

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

4
5 **Abstract**

6 TODO

7 **Introduction**

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

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

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

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

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

56 Here, we explore whether the selective feedbacks that arise during niche con-
57 struction can indefinitely maintain cooperation. We expand the model pre-
58 sented by Hammarlund et al. (2015) to allow populations to modify their
59 local environments in ways that affect fitness. We first use this model to ad-
60 dress whether niche construction can prolong the Hanksaw effect, allowing
61 cooperation to keep hitchhiking as populations continually adapt. We then
62 focus on how niche construction influences outcomes when isolated coopera-
63 tor populations encounter populations of defectors, either through migration
64 or through mutations that inevitably produce defectors that share the same

65 adaptations. Finally, niche construction has frequently been shown to increase
66 diversity (???). We explore whether this diversity helps or hinders the evolu-
67 tion of cooperation.

68 **Methods**

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

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

80 **Model Description**

81 **Individual Genotypes and Adaptation**

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

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

95 **Niche Construction and Selective Feedbacks**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

136 **Mutation**

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

145 **Migration**

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

153 **Metapopulation Initialization and Simulation**

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

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

Source Code and Software Environment

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

Results

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, affects selection. Here, we explore how niche construction influences the evolution of cooperation in the simulation environment defined by the parameter values listed in [Table 1](#).

Niche Construction Maintains Cooperation

Without any opportunity for adaptation ($L = 0$), cooperators are swiftly eliminated in competition with defectors ([Figure 1A](#)). Despite an initial lift 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 1B](#)). 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 persists in 13 of 18 repli-

199 cate populations (Figure 2A).

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

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

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

214 **Negative Niche Construction is Critical to Cooperator** 215 **Persistence**

216 Negative niche construction occurs in our model due to selection for
217 sequentially-increasing allelic states and the circular arrangement of these
218 alleles. When the genome length (L) is not evenly divided by the number

219 of adaptive alleles (A), then it is not possible for the population to be fixed
 220 for a genotype that is perfectly adapted to the constructed environment.
 221 Technically (in terms of the model) this is because the equality:

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

222 cannot simultaneously hold for all l .

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

228 We first focus on the effects of positive niche construction by removing the
 229 allelic conflict that leads to negative niche construction ($L = 5$, $A = 5$). In
 230 the absence of this conflict, cooperator presence is significantly increased (Fig-
 231 ure 2C). Within these environments, we find that positive niche construction
 232 prolongs the fitness advantage that cooperators have over defectors (Figure
 233 3C).

234 **Positive niche construction is important to cooperator** 235 **persistence**

236 To determine how negative niche construction influences the evolution of co-
 237 operation, we maximize the allelic conflict ($L = 1$, $A = 6$). Here, selection for

238 increasing allelic states among the adaptive loci means that any allelic state
239 will not be greater than at the previous allele (itself), and thus there will al-
240 ways be opportunity for adaptation. Despite this constant opportunity, niche
241 construction does not increase cooperator presence (Figure 2D).

242 **NC Enables Cooperator Spread**

243 Figure 4 - if not, could be why thinning is a must.

244 **NC Prevents Defector Invasion**

245 Figure 5

246 **How Cooperation Fuels all of this**

247 To directly explore how the increase in population size affects evolutionary
248 outcomes, we vary the maximum size that a population can reach (S_{max} , see
249 Equation 4). Figure 6A shows the result of these simulations. (**TODO** de-
250 scription of results)

251 To address how migration affects the evolutionary process in this system, we
252 vary the rate at which migration occurs (m). As seen in Figure 6B, cooperation
253 decreases as migration rate increases. This is likely because migration defines
254 the spatial structuring in this system. As migration increases, the population
255 becomes more like a well-mixed system, where defectors are better able to

256 exploit the benefits of cooperation (Griffin *et al.*, 2004; Kümmerli *et al.*, 2009).

257 # Discussion

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

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

280 (Figure 3E), negative niche construction acts to prevent this stasis. Combined,
281 we find that both positive and negative niche construction are required to main-
282 tain cooperation.

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

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

300 In our model, the environmental state was implicitly modeled, and depended
301 solely on the current state of the population. In natural settings, however, the
302 timescales at which environments are modified and reproduction are likely to

303 be decoupled. For example, a multitude of factors including protein durabil-
 304 ity (Brown and Taddei, 2007; Kümmerli and Brown, 2010), diffusion (Allison,
 305 2005; Driscoll and Pepper, 2010), and resource availability (Zhang and Rainey,
 306 2013; Ghoul *et al.*, 2014) influence both the rate and the degree to which public
 307 goods alter the environment. These factors are likely to influence evolution-
 308 ary trajectories (Laland *et al.*, 1996). Lehmann (2007) demonstrated that a
 309 cooperative, niche constructing behavior can be favored when it only affected
 310 selection for future generations, thus reducing the potential for competition
 311 among contemporary kin. The evolutionary inertia that this creates, however,
 312 may ultimately work against cooperators. When public good accumulates in
 313 the environment, cooperators must reduce their investment in production to re-
 314 main competitive (Kümmerli and Brown, 2010; Dumas and Kümmerli, 2012).
 315 Cooperation that occurs facultatively, perhaps by sensing the abiotic (Bernier
 316 *et al.*, 2011; Koestler and Waters, 2014) or biotic environment (Brown and
 317 Johnstone, 2001; Darch *et al.*, 2012), are likely to be favored in these environ-
 318 ments.

319 In many instances of cooperation, the environment is itself a biological entity,
 320 which can produce additional evolutionary feedbacks. As the host population
 321 changes, so too will selection on their symbiont populations. Here, evolution-
 322 ary outcomes depend greatly on the degree of shared interest between the host
 323 and symbiont. For example, the cooperative production of virulence factors by
 324 the human pathogen *P. aeruginosa* in lung infections is harmful to those with
 325 cystic fibrosis (Harrison, 2007). Conversely, cooperative light production by *A.*
 326 *fisheri* 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 produce into models is likely to be equally important for gaining an understanding of how cooperative behaviors evolve in these host-symbiont settings.

Acknowledgments

We thank Anuraag Pakanati for assistance with simulations. This material is based upon work supported by the National Science Foundation Postdoctoral Research Fellowship in Biology under Grant No. DBI-1309318 (to BDC) and under Cooperative Agreement No. DBI-0939454 (BEACON STC). Computational resources were provided by an award from Google (to BDC and BK).

340 Figures

341 **Figure 1**

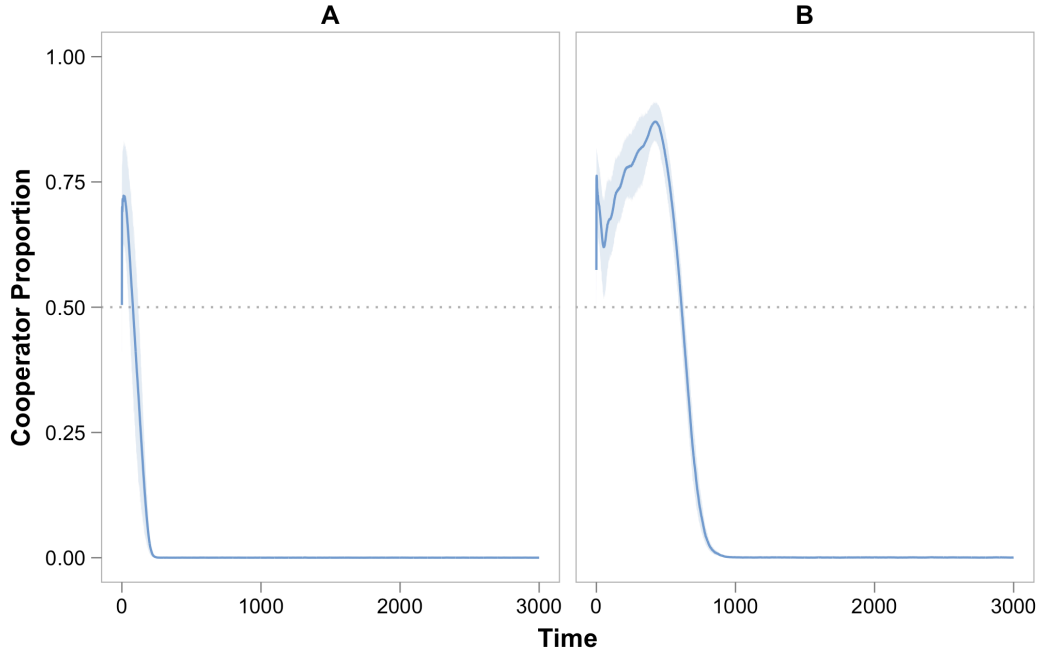


Figure 1: **Adaptation, Hitchhiking, and the Evolution of Cooperation.** The proportion of cooperators present in the population is shown for the duration of simulations. Curves show the average among replicate populations, and shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter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

342 **Figure 2**

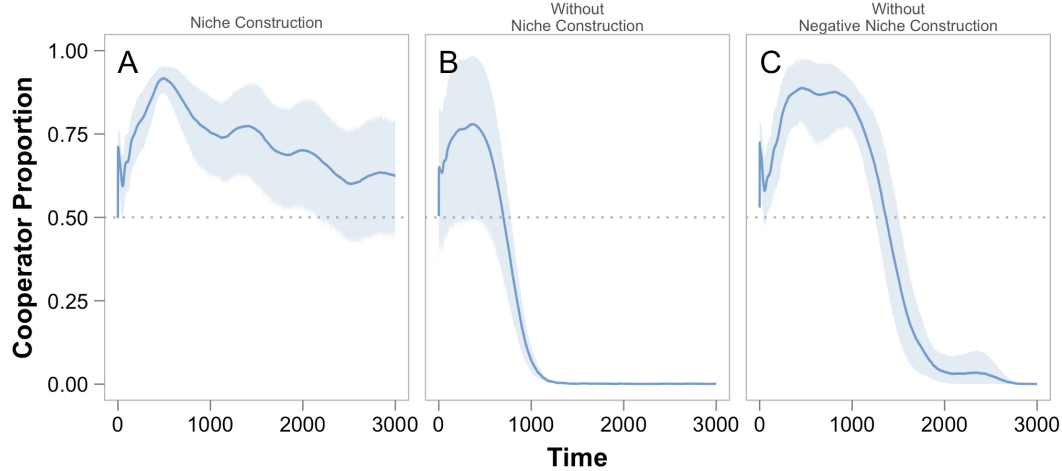


Figure 2: Niche Construction and the Evolution of Cooperation. The proportion of cooperators present in the population is shown for the duration of simulations. Curves show the average among replicate populations, and shaded areas indicate 95% confidence intervals. **(A)** Niche construction enables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

343 **Figure 3**

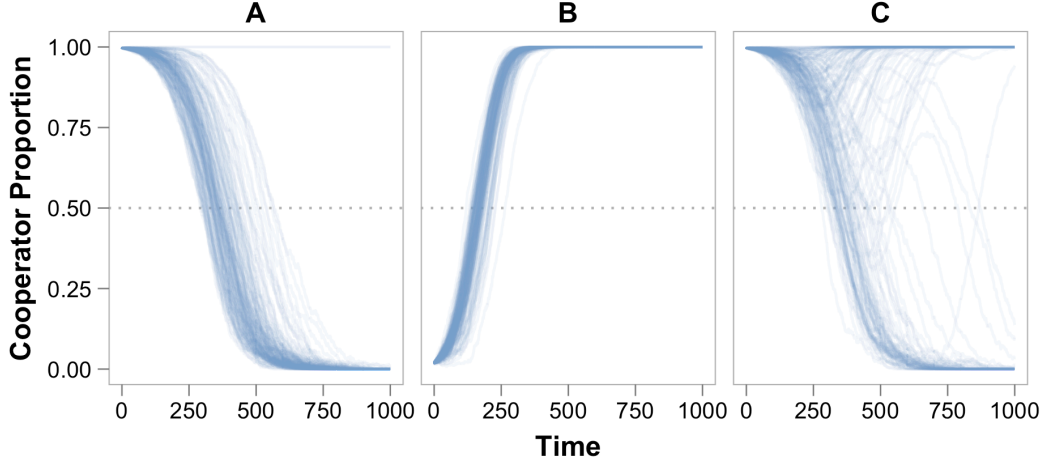


Figure 3: **Niche Construction and Invasion.** Curves trace the proportion of cooperators present in the population for the duration of 160 replicate simulations. These experiments examine whether a strategy initiated at a single population in the center of the metapopulation lattice ($N^2 = 121$) can invade. Unless otherwise noted, we disable mutations ($\mu_a = 0, \mu_c = 0$) to focus on how invasion depends on particular combinations of genotypes. **(A)** When cooperators and defectors are matched (i.e., genotypes $[1,2,3,4,5]$) and adaptation can not occur, defectors quickly drive cooperators to extinction due to the cost of cooperation. Defectors were stochastically eliminated in 2 replicate populations. **(B)** However, the adaptive opportunities produced by negative niche construction and density dependence enable an adapted cooperator (genotype $[1,2,3,4,6]$) to invade a population of defectors. **(C)** These same adaptive opportunities can allow cooperators to resist invasion by initially-matching defectors, which arise via mutation and remain a constant threat. Here, cooperation persisted in 91 populations ($\mu_a = 0.00005$, the base mutation rate).

Table 1: Model parameters and their value

Parameter	Description	Base Value
L	Number of adaptive loci	5
c	Fitness cost of cooperation	0.1
A	Number of alleles	6
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	1000

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