

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. 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 death, 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 constructed environment. Under positive niche construction,
58 selection favoring the constructor is reinforced, and evolution eventually stag-
59 nates. Under negative niche construction, the constructed environment favors
60 a different type than the constructor. In this latter case, populations find
61 themselves continually chasing beneficial mutations as their adaptive land-
62 scape perpetually shifts.

63 Here, we explore whether the selective feedbacks that result from niche con-

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

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

Methods

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

86 In our expanded model, subpopulations modify their local environment. As
87 this process occurs, environmental changes feed back to affect selection. We
88 perform simulations using this model to explore how niche construction affects
89 this adaptation process and whether selective feedbacks enable cooperation to
90 be maintained.

91 **Model Description**

92 **Individual Genotypes and Adaptation**

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

106 Niche Construction and Selective Feedbacks

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

111 We use a form of density dependent selection to favor individuals that better
 112 match their niche. Specifically, the selective value of adaptive allele a at locus l
 113 increases with the number of individuals in the subpopulation that have allele
 114 $a - 1$ at locus $l - 1$. As a consequence, genotypes with sequentially increasing
 115 allelic states will tend to evolve. We treat both adaptive loci and allelic states
 116 as “circular”: the selective value of an allele at locus 1 is affected by the
 117 allelic composition of the subpopulation at locus L . Similarly, the selective
 118 value of allele 1 at any locus increases with the number of individuals carrying
 119 allele A at the previous locus. This circularity is represented by the function
 120 $\beta(x, X)$, which gives the integer that is below an arbitrary value x in the set
 121 $\{1, 2, \dots, X\}$:

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

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

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

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

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

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

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

132 Because mutations occur randomly (see below), each subpopulation will evolve
 133 different consecutive sequences. These different sequences represent the unique
 134 niches constructed by subpopulations.

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

136 Cooperation benefits a subpopulation by enabling it to reach greater density.
 137 This benefit affects all individuals equally and accumulates linearly with the
 138 proportion of cooperators in the subpopulation. If p is the proportion of co-
 139 operators present at the beginning of a growth cycle, then that subpopulation

140 reaches the following size:

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

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

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

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

148 Mutation

149 For simplicity, we apply mutations after growth. Mutations occur indepen-
150 dently at each locus and cause an allelic state change. At the binary coopera-
151 tion locus, mutations occur at rate μ_c . These mutations flip the allelic state,
152 causing cooperators to become defectors and vice versa. Mutations occur at
153 rate μ_a at each adaptive locus. These mutations replace the existing allele
154 with a random selection from the set $\{0\} \cup \{1, 2, \dots, A\}$.

155 **Migration**

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

163 **Population Initialization and Simulation**

164 At the beginning of each simulation, subpopulations are seeded at all patches
165 with cooperator proportion p_0 and grown to density $S(p_0)$. An environmental
166 challenge is then introduced, which subjects all subpopulations to a bottleneck.
167 For each individual, the probability of survival is μ_t , which represents the
168 likelihood that tolerance arises via mutation. Because individuals have not yet
169 adapted to this new environment, the allelic state of each individual's genotype
170 is 0 at each adaptive locus. Following initialization, simulations are run for T
171 cycles, where each discrete cycle consists of subpopulation growth, mutation,
172 migration, and dilution. Dilution thins the population to support growth in
173 the next cycle. Each individual remains with probability d , regardless of allelic
174 state.

175 Simulation Source Code and Software Dependencies

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

181 Results

182 Using the model described in the previous section, we perform simulations
183 that follow the evolution of cooperation in a population consisting of subpopu-
184 lations that are connected by spatially-limited migration. Individuals compete
185 in these subpopulations by gaining a limited number of adaptations that con-
186 fer fitness benefits. While cooperation does not directly affect the selective
187 value of these adaptations, cooperation can have indirect effects on the adap-
188 tive process. Specifically, cooperation increases subpopulation density. As a
189 result, larger subpopulations of cooperators experience more mutational op-
190 portunities to gain adaptations. Cooperation can hitchhike along with these
191 adaptations, which compensate for the cost of cooperation. During this pro-
192 cess, subpopulations alter their local environments, which, in turn, influences
193 selection. Here, we explore how niche construction affects the evolution of
194 cooperation in the simulation environment defined by the parameter values

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

195 listed in Table 1.

196 Cooperation Persists with Niche Construction

197 Without any opportunity for adaptation ($L = 0$), cooperators are swiftly elim-
198 inated in competition with defectors (Figure 2A). Despite an initial lift in
199 cooperator abundance due to increased productivity, the cost of cooperation
200 becomes disadvantageous as migration mixes the initially isolated subpopu-
201 lations. When there are opportunities for adaptation ($L = 5$) but no niche
202 construction ($\epsilon = 0$), cooperators are maintained transiently (Figure 2B). Here,
203 larger cooperator subpopulations can more quickly adapt to their environment
204 as before. As previously described by Hammarlund et al. (2015), however,
205 cooperation is subsequently lost once populations become fully adapted to
206 their environment. Once this has occurred, adapted defectors that arise via
207 mutation at the cooperation locus have a selective advantage and displace
208 cooperators. However, when niche construction creates selective feedbacks, co-
209 operation persists in over 2/3 of the replicate populations (Figure 2C). We see
210 in Figure 3A that despite oscillations, cooperation is maintained at high levels
211 in these populations.

212 Fitness Increases Alone do not Support Persisting Coop- 213 eration

214 In the model, both adaptation and niche construction contribute to an indi-
215 vidual's fitness. To determine whether cooperation is maintained solely due to

the larger selective values that result from the contributions of niche construction (ϵ), we performed simulations in which these contributions were removed ($\epsilon = 0$), and we instead increased the fitness benefits conferred by adaptation ($\delta = 0.6$). In doing so, we conservatively estimate the selective effects of niche construction, as fitness benefits of this magnitude would only be given for sequential allelic states that are fixed in fully-populated subpopulations. We find that simply increasing selective values does not enable cooperators to persist (Figure 3B). Niche construction therefore plays an important role here.

Negative Niche Construction is Critical to Cooperator Persistence

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

236 Selective Feedbacks Limit Defector Invasion

237 The adaptation resulting from selective feedbacks can limit invasion by de-
238 fectors, which arise either through immigration from neighboring patches or
239 through mutation from a cooperator ancestor. The challenge is particularly
240 threatening, as they are equally adapted, yet do not incur the cost of coopera-
241 tion. When isogenic defectors (i.e., defectors with identical adaptive loci) are
242 introduced at a single patch in the center of an 11×11 population of cooperator
243 subpopulations, they quickly spread if no mutations are allowed (Figure 4A).
244 However, when resident cooperators can adapt (mutations occur at adaptive
245 loci), cooperators evade defector invasion in over half of the replicate pop-
246 ulations (Figure 4B). Figure 5 depicts one such instance where cooperators
247 gained an adaptation that stopped and eliminated invading defectors. We
248 further highlight this process in Figure 4C, where an adapted cooperator can
249 rapidly invade a population of defectors.

250 The Rate of Niche Construction Matters

251 TODO: defector can invade a diverse population of cooperators, while adapta-
252 tion to an isogenic defector can't spread to stop invasion.

253 Discussion

254 Despite their negative effects, deleterious traits can rise in abundance due to
255 genetic linkage with other traits that are strongly favored by selection (May-

256 nard Smith and Haigh, 1974). In a process termed the “Hankshaw effect”,
257 Hammarlund et al. (2015) recently demonstrated that cooperation can pro-
258 long its existence by increasing the likelihood of hitchhiking with a beneficial
259 trait. While this process does favor cooperation in the short term, it eventually
260 reaches a dead end; when the opportunities for adaptation are exhausted, and
261 cooperators can no longer hitchhike, they face extinction. In this work, we
262 have considered whether niche construction might serve to perpetually gener-
263 ate new adaptive opportunities, and thus favor cooperation indefinitely.

264 When niche construction occurs, cooperation can indeed persist (Figure 2C). In
265 our model, niche construction introduces additional selective effects that could
266 influence the evolutionary process, leading to a more pronounced Hankshaw
267 effect. However, simply raising the selective benefits provided by adaptations
268 does not prolong cooperation (Figure 3B), and indicates that niche construc-
269 tion plays an important role.

270 We find that cooperator success is due to niche construction. Further, we find
271 that it is specifically negative niche construction that maintains cooperation
272 (Figure 3C). Without adaptive opportunities, adaptation eventually grinds to
273 a halt. Once this occurs, cooperators face the threat of invasion by defectors
274 that arise de novo through mutation. Since these defectors are equally adapted
275 but do not bear the cost of cooperation, they quickly drive cooperators to ex-
276 tinction. Because every type constructs an environment in which a different
277 type is more fit, negative niche construction creates continual adaptive op-
278 portunities. These opportunities can allow cooperators to resist invasion by
279 defectors, even when defectors are equally adapted (Figure 4B). It is these

recurring cycles of invasion and adaptation that underlie the oscillations in
cooperator populations that we see in [Figure 3A](#). Here we observe another
facet of the Hawkshaw effect: because populations of cooperators are larger,
they are better able to respond to the adaptive opportunities that result from
negative niche construction. When cooperators are not able to stochastically
gain adaptations, defectors invade, and the cycle is broken.

TODO: diversity results TODO: references about diversity

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

303 By their very nature, public goods benefit populations by making their envi-
 304 ronment more hospitable (West *et al.*, 2007a). For example, bacteria produce
 305 a host of extracellular products that scavenge soluble iron (Griffin *et al.*, 2004),
 306 digest large proteins (Diggle *et al.*, 2007; Darch *et al.*, 2012), and reduce the
 307 risk of predation (Cosson *et al.*, 2002). While many studies have focused on
 308 how the environment affects the evolution of cooperative behaviors such as
 309 the production of these public goods, relatively few have examined how the
 310 resulting selective feedbacks influence evolution as public goods modify the
 311 environment. In these instances, environmental changes are likely to occur
 312 on different timescales than reproduction. These differences can have pro-
 313 found effects. For example, a multitude of factors including protein durabil-
 314 ity (Brown and Taddei, 2007; Kümmerli and Brown, 2010), diffusion (Allison,
 315 2005; Driscoll and Pepper, 2010), and resource availability (Zhang and Rainey,
 316 2013; Ghoul *et al.*, 2014) influence both the rate and the degree to which public
 317 goods alter the environment. Lehmann (2007) demonstrated that cooperative,
 318 niche constructing behaviors can be favored when they affect selection for
 319 future generations. When this occurs, conflict among contemporary kin is re-
 320 duced. The evolutionary inertia that this creates, however, may ultimately
 321 work against cooperators. When public goods accumulate in the environment,
 322 cooperators must decrease production to remain competitive (Kümmerli and
 323 Brown, 2010; Dumas and Kümmerli, 2012). This favors cooperation that oc-
 324 curs facultatively, perhaps by sensing the abiotic (Bernier *et al.*, 2011; Koestler
 325 and Waters, 2014) or biotic environment (Brown and Johnstone, 2001; Darch
 326 *et al.*, 2012).

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

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349 Figures

350 Figure 1

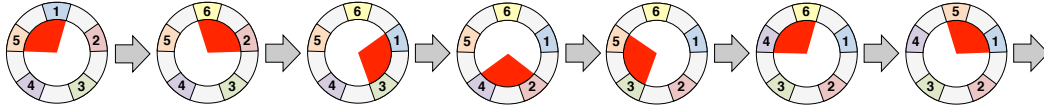


Figure 1: Negative niche construction is illustrated for the case of five adaptive loci ($L = 5$) and six alleles ($A = 6$). The adaptive loci are wrapped into a circle, where niche construction at each locus influences selection at the next locus in the clockwise direction. Suppose we start with a population 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.

351 **Figure 2**

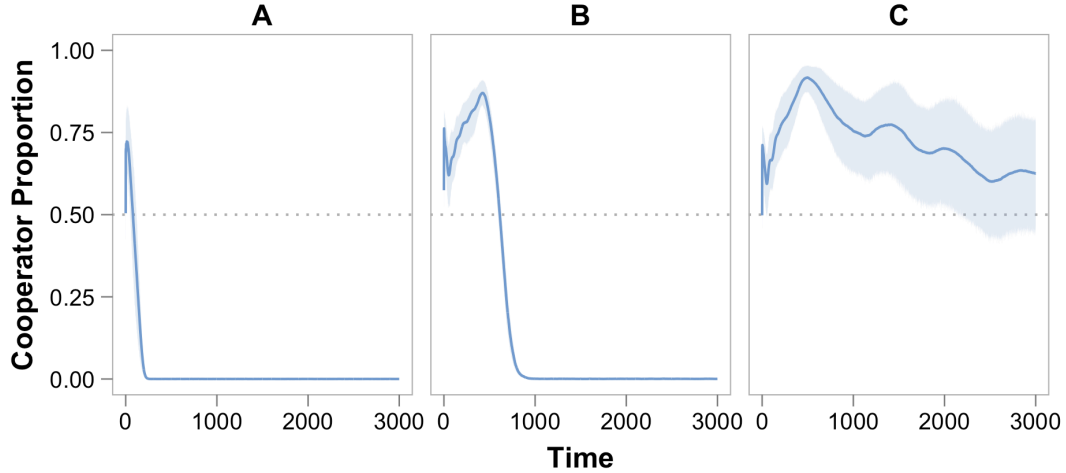


Figure 2: Adaptation, Hitchhiking, and the Evolution of Cooperation. The proportion of cooperators present in the population is shown for the duration of simulations. Curves show the average among replicate populations, and shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter 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. **(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.

352 **Figure 3**

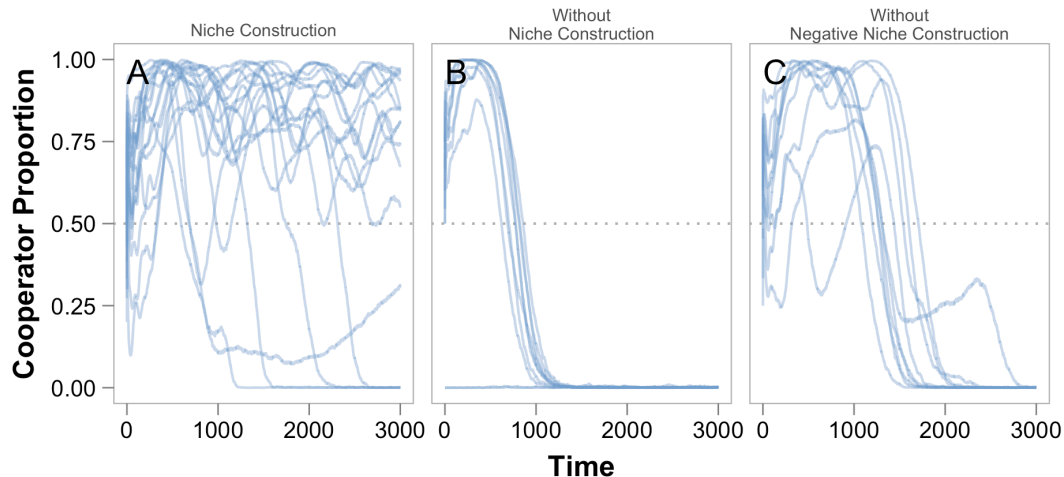


Figure 3: **Niche Construction and the Evolution of Cooperation.** The proportion of cooperators present in each replicate population is shown for the duration of simulations. **(A)** Despite some oscillations, niche construction enables cooperation to be maintained indefinitely in 14 of 18 populations. **(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 ($A = 5$).

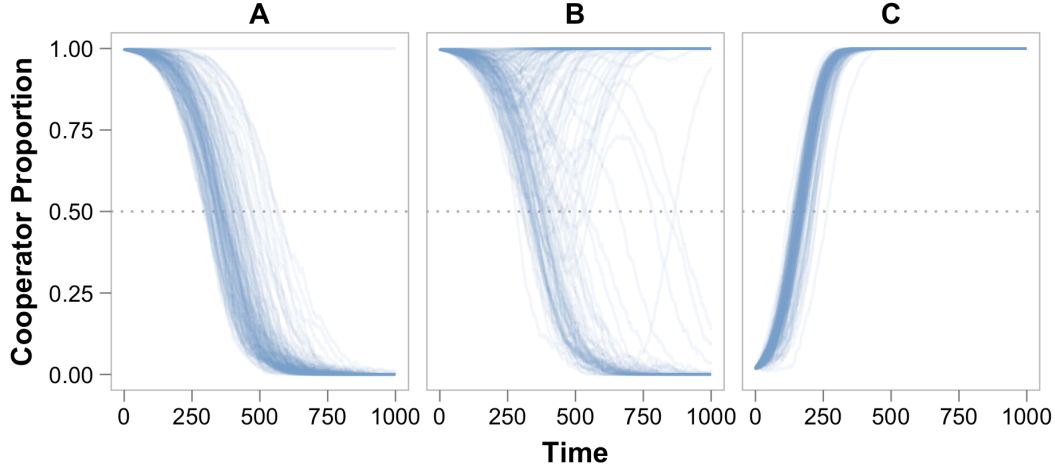
Figure 4

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.

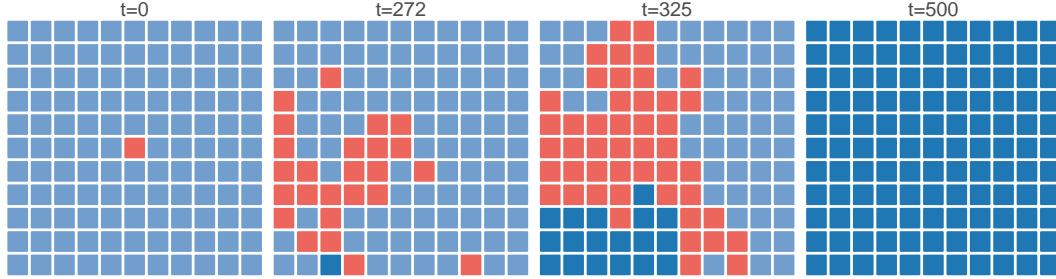
Figure 5

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.

355 **Figure 6**

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

³⁵⁸ **Supplemental Figure 1**

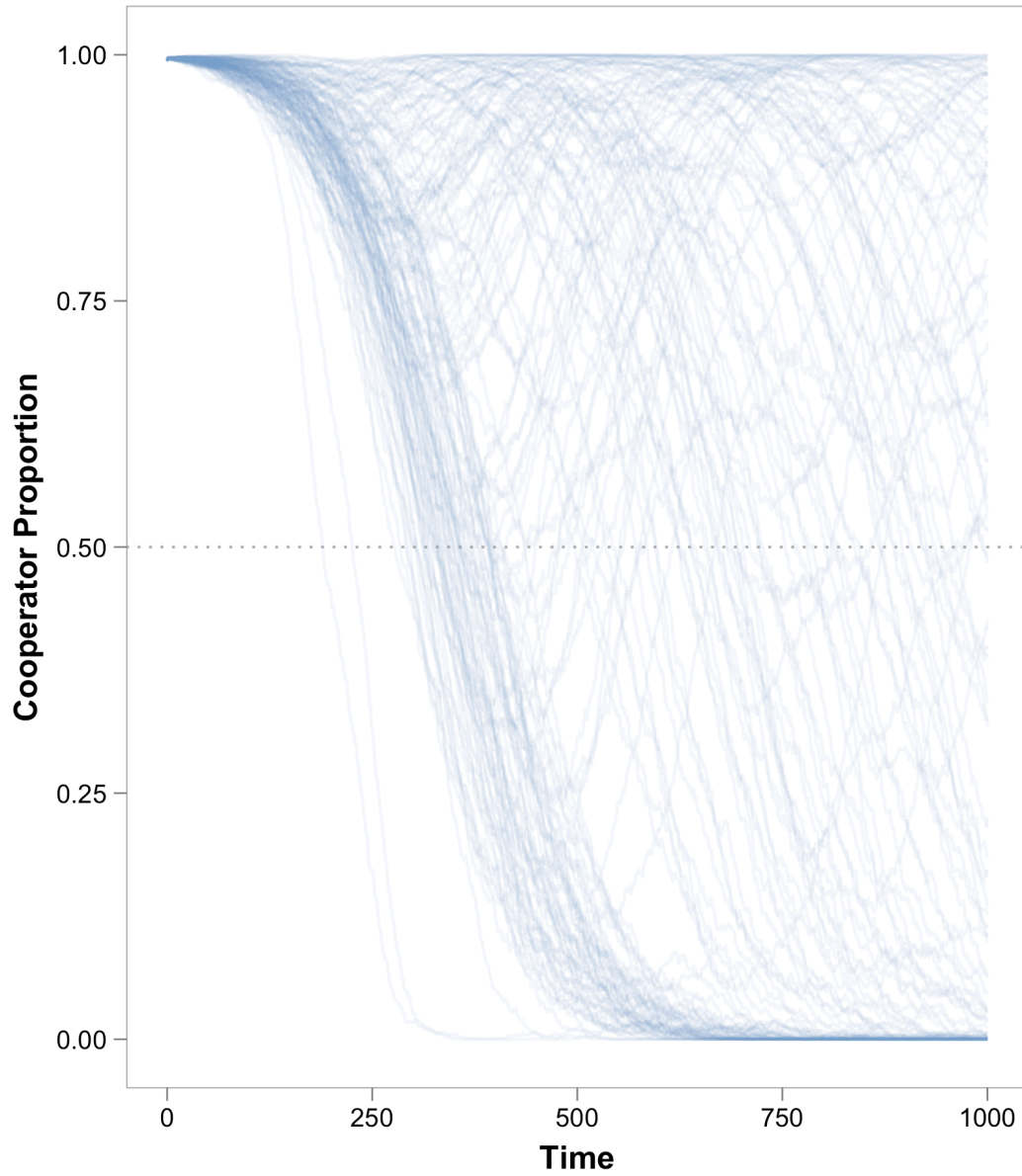


Figure S1: **Defector Invasion with Mutations.** With mutations occurring both at the adaptive loci and the cooperation locus ($\mu_a = \mu_c = 0.00005$), cooperation remains the dominant strategy in 58 replicate simulations. Curves trace the proportion of cooperators present in the population for the 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 subpopulation size	800
S_{max}	Maximum subpopulation size	2000
μ_a	Mutation rate (adaptation)	10^{-5}
μ_c	Mutation rate (cooperation)	10^{-5}
N^2	Number of patches	625
m	Migration rate	0.05
p_0	Initial cooperator proportion	0.5
μ_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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