

1 Negative Niche Construction Favors the 2 Evolution of Cooperation

3 4 **Abstract**

5 **Introduction**

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

15 Several factors can prevent this *tragedy of the commons* (Hamilton, 1964;
16 Nowak, 2006; West *et al.*, 2007). One such factor involves non-random so-

17 cial interaction, in which cooperators benefit more from the cooperative act
 18 than defectors. This can occur when cooperators are clustered together in
 19 spatially-structured populations (Fletcher and Doebeli, 2009; Nadell *et al.*,
 20 2010; Kuzdzal-Fick *et al.*, 2011) or when cooperators use communication
 21 (Brown and Johnstone, 2001; Darch *et al.*, 2012) or other cues (Sinervo *et al.*,
 22 2006; Gardner and West, 2010; Veelders *et al.*, 2010) to cooperate condition-
 23 ally with kin. Cooperation can also be bolstered by pleiotropic connections to
 24 personal benefits (Foster *et al.*, 2004; Dandekar *et al.*, 2012) or through associ-
 25 ation with alleles encoding self-benefitting traits (Asfahl *et al.*, 2015). In these
 26 cases, the alleles may provide private benefits that are completely independent
 27 from the public benefits of cooperation. In asexual populations of cooperators
 28 and defectors, this sets the stage for an “adaptive race” in which both types
 29 vie for the first highly beneficial adaptation (Waite and Shou, 2012; Morgan
 30 *et al.*, 2012). The tragedy of the commons can be deferred if a cooperator, by
 31 chance, wins the adaptive race.

32 Hammarlund et al. (2015) recently showed that in spatially-structured pop-
 33 ulations, the “Hankshaw effect” can give cooperators a substantial leg up on
 34 defectors in an adaptive race. This advantage is reminiscent of Sissy Han-
 35 kshaw, a fictional character in Tom Robbins’ *Even Cowgirls Get the Blues*,
 36 whose oversized thumbs—which were otherwise an impairment—made her a
 37 prolific hitchhiker. Similarly, cooperation is costly, but it increases local pop-
 38 ulation density. As a result, cooperators are more likely to acquire beneficial
 39 mutations. By hitchhiking along with these adaptations, cooperation can rise
 40 in abundance. Nevertheless, this advantage is fleeting. As soon as the oppor-

41 tunities for adaptation are exhausted, cooperators are once again at a selective
42 disadvantage against equally-adapted defectors that arise via mutation. How-
43 ever, Hammarlund et al. (2015) also demonstrated that cooperation can be
44 maintained when frequent environmental changes produce a steady stream of
45 new adaptive opportunities. Although organisms typically find themselves in
46 dynamic environments, the nature and frequency of these changes might not
47 ensure long-term cooperator survival.

48 However, organisms do more than simply experience changing environments
49 passively. Through their activities, their interactions with others, and even
50 their deaths, organisms constantly modify their environment. This niche con-
51 struction process can produce evolutionary feedback loops in which environ-
52 mental change alters selection, which, in turn, alters the distribution of types
53 and their corresponding influence on the environment (Odling-Smee *et al.*,
54 2003). The nature of this feedback can have dramatic evolutionary conse-
55 quences. One critical distinction is whether the constructing type is favored in
56 the resulting environment. Under positive niche construction, selection favors
57 the constructor, and evolution stagnates as this type fixes. Under negative
58 niche construction, selection favors a type other than the constructor, which
59 creates an opportunity for adaptation. If an adapted type also engages in
60 negative niche construction, cycles of construction and adaptation can ensue,
61 such that populations find themselves continually chasing beneficial mutations
62 as their adaptive landscape perpetually 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 describe 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 the evolution of coop-
79 eration; specifically, how cooperative behavior can hitchhike with adaptive
80 mutations to modified environments.

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

different integers. A binary allele at the first locus (here, locus zero) determines whether that individual is a cooperator (1), which carries fitness cost c , or a defector (0). The remaining L loci are *adaptive loci*, and are each occupied by 0 or a value from the set $\{1, 2, \dots, A\}$. Allele 0 represents a lack of adaptation, while a non-zero allele represents one of the A possible adaptations at that locus.

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

Niche Construction and Selective Feedbacks

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

In our model, the feedback from niche construction takes the form of density dependent selection, and individuals evolve to better match their niche. Specifically, the selective value of non-zero allele a at adaptive locus l —and consequently the fitness of an individual carrying that allele—increases with

107 the number of individuals in the subpopulation that have allele $a - 1$ at locus
 108 $l - 1$. For example, when $L = 5$ and $A = 6$, and allele 4 has fixed at locus 2,
 109 a genotype with allele 5 at locus 3 is favored. And once allele 5 has fixed at
 110 locus 3, the niche that this population constructs will favor allele 6 at locus
 111 4. As a consequence, genotypes with sequentially increasing allelic states will
 112 tend to evolve. We treat both adaptive loci and their non-zero allelic states as
 113 “circular”: the selective value of an allele at locus 1 is affected by the allelic
 114 composition of the subpopulation at locus L . Similarly, the selective value
 115 of allele 1 at any locus increases with the number of individuals carrying al-
 116 lele A at the previous locus. This circularity is represented by the function
 117 $\beta(x, X)$, which gives the integer that is below an arbitrary value x in the set
 118 $\{1, 2, \dots, X\}$:

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

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

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

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

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

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

128 Thus, an individual's fitness is determined both by adaptations to the exter-
 129 nal environment and by adaptations to its constructed environment. Box 1
 130 illustrates the effects of these two components. While cooperation is costly, we
 131 assume its effects are independent of the external and constructed components
 132 of the environment.

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

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

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

139 During subpopulation growth, individuals compete through differential repro-
 140 duction. Each individual's probability of success is determined by its fitness.

141 The composition of a subpopulation with size P and cooperator proportion p
 142 after growth is multinomial with parameters $S(p)$ and $\{\pi_1, \pi_2, \dots, \pi_P\}$, where
 143 π_i represents individual i 's reproductive fitness relative to others in the sub-
 144 population (using Equation 2).

145 **Mutation**

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

154 **Migration**

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

162 Population Initialization and Simulation

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

171 Simulation Source Code and Software Dependencies

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

177 Results

178 Using the model described in the previous section, we perform simulations
179 that follow the evolution of cooperation in a population consisting of subpopu-
180 lations that are connected by spatially-limited migration. Individuals increase

¹These materials will be made public prior to publication.

181 their competitiveness by gaining adaptations. While cooperation does not di-
 182 rectly affect the fitness benefits that these adaptations confer, cooperation has
 183 indirect effects on the adaptive process. Specifically, cooperation increases
 184 subpopulation density. As a result, larger subpopulations of cooperators ex-
 185 perience more mutational opportunities. Cooperation can rise in abundance
 186 by hitchhiking along with beneficial mutations, which compensate for the cost
 187 of cooperation. Importantly, subpopulations alter their local environments,
 188 which feeds back to influence selection. Here, we explore how such niche con-
 189 struction affects the evolution of cooperation.

190 **Cooperation Persists with Niche Construction**

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

203 construction feeds back to influence selection ($\epsilon > 0$), cooperation persists in
204 the majority of the replicate populations (Figure 1C). We see in Figure 2A that
205 despite oscillations in the proportion of cooperators, cooperation is maintained
206 at high levels in these populations.

207 **Fitness Increases Alone do not Support Persisting Coop-** 208 **eration**

209 In the model, adaptations to both the external environment and the con-
210 structed environment contribute to an individual's fitness. To determine
211 whether cooperation is maintained solely due to the larger selective values
212 that result from the contributions of niche construction (ϵ), we performed
213 simulations in which these contributions were removed ($\epsilon = 0$), and we in-
214 stead increased the fitness benefits conferred by adaptation to the external,
215 non-constructed environment ($\delta = 0.6$). In doing so, we conservatively esti-
216 mate the selective effects of niche construction by supplementing the selective
217 benefits of adaptations to the external environment by the maximum possible
218 selective benefit that results from niche construction. Nevertheless, we find
219 that simply increasing selective values does not enable cooperators to persist
220 (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 alleles (A) does not divide evenly into the number of adaptive loci (L). In such a case, any sequence of integers on the circular genome will always contain a break in the sequence; that is, one locus with an allele that is not one less than the allele at the next locus. Given this unavoidable mismatch, any type that has fixed will always construct a niche that favors selection for a new type. When negative niche construction is removed (by setting $L = 5$, $A = 5$), cooperators are again driven extinct after an initial lift in abundance (Figure 2C). These results indicate that the type of niche construction matters. Specifically, negative niche construction is crucial for maintaining cooperation.

Selective Feedbacks Limit Defector Invasion

The adaptation resulting from selective feedbacks can limit invasion by defectors, which arise either through immigration from neighboring patches or through mutation from a cooperator ancestor. The latter challenge is particularly threatening, as these isogenic defectors are equally adapted, yet do not incur the cost of cooperation. As demonstrated in Figure 3A, isogenic

defectors rapidly spread when introduced at a single patch in the center of a population of cooperators if mutations do not occur. However, when cooperators can gain adaptations via mutation, cooperators resist defector invasion in over half of the replicate populations (Figure 3B). Figure 4 depicts one such instance. In that population, defectors quickly began to spread. However, an adaptation arose in a neighboring cooperator population. This type spreads more quickly, stopping the spread of defectors and eventually driving them to extinction. Because this adaptation 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

265 beneficial trait. In that work and in ours, populations of cooperators grow
266 to a higher density than those of defectors. Because of this, these cooperator
267 populations experience more mutations and are therefore more likely to gain
268 adaptations. While this process does favor cooperation in the short term, it
269 eventually reaches a dead end; when the opportunities for adaptation are ex-
270 hausted and cooperators can no longer hitchhike, they face extinction. In our
271 current model, we have considered whether niche construction might serve to
272 perpetually generate new adaptive opportunities and thus favor cooperation
273 indefinitely.

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

280 Further, we find that it is specifically *negative* niche construction that main-
281 tains cooperation (Figure 2C). As cooperator and defector types gain adapta-
282 tions, they change the environment in a way that favors other types. In this
283 way, negative niche construction serves as a perpetual source of adaptation.
284 Here we observe another facet of the Hankshaw effect: because populations
285 of cooperators are larger, they are better able to respond to the adaptive op-
286 portunities that result from negative niche construction. These opportunities
287 can allow cooperators to resist invasion by defectors (Figure 3B). Although
288 defectors initially have an advantage by saving on the cost of cooperation, sub-

289 populations of cooperators can quickly gain an advantage because they are
290 larger. Even after defector invasion, subpopulations of cooperators are more
291 likely to produce the next adapted mutant, which can then displace the slower
292 evolving defectors. It is these recurring cycles of defector invasion and cooper-
293 ator adaptation that underlie the oscillations in cooperator proportion that we
294 see in [Figure 2A](#). When an adaptation to the constructed environment does
295 not occur in the cooperator background before the defector dominates, the
296 defector can drive the cooperator to extinction. This is something that we see
297 occur stochastically in [Figures 2A](#) and [3B](#).

298 **Cooperation as Niche Construction**

299 In our model, cooperation is orthogonal to niche construction, which allows us
300 to focus on hitchhiking. However, by increasing the size of the subpopulation,
301 this form of cooperation can itself be seen as form of niche construction. Co-
302 operative benefits often take similar forms in natural systems. For example,
303 bacteria produce a host of extracellular products that scavenge soluble iron
304 (Griffin *et al.*, 2004), digest large proteins (Diggle *et al.*, 2007; Darch *et al.*,
305 2012), and reduce the risk of predation (Cosson *et al.*, 2002). As in our model,
306 such cooperative acts are likely to increase local population density. While
307 many studies have focused on how the environment affects the evolution of
308 these cooperative traits, relatively few have addressed how the environmental
309 changes created by public goods feed back to influence evolution.

310 Perhaps most similar to our work, Van Dyken and Wade (2012) demonstrated

311 that when two negative niche constructing, cooperative behaviors co-evolve,
312 selection can increasingly favor these traits, which were disfavored when alone.
313 In that model, “reciprocal niche construction” occurred when the negative feed-
314 back created by one strategy positively influenced selection on the other, cre-
315 ating a perpetual cycle that maintained both forms of cooperation. Arguably,
316 this can be viewed as an instance of hitchhiking: the currently-maladaptive
317 form of cooperation is maintained by association with the adaptive form.

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

326 **Evolution at Multiple Timescales**

327 In our work, the niche is modeled implicitly by the composition of the popula-
328 tion. Any changes, therefore, in the population produce immediate effects on
329 the constructed environment and the resulting feedbacks. However, timescales
330 in our model could be de-coupled in two ways. First, cooperators modify their
331 niche by enabling their population to reach larger density (Equation 4). These
332 increased population sizes play a critical role by effectively increasing the rate

333 of evolution in these populations. Because of the importance of this process, it
334 would be very informative to explore how sensitive our results are to changes
335 in how long the increases in population size are upheld. Similarly, changes
336 in the timescale at which the niche at a patch change also have potential to
337 dramatically alter our results. Not only would changes in timescale affect the
338 selective values of alleles as the population changed, but they could also in-
339 fluence whether or not populations were able to evolve adapted types and if
340 so, how well those adapted types can propagate through the population to
341 address the threat of a defector.

342 Other studies, while not focused on cooperation, have similarly shown that the
343 timescales at which niche construction feedbacks occur can strongly influence
344 evolutionary outcomes (Laland *et al.*, 1996, 1999). This perspective is likely to
345 be crucial for understanding the evolution of cooperative behaviors like the pro-
346 duction of public goods. In these instances, environmental changes are likely
347 to occur on different timescales than growth, which can have profound effects.
348 For example, a multitude of factors including protein durability (Brown and
349 Taddei, 2007; Kümmerli and Brown, 2010), diffusion (Allison, 2005; Driscoll
350 and Pepper, 2010), and resource availability (Zhang and Rainey, 2013; Ghoul
351 *et al.*, 2014) influence both the rate and the degree to which public goods alter
352 the environment. While Lehmann (2007) showed that cooperation was favored
353 when selective feedbacks act over longer timescales, niche construction may in
354 fact hinder cooperation when selection is more quickly altered. For example,
355 when public goods accumulate in the environment, cooperators must decrease
356 production to remain competitive (Kümmerli and Brown, 2010; Dumas and

357 Kümmerli, 2012). This favors cooperation that occurs facultatively, perhaps
358 by sensing the abiotic (Bernier *et al.*, 2011; Koestler and Waters, 2014) or
359 biotic environment (Brown and Johnstone, 2001; Darch *et al.*, 2012). To allow
360 our model to address how traits such as these evolve, we would first need to
361 de-couple the niche from the composition of the population by representing
362 the niche explicitly.

363 **Cooperation and Niche Construction in Host-Symbiont** 364 **Co-Evolution**

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

373 For example, the cooperative production of virulence factors by the human
374 pathogen *P. aeruginosa* in lung infections is harmful to hosts with cystic fi-
375 brosis (Harrison, 2007). Similarly to what we have shown in this work, these
376 antagonistic, negative niche constructing behaviors might actually work to
377 maintain these infections. If this is the case, however, perhaps the case could
378 be made for developing treatments that target the selective feedback loop that

379 is created by niche construction. If these populations do indeed perpetually
380 benefit from adaptations that are created by niche construction, as we have
381 shown, case could perhaps be made for developing treatments that target the
382 selective feedback loop that provides adaptive opportunities in these spatial
383 environments. While the idea of removing negative selective feedbacks and sup-
384 porting stability may seem counterintuitive, if it makes the population more
385 susceptible, then perhaps pairing such a treatment with ones in which mutants
386 are introduced (e.g., Rumbaugh et al. (2009)), could significantly improve host
387 fitness. Expanding models such as ours to address the additional dynamics
388 present in host-symbiont systems such as these could be quite productive.

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

400 It was recently argued that incorporating the effects of niche construction is
401 critical for improving our understanding of viral evolution (Hamblin *et al.*,
402 2014) and evolution in co-infecting parasites (Hafer and Milinski, 2015). In-

403 corporating host dynamics, co-evolution, and the feedbacks that they produce
404 into models is likely to be equally important for gaining an understanding of
405 how cooperative behaviors, both positive and negative, evolve in these host-
406 symbiont settings.

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415 Figures

416 **Figure 1**

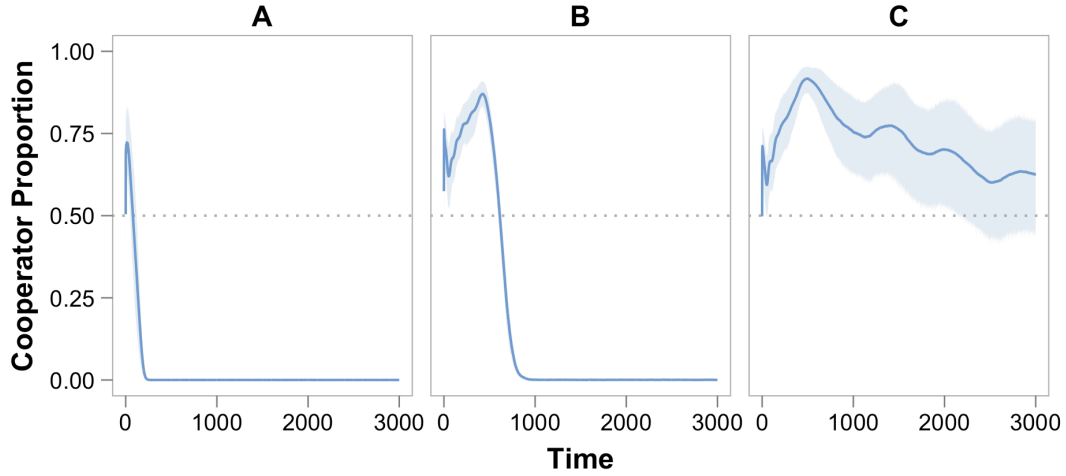


Figure 1: **Adaptation, Hitchhiking, and the Evolution of Cooperation.** Curves show the average cooperator proportion among replicate populations for the duration of simulations, and shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter values are listed in [Table 1](#).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

417 **Figure 2**

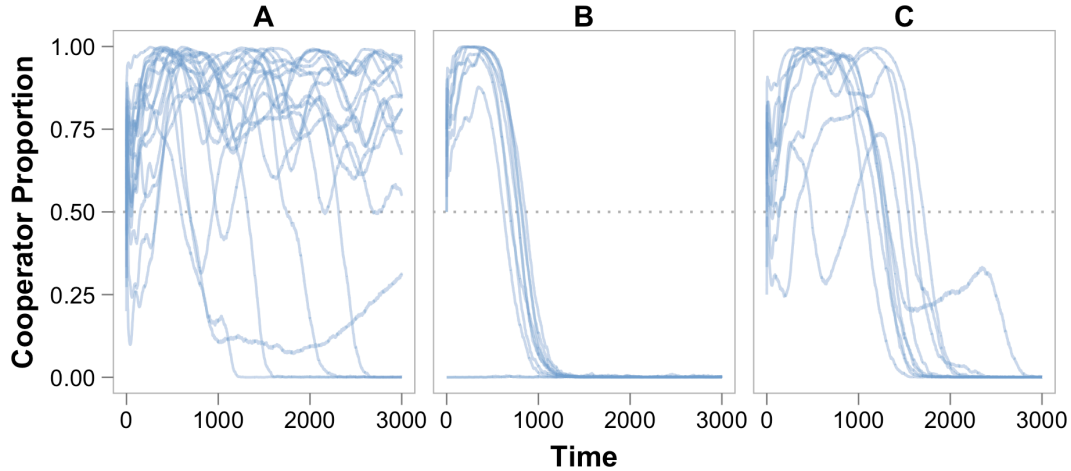


Figure 2: Niche Construction and the Evolution of Cooperation. The proportion of cooperators present in each replicate population is shown for the duration of simulations. **(A)** Despite some oscillations, cooperation dominates in 13 of 18 populations when niche construction affects selection. **(B)**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

418 **Figure 3**

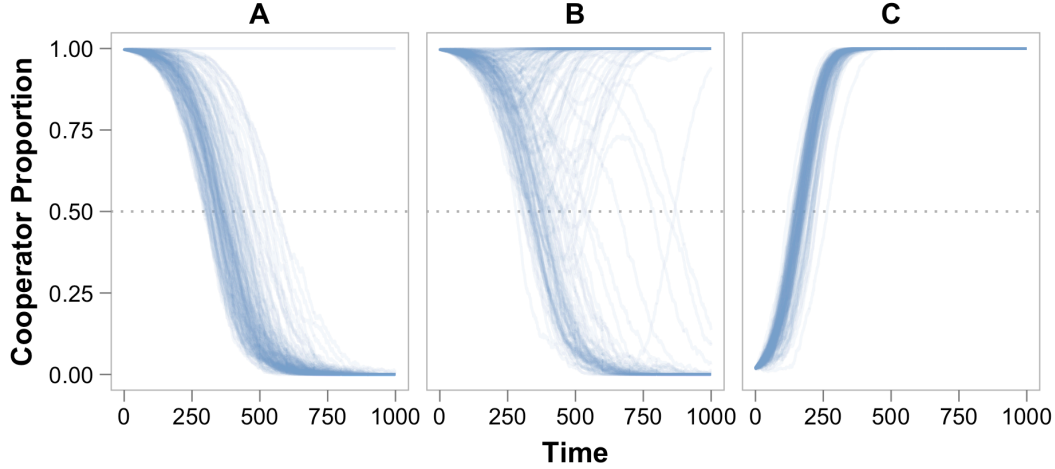


Figure 3: Niche Construction and Invasion. Curves trace the proportion of cooperators present in each replicate population for the duration of simulations ($T = 1000$). In each simulation, a rare type was initiated at a single patch in the center of the population lattice ($N^2 = 121$). Unless otherwise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

419 **Figure 4**

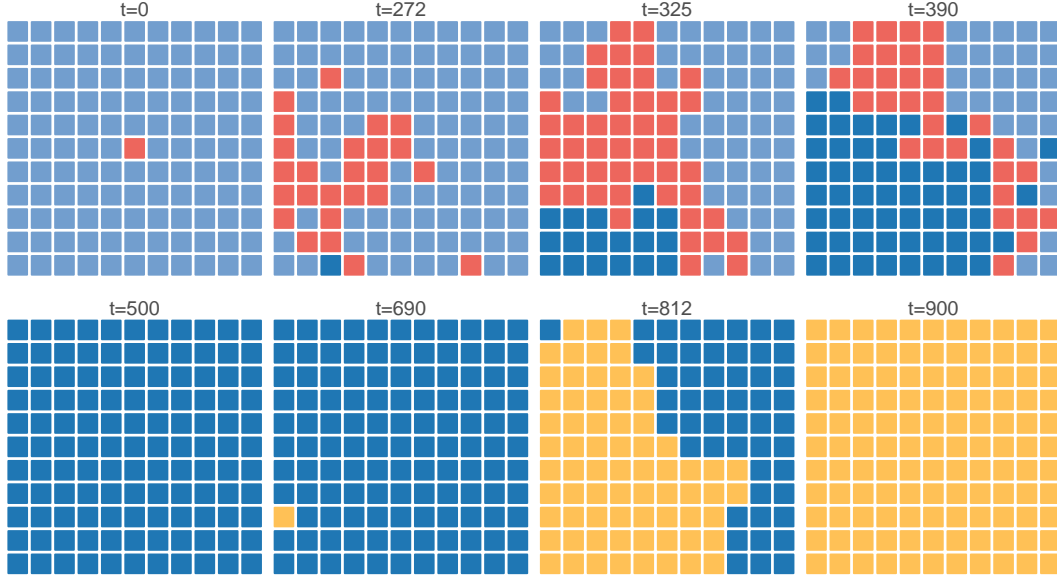


Figure 4: **Cooperator Adaptation Prevents Defector Invasion.** Here we depict the distribution of dominant types among subpopulations over time for one representative simulation in which isogenic defectors arise. To highlight the effects of adaptation, mutations did not occur at the cooperation locus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

420 **Supplemental Figure 1**

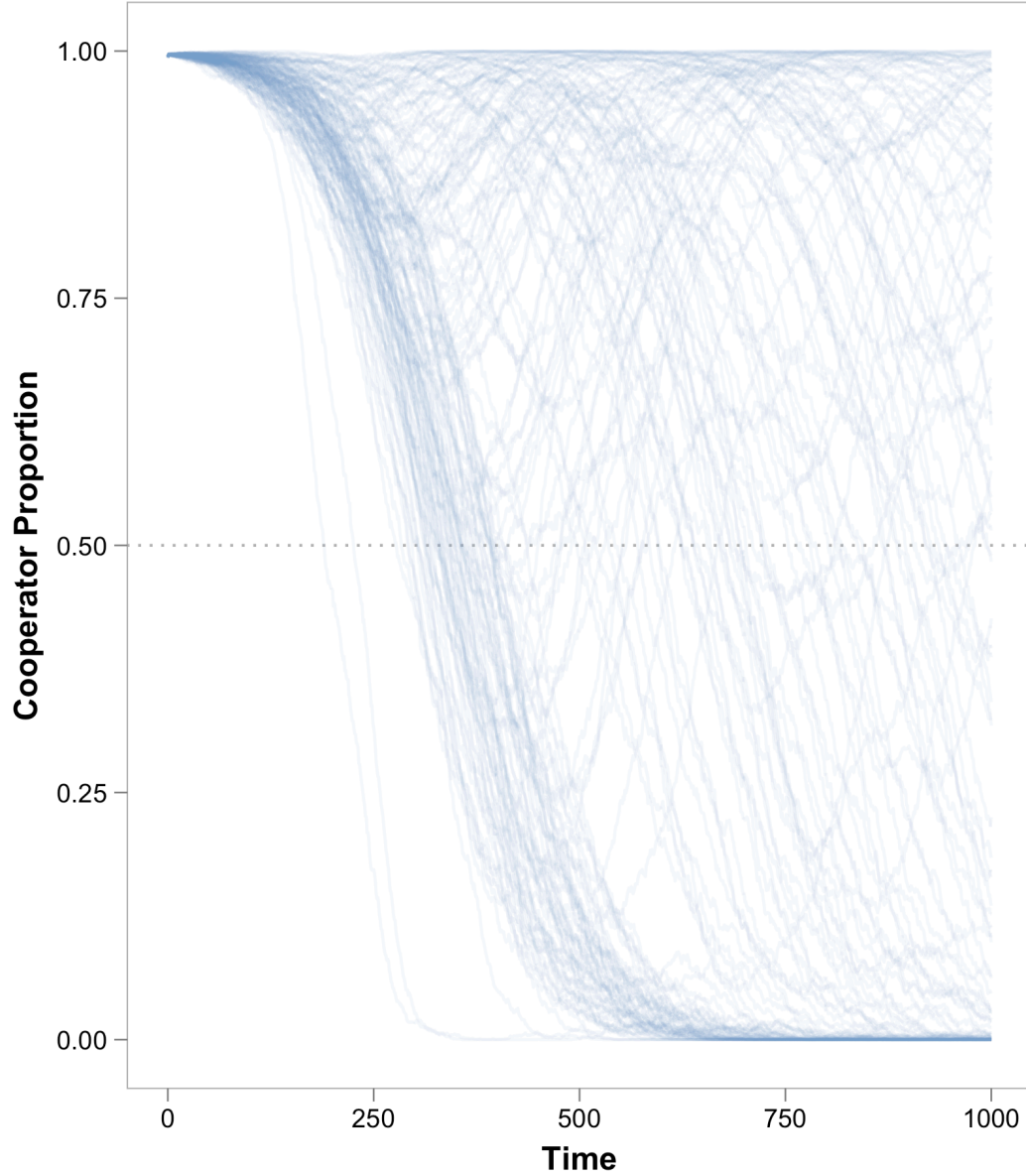


Figure S1: **Defector Invasion with Mutations.** The proportion of co-operators present in each replicate population is shown for the duration of simulations ($T = 1000$). When mutations occur both at the adaptive loci and the cooperation locus ($\mu_a = \mu_c = 0.00005$), cooperation remains dominant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