

1 Negative Niche Construction Favors the
2 Evolution of Cooperation

3
4 Brian D. Connelly¹, Katherine J. Dickinson¹, Sarah P. Hammarlund^{1,2}, and
5 Benjamin Kerr^{1,3}

6 ¹Department of Biology and BEACON Center for the Study of Evolution in
7 Action, University of Washington, Seattle, Washington, 98195, USA

8 ²Current Address: Department of Zoology, University of Oxford, Oxford OX1
9 3PS, United Kingdom

10 ³E-mail: kerrb@uw.edu

11 Abstract

12 By benefitting others at a cost to themselves, cooperators face an unrelenting
13 threat from defectors, or individuals that avail themselves of the cooperative
14 benefit without contributing. A longstanding challenge to evolutionary biol-
15 ogy is to understand the mechanisms that support the vast displays of cooper-
16 ation that nevertheless exist. Hammarlund et al. recently demonstrated that
17 cooperation can persist by hitchhiking along with beneficial non-social adapta-
18 tions. Importantly, cooperators play an active role in this process. In spatially-
19 structured environments, clustered cooperator populations reach greater densi-
20 ties, which creates more mutational opportunities to gain beneficial non-social
21 adaptations. Cooperation rises in abundance by association with these adap-
22 tations. However once adaptive opportunities have been exhausted, the free
23 ride ends as cooperators are displaced by equally-adapted defectors. Using an
24 agent-based model, we demonstrate that the selective feedback that is created
25 as populations alter their environments can maintain cooperation indefinitely.
26 We show that cooperator success depends specifically on negative niche con-
27 struction. Here, negative niche construction acts as a perpetual source of
28 adaptive opportunities. As populations adapt, they further alter their envi-
29 ronment in ways that reveal additional opportunities for adaptation. Despite
30 being independent of niche construction in our model, cooperation feeds this
31 cycle. We show that by reaching larger densities, populations of cooperators
32 are better able to adapt both to changing environments and to the constant
33 threat posed by defectors. We relate these findings to previous studies from

the niche construction literature and discuss how this model could be extended to provide a greater understanding of how cooperation evolves in the complex environments in which it is found.

37 Introduction

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

47 Several factors can prevent this *tragedy of the commons* (Hamilton, 1964;
48 Nowak, 2006; West *et al.*, 2007b). One such factor involves non-random so-
49 cial interaction, in which cooperators benefit more from the cooperative act
50 than defectors. This can occur when cooperators are clustered together in
51 spatially-structured populations (Fletcher and Doebeli, 2009; Nadell *et al.*,
52 2010; Kuzdzal-Fick *et al.*, 2011) or when cooperators use communication
53 (Brown and Johnstone, 2001; Darch *et al.*, 2012) or other cues (Sinervo *et al.*,
54 2006; Gardner and West, 2010; Veelders *et al.*, 2010) to cooperate condition-
55 ally with kin. Cooperation can also be bolstered by pleiotropic connections to
56 personal benefits (Foster *et al.*, 2004; Dandekar *et al.*, 2012) or through associ-
57 ation with alleles encoding self-benefitting traits (Asfahl *et al.*, 2015). In these
58 cases, the alleles may provide private benefits that are completely independent
59 from the public benefits of cooperation. In asexual populations of cooperators

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

64 Hammarlund et al. (2015) recently showed that in spatially-structured pop-
65 ulations, the “Hankshaw effect” can give cooperators a substantial leg up on
66 defectors in an adaptive race. This advantage is reminiscent of Sissy Han-
67 kshaw, a fictional character in Tom Robbins’ *Even Cowgirls Get the Blues*,
68 whose oversized thumbs—which were otherwise an impairment—made her a
69 prolific hitchhiker. Similarly, cooperation is costly, but it increases local pop-
70 ulation density. As a result, cooperators are more likely to acquire beneficial
71 mutations. By hitchhiking along with these adaptations, cooperation can rise
72 in abundance. Nevertheless, this advantage is fleeting. As soon as the oppor-
73 tunities for adaptation are exhausted, cooperators are once again at a selective
74 disadvantage against equally-adapted defectors that arise via mutation. How-
75 ever, Hammarlund et al. (2015) also demonstrated that cooperation can be
76 maintained when frequent environmental changes produce a steady stream of
77 new adaptive opportunities. Although organisms typically find themselves in
78 dynamic environments, the nature and frequency of these changes might not
79 ensure long-term cooperator survival.

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

84 mental change alters selection, which, in turn, alters the distribution of types
85 and their corresponding influence on the environment (Odling-Smee *et al.*,
86 2003). The nature of this feedback can have dramatic evolutionary conse-
87 quences. One critical distinction is whether the constructing type is favored in
88 the resulting environment. Under positive niche construction, selection favors
89 the constructor, and evolution stagnates as this type fixes. Under negative
90 niche construction, selection favors a type other than the constructor, which
91 creates an opportunity for adaptation. If an adapted type also engages in
92 negative niche construction, cycles of construction and adaptation can ensue,
93 such that populations find themselves continually chasing beneficial mutations
94 as their adaptive landscape perpetually shifts.

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

101 **Methods**

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

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

108 In this expanded model, subpopulations additionally modify their local envi-
109 ronment. As this process occurs, environmental changes feed back to affect
110 selection. We explore how niche construction affects the evolution of coop-
111 eration; specifically, how cooperative behavior can hitchhike with adaptive
112 mutations to modified environments. Box 1 provides additional information
113 about the model.

114 **Model Description**

115 **Individual Genotypes and Adaptation**

116 Each individual has a haploid genome with $L + 1$ loci (see [Table 1](#) for model
117 parameters and their values). Different alleles at each locus are represented by
118 different integers. A binary allele at the first locus (here, locus zero) determines
119 whether that individual is a cooperator (1), which carries fitness cost c , or a
120 defector (0). The remaining L loci are *adaptive loci*, and are each occupied by
121 0 or a value from the set $\{1, 2, \dots, A\}$. Allele 0 represents a lack of adaptation,
122 while a non-zero allele represents one of the A possible adaptations at that
123 locus.

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

128 minimally adapted cooperator to recoup the cost of cooperation and gain a
129 fitness advantage.

130 Niche Construction and Selective Feedbacks

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

136 In our model, the feedback from niche construction takes the form of den-
137 sity dependent selection, and individuals evolve to better match their niche.
138 Specifically, the selective value of non-zero allele a at adaptive locus l —and
139 consequently the fitness of an individual carrying that allele—increases with
140 the number of individuals in the subpopulation that have allele $a - 1$ at locus
141 $l - 1$. For example, when $L = 5$ and $A = 6$, and allele 4 has fixed at locus 2,
142 a genotype with allele 5 at locus 3 is favored. And once allele 5 has fixed at
143 locus 3, the niche that this population constructs will favor allele 6 at locus 4
144 (see Box 1). As a consequence, genotypes with sequentially increasing allelic
145 states will tend to evolve. We treat both adaptive loci and their non-zero al-
146 lelic states as “circular”: the selective value of an allele at locus 1 is affected by
147 the allelic composition of the subpopulation at locus L . Similarly, the selective
148 value of allele 1 at any locus increases with the number of individuals carrying
149 allele A at the previous locus. This circularity is represented by the function

150 $\beta(x, X)$, which gives the integer that is below an arbitrary value x in the set
 151 $\{1, 2, \dots, X\}$:

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

152 Here, $\text{mod}_X(x)$ is the integer remainder when dividing x by X . Using this
 153 function, the selective value of allele a at adaptive locus l is increased by ϵ for
 154 each individual in the subpopulation that has allele $\beta(a, A)$ at locus $\beta(l, L)$.
 155 Thus, ϵ specifies the intensity of selection due to niche construction.

156 Consider a genotype g with allelic state $a_{g,l}$ at locus l ; the fitness of an indi-
 157 vidual with this genotype is defined as:

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

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

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

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

163 illustrates the process of adaptation to the constructed environment. While
 164 cooperation is costly, we assume its effects are independent of the external and
 165 constructed components of the environment.

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

167 Cooperation enables a subpopulation to reach a greater density. This benefit
 168 affects all individuals equally and accumulates linearly with the proportion
 169 of cooperators in the subpopulation. If p is the proportion of cooperators
 170 present at the beginning of a growth cycle, then that subpopulation reaches
 171 the following size:

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

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

178 **Mutation**

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

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

187 **Migration**

188 Populations are composed of N^2 patches arranged as an $N \times N$ lattice, where
 189 each patch can support a subpopulation. After mutation, individuals emigrate
 190 to an adjacent patch with probability m . During each migration event, a single
 191 destination patch is randomly chosen from each source patch's Moore neigh-
 192 borhood, which is composed of the nearest 8 patches on the lattice. Because
 193 the population lattice has boundaries, patches located on the periphery have
 194 smaller neighborhoods.

195 **Population Initialization and Simulation**

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

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

Simulation Source Code and Software Dependencies

The simulation software and configurations for the experiments reported are available online.¹ 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 population consisting of subpopulations that are connected by spatially-limited migration. Individuals increase their competitiveness by gaining adaptations. While cooperation does not directly affect the fitness benefits that these adaptations confer, cooperation has indirect effects on the adaptive process. Specifically, cooperation increases subpopulation density. As a result, larger subpopulations of cooperators experience more mutational opportunities. Cooperation can rise in abundance by hitchhiking along with beneficial mutations, which compensate for the cost of cooperation. Importantly, subpopulations alter their local environments,

¹These materials will be made public prior to publication.

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

223 Cooperation Persists with Niche Construction

224 Without any opportunity for adaptation ($L = 0$), cooperators are swiftly elim-
225 inated in competition with defectors (Figure 1A). Despite an initial lift in
226 cooperator abundance due to increased productivity, the cost of cooperation
227 becomes disadvantageous as migration mixes the initially isolated subpopula-
228 tions. When populations can adapt to the external environment ($L = 5$ and
229 $\delta > 0$), but niche construction is absent ($\epsilon = 0$), cooperators are maintained
230 only transiently (Figure 1B). Here, larger cooperator subpopulations can more
231 quickly adapt to their external environment. However, as previously described
232 by Hammarlund et al. (2015), cooperation is subsequently lost once popula-
233 tions become fully adapted to their environment. This occurs when isogenic
234 defectors (i.e., defectors with identical adaptive loci) arise via mutation and
235 displace cooperators due to their selective advantage. However, when niche
236 construction feeds back to influence selection ($\epsilon > 0$), cooperation persists in
237 the majority of the replicate populations (Figure 1C). We see in Figure 2A that
238 despite oscillations in the proportion of cooperators, cooperation is maintained
239 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-

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

270 **Selective Feedbacks Limit Defector Invasion**

271 The adaptation resulting from selective feedbacks can limit invasion by de-
 272 fectors, which arise either through immigration from neighboring patches or
 273 through mutation from a cooperator ancestor. The latter challenge is par-
 274 ticularly threatening, as these isogenic defectors are equally adapted, yet do
 275 not incur the cost of cooperation. As demonstrated in Figure 3A, isogenic
 276 defectors rapidly spread when introduced at a single patch in the center of a
 277 population of cooperators if mutations do not occur. However, when coopera-
 278 tors can gain adaptations via mutation, cooperators resist defector invasion in
 279 over half of the replicate populations (Figure 3B). Figure 4 depicts one such
 280 instance. In that population, defectors quickly began to spread. However, an
 281 adaptation arose in a neighboring cooperator population. This type spreads
 282 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. Here, we have considered whether niche construction might serve to perpetually generate new adaptive

305 opportunities and thus favor cooperation indefinitely.
 306 When niche construction occurs, cooperation can indeed persist (Figures 1C
 307 and 2A). In our model, niche construction introduces additional selective ef-
 308 fects that influence the evolutionary process, leading to a more pronounced
 309 Hankshaw effect. However, these fitness benefits alone do not maintain coop-
 310 erators at high proportion (Figure 2B). Niche construction and the selective
 311 feedbacks that it produces play a crucial role.
 312 We find that it is specifically *negative* niche construction that maintains coop-
 313 eration (Figure 2C). As cooperator and defector types gain adaptations, they
 314 alter their environment ways that favor other types. Because of this, negative
 315 niche construction serves as a perpetual source of adaptation. Here we observe
 316 another facet of the Hankshaw effect: because populations of cooperators are
 317 larger, they are better able to respond to the adaptive opportunities that fol-
 318 low from negative niche construction. By gaining adaptations more quickly,
 319 cooperators resist invasion by defectors (Figure 3B). Although defectors ini-
 320 tially have an advantage by saving on the cost of cooperation, subpopulations
 321 of cooperators can quickly gain an advantage because they are larger. Even in
 322 the presence of an equally-adapted defector tyoe, cooperator subpopulations
 323 are more likely to produce the next adapted mutant, which can then displace
 324 the slower evolving defectors. These recurring cycles of defector invasion and
 325 cooperator adaptation underlie the oscillations in cooperator proportion seen
 326 in Figure 2A. When cooperators do not gain these adaptations, it is driven to
 327 extinction by the defector. This is something that we see occur stochastically
 328 in Figures 2A and 3B.

Cooperation as Niche Construction

In our model, niche construction and adaptation are independent of cooperation, 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), among many others (West *et al.*, 2007a). As in our model, these forms of cooperation 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 this study, 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 resulting from one strategy positively influenced selection on the other, creating a perpetual cycle that maintained both forms of cooperation. Arguably, this can be seen as an instance of hitchhiking: the currently-maladaptive form of cooperation is maintained by association with the adaptive form.

When dispersal is limited, competition among kin can undermine cooperation.

352 To separate kin competition from kin selection, Lehmann (2007) developed
353 a model in which a cooperative, niche-constructing behavior only benefitted
354 future generations. Kin competition thereby was reduced, and cooperation
355 instead benefitted descendants. This work highlights an important aspect of
356 niche construction—often, the rate of selective feedback from niche construc-
357 tion is different from the rate at which populations grow.

358 **Evolution at Multiple Timescales**

359 In our work, the niche is modeled implicitly by the composition of the popula-
360 tion. Any changes in the population, therefore, produce immediate effects on
361 the constructed environment and the resulting feedbacks. However, timescales
362 in our model could be de-coupled in two ways. First, cooperators modify their
363 niche by enabling their population to reach larger density (Equation 4). These
364 increased population sizes play a critical role by effectively increasing the rate
365 of evolution in these populations. Because of the importance of this process, it
366 would be very informative to explore how sensitive our results are to changes
367 in how long the increases in population size are upheld. Similarly, changes
368 in the rate at which a niche changes in response to subpopulation changes
369 have potential to dramatically alter our results. Not only would such changes
370 in timescale affect the selective values of alleles as the population changed,
371 but they could also influence whether or not populations were able to evolve
372 adapted types and if so, how well those adapted types can propagate through
373 the population to address the threat of a defector.

374 Other studies, while not focused on cooperation, have similarly shown that the
 375 timescales at which niche construction feedbacks occur can strongly influence
 376 evolutionary outcomes (Laland *et al.*, 1996, 1999). This perspective is likely to
 377 be crucial for understanding the evolution of cooperative behaviors like the pro-
 378 duction of public goods. In these instances, environmental changes are likely
 379 to occur on different timescales than growth, which can have profound effects.
 380 For example, a multitude of factors including protein durability (Brown and
 381 Taddei, 2007; Kümmerli and Brown, 2010), diffusion (Allison, 2005; Driscoll
 382 and Pepper, 2010), and resource availability (Zhang and Rainey, 2013; Ghoul
 383 *et al.*, 2014) influence both the rate and the degree to which public goods alter
 384 the environment. While Lehmann (2007) showed that cooperation was favored
 385 when selective feedbacks act over longer timescales, niche construction may in
 386 fact hinder cooperation when selection is more quickly altered. For example,
 387 when public goods accumulate in the environment, cooperators must decrease
 388 production to remain competitive (Kümmerli and Brown, 2010; Dumas and
 389 Kümmerli, 2012). This favors cooperation that occurs facultatively, perhaps
 390 by sensing the abiotic (Bernier *et al.*, 2011; Koestler and Waters, 2014) or
 391 biotic environment (Brown and Johnstone, 2001; Darch *et al.*, 2012). To allow
 392 our model to address how traits such as these evolve, we would first need to
 393 de-couple the niche from the composition of the population by representing
 394 the niche explicitly.

395 Cooperation and Niche Construction in Host-Symbiont

396 Co-Evolution

397 As the niche becomes more independent from the population, it develops its
398 own state and dynamics. A logical next step, then, could be to treat the
399 environment as a biological entity itself, which could introduce additional evo-
400 lutionary feedbacks. As the host population changes, so too does selection on
401 their symbiont populations. Here, evolutionary outcomes depend greatly on
402 the degree of shared interest between the host and symbiont. Future models
403 could explicitly capture the environment as a biological entity to explore the
404 rich coevolutionary dynamics that these systems might offer.

405 For example, the cooperative production of virulence factors by the human
406 pathogen *P. aeruginosa* in lung infections is harmful to hosts with cystic fibro-
407 sis (Harrison, 2007). Following what we have shown in this work, these antag-
408 onistic, negative niche constructing behaviors might actually work to maintain
409 these infections. If these populations do indeed perpetually benefit from adap-
410 tations that are created by niche construction, as we have shown, case could
411 perhaps be made for developing treatments that target the selective feedback
412 loop that provides adaptive opportunities in these spatial environments. While
413 the idea of removing negative selective feedbacks and supporting stability may
414 seem counterintuitive, if it makes the infecting population more susceptible,
415 then perhaps pairing such a treatment with ones in which mutants are intro-
416 duced (e.g., Rumbaugh et al. (2009)), could significantly improve host fitness.
417 Expanding models such as ours to address the additional dynamics present in

418 host-symbiont systems such as these could be quite productive.

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

430 It was recently argued that incorporating the effects of niche construction is
431 critical for improving our understanding of viral evolution (Hamblin *et al.*,
432 2014) and evolution in co-infecting parasites (Hafer and Milinski, 2015). In-
433 corporating host dynamics, co-evolution, and the feedbacks that they produce
434 into models is likely to be equally important for gaining an understanding of
435 how cooperative behaviors, both positive and negative, evolve in these host-
436 symbiont settings.

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Box 1: Description of niche construction in our model

See [Figure B1](#)

(A) Individuals. The genome of each individual consists of a single *cooperation locus* and L *adaptive loci* (here, $L = 5$). At the cooperation locus (labeled 0), this individual has allele 1, making it a cooperator. The adaptive loci (labeled 1-5) are arranged as a circular chromosome, where each locus has an integer allele between 0 and A , inclusive. In the description that follows, we focus exclusively on these adaptive loci. Genotypes are given by their allelic states starting with locus 1. For instance, the genotype shown here is $[2,0,5,2,1]$. Because of their circular structure, allele 2 at the first locus follows allele 1 at the fifth locus.

(B) Niche Construction. Consider a subpopulation fixed for genotype $[1,2,0,0,0]$. This subpopulation constructs environment $E_{[1,2,0,0,0]}$. Every non-zero allele influences selection at the next locus, favoring sequential allelic states. In this constructed environment, allele 3 at locus 3 would be favored. If genotype $[1,2,3,0,0]$ arises via mutation, it is expected to fix. However, genotype $[1,2,3,0,0]$ affects the environment differently than its ancestor. As $[1,2,3,0,0]$ rises in abundance, the constructed environment changes from $E_{[1,2,0,0,0]}$ to $E_{[1,2,3,0,0]}$, which favors $[1,2,3,4,0]$.

(C) Niche Construction and Adaptation. The evolutionary transition shown in Part B is indicated in the dashed box. Here, we depict entire sub-

467 populations fixed for a genotype using a single instance of that genotype. Simi-
 468 larly, an arrow represents niche construction and adaptation to the constructed
 469 environment. We start with a case in which there are five alleles ($A = 5$). Sub-
 470 populations begin with the non-adapted genotype $[0,0,0,0,0]$, shown on the far
 471 left. A non-zero allele is introduced via mutation, which represents an adapta-
 472 tion to external aspects of the environment. Here, allele 1 arises and fixes at
 473 locus 1. The remainder of this figure focuses on adaptation to the constructed
 474 aspects of the environment. This genotype has a “mismatch” (shown by the
 475 red sector), because $E_{[1,0,0,0,0]}$ favors $[1,2,0,0,0]$. Assuming allele 2 arises at the
 476 second locus, it will be selected, creating a “match” at the first and second
 477 loci (green sector). Now there is a mismatch between the second and third
 478 loci in the resulting environment, which a new round of mutation and selection
 479 corrects, and so on. The green sector grows as the red sector shifts clockwise.
 480 Since allele 1 follows allele 5 when $A = 5$, there is no mismatch as we cycle
 481 through the circular genotype $[1,2,3,4,5]$. This genotype will now remain in
 482 the subpopulation.

483 **(D) Negative Niche Construction.** A different case emerges when a mis-
 484 match exists as the genotype cycles back to where we started. Here, we change
 485 the number of alleles to six ($A = 6$). As shown on the far left, we begin with
 486 a subpopulation fixed for genotype $[1,2,3,4,5]$. This genotype has a mismatch,
 487 because the niche constructed by allele 5 favors allele 6 (not 1) at the next
 488 locus (in this case locus 1). A mutant with genotype $[6,2,3,4,5]$ has a fitness ad-
 489 vantage and can fix in $E_{[1,2,3,4,5]}$. However, as this type constructs $E_{[6,2,3,4,5]}$, a
 490 new mismatch appears. In this instance of negative niche construction, adapt-

491 ing to correct one mismatch generates a new mismatch. This system can never
492 escape its mismatches—the red sector just shifts clockwise around the genome
493 perpetually.

494 Figures

495 Figure 1

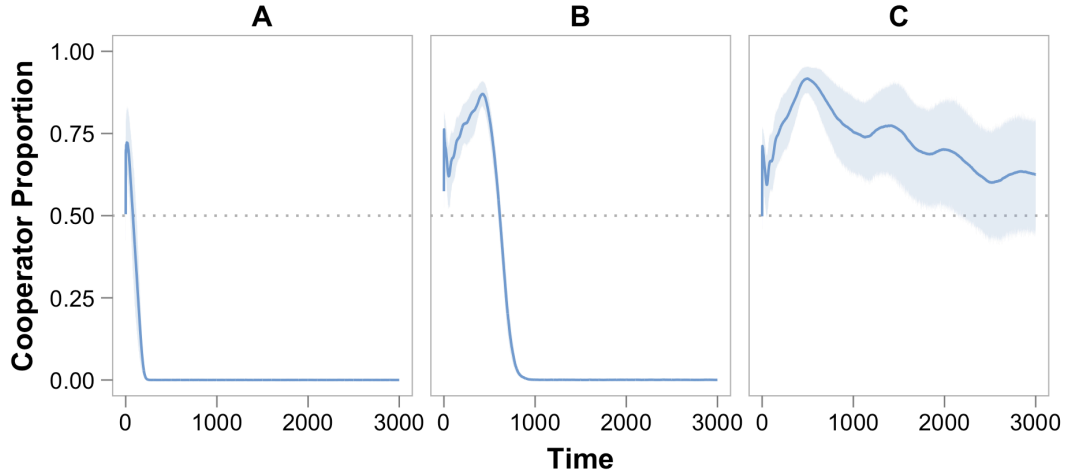


Figure 1: **Adaptation, Hitchhiking, and the Evolution of Cooperation.** Curves show the average cooperator proportion among replicate populations for the duration of simulations, and shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter values are listed in [Table 1](#). **(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.

496 **Figure 2**

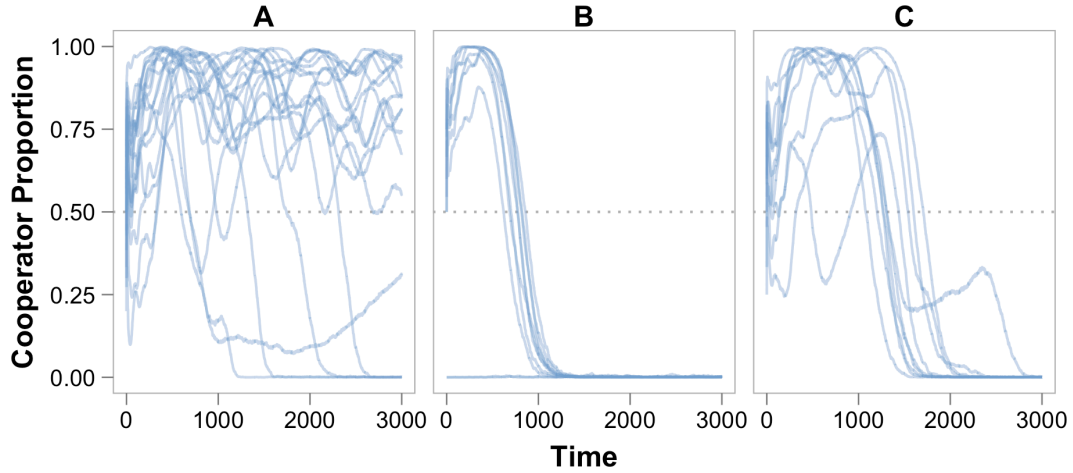


Figure 2: Niche Construction and the Evolution of Cooperation. The proportion of cooperators present in each replicate population is shown for the duration of simulations. **(A)** Despite some oscillations, cooperation dominates in 13 of 18 populations when niche construction affects selection. **(B)** 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 ($A = 5$).

497 **Figure 3**

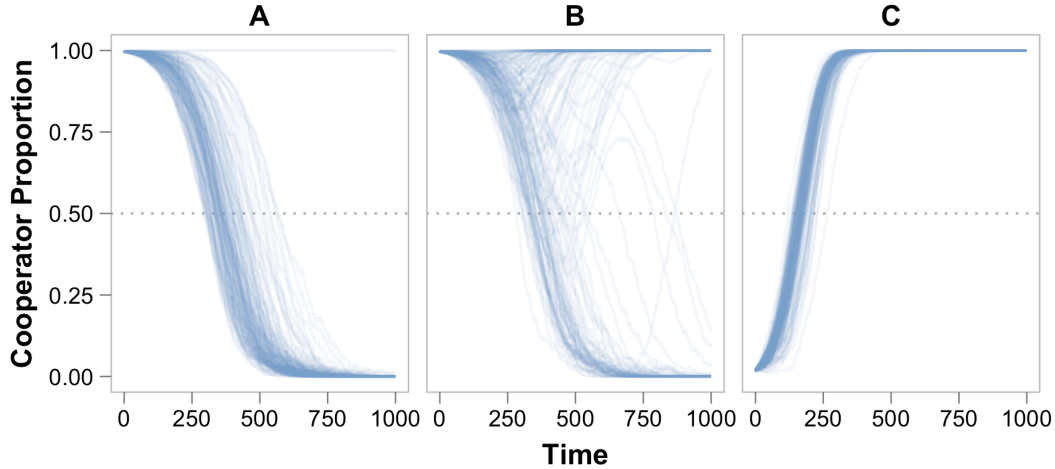


Figure 3: Niche Construction and Invasion. Curves trace the proportion of cooperators present in each replicate population for the duration of simulations ($T = 1000$). In each simulation, a rare type was initiated at a single patch in the center of the population lattice ($N^2 = 121$). Unless otherwise 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.

498 **Figure 4**

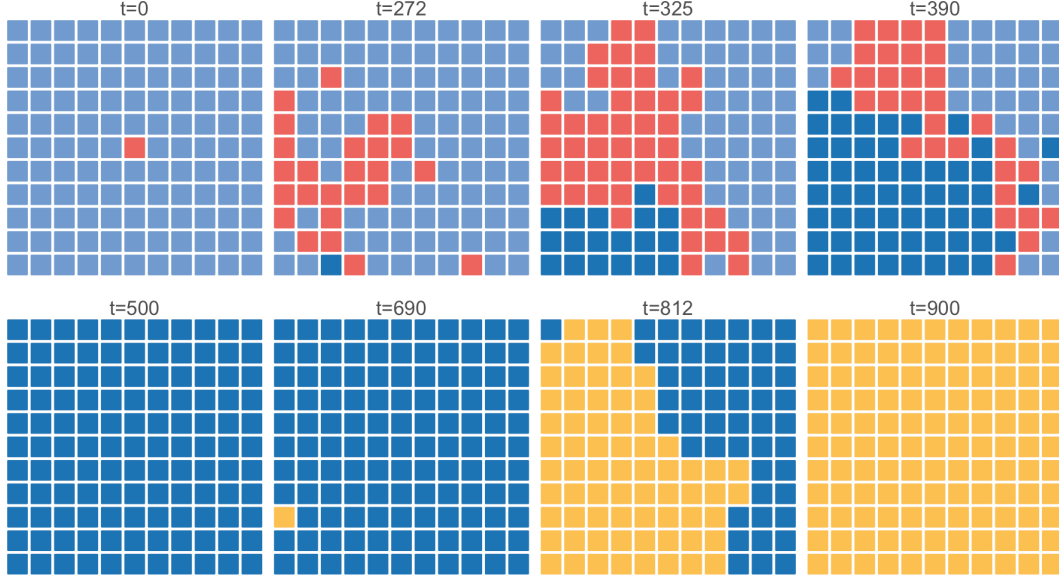


Figure 4: **Cooperator Adaptation Prevents Defector Invasion.** Here we depict the distribution of dominant types among subpopulations over time for one representative simulation in which isogenic defectors arise. To highlight the effects of adaptation, mutations did not occur at the cooperation locus ($\mu_c = 0$). 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.

499 **Box 1 Figures**

500 **Figure B1**

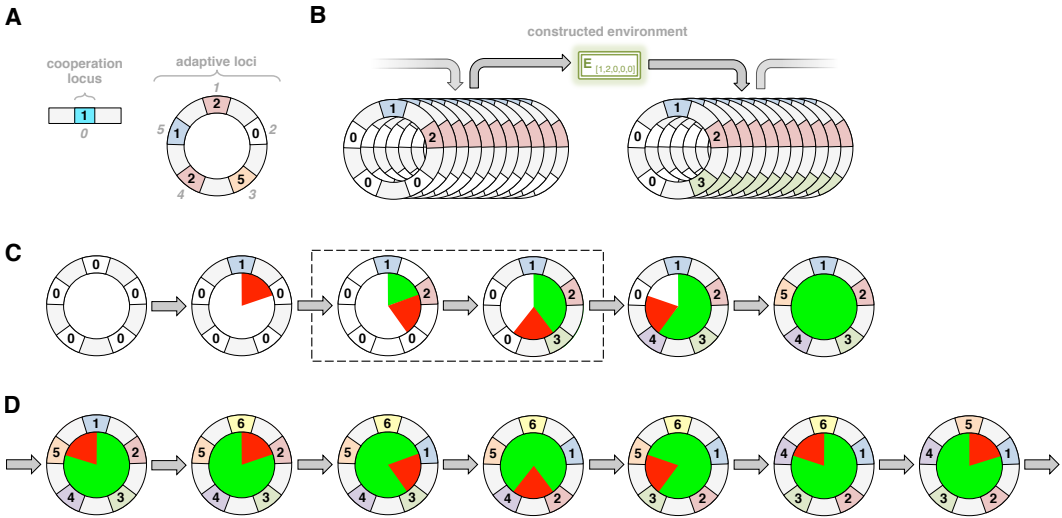


Figure B1: Figure for Box 1

501 **Supplemental Figures**

502 **Figure S1**

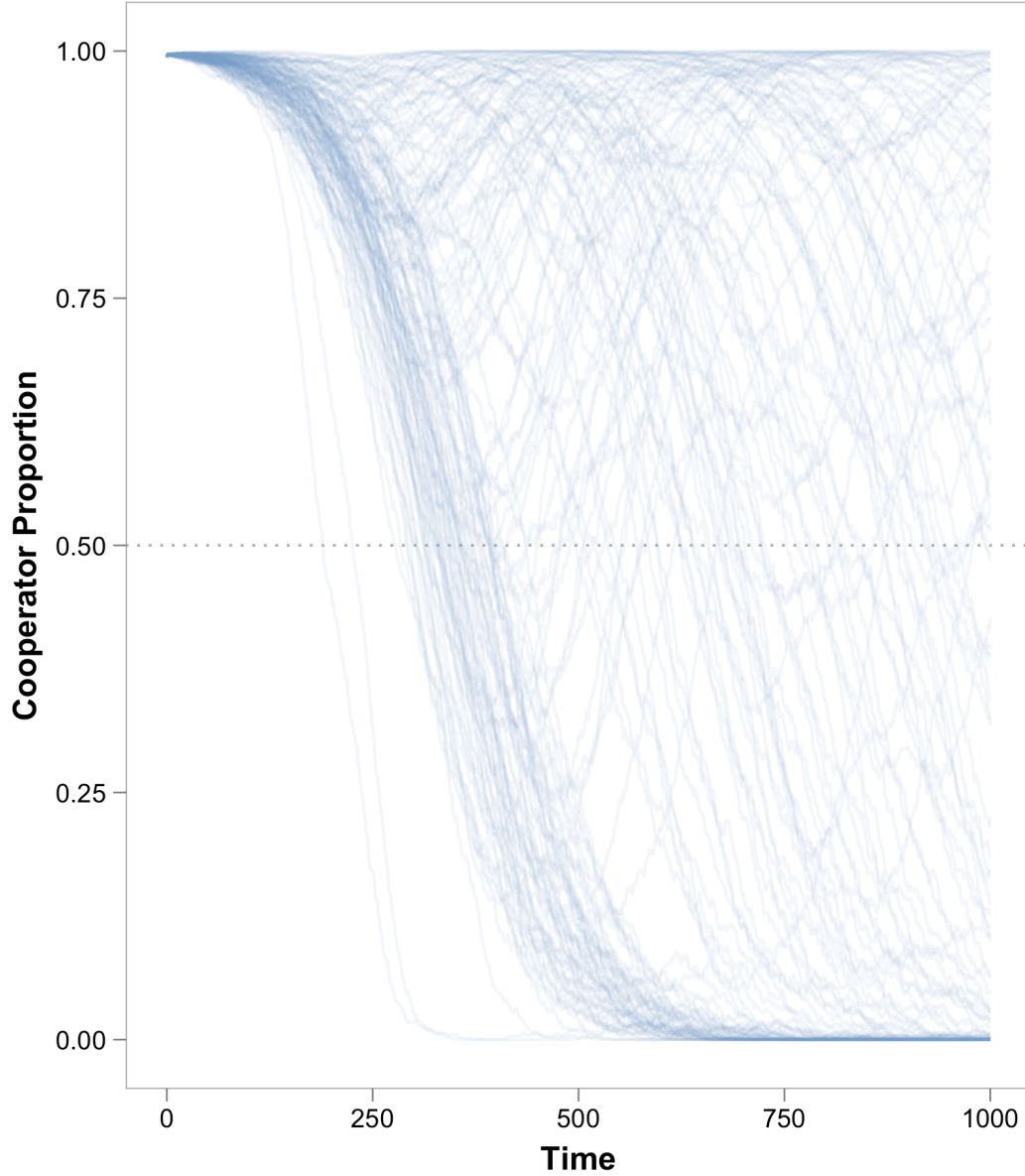


Figure S1: **Defector Invasion with Mutations.** The proportion of co-operators present in each replicate population is shown for the duration of simulations ($T = 1000$). When mutations occur both at the adaptive loci and the cooperation locus ($\mu_a = \mu_c = 0.00005$), cooperation remains dominant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