

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

55 Here, we explore whether the selective feedbacks that result from niche con-
56 struction can prolong cooperation. We build upon the model presented by
57 Hammarlund et al. (2015) to allow populations to modify their local environ-
58 ments in ways that affect fitness. We first use this model to address whether
59 niche construction can extend the 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 **Methods**

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

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

79 **Model Description**

80 **Individual Genotypes and Adaptation**

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

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

94 Niche Construction and Selective Feedbacks

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

135 **Mutation**

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

144 **Migration**

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

152 **Metapopulation Initialization and Simulation**

153 Metapopulations are initiated in a state that follows an environmental change,
154 which leaves most patches empty. First, populations are seeded at all patches
155 with cooperator proportion p_0 and grown to density $S(p_0)$. An environmental

challenge is then introduced, which subjects all populations to a bottleneck. For each individual, the probability of survival is μ_t , which represents the likelihood that tolerance to the new environmental conditions arises via mutation. Because individuals have not yet adapted to this new environment, the allelic state of each individual's genotype is 0 at each adaptive locus. Following initialization, simulations are run for T cycles, where each discrete cycle consists of population growth, mutation, and migration. At the end of each cycle, populations are thinned to allow for growth in the next cycle. Each individual persists with probability d , regardless of allelic state.

Source Code and Software Environment

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

Results

Using the model described in the previous section, we perform simulations that follow the evolution of cooperation in a metapopulation consisting of populations connected by spatially-limited migration. Individuals compete in these populations by gaining a limited number of adaptations that confer fit-

ness benefits. While cooperation does not directly affect the selective value of these adaptations, cooperation can have indirect effects on the adaptive process. Specifically, cooperation increases population density. As a result, larger populations of cooperators experience more mutational opportunities to gain adaptations. Cooperation can hitchhike along with these adaptations, which compensate for the cost of cooperation. During this process, populations alter their local environments, which, in turn, influences selection. Here, we explore how niche construction affects the evolution of cooperation in the simulation environment defined by the parameter values listed in [Table 1](#).

Cooperation Persists with Niche Construction

Without any opportunity for adaptation ($L = 0$), cooperators are swiftly eliminated in competition with defectors ([Figure 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 previously described by Hammarlund et al. (2015), however, cooperation is subsequently lost once populations become fully adapted to their environment. Once this has occurred, adapted defectors that arise via mutation at the cooperation locus have a selective advantage and drive cooperators from the population. However, when niche construction creates selective feedbacks, cooperation per-

198 sists in 13 of 18 replicate populations (Figure 3A).

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 (ϵ), we performed simulations in which these contributions were removed
205 ($\epsilon = 0$), and we instead increased the fitness benefits conferred by adaptation
206 ($\delta = 0.6$). In doing so, we conservatively mimic the selective effects of niche
207 construction, as fitness benefits of this magnitude would only be given for se-
208 quential allelic states that are fixed in full populations. We find that simply
209 increasing selective values does not allow cooperators to persist (Figure 3B).

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

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

218 This allelic conflict exists with our base parameter values (Table 1), where
 219 $L = 5$ and $A = 6$. Here, a mutation that produces genotype $[1, 2, 3, 4, 6]$ is
 220 beneficial in a population where $[1, 2, 3, 4, 5]$ has fixed, as a 6 at the last locus
 221 precedes the 1 at the first locus. However, once $[1, 2, 3, 4, 6]$ fixes, genotype
 222 $[1, 2, 3, 5, 6]$ will be favored, and so on. When we remove negative niche con-
 223 struction ($L = 5$, $A = 5$), cooperators are again driven to extinction after
 224 an initial lift in abundance (Figure 3C). Here we observe that because niche
 225 construction presents additional opportunities for hitchhiking, the Hanksaw
 226 effect extends the initial lift in cooperation. However, once a genotype with
 227 sequential allelic states fixes, cooperation...

228 **Selective Feedbacks Limit Defector Invasion**

229 The adaptation resulting from selective feedbacks can limit invasion by de-
 230 fectors, which arise either through immigration from neighboring patches or
 231 through mutation from a cooperator ancestor. The challenge is particularly
 232 threatening, as they are equally adapted, yet do not incur the cost of coopera-
 233 tion. When homologous defectors (i.e., defectors with identical adaptive loci)
 234 are introduced as a single population in the center of an 11×11 metapopulation
 235 of cooperators, they quickly spread (Figure 4A). However, when resident co-
 236 operators can adapt and respond to defector invasion, the situation improves
 237 dramatically, allowing cooperation to evade defector invasion in 91 of 160 repli-
 238 cate simulations (57%; Figure 4B). Figure 5 depicts one such instance where
 239 cooperators gained an adaptation that stopped and eliminated invading de-

240 defectors. We further highlight this process in [Figure 4C](#), where an adapted
241 cooperator genotype can rapidly invade a population of defectors.

242 **Diversity Hampers the Evolution of Cooperation**

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

245 **Discussion**

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

256 When niche construction occurs, cooperation can indeed persist ([Figure 3A](#)). In
257 our model, niche construction introduces additional selective effects that could
258 influence the evolutionary process, leading to a more pronounced Hankshaw
259 effect. However, simply raising the selective benefits provided by adaptations

260 does not prolong cooperation (Figure 3B), and indicates that niche construc-
261 tion plays an important role.

262 We find that cooperator success is due to niche construction. Further, we
263 find that it is specifically negative niche construction that maintains coopera-
264 tion (Figure 3C). Without adaptive opportunities, adaptation eventually slows.
265 Once this occurs, cooperators face the threat of invasion by defectors that arise
266 de novo through mutation. Since these defectors are equally adapted but do
267 not bear the cost of cooperation, they are favored by selection, and quickly
268 drive cooperators to extinction. By reducing fitness, negative niche construc-
269 tion creates adaptive opportunities. These opportunities can allow cooperators
270 to resist invasion by defectors, even when defectors are equally adapted (Figure
271 4B). Here we observe another facet of the Hankshaw effect: because popula-
272 tions of cooperators are larger, they are better able to respond to the adaptive
273 opportunities that result from negative niche construction.

274 TODO: diversity results TODO: references about diversity

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

283 be considered deleterious, so introducing selective feedbacks from cooperation
284 could further bolster cooperation. Van Dyken and Wade (2012) showed that
285 when two cooperative behaviors co-evolve and niche construction feedbacks
286 benefit the other type, niche construction can increasingly favor these traits,
287 which were otherwise disfavored when alone. Arguably, this can be viewed
288 as another instance of hitchhiking: the maladaptive form of cooperation is
289 maintained by association with the adaptive form. However, negative niche
290 construction then reverses these roles and perpetuates the cycle.

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

307 future generations. When this occurs, conflict among contemporary kin is re-
308 duced. The evolutionary inertia that this creates, however, may ultimately
309 work against cooperators. When public goods accumulate in the environment,
310 cooperators must decrease production to remain competitive (Kümmerli and
311 Brown, 2010; Dumas and Kümmerli, 2012). This favors cooperation that oc-
312 curs facultatively, perhaps by sensing the abiotic (Bernier *et al.*, 2011; Koestler
313 and Waters, 2014) or biotic environment (Brown and Johnstone, 2001; Darch
314 *et al.*, 2012).

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

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335 BK).

336 **Figures**

337 **Figure 1**

338 TODO: diagram of model

339 **Figure 2**

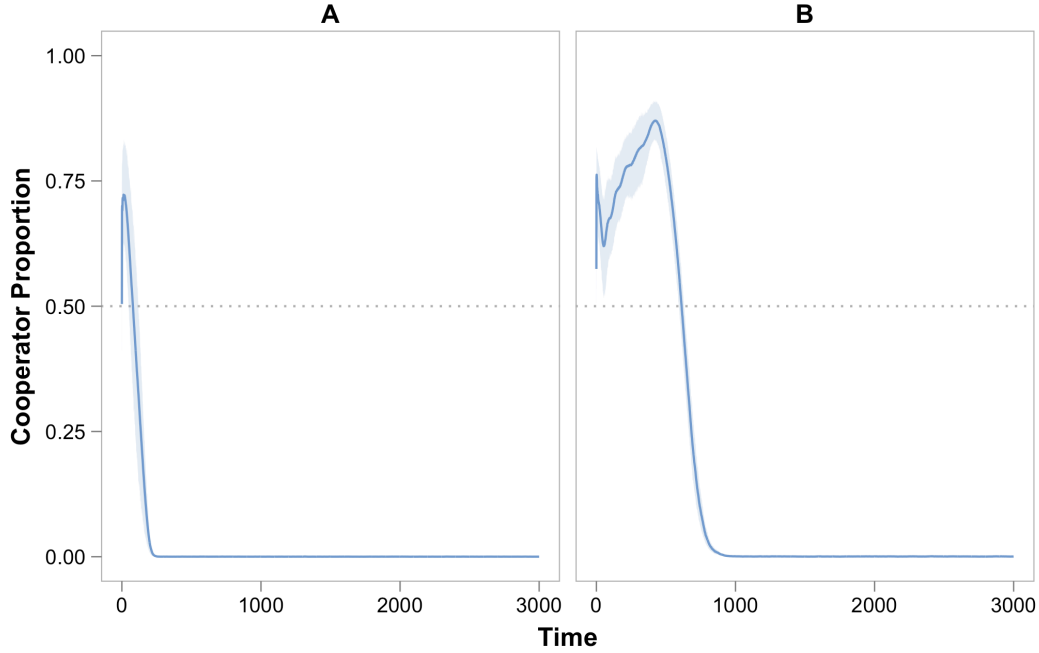


Figure 1: Adaptation, Hitchhiking, and the Evolution of Cooperation. The proportion of cooperators present in the population is shown for the duration of simulations. Curves show the average among replicate populations, and shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter values are listed in [Table 1](#). **(A)** Without any opportunity to adapt (L , the number of adaptive loci, is zero), cooperation is quickly lost. **(B)** When adaptation can occur ($L = 5$), but populations do not alter their environment (ϵ , the intensity of niche construction, is zero), cooperation hitchhikes along with adaptations, allowing cooperators to temporarily rise in abundance before eventually going extinct.

340 **Figure 3**

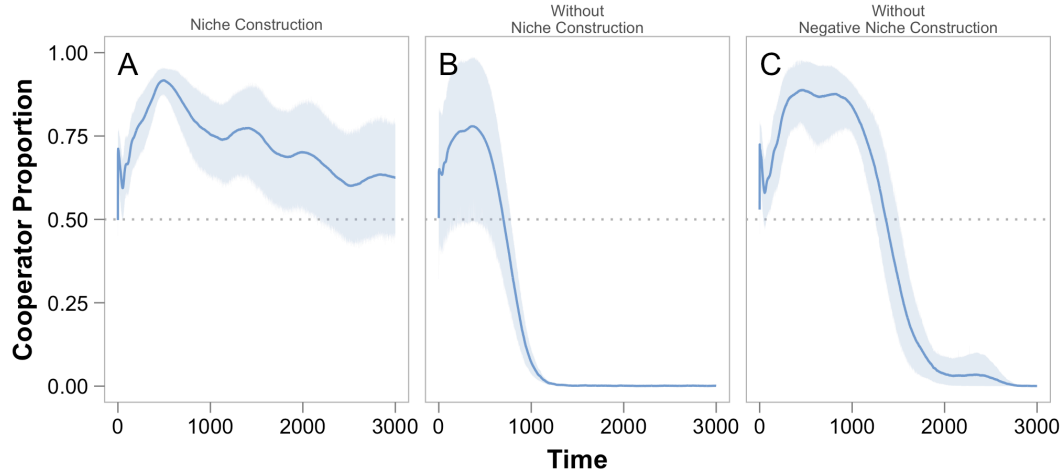


Figure 2: Niche Construction and the Evolution of Cooperation. The proportion of cooperators present in the population is shown for the duration of simulations. Curves show the average among replicate populations, and shaded areas indicate 95% confidence intervals. **(A)** Niche construction enables cooperation to be maintained indefinitely. In the majority of populations (13/18), cooperation remained the dominant strategy. **(B)** When niche construction is removed and the fitness benefit of adaptation is increased as compensation ($\epsilon = 0$, $\delta = 0.6$), adapted defectors arise and drive cooperators to extinction. **(C)** Without negative niche construction, cooperation is not maintained ($A = 5$). Here again, cooperators are at a selective disadvantage against equally-adapted defectors that arise via mutation.

341 **Figure 4**

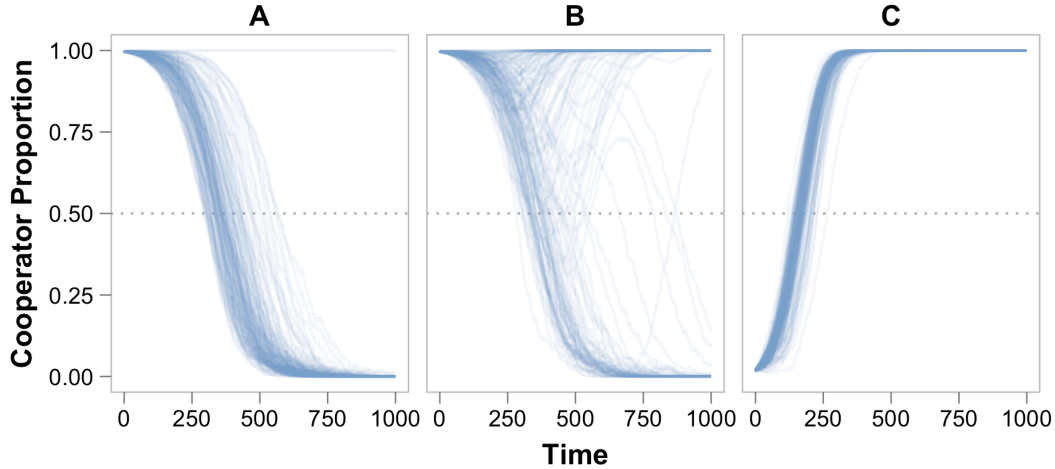


Figure 3: **Niche Construction and Invasion.** Curves trace the proportion of cooperators present in the population for the duration of 160 replicate simulations ($T = 1000$). These experiments examine whether a rare cooperator or defector strategy can invade when initiated at a single population in 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. This limitation is removed in the results shown in Figure SX. **(A)** When cooperators and defectors are matched (i.e., genotypes $[1,2,3,4,5]$) and adaptation 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.

342 **Figure 5**

343 TODO: snapshots of cooperators adapting to thwart defector invasion

344 **Figure 6**

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

³⁴⁷ **Supplemental Figure 1**

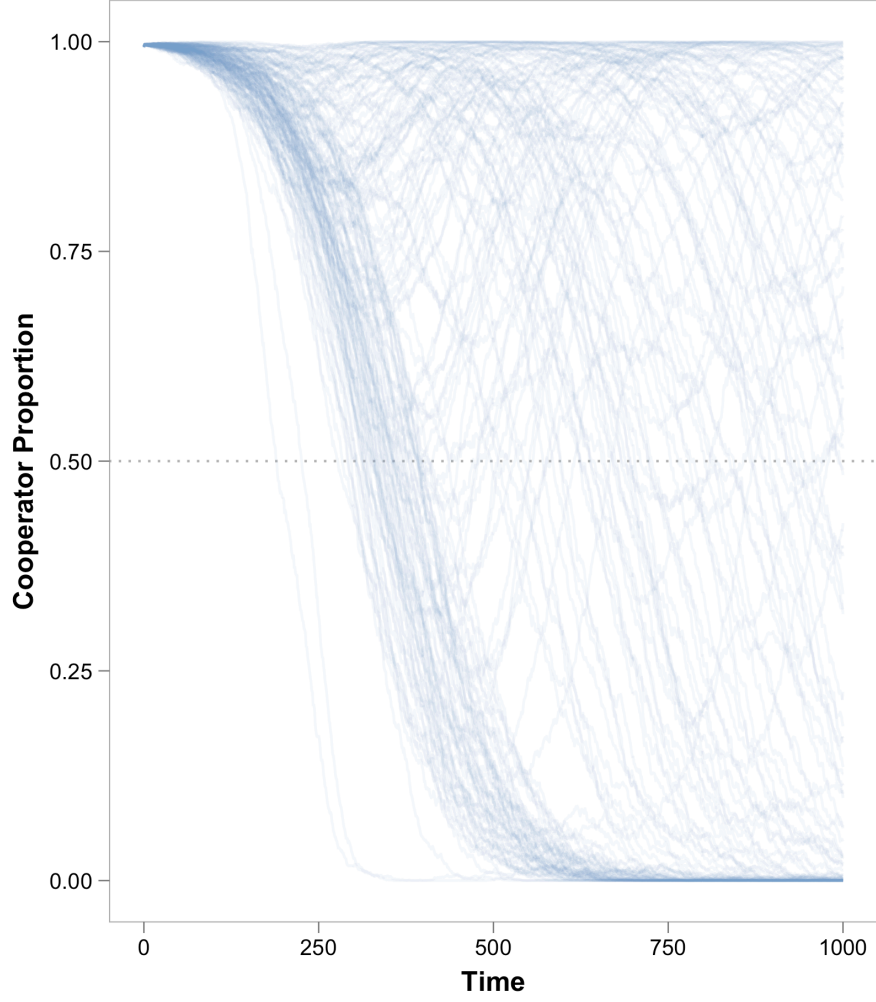


Figure S1: **Defector Invasion with Mutations.** With mutations occurring both at the adaptive loci and the cooperation locus ($\mu_a = \mu_c = 0.00005$), cooperation remains the dominant strategy in 58 replicate simulations. Curves trace the proportion of cooperators present in the population for the 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
p_0	Initial cooperator proportion	0.5
μ_t	Mutation rate (tolerance to new environment)	10^{-5}
d	Population dilution factor	0.1
T	Number of simulation cycles	3000

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