

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.*, 2007). 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 al.*,
23 2006; Gardner and West, 2010; Veelders *et al.*, 2010) to cooperate condition-
24 ally with kin. Cooperation can also be bolstered by pleiotropic connections to
25 personal benefits (Foster *et al.*, 2004; Dandekar *et al.*, 2012) or through associ-
26 ation with alleles encoding self-benefitting traits (Asfahl *et al.*, 2015). In these
27 cases, the alleles may provide private benefits that are completely independent
28 from the public benefits of cooperation. In asexual populations of cooperators

29 and defectors, this sets the stage for an “adaptive race” in which both types
30 vie for the first highly beneficial adaptation (Waite and Shou, 2012; Morgan
31 *et al.*, 2012). The tragedy of the commons can be deferred if a cooperator, by
32 chance, wins the adaptive race.

33 Hammarlund et al. (2015) recently showed that in spatially-structured pop-
34 ulations, the “Hankshaw effect” can give cooperators a substantial leg up on
35 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 rise
41 in abundance. Nevertheless, this advantage is fleeting. As soon as the oppor-
42 tunities for adaptation are exhausted, cooperators are once again at a selective
43 disadvantage against equally-adapted defectors that arise via mutation. How-
44 ever, Hammarlund et al. (2015) also demonstrated that cooperation can be
45 maintained when frequent environmental changes produce a steady stream of
46 new adaptive opportunities. Although organisms typically find themselves in
47 dynamic environments, the nature and frequency of these changes might not
48 ensure long-term cooperator survival.

49 However, organisms do more than simply experience changing environments
50 passively. Through their activities, their interactions with others, and even
51 their deaths, organisms constantly modify their environment. This niche con-
52 struction process can produce evolutionary feedback loops in which environ-

53 mental change alters selection, which, in turn, alters the distribution of types
54 and their corresponding influence on the environment (Odling-Smee *et al.*,
55 2003). The nature of this feedback can have dramatic evolutionary conse-
56 quences. One critical distinction is whether the constructing type is favored in
57 the resulting environment. Under positive niche construction, selection favors
58 the constructor, and evolution stagnates as this type fixes. Under negative
59 niche construction, selection favors a type other than the constructor, which
60 creates an opportunity for adaptation. If an adapted type also engages in
61 negative niche construction, cycles of construction and adaptation can ensue,
62 such that populations find themselves continually chasing beneficial mutations
63 as their adaptive landscape perpetually shifts.

64 Here, we show that the selective feedbacks that result from niche construction
65 can maintain cooperation indefinitely. We find that it is specifically negative
66 niche construction that is responsible for this result because of the endless
67 opportunities for adaptation that it produces. These results indicate that
68 cooperators can ensure their survival when they play an active role in their
69 own evolution.

70 **Methods**

71 Building upon Hammarlund *et al.* (2015), we describe an individual-based
72 model in which cooperators and defectors evolve and compete in a population
73 of subpopulations (i.e., a metapopulation). Through mutations, individuals
74 gain adaptations to their environment, which increase reproductive fitness,

75 and allow those lineages to rise in abundance. More successful lineages spread
76 to neighboring subpopulations by migration.

77 In this expanded model, subpopulations additionally modify their local envi-
78 ronment. As this process occurs, environmental changes feed back to affect
79 selection. We explore how niche construction affects the evolution of coop-
80 eration; specifically, how cooperative behavior can hitchhike with adaptive
81 mutations to modified environments.

82 **Model Description**

83 **Individual Genotypes and Adaptation**

84 Each individual has a haploid genome with $L + 1$ loci (see [Table 1](#) for model
85 parameters and their values). Different alleles at each locus are represented by
86 different integers. A binary allele at the first locus (here, locus zero) determines
87 whether that individual is a cooperator (1), which carries fitness cost c , or a
88 defector (0). The remaining L loci are *adaptive loci*, and are each occupied by
89 0 or a value from the set $\{1, 2, \dots, A\}$. Allele 0 represents a lack of adaptation,
90 while a non-zero allele represents one of the A possible adaptations at that
91 locus.

92 These non-zero alleles signify two types of adaptations, both of which increase
93 fitness. First, adaptations to the external environment confer a fitness benefit δ .
94 This selective value is the same regardless of which non-zero allele is present
95 and is not affected by other individuals. We assume $\delta > c$, which allows a

96 minimally adapted cooperator to recoup the cost of cooperation and gain a
97 fitness advantage.

98 **Niche Construction and Selective Feedbacks**

99 Individual fitness is also affected by aspects of the local environment that are
100 affected by organisms. We represent this constructed “niche” implicitly based
101 on the specific allelic states present in the subpopulation. As allelic states
102 change, the subpopulation alters its environment, creating a unique niche. As
103 described below, the specific alleles that are present at each locus matter.

104 In our model, the feedback from niche construction takes the form of den-
105 sity dependent selection, and individuals evolve to better match their niche.
106 Specifically, the selective value of non-zero allele a at adaptive locus l —and
107 consequently the fitness of an individual carrying that allele—increases with
108 the number of individuals in the subpopulation that have allele $a - 1$ at locus
109 $l - 1$. For example, when $L = 5$ and $A = 6$, and allele 4 has fixed at locus 2,
110 a genotype with allele 5 at locus 3 is favored. And once allele 5 has fixed at
111 locus 3, the niche that this population constructs will favor allele 6 at locus
112 4. As a consequence, genotypes with sequentially increasing allelic states will
113 tend to evolve. We treat both adaptive loci and their non-zero allelic states as
114 “circular”: the selective value of an allele at locus 1 is affected by the allelic
115 composition of the subpopulation at locus L . Similarly, the selective value
116 of allele 1 at any locus increases with the number of individuals carrying al-
117 lele A at the previous locus. This circularity is represented by the function

118 $\beta(x, X)$, which gives the integer that is below an arbitrary value x in the set
 119 $\{1, 2, \dots, X\}$:

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

120 Here, $\text{mod}_X(x)$ is the integer remainder when dividing x by X . Using this
 121 function, the selective value of allele a at adaptive locus l is increased by ϵ for
 122 each individual in the subpopulation that has allele $\beta(a, A)$ at locus $\beta(l, L)$.
 123 Thus, ϵ specifies the intensity of selection due to niche construction.
 124 Consider a genotype g with allelic state $a_{g,l}$ at locus l ; the fitness of an indi-
 125 vidual with this genotype is defined as:

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

126 where z is a baseline fitness, $n(a, l)$ is the number of individuals in the sub-
 127 population with allele a at locus l , and $I(a)$ indicates whether a given allele is
 128 non-zero:

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

129 Thus, an individual's fitness is determined both by adaptations to the exter-
 130 nal environment and by adaptations to its constructed environment. Box 1

131 illustrates the effects of these two components. While cooperation is costly, we
 132 assume its effects are independent of the external and constructed components
 133 of the environment.

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

135 Cooperation enables a subpopulation to reach a greater density. This benefit
 136 affects all individuals equally and accumulates linearly with the proportion
 137 of cooperators in the subpopulation. If p is the proportion of cooperators
 138 present at the beginning of a growth cycle, then that subpopulation reaches
 139 the following size:

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

140 During subpopulation growth, individuals compete through differential repro-
 141 duction. Each individual's probability of success is determined by its fitness.
 142 The composition of a subpopulation with size P and cooperator proportion p
 143 after growth is multinomial with parameters $S(p)$ and $\{\pi_1, \pi_2, \dots, \pi_P\}$, where
 144 π_i represents individual i 's reproductive fitness relative to others in the sub-
 145 population (using Equation 2).

146 **Mutation**

147 For simplicity, we apply mutations after subpopulation growth. Mutations
 148 occur independently at each locus and cause an allelic state change. At the

149 binary cooperation locus, mutations occur at rate μ_c . These mutations flip
 150 the allelic state, causing cooperators to become defectors and vice versa. Mu-
 151 tations occur at rate μ_a at each adaptive locus. These mutations replace the
 152 existing allele with a random selection from the set $\{0\} \cup \{1, 2, \dots, A\}$. Be-
 153 cause mutations are stochastic, the allelic sequences that evolve depend on
 154 which allele arises first and at which locus.

155 **Migration**

156 Populations are composed of 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 single
 159 destination patch is randomly chosen from each source patch's Moore neigh-
 160 borhood, which is composed of the nearest 8 patches on the lattice. Because
 161 the population lattice has boundaries, patches located on the periphery have
 162 smaller neighborhoods.

163 **Population Initialization and Simulation**

164 Following Hammarlund et al. (2015), we begin simulations with sparse pop-
 165 ulations. Subpopulations are first seeded at all patches with size $S(p_0)$ and
 166 cooperator proportion p_0 . The population is then thinned. Each individual
 167 survives this bottleneck with probability σ . Starting from this initial state,
 168 simulations then proceed for T cycles, where each discrete cycle consists of
 169 subpopulation growth, mutation, migration, and dilution. Dilution reduces

170 the population to support growth in the next cycle. Each individual remains
171 with probability d , regardless of its genotype.

172 **Simulation Source Code and Software Dependencies**

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

178 **Results**

179 Using the model described in the previous section, we perform simulations
180 that follow the evolution of cooperation in a population consisting of subpopu-
181 lations that are connected by spatially-limited migration. Individuals increase
182 their competitiveness by gaining adaptations. While cooperation does not di-
183 rectly affect the fitness benefits that these adaptations confer, cooperation has
184 indirect effects on the adaptive process. Specifically, cooperation increases
185 subpopulation density. As a result, larger subpopulations of cooperators ex-
186 perience more mutational opportunities. Cooperation can rise in abundance
187 by hitchhiking along with beneficial mutations, which compensate for the cost
188 of cooperation. Importantly, subpopulations alter their local environments,

¹These materials will be made public prior to publication.

189 which feeds back to influence selection. Here, we explore how such niche con-
190 struction affects the evolution of cooperation.

191 **Cooperation Persists with Niche Construction**

192 Without any opportunity for adaptation ($L = 0$), cooperators are swiftly elim-
193 inated in competition with defectors (Figure 1A). Despite an initial lift in
194 cooperator abundance due to increased productivity, the cost of cooperation
195 becomes disadvantageous as migration mixes the initially isolated subpopula-
196 tions. When populations can adapt to the external environment ($L = 5$ and
197 $\delta > 0$), but niche construction is absent ($\epsilon = 0$), cooperators are maintained
198 only transiently (Figure 1B). Here, larger cooperator subpopulations can more
199 quickly adapt to their external environment. However, as previously described
200 by Hammarlund et al. (2015), cooperation is subsequently lost once popula-
201 tions become fully adapted to their environment. This occurs when isogenic
202 defectors (i.e., defectors with identical adaptive loci) arise via mutation and
203 displace cooperators due to their selective advantage. However, when niche
204 construction feeds back to influence selection ($\epsilon > 0$), cooperation persists in
205 the majority of the replicate populations (Figure 1C). We see in Figure 2A that
206 despite oscillations in the proportion of cooperators, cooperation is maintained
207 at high levels in these populations.

Fitness Increases Alone do not Support Persisting Cooperation

In the model, adaptations to both the external environment and the constructed environment contribute to an individual'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 to the external, non-constructed environment ($\delta = 0.6$). In doing so, we conservatively estimate the selective effects of niche construction by supplementing the selective benefits of adaptations to the external environment by the maximum possible selective benefit that results from niche construction. Nevertheless, we find that simply increasing selective values does not enable cooperators to persist (Figure 2B). Niche construction, therefore, plays a decisive role here.

Negative Niche Construction is Critical to Cooperator Persistence

In our model, an adaptation to a constructed aspect of the environment initiates a new instance of niche construction, leading to sequentially increasing allelic states across the adaptive loci. Under certain conditions, this construction always makes the constructor suboptimal for the niche it creates (see Box 1). This negative niche construction occurs when the number of adaptive al-

229 leles (A) does not divide evenly into the number of adaptive loci (L). In such
 230 a case, any sequence of integers on the circular genome will always contain a
 231 break in the sequence; that is, one locus with an allele that is not one less than
 232 the allele at the next locus. Given this unavoidable mismatch, any type that
 233 has fixed will always construct a niche that favors selection for a new type.
 234 When negative niche construction is removed (by setting $L = 5$, $A = 5$), coop-
 235 erators are again driven extinct after an initial lift in abundance (Figure 2C).
 236 These results indicate that the type of niche construction matters. Specifically,
 237 negative niche construction is crucial for maintaining cooperation.

238 **Selective Feedbacks Limit Defector Invasion**

239 The adaptation resulting from selective feedbacks can limit invasion by de-
 240 fectors, which arise either through immigration from neighboring patches or
 241 through mutation from a cooperator ancestor. The latter challenge is par-
 242 ticularly threatening, as these isogenic defectors are equally adapted, yet do
 243 not incur the cost of cooperation. As demonstrated in Figure 3A, isogenic
 244 defectors rapidly spread when introduced at a single patch in the center of a
 245 population of cooperators if mutations do not occur. However, when coopera-
 246 tors can gain adaptations via mutation, cooperators resist defector invasion in
 247 over half of the replicate populations (Figure 3B). Figure 4 depicts one such
 248 instance. In that population, defectors quickly began to spread. However, an
 249 adaptation arose in a neighboring cooperator population. This type spreads
 250 more quickly, stopping the spread of defectors and eventually driving them to

extinction. Because this adaption occurred in a cooperator population, cooperation was able to hitchhike to safety. Importantly, this new cooperator was favored because of the niche that its ancestor created. Here, cooperators can find safety in numbers—because their larger populations have more mutational opportunities, they are more likely to gain adaptations that rescue them from invasion. Further, the larger number of cooperators more strongly construct their niche, and thus more strongly favors an adapted type. This allows that type to appear and to spread more quickly in the population. **Figure 3C** shows how quickly an adapted cooperator type can invade a population of defectors.

Discussion

Despite their negative effects, deleterious traits can rise in abundance due to genetic linkage with other traits that are strongly favored by selection (Maynard Smith and Haigh, 1974). In a process termed the “Hankshaw effect”, Hammarlund et al. (2015) recently demonstrated that cooperation can actively prolong its existence by increasing its likelihood of hitchhiking with a beneficial trait. In that work and in ours, populations of cooperators grow to a higher density than those of defectors. Because of this, these cooperator populations experience more mutations and are therefore more likely to gain adaptations. While this process does favor cooperation in the short term, it eventually reaches a dead end; when the opportunities for adaptation are exhausted and cooperators can no longer hitchhike, they face extinction. In our current model, we have considered whether niche construction might serve to

273 perpetually generate new adaptive opportunities and thus favor cooperation
274 indefinitely.

275 When niche construction occurs, cooperation can indeed persist (Figures 1C
276 and 2A). In our model, niche construction introduces additional selective ef-
277 fects that influence the evolutionary process, leading to a more pronounced
278 Hankshaw effect. However, simply raising the fitness benefits conferred by
279 adaptations does not maintain cooperators at high proportion (Figure 2B).
280 This indicates that niche construction does play a crucial role.

281 Further, we find that it is specifically *negative* niche construction that main-
282 tains cooperation (Figure 2C). As cooperator and defector types gain adapta-
283 tions, they change the environment in a way that favors other types. In this
284 way, negative niche construction serves as a perpetual source of adaptation.
285 Here we observe another facet of the Hankshaw effect: because populations
286 of cooperators are larger, they are better able to respond to the adaptive op-
287 portunities that result from negative niche construction. These opportunities
288 can allow cooperators to resist invasion by defectors (Figure 3B). Although
289 defectors initially have an advantage by saving on the cost of cooperation, sub-
290 populations of cooperators can quickly gain an advantage because they are
291 larger. Even after defector invasion, subpopulations of cooperators are more
292 likely to produce the next adapted mutant, which can then displace the slower
293 evolving defectors. It is these recurring cycles of defector invasion and cooper-
294 ator adaptation that underlie the oscillations in cooperator proportion that we
295 see in Figure 2A. When an adaptation to the constructed environment does
296 not occur in the cooperator background before the defector dominates, the

defector can drive the cooperator to extinction. This is something that we see occur stochastically in Figures 2A and 3B.

Cooperation as Niche Construction

In our model, cooperation is orthogonal to niche construction, which allows us to focus on hitchhiking. However, by increasing the size of the subpopulation, this form of cooperation can itself be seen as form of niche construction. Cooperative benefits often take similar forms in natural systems. For example, bacteria produce a host of extracellular products that scavenge soluble iron (Griffin *et al.*, 2004), digest large proteins (Diggle *et al.*, 2007; Darch *et al.*, 2012), and reduce the risk of predation (Cosson *et al.*, 2002). As in our model, such cooperative acts are likely to increase local population density. While many studies have focused on how the environment affects the evolution of these cooperative traits, relatively few have addressed how the environmental changes created by public goods feed back to influence evolution.

Perhaps most similar to our work, Van Dyken and Wade (2012) demonstrated that when two negative niche constructing, cooperative behaviors co-evolve, selection can increasingly favor these traits, which were disfavored when alone. In that model, “reciprocal niche construction” occurred when the negative feedback created by one strategy positively influenced selection on the other, creating a perpetual cycle that maintained both forms of cooperation. Arguably, this can be viewed as an instance of hitchhiking: the currently-maladaptive form of cooperation is maintained by association with the adaptive form.

319 When dispersal is limited, competition among kin can undermine cooperation.
320 To separate kin competition from kin selection, Lehmann (2007) developed
321 a model in which the selective feedbacks produced by a cooperative, niche-
322 constructing behavior only benefitted future generations. Kin competition
323 thereby was reduced, and cooperation instead benefitted descendants. This
324 work highlights an important aspect of niche construction—often, the rate of
325 selective feedback from niche construction is different from the rate at which
326 populations grow.

327 **Evolution at Multiple Timescales**

328 In our work, the niche is modeled implicitly by the composition of the popula-
329 tion. Any changes, therefore, in the population produce immediate effects on
330 the constructed environment and the resulting feedbacks. However, timescales
331 in our model could be de-coupled in two ways. First, cooperators modify their
332 niche by enabling their population to reach larger density (Equation 4). These
333 increased population sizes play a critical role by effectively increasing the rate
334 of evolution in these populations. Because of the importance of this process, it
335 would be very informative to explore how sensitive our results are to changes
336 in how long the increases in population size are upheld. Similarly, changes
337 in the timescale at which the niche at a patch change also have potential to
338 dramatically alter our results. Not only would changes in timescale affect the
339 selective values of alleles as the population changed, but they could also in-
340 fluence whether or not populations were able to evolve adapted types and if

341 so, how well those adapted types can propagate through the population to
342 address the threat of a defector.

343 Other studies, while not focused on cooperation, have similarly shown that the
344 timescales at which niche construction feedbacks occur can strongly influence
345 evolutionary outcomes (Laland *et al.*, 1996, 1999). This perspective is likely to
346 be crucial for understanding the evolution of cooperative behaviors like the pro-
347 duction of public goods. In these instances, environmental changes are likely
348 to occur on different timescales than growth, which can have profound effects.
349 For example, a multitude of factors including protein durability (Brown and
350 Taddei, 2007; Kümmerli and Brown, 2010), diffusion (Allison, 2005; Driscoll
351 and Pepper, 2010), and resource availability (Zhang and Rainey, 2013; Ghoul
352 *et al.*, 2014) influence both the rate and the degree to which public goods alter
353 the environment. While Lehmann (2007) showed that cooperation was favored
354 when selective feedbacks act over longer timescales, niche construction may in
355 fact hinder cooperation when selection is more quickly altered. For example,
356 when public goods accumulate in the environment, cooperators must decrease
357 production to remain competitive (Kümmerli and Brown, 2010; Dumas and
358 Kümmerli, 2012). This favors cooperation that occurs facultatively, perhaps
359 by sensing the abiotic (Bernier *et al.*, 2011; Koestler and Waters, 2014) or
360 biotic environment (Brown and Johnstone, 2001; Darch *et al.*, 2012). To allow
361 our model to address how traits such as these evolve, we would first need to
362 de-couple the niche from the composition of the population by representing
363 the niche explicitly.

364 Cooperation and Niche Construction in Host-Symbiont

365 Co-Evolution

366 As niche construction becomes more independent, it develops its own state and
367 dynamics. A logical next step, then, could be to treat the environment as a bi-
368 ological entity itself, which could introduce additional evolutionary feedbacks.
369 As the host population changes, so too does selection on their symbiont pop-
370 ulations. Here, evolutionary outcomes depend greatly on the degree of shared
371 interest between the host and symbiont. Future models could explicitly cap-
372 ture the environment as a biological entity to explore the rich coevolutionary
373 dynamics that these systems might offer.

374 For example, the cooperative production of virulence factors by the human
375 pathogen *P. aeruginosa* in lung infections is harmful to hosts with cystic fi-
376 brosis (Harrison, 2007). Similarly to what we have shown in this work, these
377 antagonistic, negative niche constructing behaviors might actually work to
378 maintain these infections. If this is the case, however, perhaps the case could
379 be made for developing treatments that target the selective feedback loop that
380 is created by niche construction. If these populations do indeed perpetually
381 benefit from adaptations that are created by niche construction, as we have
382 shown, case could perhaps be made for developing treatments that target the
383 selective feedback loop that provides adaptive opportunities in these spatial
384 environments. While the idea of removing negative selective feedbacks and sup-
385 porting stability may seem counterintuitive, if it makes the population more
386 susceptible, then perhaps pairing such a treatment with ones in which mutants

are introduced (e.g., Rumbaugh et al. (2009)), could significantly improve host fitness. Expanding models such as ours to address the additional dynamics present in host-symbiont systems such as these could be quite productive.

Or conversely, cooperative light production by *A. fischeri* is vital for the survival of its host, the Hawaiian bobtail squid (Ruby, 1996). While our current model and that of Van Dyken and Wade (2012) have showed that negative niche construction can play a decisive role in the evolution of cooperation, this instance of positive niche construction is a textbook example of cooperation and mutualism. Therefore, a greater understanding of the additional feedbacks created in symbioses such as these could be gained from modeling. Similar to our model, these host-symbiont systems likely have many other traits that are orthogonal to cooperation. Perhaps combinations of certain types of behaviors are important for maintaining cooperation, similar to what was shown by Van Dyken and Wade (2012).

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, both positive and negative, evolve in these host-symbiont settings.

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415 resources were provided by an award from Google Inc. (to BDC and BK).

416 Figures

417 **Figure 1**

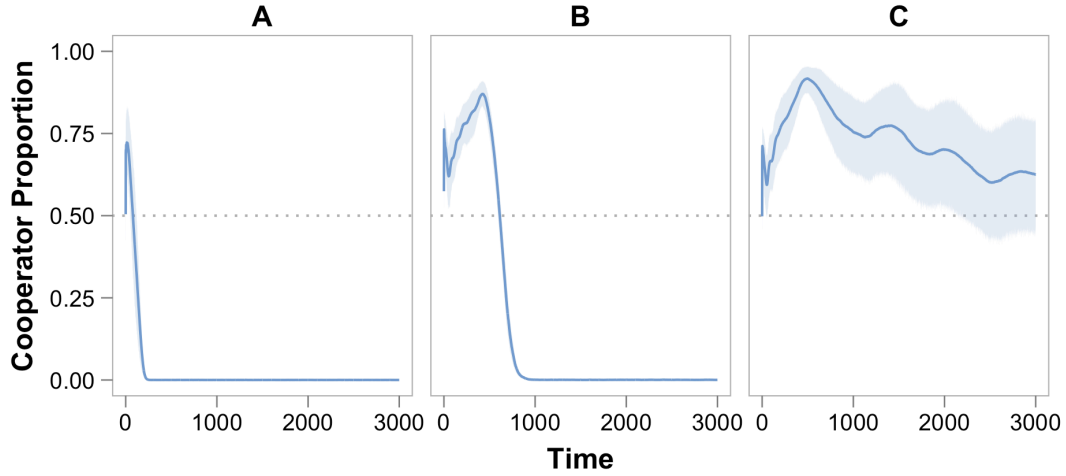


Figure 1: **Adaptation, Hitchhiking, and the Evolution of Cooperation.** Curves show the average cooperator proportion among replicate populations for the duration of simulations, and shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter values are listed in [Table 1](#). **(A)** Without any opportunity to adapt ($L = 0$), cooperation is quickly lost. **(B)** When adaptation can occur ($L = 5$), but niche construction does not affect selection ($\epsilon = 0$), cooperators rise in abundance by hitchhiking along with adaptations to the external environment. Nevertheless, this effect is transient, and cooperators eventually become extinct. **(C)** Niche construction enables cooperation to be maintained indefinitely. In the majority of populations, cooperation remained the dominant strategy. The trajectories of individual populations are shown in Figure 2A.

418 **Figure 2**

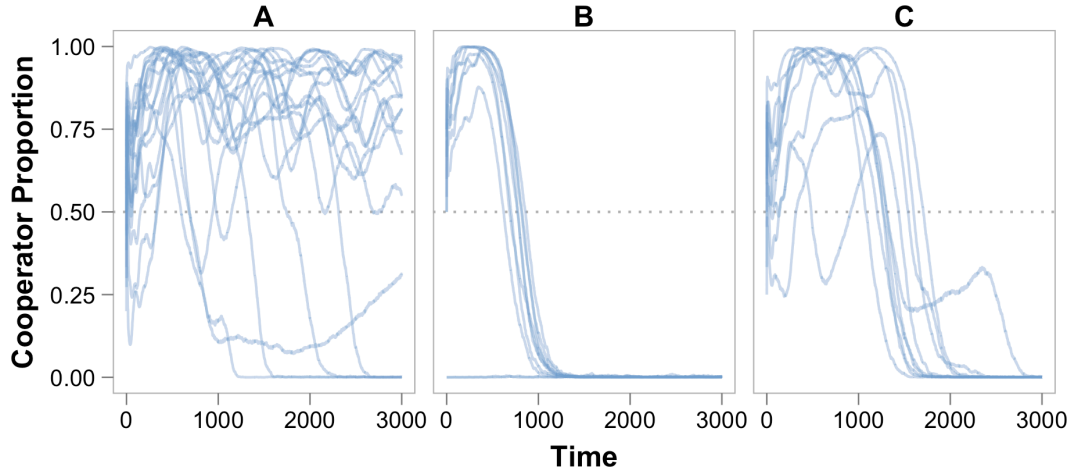


Figure 2: Niche Construction and the Evolution of Cooperation. The proportion of cooperators present in each replicate population is shown for the duration of simulations. **(A)** Despite some oscillations, cooperation dominates in 13 of 18 populations when niche construction affects selection. **(B)** When the selective effects of niche construction (ϵ) are removed, and the selective benefit of adaptation to the external environment (δ) is increased to compensate, cooperators are driven to extinction by isogenic defectors that arise by mutation ($\epsilon = 0$, $\delta = 0.6$). Note that cooperation was not present after initialization in one replicate population. **(C)** Cooperators are also driven to extinction without negative niche construction ($A = 5$).

419 **Figure 3**

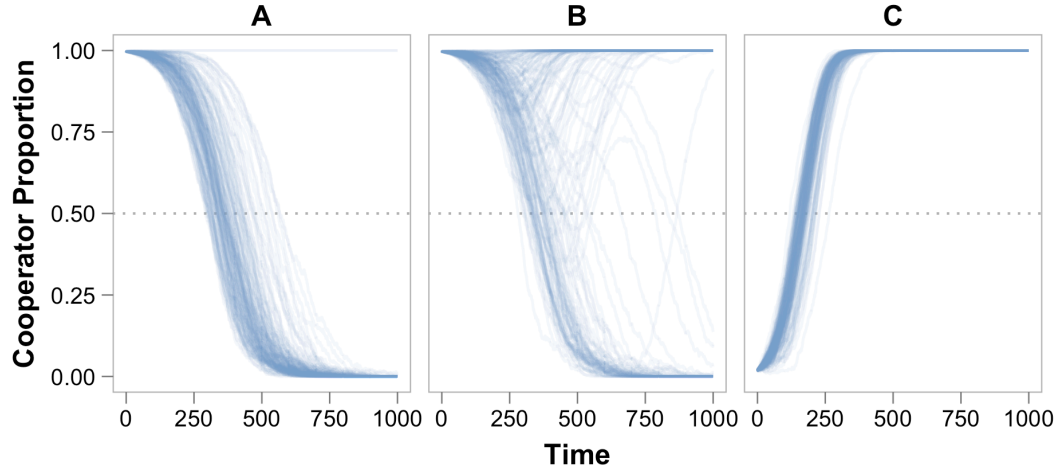


Figure 3: Niche Construction and Invasion. Curves trace the proportion of cooperators present in each replicate population for the duration of simulations ($T = 1000$). In each simulation, a rare type was initiated at a single patch in the center of the population lattice ($N^2 = 121$). Unless otherwise noted, mutations are disabled in these ecological simulations to highlight the dynamics of invasion ($\mu_a = 0, \mu_c = 0$). **(A)** When cooperators and defectors are isogenic (i.e., both types have stress alleles [1,2,3,4,5]), 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, negative niche construction creates adaptive opportunities that enable cooperators to resist invasion by isogenic defectors. Here, cooperation remained the dominant in 91 of 160 populations ($\mu_a = 0.00005$). Results from simulations where mutations also occurred at the cooperation locus are shown in Figure S1. **(C)** In fact, an adapted cooperator type (stress alleles [6,2,3,4,5], see Box 1) can swiftly displace defectors when isogenic defectors cannot arise or adapt via mutation.

420 **Figure 4**

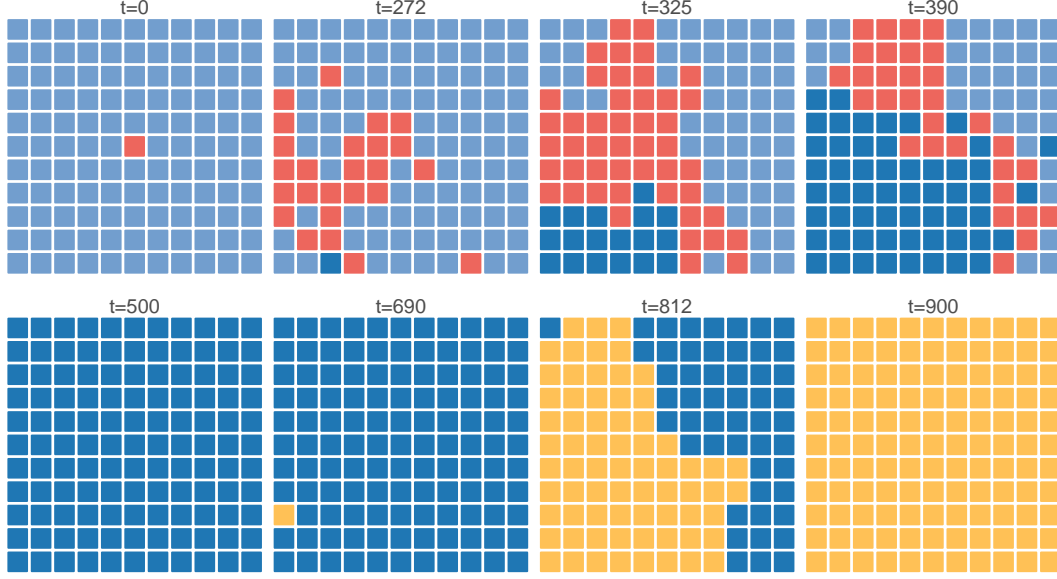


Figure 4: **Cooperator Adaptation Prevents Defector Invasion.** Here we depict the distribution of dominant types among subpopulations over time for one representative simulation in which isogenic defectors arise. To highlight the effects of adaptation, mutations did not occur at the cooperation locus ($\mu_c = 0$). At time $t = 0$ (upper left panel), a single isogenic defector population (red) is placed among cooperator populations (light blue). Because these defectors do not bear the costs of cooperation, they spread ($t = 272$). However, cooperators in one population gain an adaptation that gives them a fitness advantage over defectors (second panel, dark blue, lower left). At $t = 325$, defectors continue to invade cooperator populations. However, the adapted cooperator type spreads more quickly due to its fitness advantage, invading both defector populations and ancestral cooperator populations ($t = 390$), until it eventually fixes in the population ($t = 500$). At $t = 690$, a new cooperator type emerges that is favored due to negative niche construction (orange). This new type spreads rapidly ($t = 812$) until reaching fixation ($t = 900$). At this point, it becomes susceptible to invasion by the next “adapted” cooperator type, and the cycle continues.

⁴²¹ **Supplemental Figure 1**

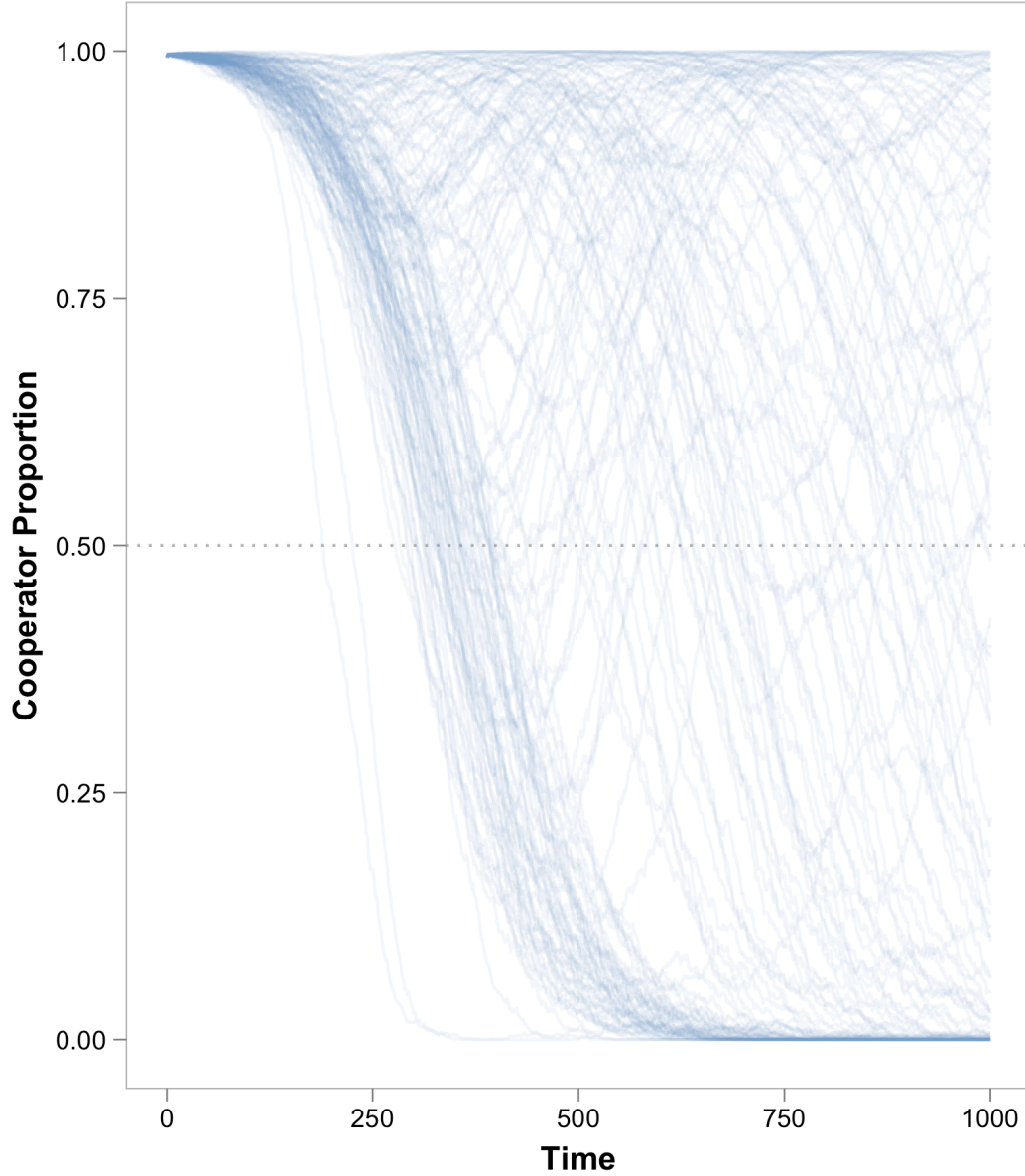


Figure S1: **Defector Invasion with Mutations.** The proportion of co-operators present in each replicate population is shown for the duration of simulations ($T = 1000$). When mutations occur both at the adaptive loci and the cooperation locus ($\mu_a = \mu_c = 0.00005$), cooperation remains dominant in 58 of 160 replicate populations.

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, adaptation to external environment	0.3
ϵ	Fitness benefit, adaptation to constructed environment	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
σ	Survival rate at population initialization	10^{-5}
T	Number of simulation cycles	3000
d	Subpopulation dilution factor	0.1

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