

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 Importantly, however, organisms do more than simply experience changing en-  
50 vironments passively. Through their activities, their interactions with others,  
51 and even their deaths, organisms constantly modify their environment. This  
52 niche construction process can produce evolutionary feedback loops in which  
53 environmental change alters selection, which, in turn, alters the distribution  
54 of types and their corresponding influence on the environment (Odling-Smee  
55 *et al.*, 2003). The nature of this feedback can have dramatic evolutionary con-  
56 sequences. One critical distinction is whether the constructing type or some  
57 other type is most adapted in the resulting environment. Under positive niche  
58 construction, selection favors the constructor, and evolution stagnates as this  
59 type fixes. Under negative niche construction, selection favors a type other  
60 than the constructor. In this latter case, populations find themselves con-  
61 tinually chasing beneficial mutations as their adaptive landscape perpetually  
62 shifts.

63 Here, we show that the selective feedbacks that result from niche construction

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

## 69 **Methods**

70 Building upon Hammarlund et al. (2015), we develop an individual-based  
71 model in which cooperators and defectors evolve and compete in a population  
72 of subpopulations (i.e., a metapopulation). Through mutations, individuals  
73 gain adaptations to their environment, which increase reproductive fitness,  
74 and allow those lineages to rise in abundance. More successful lineages spread  
75 to neighboring subpopulations by migration.

76 In this expanded model, subpopulations additionally modify their local envi-  
77 ronment. As this process occurs, environmental changes feed back to affect  
78 selection. We explore how niche construction affects this process hitchhiking  
79 along with adaptations, and whether cooperation can be maintained by selec-  
80 tive feedbacks.

## 81 **Model Description**

### 82 **Individual Genotypes and Adaptation**

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

91 These non-zero alleles signify two types of adaptations, both of which increase  
92 fitness. First, adaptations to the external environment confer a fitness benefit  
93  $\delta$ . This selective value is the same regardless of which non-zero allele is present  
94 and is not affected by other individuals or the local niche. We assume  $\delta > c$ ,  
95 which allows a minimally adapted cooperator to recoup the cost of cooperation  
96 and gain a fitness advantage.

### 97 **Niche Construction and Selective Feedbacks**

98 Individual fitness is also affected by the current state of the local environment.  
99 We represent the “niche” implicitly based on the specific allelic states present  
100 in the subpopulation. As allelic states change, subpopulations alter aspects of  
101 their environment, creating a unique niche. As described below, the specific

alleles that are present at each locus matter.  
 Niche construction takes the form of density dependent selection, and individuals evolve to better match their niche by an additional form of adaptation. The niche is defined by the distribution of alleles at each locus. Non-zero alleles that are more common will improve fitness by a larger selective value (beyond  $\delta$ ). Specifically, the selective value of adaptive allele  $a$  at locus  $l$ , and consequently the fitness of an individual carrying that allele, increases with the number of individuals in the subpopulation that have allele  $a - 1$  at locus  $l - 1$ . As a consequence, genotypes with sequentially increasing allelic states will tend to evolve. We treat both adaptive loci and allelic states as “circular”: the selective value of an allele at locus 1 is affected by the allelic composition of the subpopulation at locus  $L$ . Similarly, the selective value of allele 1 at any locus increases with the number of individuals carrying allele  $A$  at the previous locus. This circularity is represented by the function  $\beta(x, X)$ , which gives the integer that is below an arbitrary value  $x$  in the set  $\{1, 2, \dots, X\}$ :

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

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

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

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

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

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

Thus, an individual's fitness is determined both by adaptations to the external environment ( $\delta$ ) and by adaptations to its constructed environment ( $\epsilon$ ). **Figure 1** illustrates the effects of these two components.

## Population Growth and the Benefit of Cooperation

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

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

During growth, individuals compete through differential reproduction. Each

individual's probability of success is determined by its fitness. The composition of a subpopulation with size  $P$  and cooperator proportion  $p$  after growth is multinomial with parameters  $S(p)$  and  $\{\pi_1, \pi_2, \dots, \pi_P\}$ , where  $\pi_i$  represents individual  $i$ 's reproductive fitness relative to others in the subpopulation.

## Mutation

For simplicity, we apply mutations after growth. Mutations occur independently at each locus and cause an allelic state change. At the binary cooperation locus, mutations occur at rate  $\mu_c$ . These mutations flip the allelic state, causing cooperators to become defectors and vice versa. Mutations occur at rate  $\mu_a$  at each adaptive locus. These mutations replace the existing allele with a random selection from the set  $\{0\} \cup \{1, 2, \dots, A\}$ . Because mutations are stochastic, the allelic sequences that evolve depend on which allele arises first and at which locus.

## Migration

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



## 157 **Population Initialization and Simulation**

158 Following Hammarlund et al. (2015), we begin simulations with sparse pop-  
159 ulations. Subpopulations are first seeded at all patches with size  $S(p_0)$  and  
160 cooperator proportion  $p_0$ . The population is then thinned to create empty  
161 patches. Each individual survives this bottleneck with probability  $\sigma$ . Start-  
162 ing from this initial state, simulations then proceed for  $T$  cycles, where each  
163 discrete cycle consists of subpopulation growth, mutation, migration, and dilu-  
164 tion. Dilution thins the population to support growth in the next cycle. Each  
165 individual remains with probability  $d$ , regardless of allelic state.

## 166 **Simulation Source Code and Software Dependencies**

167 The simulation software and configurations for the experiments reported are  
168 available online.<sup>1</sup> Simulations used Python 3.4, NumPy 1.9.1, Pandas 0.15.2  
169 (McKinney, 2010), and NetworkX 1.9.1 (Hagberg *et al.*, 2008). Data analy-  
170 ses were performed with R 3.1.3 (R Core Team, 2015). Reported confidence  
171 intervals were estimated by bootstrapping with 1000 resamples.

## 172 **Results**

173 Using the model described in the previous section, we perform simulations that  
174 follow the evolution of cooperation in a population consisting of subpopulations  
175 that are connected by spatially-limited migration. Individuals increase their

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<sup>1</sup>These materials will be made public prior to publication.

176 competitiveness by gaining a limited number of adaptations. While coopera-  
 177 tion does not directly affect the fitness benefits that these adaptations confer,  
 178 cooperation has indirect effects on the adaptive process. Specifically, coopera-  
 179 tion increases subpopulation density. As a result, larger subpopulations of  
 180 cooperators experience more mutational opportunities to gain adaptations. Co-  
 181 operation can rise in abundance by hitchhiking along with these adaptations,  
 182 which compensate for the cost of cooperation. During this process, subpopu-  
 183 lations alter their local environments, which feeds back to influence selection.  
 184 Here, we explore how niche construction affects the evolution of cooperation.

## 185 **Cooperation Persists with Niche Construction**

186 Without any opportunity for adaptation ( $L = 0$ ), cooperators are swiftly elim-  
 187 inated in competition with defectors (Figure 2A). Despite an initial lift in  
 188 cooperator abundance due to increased productivity, the cost of cooperation  
 189 becomes disadvantageous as migration mixes the initially isolated subpopula-  
 190 tions. When populations can adapt to the external environment ( $L = 5$ ), but  
 191 niche construction is absent ( $\epsilon = 0$ ), cooperators are maintained only tran-  
 192 siently (Figure 2B). Here, larger cooperator subpopulations can more quickly  
 193 adapt to their external environment as before. However, as previously de-  
 194 scribed by Hammarlund et al. (2015), cooperation is subsequently lost once  
 195 populations become fully adapted to their environment. This occurs when iso-  
 196 genic defectors (i.e., defectors with identical adaptive loci) arise via mutation  
 197 and displace cooperation due to their selective advantage. However, when

198 niche construction feeds back to influence selection, cooperation persists in  
199 over 2/3 of the replicate populations (Figure 2C). We see in Figure 3A that  
200 despite oscillations in the proportion of cooperators, cooperation is maintained  
201 at high levels in these populations.

## 202 **Fitness Increases Alone do not Support Persisting Coop-** 203 **eration**

204 In the model, adaptations to both the external environment and the con-  
205 structed environment contribute to an individual's fitness. To determine  
206 whether cooperation is maintained solely due to the larger selective values  
207 that result from the contributions of niche construction ( $\epsilon$ ), we performed  
208 simulations in which these contributions were removed ( $\epsilon = 0$ ), and we in-  
209 stead increased the fitness benefits conferred by adaptation to the external,  
210 non-constructed environment ( $\delta = 0.6$ ). In doing so, we conservatively esti-  
211 mate the selective effects of niche construction by supplementing the selective  
212 benefits of adaptations to the external environment by the maximum possible  
213 selective benefit that results from niche construction. Nevertheless, we find  
214 that simply increasing selective values does not enable cooperators to persist  
215 (Figure 3B). Niche construction, therefore, plays a decisive role here.

## 216 Negative Niche Construction is Critical to Cooperator 217 Persistence

218 Adaptations can negatively effect fitness in our model due to selection for  
219 sequentially-increasing allelic states and the circular arrangement of these al-  
220 leles (see [Figure 1](#)). This negative niche construction occurs when the number  
221 of adaptive alleles ( $A$ ) does not divide evenly into the number of adaptive loci  
222 ( $L$ ). In such a case, any sequence of integers on the circular genome will always  
223 contain a break in the sequence; that is, one locus with an allele that is not  
224 one less than the allele at the next locus. Given this unavoidable mismatch,  
225 any type that has fixed will always construct a niche that favors selection for  
226 a new type. When negative niche construction is removed (by setting  $L = 5$ ,  
227  $A = 5$ ), cooperators are again driven extinct after an initial lift in abundance  
228 ([Figure 3C](#)). These results indicate that the type of niche construction matters.  
229 Specifically, negative niche construction is crucial for maintaining cooperation.

## 230 Selective Feedbacks Limit Defector Invasion

231 The adaptation resulting from selective feedbacks can limit invasion by de-  
232 fectors, which arise either through immigration from neighboring patches or  
233 through mutation from a cooperator ancestor. The latter challenge is partic-  
234 ularly threatening, as these isogenic defectors are equally adapted, yet do not  
235 incur the cost of cooperation. As demonstrated in [Figure 4A](#), isogenic defectors  
236 rapidly spread when introduced at a single patch in the center of a population  
237 of cooperators if mutations do not occur. However, when resident coopera-

238 tors can gain adaptations via mutation, cooperators resist defector invasion in  
 239 over half of the replicate populations (Figure 4B). Figure 5 depicts one such  
 240 instance where cooperation survived. In that population, defectors quickly  
 241 began to spread. However, an adaptation arose in a neighboring cooperator  
 242 population. This type spread more quickly, halting defectors and eventually  
 243 driving them to extinction. Because this adaption occurred in a cooperator  
 244 population, cooperation was able to hitchhike to safety. Figure 4C shows how  
 245 quickly an adapted cooperator type can invade a population of defectors.

## 246 **Negative Niche Construction Must Follow a Path**

247 We have seen that negative niche construction plays a critical role in main-  
 248 taining cooperation by creating adaptive “escape routes” for cooperators. But  
 249 in some cases, cooperator populations were not able to gain these adaptations  
 250 quickly enough, which led to extinction (Figure 3A). To determine whether  
 251 stronger negative feedbacks from niche construction would increase the rate at  
 252 which cooperator populations gained the adaptations needed to escape defec-  
 253 tor invasion, we performed simulations in which the allelic state at each locus  
 254 was always mismatched. This was accomplished in the model by removing  
 255 selection for sequential allelic states. Instead, the selective value of an allele  
 256 at each locus increased with the number of individuals in the population that  
 257 had the next allelic state at that *same* locus. For example, selection in this  
 258 modified model would favor a type with  $[2, 5, 1, 4, 4]$  in a niche constructed  
 259 by  $[1, 4, 6, 3, 3]$  ( $L = 5$ ,  $A = 6$ ). However, this strongly negative niche con-

struction does not better enable cooperators to stave off defection. In fact, cooperation is quickly lost under these conditions (Figure 6A).

We then performed simulations to determine whether it is the rate of adaptation in response to negative niche construction that is important, not the strength of its feedback. When the mutation rate at adaptive loci is raised 100-fold ( $\mu_a = 0.001$ ), cooperation is maintained at higher levels and in more replicate populations (Figure 6B).

## 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. 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 this work, we have considered whether niche construction might serve to perpetually generate new adaptive opportunities and thus favor cooperation indefinitely.

When niche construction occurs, cooperation can indeed persist (Figures 2C and 3A). In our model, niche construction introduces additional selective effects that could influence the evolutionary process, leading to a more pro-

nounced Hankshaw effect. However, simply raising the fitness benefits conferred by adaptations does not prolong cooperation (Figure 3B), which indicates that niche construction and the selective feedbacks that it produces play a crucial role.

Further, we find that it is specifically negative niche construction that maintains cooperation (Figure 3C). Here we observe another facet of the Hankshaw effect: because populations of cooperators are larger, they are better able to respond to the adaptive opportunities that result from negative niche construction. Without these adaptive opportunities, adaptation eventually grinds to a halt. Once this occurs, cooperators face the threat of invasion by isogenic defectors. Since these defectors are equally adapted but do not bear the cost of cooperation, they quickly drive cooperators to extinction. Importantly, because every type constructs an environment in which a different type is more fit, negative niche construction creates continual adaptive opportunities. These opportunities can allow cooperators to resist invasion by defectors, even when defectors are equally adapted (Figure 4B). It is these recurring cycles of invasion and adaptation that underlie the oscillations in cooperator populations that we see in Figure 3A. When stochastic mutations do not engender these adaptations, defectors invade, and the cycle is broken.

While negative niche construction is necessary, we find that making the selective effects of niche construction more negative is disruptive to cooperation (Figure 6A). Instead, it is the rate at which cooperators gain adaptations that allow them to escape invasion. When the mutation rate at adaptive loci was increased, cooperation was maintained in more populations, despite the

306 increased opportunity for gaining deleterious mutations (Figure 6B). Taken  
307 together, these results indicate that cooperators are better able to escape de-  
308 fector invasion when adaptation has a clear path.

309 When the selective effects of niche construction are more negative, popula-  
310 tions become more diverse. This diversity could potentially mean that when  
311 a defector arises, the type that outcompetes it may already be present in the  
312 population. But diversity is a double edged sword. Because a neighboring  
313 patch in a diverse population is also more likely to have constructed a differ-  
314 ent niche. This greatly limits how quickly an adapted type can spread, since  
315 the immigrant type evolved in a different niche and is therefore maladapted to  
316 the new environment. Instead, when a cooperator population is homogeneous,  
317 the evolutionary trajectories of its subpopulations are more aligned. As we see  
318 in Figure 5, when an adapted type emerges in a more homogeneous population,  
319 that type can quickly spread throughout the population, thwarting invasion  
320 by isogenic defector types.

## 321 Niche Construction and the Evolution of Cooperation

322 In our model, cooperation is orthogonal to niche construction, which allows us  
323 to focus on hitchhiking. However, by increasing the size of the local patch, this  
324 form of cooperation could itself be seen as form of niche construction. Previous  
325 studies have more directly explored how niche construction and cooperation  
326 interact. Lehmann (2007) showed that cooperation can be favored when niche  
327 construction acted to decouple kin competition from kin selection in spatially-



structured populations. Perhaps most similar 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. Outside of the context of cooperation, Laland, Odling-Smee, and Feldman have shown that niche construction can allow deleterious alleles to be maintained (1996, 1999). Indeed, cooperation, especially in competition against equally-adapted defectors, can be considered deleterious.

## Evolution at Multiple Timescales

In the model described by Lehmann (2007), the selective feedbacks produced by the cooperative, niche-constructing behavior only affected future generations. Kin competition thereby was reduced, and cooperation instead benefited descendants. Other studies, while not focused on cooperation, have similarly shown that the timescales at which niche construction feedbacks occur can strongly influence evolutionary outcomes (Laland *et al.*, 1996, 1999). This perspective is likely to be crucial for understanding the evolution of cooperative behaviors like the production of public goods.

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). 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. In these instances, environmental changes are likely to occur on different timescales than growth, which can have profound effects. For example, a multitude of factors including protein durability (Brown and Taddei, 2007; Kümmerli and Brown, 2010), diffusion (Allison, 2005; Driscoll and Pepper, 2010), and resource availability (Zhang and Rainey, 2013; Ghoul *et al.*, 2014) influence both the rate and the degree to which public goods alter the environment. While Lehmann (2007) showed that cooperation was favored when selective feedbacks act over longer timescales, niche construction may in fact hinder cooperation when selection is more quickly altered. For example, when public goods accumulate in the environment, cooperators must decrease production to remain competitive (Kümmerli and Brown, 2010; Dumas and Kümmerli, 2012). This favors cooperation that occurs facultatively, perhaps by sensing the abiotic (Bernier *et al.*, 2011; Koestler and Waters, 2014) or biotic environment (Brown and Johnstone, 2001; Darch *et al.*, 2012).

## Cooperation and Niche Construction in Host-Symbiont

## Co-Evolution

In many instances where cooperation occurs, the environment is itself a biological entity. This can introduce additional evolutionary feedbacks. As the host population changes, so too does selection on their symbiont populations. Here, evolutionary outcomes depend greatly on the degree of shared interest between the host and symbiont. For example, the cooperative production of virulence factors by the human pathogen *P. aeruginosa* in lung infections is harmful to hosts with cystic fibrosis (Harrison, 2007). Conversely, cooperative light production by *A. fischeri* 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.

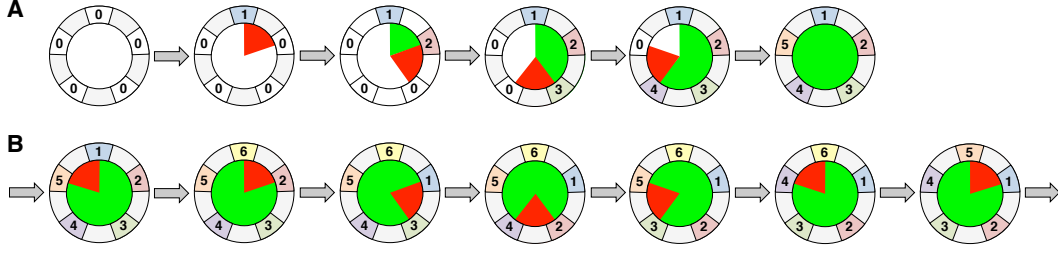
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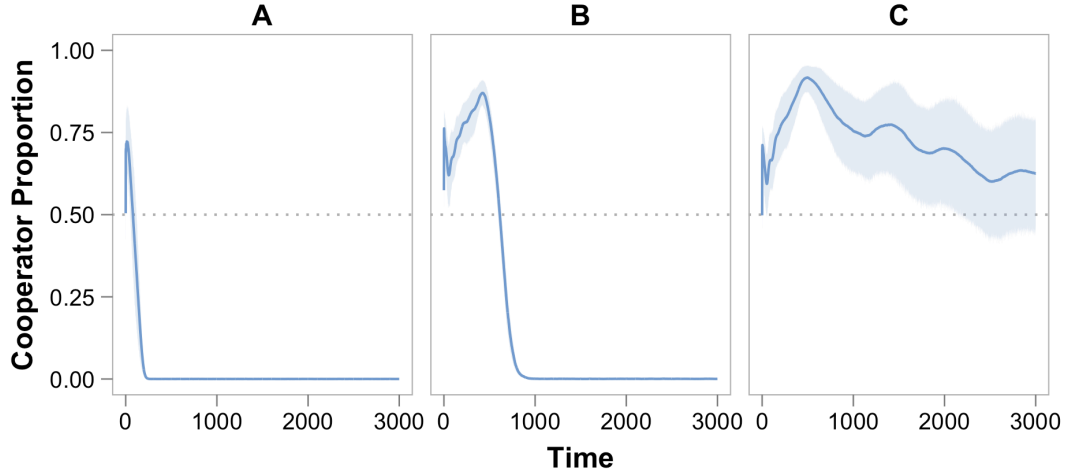
394 **Figures**

395 **Figure 1**



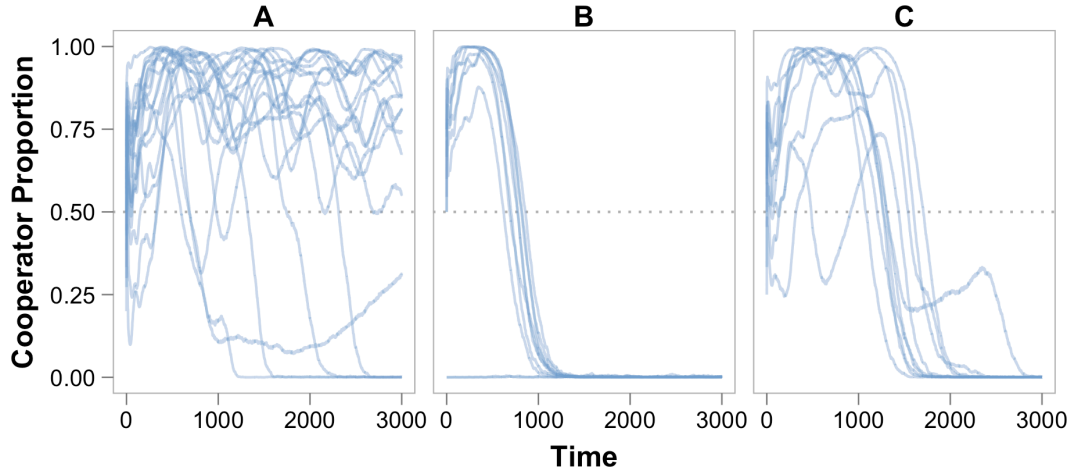
**Figure 1: Adaptation to External and Constructed Environments.** (A) We begin with the case with five adaptive loci ( $L = 5$ ) and five non-zero alleles ( $A = 5$ ). All simulations are initialized with a non-adapted genotype with allele 0 at every locus (far left). Random mutation will introduce a non-zero allele, which will increase in frequency. In this example, allele 1 arises at the first locus (in the “12 o’clock” position). The rest of this schematic focuses on niche construction. Every non-zero allele at any locus influences selection at the next locus in the clockwise direction. There is a “mismatch” in this genotype (highlighted by the red sector), because the niche constructed by allele 1 at the first locus favors allele 2, not 0, at its immediate clockwise neighbor (the second locus). Once the appropriate allele arises, it will be selected. In this case, the genotype  $[1,2,0,0,0]$  receives an epsilon effect in addition to the extra delta. The “match” at the first and second locus is highlighted as a green sector. However, now there is a new mismatch between the second and third locus, which a new round of mutation and selection corrects, and so on. The green sector grows as the red sector ticks clockwise. Importantly, because  $A$  divides evenly into  $L$ , this genotype can evolve into a perfectly reinforcing sequence  $[1,2,3,4,5]$ , which enjoys a maximal epsilon increment of fitness due to niche construction. (B) The case of negative niche construction is illustrated for the case of five loci ( $L = 5$ ) and six non-zero alleles ( $A = 6$ ). Here we start with a population fixed for the genotype on the far left  $[1,2,3,4,5]$ . There is a single mismatch in this genotype (highlighted by the red sector), because the niche constructed by allele 5 favors allele 6, not 1, at its immediate clockwise neighbor. If the fitter mutant  $[6,2,3,4,5]$  arises (see next genotype to the right), it will fix. (We note that the strength of selection will drop as its frequency increases). However, now there is a new mismatch in the genotype (highlighted again with a red sector). We see that correcting one mismatch generates a new mismatch. Thus, this system will never escape its mismatches—the red sector just clicks clockwise around the genome. Indeed, after six (or  $A$ ) rounds of mismatch correction and generation, we have ended back where we started with the original genotype turned clockwise by one locus. Here, the adaptation to previous niche construction generates further niche construction that leads to novel adaptation.

396 **Figure 2**



**Figure 2: 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 3A.

397 **Figure 3**



**Figure 3: Niche Construction and the Evolution of Cooperation.** The proportion of cooperators present in each replicate population is shown for the duration of simulations. **(A)** Despite some oscillations, cooperation dominates in 13 of 18 populations when niche construction affects selection. **(B)** When the selective effects of niche construction ( $\epsilon$ ) are removed, and the selective benefit of adaptation to the external environment ( $\delta$ ) 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 ( $A = 5$ ).



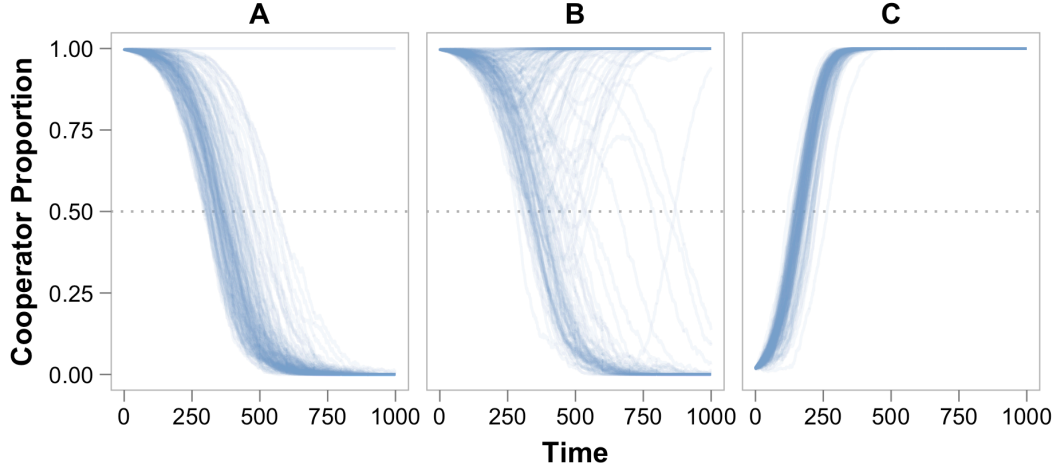
**Figure 4**

Figure 4: **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 Figure 1) can swiftly displace defectors when isogenic defectors cannot arise or adapt via mutation.

399 **Figure 5**

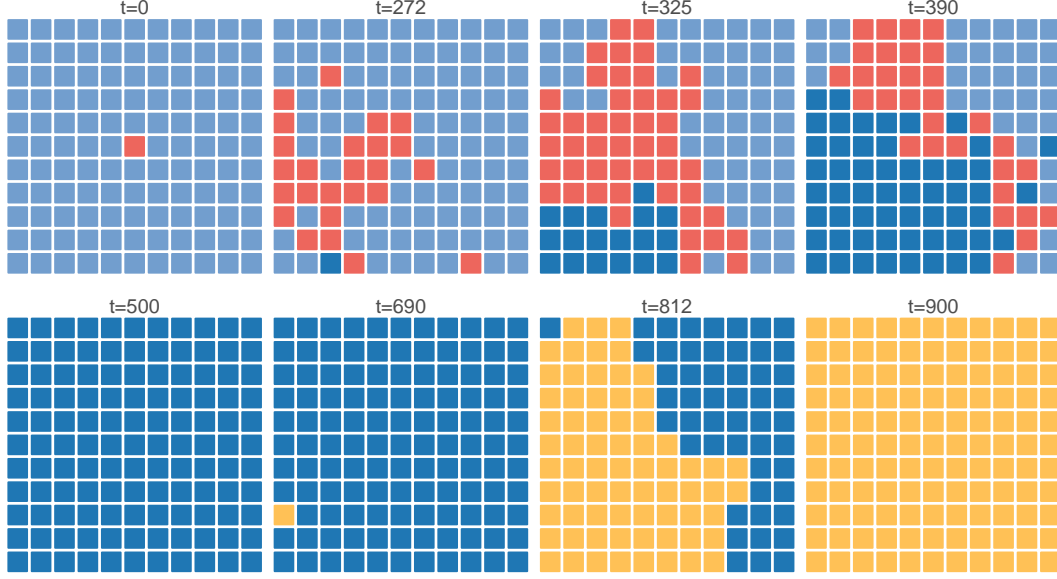


Figure 5: **Cooperator Adaptation Prevents Defector Invasion.** Here we depict the distribution of dominant types among subpopulations over time for one representative simulation in which isogenic defectors arise. To highlight the effects of adaptation, mutations did not occur at the cooperation locus ( $\mu_c = 0$ ). 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.

400 **Figure 6**

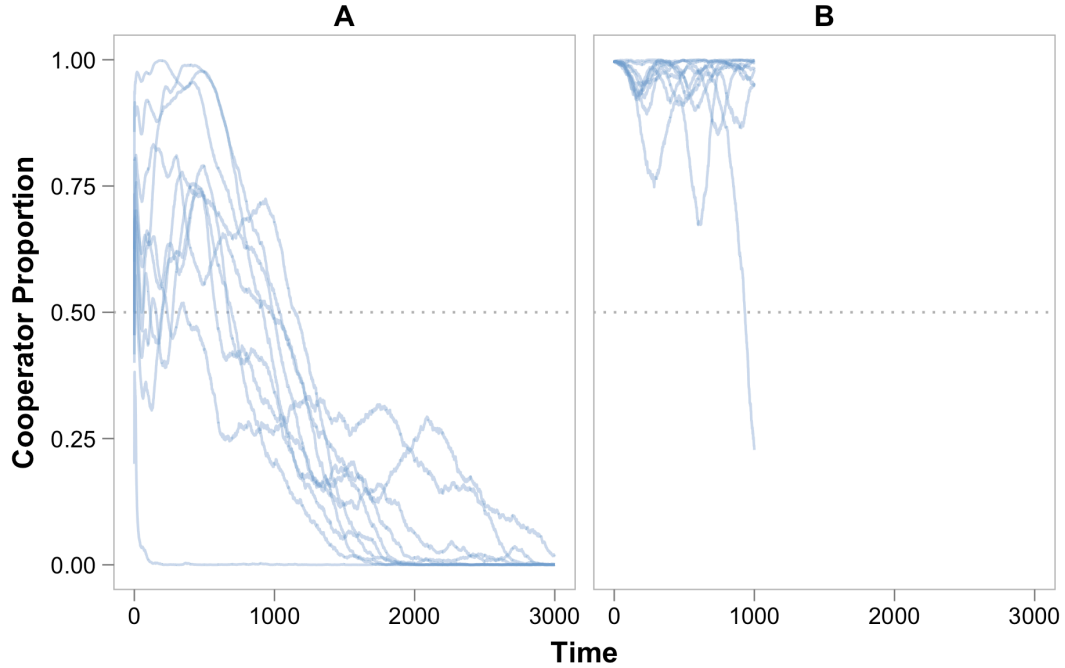


Figure 6: **Negative Niche Construction and Adaptive Paths.** The proportion of cooperators present in each replicate population is shown for the duration of simulations. **(A)** When the effects of negative niche construction are magnified, cooperators are eliminated from all replicate populations ( $n=10$ ). **(B)** Instead, when the mutation rate at adaptive loci is increased 100-fold, cooperators remain dominant in  $\frac{1}{10}$  of  $\frac{1}{10}$  replicate populations ( $\mu_a = 0.001$ ).

401 **Supplemental Figure 1**

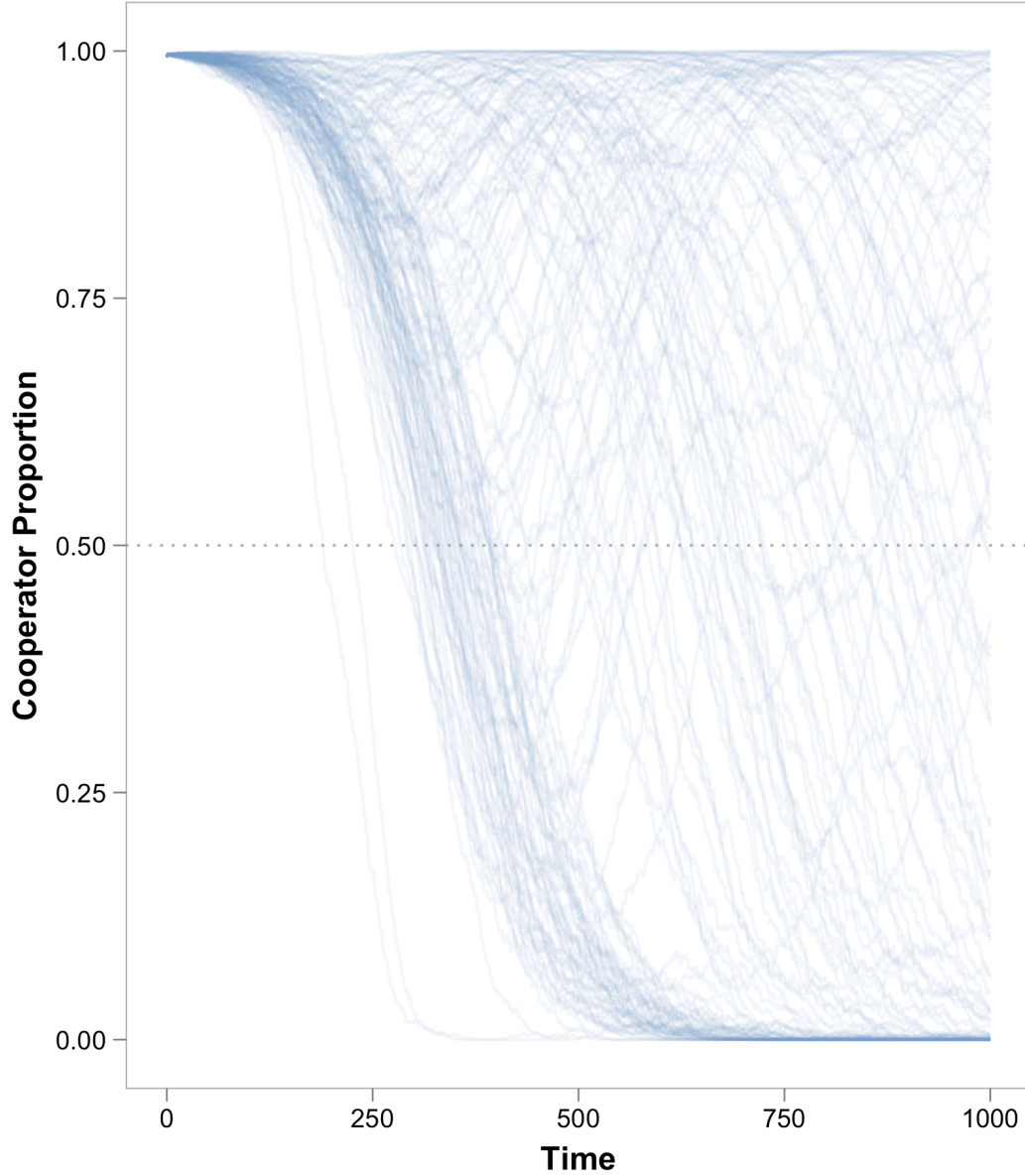


Figure S1: **Defector Invasion with Mutations.** The proportion of co-operators present in each replicate population is shown for the duration of simulations ( $T = 1000$ ). When mutations occur both at the adaptive loci and the cooperation locus ( $\mu_a = \mu_c = 0.00005$ ), cooperation remains dominant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

402 **Supplemental Figure 2**

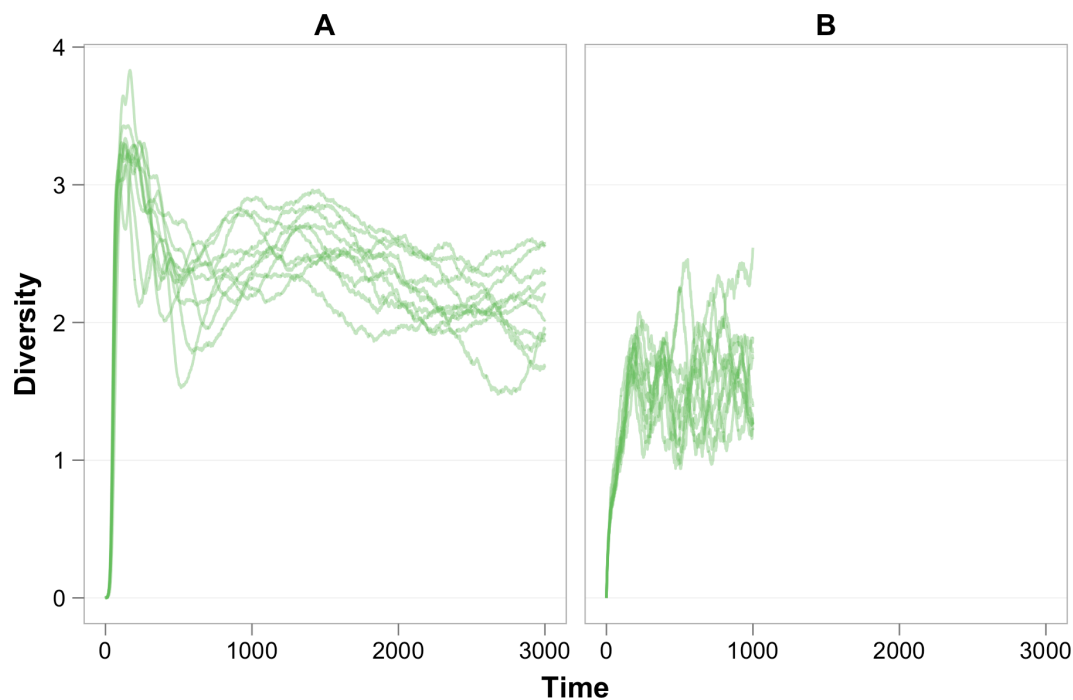


Figure S2: **TODO Diversity something.** TODO. Also explain Shannon  
(A) TODO. (n=TODO) (B) TODO. (n=TODO)

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
$\delta$	Fitness benefit, nonzero alleles	0.3
$\epsilon$	Fitness benefit, sequential alleles	0.00015
$z$	Baseline fitness	1
$S_{min}$	Minimum subpopulation size	800
$S_{max}$	Maximum subpopulation size	2000
$\mu_a$	Mutation rate (adaptation)	$10^{-5}$
$\mu_c$	Mutation rate (cooperation)	$10^{-5}$
$N^2$	Number of patches	625
$m$	Migration rate	0.05
$p_0$	Initial cooperator proportion	0.5
$\sigma$	Survival rate at population initialization	$10^{-5}$
$T$	Number of simulation cycles	3000
$d$	Subpopulation dilution factor	0.1



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