

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

4  
5 **Abstract**

6 TODO

## 7 **Introduction**

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

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

34 Hammarlund *et al.* (2015) recently showed that in spatially structured popu-  
35 lations, cooperators can gain a substantial leg up on defectors in an adaptive  
36 race. Specifically, cooperation increases local population density, thus increas-  
37 ing the likelihood of acquiring beneficial mutations. By hitchhiking along with  
38 these adaptations, the cooperative trait can rapidly rise in abundance. Never-  
39 theless, this advantage is fleeting. As soon as the opportunities for adaptation  
40 are exhausted, cooperators are once again at a disadvantage against adapted

41 defectors. However, Hammarlund et al. (2015) demonstrated that cooperation  
42 can be maintained indefinitely when frequent environmental changes produce  
43 a steady stream of adaptive opportunities. Although organisms typically find  
44 themselves in dynamic environments, change might not occur at a rate that  
45 provides sufficient adaptive opportunities to ensure long-term cooperator per-  
46 sistence.

47 In this work, we explore whether cooperation can be maintained indefinitely  
48 by niche construction. We expand upon the model presented in Hammarlund  
49 et al. (2015) to allow populations to alter their local environment. As environ-  
50 ments change, so too does selection, which creates an eco-evolutionary feedback  
51 whereby selection is dependent on the genotypes present in the population, and  
52 the composition of genotypes is dependent on selection. Niche construction  
53 can be positive or negative, depending on whether the environmental change  
54 increases or decreases the fitness of the niche-constructing individual. We in-  
55 vestigate whether these selective feedbacks can act as a continual source of  
56 adaptive opportunities for cooperators.

57 Although niche construction occurs independently of cooperation in our model,  
58 the increase in density that results from cooperation has a profound effect on  
59 how populations evolve in the presence of selective feedbacks. First, these pop-  
60 ulations exert greater influence on their environments, which better enables  
61 them to benefit from positive niche construction. Additionally, as environ-  
62 ments change, either through negative niche construction or external influ-  
63 ences, these larger populations can adapt more quickly. Finally, because large  
64 populations produce more emigrants, these populations will exert a stronger in-

fluence on neighboring populations, effectively exporting their niche. Because of these potential benefits, we also focus our attention on how population size and migration rate influence evolutionary outcomes in these environments.

## Methods

We build upon the model described in Hammarlund et al. (2015), in which cooperators and defectors compete and evolve in a metapopulation (a collection of populations). Individuals in each of the populations reproduce, mutate, and migrate to neighboring populations. Importantly, adaptation can occur. In our model here, we further allow populations to modify their local environment, and these modifications feed back to affect selection.

## Model Description

Our simulated environment consists of  $N^2$  patches arranged as an  $N \times N$  lattice (see Table 1 for model parameters and their values), where each patch can support a population.

## Individuals and Genotypes

Each individual in a population has a genotype, which is an ordered list of  $L + 1$  integers (loci). A binary allele at the last locus ( $L + 1$ ) determines whether that individual is a cooperator (1) or a defector (0). Cooperators incur a fitness cost  $c$ . The first  $L$  loci are *adaptive loci*, and are each occupied

by 0 or an integer from the set  $\{1, 2, \dots, A\}$ , where  $A$  is the number of alleles conferring a selective benefit. Specifically, the presence of any non-zero allele at any of these loci represents an adaptation that confers a fitness benefit  $\delta$ . We choose  $\delta > c$ , which allows a minimally adapted cooperator to recoup the cost of cooperation. The fitness benefits of these adaptations are purely endogenous, and are not affected by other individuals or the environment.

## Niche Construction

Populations also influence their environment, which feeds back to affect selection. This process adds a second, exogenous component to each individual's fitness. Here, the “niche” is defined implicitly by the allelic states present in the population. As allelic states change, a population constructs its unique niche. We use a form of density dependent selection to increasingly favors individuals that match their niche.

Specifically, the selective value of adaptive allele  $a$  at locus  $l$  increases with the number of individuals in the population that have allele  $a + 1$  at locus  $l + 1$ . We treat both adaptive loci and allelic states as “circular”, so the allelic state at locus  $L$  is affected by the allelic composition of the population at locus 1, and the selective value of allele  $A$  at any locus increases with the number of individuals carrying allele 1 at the next locus. For the remainder of this section, this circularity is represented by the function below, which gives the integer that follows an arbitrary value  $x$  in the set  $\{1, 2, \dots, X\}$ .

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

Here,  $\text{mod}_Y(y)$  is the integer remainder when dividing  $y$  by  $Y$ . Thus, the selective value of adaptive allele  $a$  at locus  $l$  increases with the number of individuals that have allele  $\beta(a, A)$  at locus  $\beta(l, L)$ . The slope of this increase is  $\epsilon$ , which specifies the intensity of niche construction. Consider a genotype  $g$  with allelic state at locus  $l$  given by  $a_{g,l}$ ; its fitness is defined as:

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

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

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

As a consequence of this form of density dependent selection, genotypes with sequentially increasing allelic states will tend to evolve. Because mutations are random (see below), each population will evolve different consecutive sequences. These different sequences represent the unique niches constructed by populations.

## 117 **Population Growth and the Benefit of Cooperation**

118 Cooperation allows the population to reach greater density. If  $p$  is the propor-  
119 tion of cooperators in a population at the beginning of a growth cycle, then  
120 that population reaches the following size:

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

121 The function  $S(p)$  reflects the benefit of cooperation. During growth, individ-  
122 uals compete for inclusion in the resulting population. The composition of a  
123 population with size  $P$  and cooperator proportion  $p$  after growth is multino-  
124 mial with parameters  $S(p)$  and  $\{\pi_1, \pi_2, \dots, \pi_P\}$ , where:

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

125 Here,  $W_{\gamma(i)}$  is the fitness of an individual  $i$  with genotype  $\gamma(i)$  (see Equation  
126 2). The value  $\pi_i$  therefore reflects an individual's reproductive fitness relative  
127 to others' in the population.

## 128 **Mutation**

129 For simplicity, we apply mutations after population growth. Mutations occur  
130 independently at each locus and cause an allelic state change. At each adaptive  
131 locus, mutations occur at rate  $\mu_a$ . These mutations replace the current allele  
132 with a random selection from the set  $\{0\} \cup \{1, 2, \dots, A\}$ . Note that this allows

133 for the possibility of an allele replacing itself, thus slightly reducing the effective  
134 mutation rate. At the binary cooperation locus, mutations occur at rate  $\mu_c$ .  
135 These mutations flip the allelic state, causing cooperators to become defectors  
136 and vice versa.

## 137 **Migration**

138 After mutation, individuals emigrate to an adjacent patch at rate  $m$ . The  
139 destination patch is randomly chosen with uniform probability from the source  
140 patch's Moore neighborhood, which is composed of the nearest 8 patches on the  
141 lattice. Because the metapopulation lattice has boundaries, patches located  
142 on an edge have smaller neighborhoods.

## 143 **Metapopulation Initialization and Simulation**

144 Metapopulations are initiated in a state that follows an environmental change.  
145 First, populations are seeded at all patches with cooperator proportion  $p_0$  and  
146 grown to density  $S(p_0)$ . An environmental challenge is then introduced, which  
147 subjects the population to a bottleneck. For each individual, the probability  
148 of survival is  $\mu_t$ , which represents the likelihood that a mutation occurs that  
149 confers tolerance. Survivors are chosen by binomial sampling. Because indi-  
150 viduals have not yet adapted to this new environment, the allelic state of each  
151 individual's genotype is set to 0 at each adaptive locus. Following initializa-  
152 tion, simulations are run for  $T$  cycles, where each discrete cycle consists of  
153 population growth, mutation, and migration. At the end of each cycle, popu-



154 lations are thinned to allow for growth in the next cycle. The individuals that  
155 remain are chosen by binomial sampling, where each individual persists with  
156 probability  $d$ , regardless of allelic state.

## 157 **Source Code and Software Environment**

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

## 163 **Results**

164 We follow the evolution of cooperation in a metapopulation consisting of pop-  
165 ulations connected by spatially-limited migration. Individuals in these popu-  
166 lations can gain a limited number of adaptations that confer selective benefits.  
167 While the allele at an individual’s cooperation locus does not directly affect  
168 the value of alleles at adaptive loci, cooperation can have indirect effects on the  
169 process of adaptation. Specifically, because cooperation increases population  
170 density, isolated cooperators experience more mutational opportunities to gain  
171 adaptations. Cooperation can hitchhike along with these adaptations, which  
172 compensate for the cost of cooperation. Additionally, populations alter their  
173 environment. Here, we explore how niche construction can favor the evolution

174 of cooperation. Our simulation environment is defined by the parameter val-  
175 ues listed in Table 1. Unless otherwise noted, 10 replicate simulations were  
176 performed for each experiment. We quantify cooperator success using the area  
177 under the cooperator proportion curve. This measure of cooperator presence  
178 increases as cooperators rise in abundance or remain in the population longer.

## 179 Niche Construction Maintains Cooperation

180 Without any opportunity for adaptation ( $L = 0$ ), cooperators are swiftly elim-  
181 inated in competition with defectors (Figure 1A). Despite an initial lift due  
182 to increased productivity, the cost of cooperation becomes disadvantageous as  
183 migration mixes the initially isolated populations. When there are opportu-  
184 nities for adaptation ( $L = 5$ ) but no niche construction ( $\epsilon = 0$ ), cooperators are  
185 maintained transiently (Figure 1B). Here, the additional mutational oppor-  
186 tunities provided by their larger sizes allows cooperator populations to more  
187 quickly adapt to their environment. As previously described by Hammarlund  
188 et al. (2015), however, cooperation is subsequently lost as *adapted* defector  
189 populations arise via mutation. When niche construction is incorporated,  
190 cooperation persists (Figure 1C).

## 191 Fitness Increases Alone do not Support Persisting Coop- 192 eration

193 In our model, niche construction introduces additional selective benefits. To  
194 determine how these selective effects influence evolutionary outcomes, we per-

195 formed simulations in which the selective effects of niche construction were  
196 removed ( $\epsilon = 0$ ), and we instead increased the fitness benefits conferred by  
197 adaptation ( $\delta = 0.6$ ). Here, we are conservative by lifting the selective value of  
198 exogenous adaptation by the maximum value possible from niche construction.

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

## 204 **Negative Niche Construction is Critical to Cooperator** 205 **Persistence**

206 Negative niche construction occurs in our model due to selection for  
207 sequentially-increasing allelic states and the circular arrangement of these  
208 alleles. When the genome length ( $L$ ) is not evenly divided by the number  
209 of adaptive alleles ( $A$ ), then it is not possible for the population to be fixed  
210 for a genotype that is perfectly adapted to the constructed environment.  
211 Technically (in terms of the model) this is because the equality:

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

212 cannot simultaneously hold for all  $l$ .

213 For example, consider genotype  $(1, 2)$  when  $L = 2$  and  $A = 3$ . Here, allelic

state 2 at locus 2 will be beneficial, because it follows allelic state 1 at locus 1. However, due to the circular effects, allelic state 1 at locus 1 will be deleterious relative to allelic state 3 at locus 1. Yet, fixation for genotype (3, 2) does not solve the problem, because a mutant (3, 1) is fitter, and so on.

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

## **Positive niche construction is important to cooperator persistence**

To determine how negative niche construction influences the evolution of co-operation, we maximize the allelic conflict ( $L = 1$ ,  $A = 6$ ). Here, selection for increasing allelic states among the adaptive loci means that any allelic state will not be greater than at the previous allele (itself), and thus there will always be opportunity for adaptation. Despite this constant opportunity, niche construction does not increase cooperator presence (Figure 2D).

## **NC Enables Cooperator Spread**

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

## 234 NC Prevents Defector Invasion

235 Figure 5

## 236 How Cooperation Fuels all of this

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

241 To address how migration affects the evolutionary process in this system, we  
242 vary the rate at which migration occurs ( $m$ ). As seen in Figure 6B, cooperation  
243 decreases as migration rate increases. This is likely because migration defines  
244 the spatial structuring in this system. As migration increases, the population  
245 becomes more like a well-mixed system, where defectors are better able to  
246 exploit the benefits of cooperation (Griffin *et al.*, 2004; Kümmerli *et al.*, 2009).

## 247 # Discussion

248 Despite their negative effects, deleterious traits can rise in abundance due to  
249 genetic linkage with other traits that are strongly favored by selection (May-  
250 nard Smith and Haigh, 1974). In a process termed the “Hankshaw effect”,  
251 Hammarlund *et al.* (2015) recently demonstrated that cooperative behaviors  
252 can prolong their existence by actively increasing their likelihood of hitchhik-  
253 ing with a beneficial trait. While this process does favor cooperation in the  
254 short term, it eventually reaches a dead end. When the opportunities for  
255 adaptation are exhausted, and cooperators can no longer hitchhike, they face

extinction. In this work, we have considered whether niche construction can maintain cooperation indefinitely.

We demonstrate that when niche construction occurs, cooperation can indeed persist (Figure 1C). But what aspects of niche construction produce this result? In our model, niche construction introduces additional selective effects that could influence the evolutionary process. However, simply raising the selective benefits provided by adaptations does not significantly increase cooperator presence (Figure 2B), and indicates that niche construction plays an important role. Although cooperators benefit greatly from positive niche construction, it does not fully explain our results (Figure 2C). Indeed, despite an initial increase in abundance, cooperators are eventually driven to extinction when environmental change produces only positive fitness effects. As with the Hankshaw effect, adaption eventually slows, allowing defectors to outcompete cooperators (Figure 3C). While it does not benefit cooperation when alone (Figure 3E), negative niche construction acts to prevent this stasis. Combined, we find that both positive and negative niche construction are required to maintain cooperation.

When successful, we observe that populations do not reach the maximum possible fitness (Figure 3A). Although cooperation is the focus of this study, it can be seen as deleterious. Previous work has shown that niche construction can favor deleterious alleles (Laland *et al.*, 1996, 1999). Similarly here, cooperation is maintained in the presence of niche construction, but lost otherwise. Van Dyken and Wade (2012) showed that when two cooperative behaviors co-evolve and niche construction feedbacks benefit the other type, niche con-

struction can increasingly favor these traits, which were otherwise disfavored when alone.

By their very nature, public goods benefit populations by making their environment more hospitable (West *et al.*, 2007a). For example, bacteria produce a host of extracellular products that find 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 explored how the environment affects the evolution of cooperative behaviors such as these, relatively few have examined how those behaviors affect the environment and how the resulting feedbacks influence evolutionary trajectories.

In our model, the environmental state was implicitly modeled, and depended solely on the current state of the population. In natural settings, however, the timescales at which environments are modified and reproduction are likely to be decoupled. 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. These factors are likely to influence evolutionary trajectories (Laland *et al.*, 1996). Lehmann (2007) demonstrated that a cooperative, niche constructing behavior can be favored when it only affected selection for future generations, thus reducing the potential for competition among contemporary kin. The evolutionary inertia that this creates, however, may ultimately work against cooperators. When public good accumulates in the environment, cooperators must reduce their investment in production to re-

304 main competitive (Kümmerli and Brown, 2010; Dumas and Kümmerli, 2012).  
305 Cooperation that occurs facultatively, perhaps by sensing the abiotic (Bernier  
306 *et al.*, 2011; Koestler and Waters, 2014) or biotic environment (Brown and  
307 Johnstone, 2001; Darch *et al.*, 2012), are likely to be favored in these environ-  
308 ments.

309 In many instances of cooperation, the environment is itself a biological entity,  
310 which can produce additional evolutionary feedbacks. As the host population  
311 changes, so too will selection on their symbiont populations. Here, evolution-  
312 ary outcomes depend greatly on the degree of shared interest between the host  
313 and symbiont. For example, the cooperative production of virulence factors by  
314 the human pathogen *P. aeruginosa* in lung infections is harmful to those with  
315 cystic fibrosis (Harrison, 2007). Conversely, cooperative light production by *A.*  
316 *fischeri* is vital for the survival of its host, the Hawaiian bobtail squid (Ruby,  
317 1996). It was recently argued that incorporating the effects of niche construc-  
318 tion is critical for improving our understanding of viral evolution (Hamblin *et*  
319 *al.*, 2014) and evolution in co-infecting parasites (Hafer and Milinski, 2015).  
320 Incorporating host dynamics, co-evolution, and the feedbacks that they pro-  
321 duce into models is likely to be equally important for gaining an understanding  
322 of how cooperative behaviors evolve in these host-symbiont settings.

## 323 Acknowledgments

324 We thank Anuraag Pakanati for assistance with simulations. This material  
325 is based upon work supported by the National Science Foundation Postdoc-



326 toral Research Fellowship in Biology under Grant No. DBI-1309318 (to BDC)  
327 and under Cooperative Agreement No. DBI-0939454 (BEACON STC). Com-  
328 putational resources were provided by an award from Google (to BDC and  
329 BK).

## 330 Figures

331 **Figure 1**

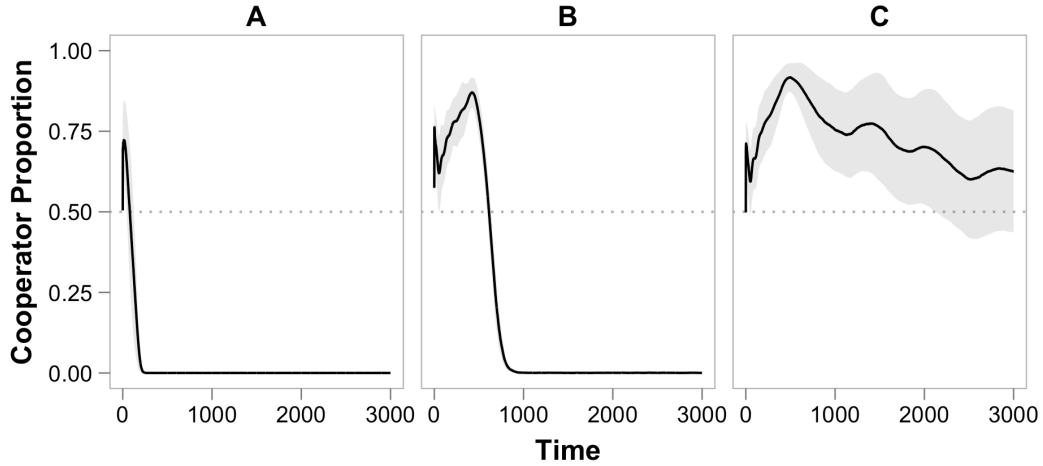
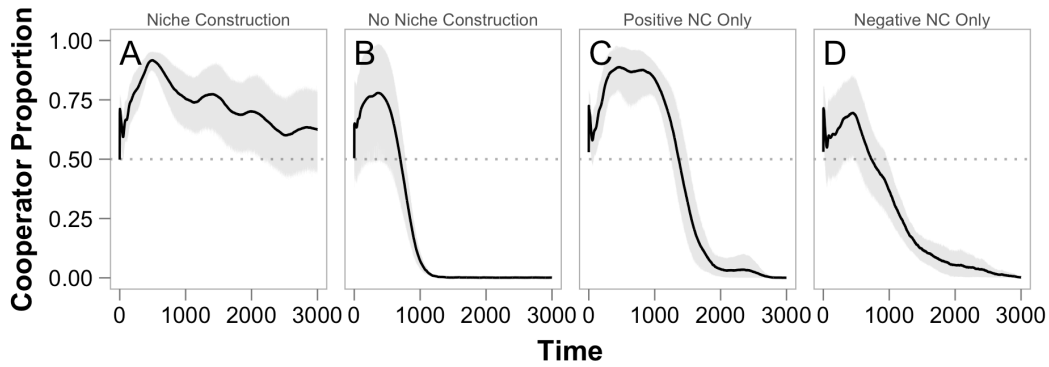


Figure 1: **Adaptation, niche construction, and the evolution of cooperation.** The proportion of cooperators present in the population is shown for the duration of simulations. Curves show the average among replicates, and shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter values used are listed in [Table 1](#). **(A)** When there is no opportunity for adaptation ( $L$ , the number of adaptive loci, is zero), cooperation is quickly lost. **(B)** When adaptation can occur ( $L = 5$ ), but populations do not alter their environment ( $\epsilon$ , the intensity of niche construction, is zero), cooperators temporarily rise in abundance before eventually going extinct. **(C)** Niche construction enables cooperation to be maintained indefinitely. After 3000 cycles, cooperation was the dominant phenotype in 13 of 18 replicate populations.

332 **Figure 2**



**Figure 2: Niche Construction and the Evolution of Cooperation.** The proportion of cooperators present in the population is shown for the duration of simulations. Curves show the average among replicates, and shaded areas indicate 95% confidence intervals. **(A)** Niche construction enables cooperation to be maintained indefinitely. In the majority of populations, cooperation remained as the dominant strategy. **(B)** When niche construction is removed ( $\epsilon = 0$ ) and the fitness benefit of adaptation is increased as compensation ( $\delta = 0.6$ ), cooperation is quickly lost when adapted defectors arise. **(C)** Positive niche construction alone can not maintain cooperation ( $A = 5$ ). Here again, cooperation is driven to extinction by equally-adapted defectors. **(D)** However, negative niche construction alone is also not sufficient to maintain cooperation, and cooperators are rapidly lost. (TODO do we know how?)

333 **Figure 3**

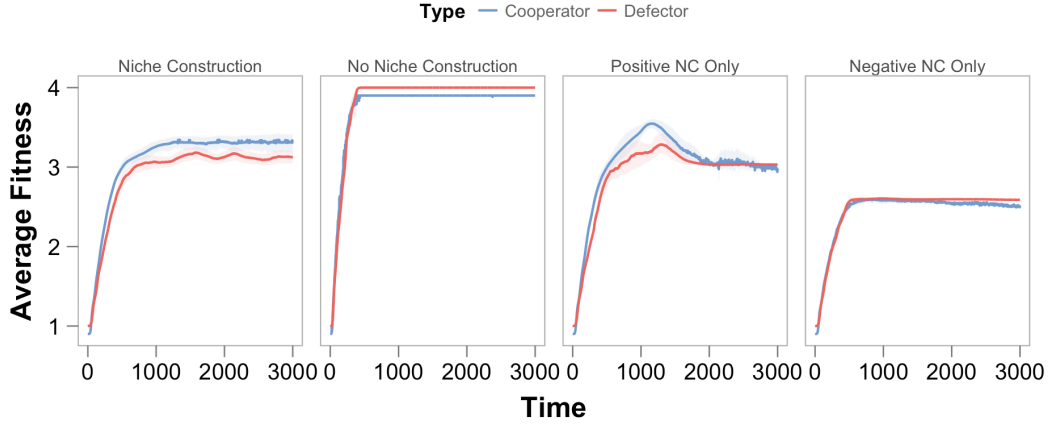


Figure 3: **Fitness Effects of Mutation Accumulation by Cooperators and Defectors.** Lines indicate the grand mean of cooperator (blue) and defector (red) fitness among replicate populations, while shaded areas indicate 95% confidence intervals. Upper and lower dotted lines indicate the maximum fitness values achievable by defectors and cooperators, respectively. **(A)** In the presence of niche construction, cooperators persist in the population by maintaining a greater mean fitness. **(B)** When selective values are increased ( $\delta = 0.6$ ), populations rapidly adapt. In the absence of niche construction ( $\epsilon = 0$ ), defectors eventually become equally adapted and surpass cooperators. At this point, cooperators are driven from the population due to the cost of cooperation. **(C)** With the effects of niche construction removed ( $\epsilon = 0$ ), positive niche construction prolongs the time when cooperators are at an advantage over defectors. Once again, however, defectors eventually become equally adapted, leading to the loss of cooperation. **(D)** Without positive niche construction or further adaptive opportunities ( $L = 1$ ,  $a_{max} = 6$ ) cooperators do not benefit from niche construction.

334 **Figure 4**

335 Cooperators invade defector population. Fully adapted but mismatched. Neg-  
336 ative NC.

337 **Figure 5**

338 Defectors invade cooperator population. Fully adapted and matched. Role of  
339 Export.

340 **Figure 6**

341 **Figure 6A - Effect of Public Good Benefit ( $S_{\max}-S_{\min}$ )**

342 **Figure 6B - Effect of Migration Rate ( $m$ )**

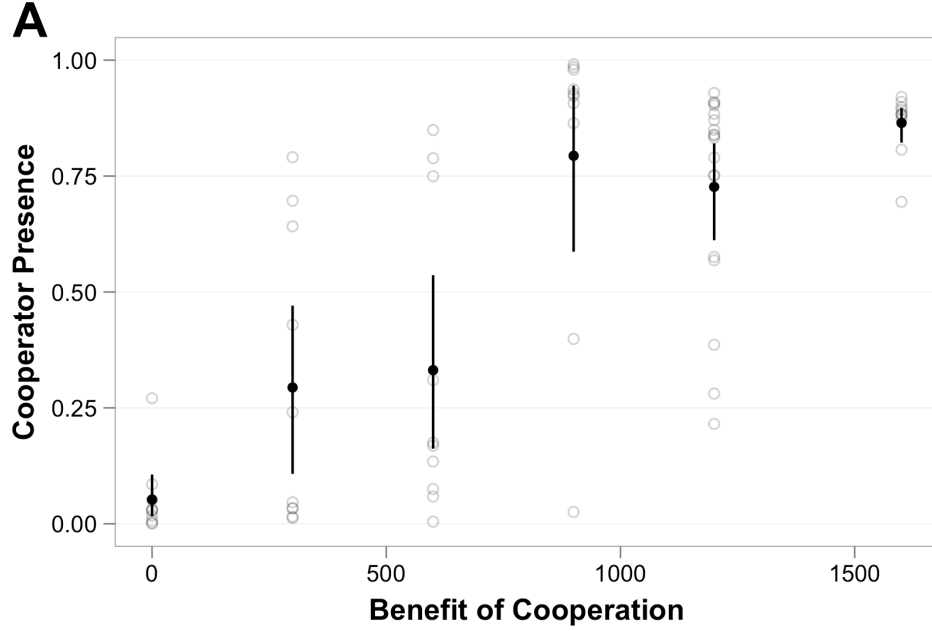


Figure 4: **Cooperator Presence as a Function of Population Size and Migration Rate.** Cooperator presence for each replicate population is shown as an open circle. The mean among these replicates is represented by a filled circle, and bars indicate 95% confidence intervals. **(A)** Cooperator presence increases proportional to increases in population size. Here, the benefit of cooperation ( $S_{max}$ ) is varied (the density-dependent fitness effects of niche construction are adjusted accordingly in the model parameter  $\epsilon$ ). **(B)** Cooperator presence decreases with migration rate ( $m$ ). When migration is low, cooperators can not export their niche, which limits expansion. When migration is high, the defectors immigrate into populations more quickly than cooperators can adapt.

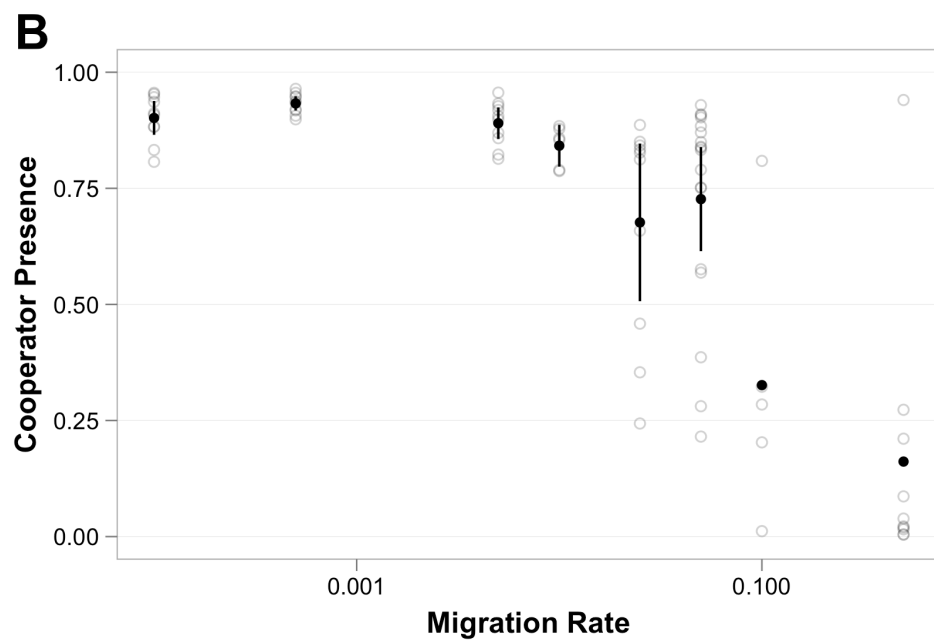


Figure 5: Will share caption with 6A

Table 1: Model parameters and their value

Parameter	Description	Base Value
$N^2$	Number of metapopulation sites	625
$L$	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 population size	800
$S_{max}$	Maximum population size	2000
$\mu_a$	Mutation rate (adaptation)	$10^{-5}$
$\mu_c$	Mutation rate (cooperation)	$10^{-5}$
$m$	Migration rate	0.05
$p_0$	Initial cooperator proportion	0.5
$\mu_t$	Mutation rate (tolerance to new environment)	$10^{-5}$
$T$	Number of simulation cycles	1000
$d$	Population dilution factor	0.1



## References

Allison, S.D. 2005. Cheaters, diffusion and nutrients constrain decomposition by microbial enzymes in spatially structured environments. *Ecology Letters*, **8**: 626–635.

Asfahl, K.L., Walsh, J., Gilbert, K. and Schuster, M. 2015. Non-social adaptation defers a tragedy of the commons in *Pseudomonas aeruginosa* quorum sensing. *The ISME Journal*, doi: [10.1038/ismej.2014.259](https://doi.org/10.1038/ismej.2014.259).

Bernier, S.P., Ha, D.-G., Khan, W., Merritt, J.H.M. and O'Toole, G.A. 2011. Modulation of *Pseudomonas aeruginosa* surface-associated group behaviors by individual amino acids through c-di-GMP signaling. *Research in Microbiology*, **162**: 680–688.

Brown, S.P. and Johnstone, R.A. 2001. Cooperation in the dark: Signalling and collective action in quorum-sensing bacteria. *Proceedings of the Royal Society of London B: Biological Sciences*, **268**: 961–965.

Brown, S.P. and Taddei, F. 2007. The durability of public goods changes the dynamics and nature of social dilemmas. *PLoS ONE*, **2**: e593. Public Library of Science.

Cosson, P., Zulianello, L., Join-Lambert, O., Faurisson, F., Gebbie, L. and Benghezal, M.*et al.* 2002. *Pseudomonas aeruginosa* virulence analyzed in a *Dictyostelium discoideum* host system. *Journal of Bacteriology*, **184**: 3027–3033.

Dandekar, A.A., Chugani, S. and Greenberg, E.P. 2012. Bacterial quorum

366 sensing and metabolic incentives to cooperate. *Science*, **338**: 264–266.

367 Darch, S.E., West, S.A., Winzer, K. and Diggle, S.P. 2012. Density-dependent  
368 fitness benefits in quorum-sensing bacterial populations. *Proceedings of the*  
369 *National Academy of Sciences*, **109**: 8259–8263.

370 Diggle, S.P., Griffin, A.S., Campbell, G.S. and West, S.A. 2007. Cooperation  
371 and conflict in quorum-sensing bacterial populations. *Nature*, **450**: 411–414.

372 Driscoll, W.W. and Pepper, J.W. 2010. Theory for the evolution of diffusible  
373 external goods. *Evolution*, **64**: 2682–2687.

374 Dumas, Z. and Kümmerli, R. 2012. Cost of cooperation rules selection for  
375 cheats in bacterial metapopulations. *Journal of Evolutionary Biology*, **25**:  
376 473–484.

377 Fletcher, J.A. and Doebeli, M. 2009. A simple and general explanation for the  
378 evolution of altruism. *Proceedings of the Royal Society B: Biological Sciences*,  
379 **276**: 13–19.

380 Foster, K., Shaulsky, G., Strassmann, J., Queller, D. and Thompson, C. 2004.  
381 Pleiotropy as a mechanism to stabilize cooperation. *Nature*, **431**: 693–696.  
382 Nature Publishing Group.

383 Gardner, A. and West, S.A. 2010. Greenbeards. *Evolution*, **64**: 25–38.

384 Ghoul, M., West, S.A., Diggle, S.P. and Griffin, A.S. 2014. An experimental  
385 test of whether cheating is context dependent. *Journal of Evolutionary Biology*,  
386 **27**: 551–556.

387 Griffin, A.S., West, S.A. and Buckling, A. 2004. Cooperation and competition

in pathogenic bacteria. *Nature*, **430**: 1024–1027.

Hafer, N. and Milinski, M. 2015. When parasites disagree: Evidence for parasite-induced sabotage of host manipulation. *Evolution*, doi: [10.1111/evo.12612](https://doi.org/10.1111/evo.12612).

Hagberg, A.A., Schult, D.A. and Swart, P.J. 2008. Exploring network structure, dynamics, and function using NetworkX. In: *Proceedings of the 7th Python in Science Conference (SciPy2008)*, pp. 11–15.

Hamblin, S.R., White, P.A. and Tanaka, M.M. 2014. Viral niche construction alters hosts and ecosystems at multiple scales. *Trends in Ecology & Evolution*, **29**: 594–599.

Hamilton, W.D. 1964. The genetical evolution of social behaviour I & II. *Journal of Theoretical Biology*, **7**: 1–52.

Hammarlund, S., Connelly, B.D., Dickinson, K. and Kerr, B. 2015. The evolution of cooperation by the hankshaw effect. *TODO*, **0**: 0–0.

Hardin, G. 1968. The tragedy of the commons. *Science*, **162**: 1243–1248.

Harrison, F. 2007. Microbial ecology of the cystic fibrosis lung. *Microbiology*, **153**: 917–923.

Koestler, B.J. and Waters, C.M. 2014. Bile acids and bicarbonate inversely regulate intracellular cyclic di-GMP in *Vibrio cholerae*. *Infection and Immunity*, **82**: 3002–3014.

Kuzdzal-Fick, J.J., Fox, S.A., Strassmann, J.E. and Queller, D.C. 2011. High relatedness is necessary and sufficient to maintain multicellularity in Dic-

410 tyostelium. *Science*, **334**: 1548–1551.

411 Kümmerli, R. and Brown, S.P. 2010. Molecular and regulatory properties of  
412 a public good shape the evolution of cooperation. *Proceedings of the National*  
413 *Academy of Sciences*, **107**: 18921–18926.

414 Kümmerli, R., Griffin, A.S., West, S.A., Buckling, A. and Harrison, F.  
415 2009. Viscous medium promotes cooperation in the pathogenic bacterium  
416 *Pseudomonas aeruginosa*. *Proceedings of the Royal Society of London B:*  
417 *Biological Sciences*, **282**.

418 Laland, K.N., Odling-Smee, F.J. and Feldman, M.W. 1999. Evolutionary con-  
419 sequences of niche construction and their implications for ecology. *Proceedings*  
420 *of the National Academy of Sciences*, **96**: 10242–10247.

421 Laland, K.N., Odling-Smee, F.J. and Feldman, M.W. 1996. The evolutionary  
422 consequences of niche construction: A theoretical investigation using two-locus  
423 theory. *Journal of Evolutionary Biology*, **9**: 293–316.

424 Lehmann, L. 2007. The evolution of trans-generational altruism: Kin selec-  
425 tion meets niche construction. *Journal of Evolutionary Biology*, **20**: 181–189.  
426 Blackwell Publishing Ltd.

427 Maynard Smith, J. and Haigh, J. 1974. The hitch-hiking effect of a favourable  
428 gene. *Genetics Research*, **23**: 23–35.

429 McKinney, W. 2010. Data structures for statistical computing in Python. In:  
430 *Proceedings of the 9th Python in Science Conference* (S. van der Walt and J.  
431 Millman, eds), pp. 51–56.

432 Morgan, A.D., Quigley, B.J.Z., Brown, S.P. and Buckling, A. 2012. Selection  
433 on non-social traits limits the invasion of social cheats. *Ecology Letters*, **15**:  
434 841–846.

435 Nadell, C.D., Foster, K.R. and Xavier, J.B. 2010. Emergence of spatial struc-  
436 ture in cell groups and the evolution of cooperation. *PLoS Computational*  
437 *Biology*, **6**: e1000716.

438 Nowak, M.A. 2006. Five rules for the evolution of cooperation. *Science*, **314**:  
439 1560–1563.

440 R Core Team. 2015. *R: A language and environment for statistical computing*.  
441 Vienna, Austria: R Foundation for Statistical Computing.

442 Ruby, E.G. 1996. Lessons from a cooperative, bacterial-animal association:  
443 The *Vibrio fischeri*–*Euprymna scolopes* light organ symbiosis. *Annual Review*  
444 *of Microbiology*, **50**: 591–624.

445 Sinervo, B., Chaine, A., Clobert, J., Calsbeek, R., Hazard, L. and Lancaster,  
446 L.*et al.* 2006. Self-recognition, color signals, and cycles of greenbeard mutu-  
447 alism and altruism. *Proceedings of the National Academy of Sciences*, **103**:  
448 7372–7377.

449 Van Dyken, J.D. and Wade, M.J. 2012. Origins of altruism diversity II: Run-  
450 away coevolution of altruistic strategies via “reciprocal niche construction”.  
451 *Evolution*, **66**: 2498–2513.

452 Veelders, M., Brückner, S., Ott, D., Unverzagt, C., Mösch, H.-U. and Essen,  
453 L.-O. 2010. Structural basis of flocculin-mediated social behavior in yeast.  
454 *Proceedings of the National Academy of Sciences*, **107**: 22511–22516.

- 455 Waite, A.J. and Shou, W. 2012. Adaptation to a new environment allows coop-  
456 erators to purge cheaters stochastically. *Proceedings of the National Academy*  
457 *of Sciences*, **109**: 19079–19086.
- 458 West, S.A., Diggle, S.P., Buckling, A., Gardner, A. and Griffin, A.S. 2007a.  
459 The social lives of microbes. *Annual Review of Ecology, Evolution, and Sys-*  
460 *tematics*, **38**: 53–77.
- 461 West, S.A., Griffin, A.S. and Gardner, A. 2007b. Evolutionary explanations  
462 for cooperation. *Current Biology*, **17**: R661–R672.
- 463 Zhang, X.-X. and Rainey, P.B. 2013. Exploring the sociobiology of pyoverdin-  
464 producing *Pseudomonas*. *Evolution*, **67**: 3161–3174.