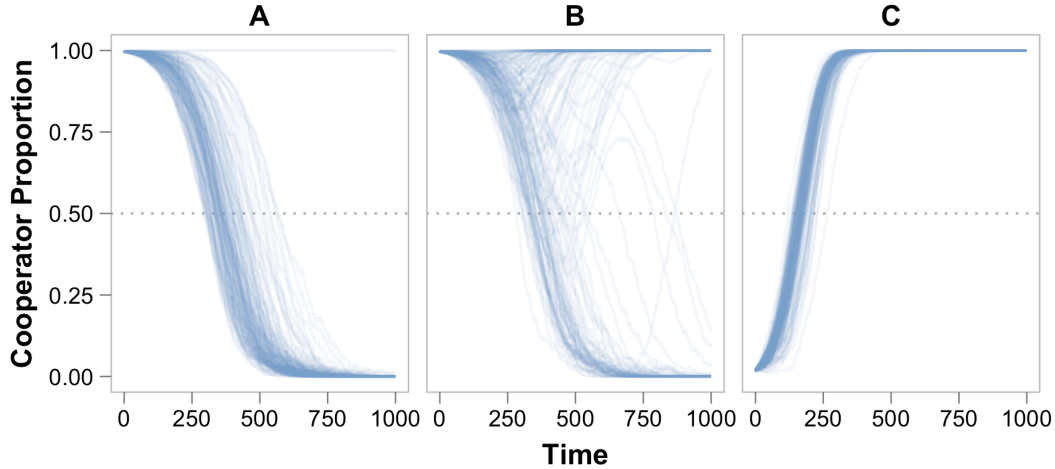


Figure 4: **Niche Construction and Invasion.** Curves trace the proportion of cooperators present in the population for the duration of 160 replicate simulations ($T = 1000$). These experiments examine whether a rare cooperator or defector strategy can invade when initiated at a single population in the center of the metapopulation lattice ($N^2 = 121$). Unless otherwise noted, mutations ($\mu_a = 0, \mu_c = 0$) are disabled in these ecological simulations to focus on the dynamics of invasion. Figure S1 shows results from simulations where this limitation is removed. **(A)** When cooperators and defectors are matched at their adaptive loci (i.e., genotypes $[1,2,3,4,5]$) 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 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 cannot arise or adapt via mutation.

340 **Figure 5**

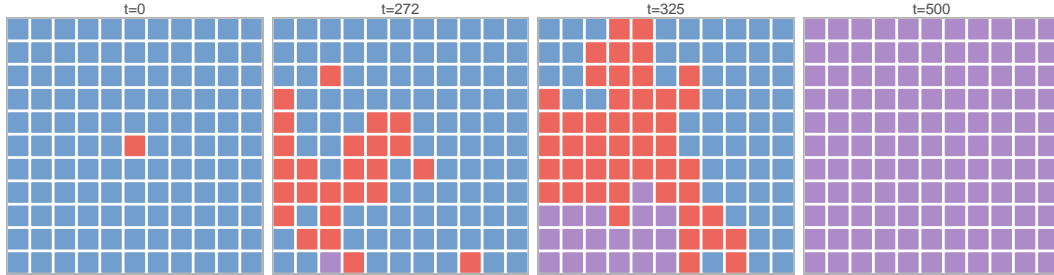


Figure 5: **Defector Invasion Stopped by Cooperator Adaptation.** Here we depict the distribution of dominant genotypes among populations over time for one representative simulation in which matched defectors arise. For clarity, mutations occurred at the adaptive loci, but not at the cooperation locus ($\mu_c = 0$) during this ecological simulation. A time $t = 0$ (leftmost panel), a single matched defector population (red) is placed among cooperator populations (blue). Because it does not bear the costs of cooperation, it spreads ($t = 272$, second panel). However, one cooperator population gains an adaptation giving it a fitness advantage over defectors (purple, lower left). At $t = 325$ (third panel), defectors continue to invade cooperator populations. However, the adapted cooperator genotype, which can invade both defector populations and ancestral cooperator populations, can spread more quickly as populations with that genotype reach greater densities. Eventually, this strategy spreads and fixes in all populations (rightmost panel).

341 **Figure 6**

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

³⁴⁴ **Supplemental Figure 1**

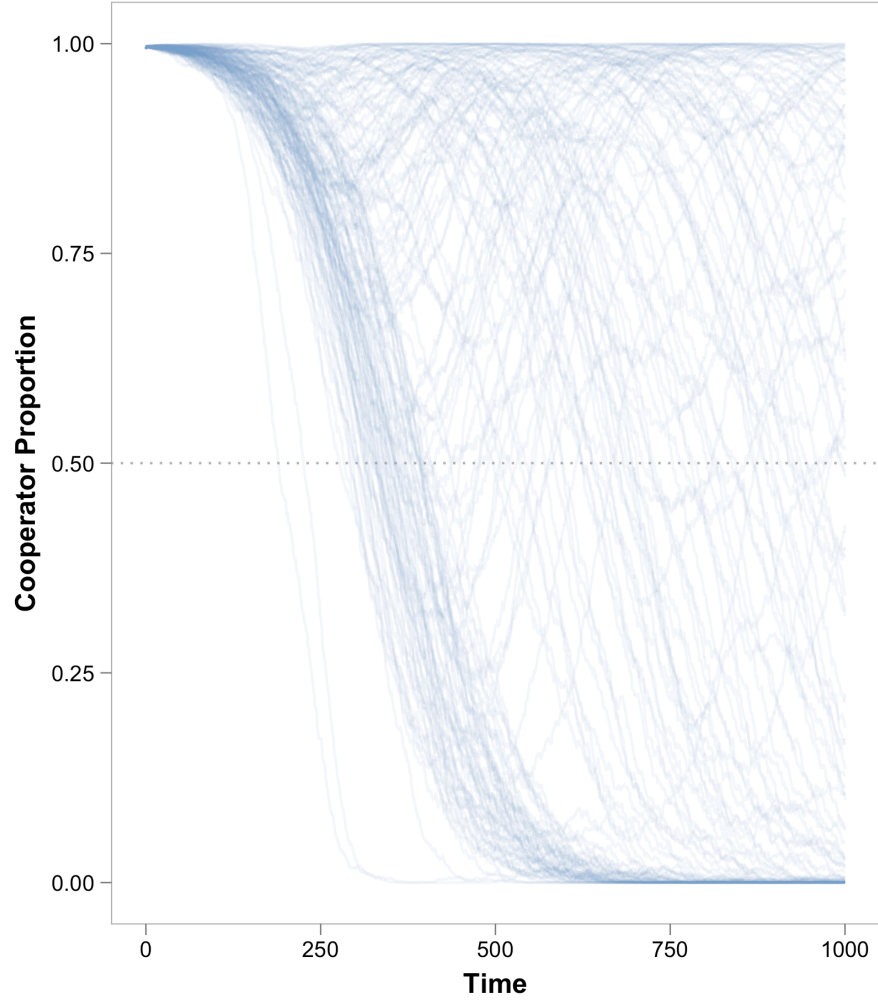


Figure S1: **Defector Invasion with Mutations.** With mutations occurring both at the adaptive loci and the cooperation locus ($\mu_a = \mu_c = 0.00005$), cooperation remains the dominant strategy in 58 replicate simulations. Curves trace the proportion of cooperators present in the population for the 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
δ	Fitness benefit, nonzero alleles	0.3
ϵ	Fitness benefit, sequential alleles	0.00015
z	Baseline fitness	1
S_{min}	Minimum population size	800
S_{max}	Maximum population size	2000
μ_a	Mutation rate (adaptation)	10^{-5}
μ_c	Mutation rate (cooperation)	10^{-5}
N^2	Number of metapopulation sites	625
m	Migration rate	0.05
d	Population dilution factor	0.1
p_0	Initial cooperator proportion	0.5
μ_t	Mutation rate (tolerance to new environment)	10^{-5}
T	Number of simulation cycles	3000

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