

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. Each individual in a population has a genotype, which is an ordered list of $L + 1$ integers (loci). 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 fitness benefit δ . A binary allele at locus $L + 1$ determines whether or not that individual is a cooperator. Individuals with allelic state 1 at this locus

are cooperators, carrying a cost c , while individuals with allelic state 0 are defectors. When $\delta \geq c$, a minimally adapted cooperator recoups the cost of cooperation.

Organisms also influence their environment, which, in turn, influences selection. We model this as a form of density dependent selection. 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 1 is affected by the allelic composition of the population at locus L , and the selective value of allele 1 at any locus increases with the number of individuals carrying allele A at the previous locus. For the remainder of this section, this circularity is represented by the function below, which gives the integer below x in the set $\{1, 2, \dots, X\}$.

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

Here, $\text{mod}_Y(y)$ is the integer remainder after dividing y by Y . Thus, the 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 ϵ , 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:

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

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

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

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

110 Cooperation allows the population to reach greater density. If p is the propor-
 111 tion of cooperators in a population at the beginning of a growth cycle, then
 112 that population reaches the following size during the growth phase:

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

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

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

Here, $W_{\gamma(i)}$ is the fitness of an individual i with genotype $\gamma(i)$ (see Equation
 2). The value π_i therefore reflects an individual's relative reproductive fitness.
 For simplicity, we apply mutations after population growth. Mutations occur
 independently at each locus and cause the allelic state to change. Mutations
 occur at each adaptive locus at rate μ_a , in which a new allele is chosen at
 random from the set $\{0\} \cup \{1, 2, \dots, A\}$. At the binary cooperation locus,
 mutations occur at rate μ_c . These mutations flip the allelic state, causing
 cooperators to become defectors and vice versa.
 After mutation, individuals emigrate to an adjacent patch at rate m . The
 destination patch is randomly chosen with uniform probability from the source
 patch's Moore neighborhood, which is composed of the nearest 8 patches on the
 lattice. Because the metapopulation lattice has boundaries, patches located
 on an edge have smaller neighborhoods.
 Metapopulations are initiated in a state that follows an environmental change.
 First, populations are seeded at all patches with cooperator proportion p_0 and
 grown to density $S(p_0)$. An environmental challenge is then introduced, which
 subjects the population to a bottleneck. For each individual, the probability
 of survival is μ_t , which represents the likelihood that a mutation occurs that
 confers tolerance. Survivors are chosen by binomial sampling. Because indi-
 viduals have not yet adapted to this new environment, the allelic state of each
 individual's genotype is set to 0 at each adaptive locus. Following initializa-
 tion, simulations are run for T cycles, where each discrete cycle consists of
 population growth, mutation, and migration. At the end of each cycle, popu-

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

143 **Source Code and Software Environment**

144 The simulation software and configurations for the experiments reported are
145 available online. Simulations used Python 3.4.0, NumPy 1.9.1, Pandas 0.15.2
146 (McKinney, 2010), and NetworkX 1.9.1 (Hagberg *et al.*, 2008). Data analyses
147 were performed with R 3.1.3 (R Core Team, 2015). Confidence intervals were
148 estimated by bootstrapping with 1000 resamples.

149 **Results**

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

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

165 Niche Construction Maintains Cooperation

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

177 Fitness Increases Alone do not Support Persisting Coop- 178 eration

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

181 formed simulations in which the selective effects of niche construction were
 182 removed ($\epsilon = 0$), and we instead increased the fitness benefits conferred by
 183 adaptation ($\delta = 0.6$). Here, we are conservative by lifting the selective value of
 184 exogenous adaptation by the maximum value possible from niche construction.
 185 We find that higher selective values do not provide a significant increase in
 186 cooperator presence (Figure 2B). As shown in Figure 3, cooperators gain adap-
 187 tations more quickly than defectors, which provides a fitness advantage. How-
 188 ever, the cost of cooperation puts defectors at an advantage once these popu-
 189 lations become fully adapted.

190 **Negative Niche Construction is Critical to Cooperator** 191 **Persistence**

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

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

198 cannot simultaneously hold for all l .

199 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.

220 NC Prevents Defector Invasion

221 Figure 5

222 How Cooperation Fuels all of this

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

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

233 # Discussion

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

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

244 We demonstrate that when niche construction occurs, cooperation can indeed
245 persist (Figure 1C). But what aspects of niche construction produce this re-
246 sult? In our model, niche construction introduces additional selective effects
247 that could influence the evolutionary process. However, simply raising the
248 selective benefits provided by adaptations does not significantly increase co-
249 operator presence (Figure 2B), and indicates that niche construction plays an
250 important role. Although cooperators benefit greatly from positive niche con-
251 struction, it does not fully explain our results (Figure 2C). Indeed, despite an
252 initial increase in abundance, cooperators are eventually driven to extinction
253 when environmental change produces only positive fitness effects. As with the
254 Hankshaw effect, adaption eventually slows, allowing defectors to outcompete
255 cooperators (Figure 3C). While it does not benefit cooperation when alone
256 (Figure 3E), negative niche construction acts to prevent this stasis. Combined,
257 we find that both positive and negative niche construction are required to main-
258 tain cooperation.

259 When successful, we observe that populations do not reach the maximum pos-
260 sible fitness (Figure 3A). Although cooperation is the focus of this study, it
261 can be seen as deleterious. Previous work has shown that niche construction
262 can favor deleterious alleles (Laland *et al.*, 1996, 1999). Similarly here, coop-
263 eration is maintained in the presence of niche construction, but lost otherwise.
264 Van Dyken and Wade (2012) showed that when two cooperative behaviors
265 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-

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

295 In many instances of cooperation, the environment is itself a biological entity,
296 which can produce additional evolutionary feedbacks. As the host population
297 changes, so too will selection on their symbiont populations. Here, evolution-
298 ary outcomes depend greatly on the degree of shared interest between the host
299 and symbiont. For example, the cooperative production of virulence factors by
300 the human pathogen *P. aeruginosa* in lung infections is harmful to those with
301 cystic fibrosis (Harrison, 2007). Conversely, cooperative light production by *A.*
302 *fischeri* is vital for the survival of its host, the Hawaiian bobtail squid (Ruby,
303 1996). It was recently argued that incorporating the effects of niche construc-
304 tion is critical for improving our understanding of viral evolution (Hamblin *et*
305 *al.*, 2014) and evolution in co-infecting parasites (Hafer and Milinski, 2015).
306 Incorporating host dynamics, co-evolution, and the feedbacks that they pro-
307 duce into models is likely to be equally important for gaining an understanding
308 of how cooperative behaviors evolve in these host-symbiont settings.

309 Acknowledgments

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

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

316 Figures

317 **Figure 1**

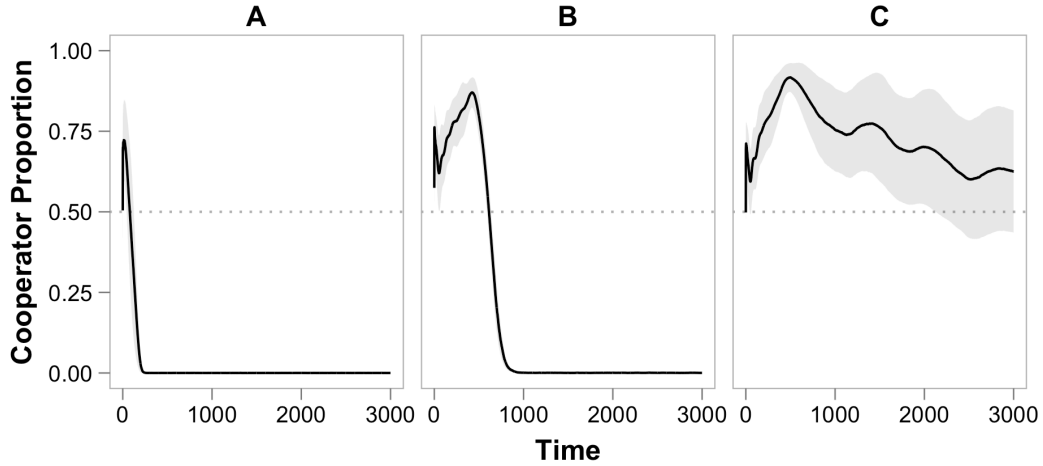


Figure 1: **Adaptation, niche construction, and the evolution of cooperation.** The proportion of cooperators present in the population is shown for the duration of simulations. Curves show the average among replicates, and shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter 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 (ϵ , 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.

318 **Figure 2**

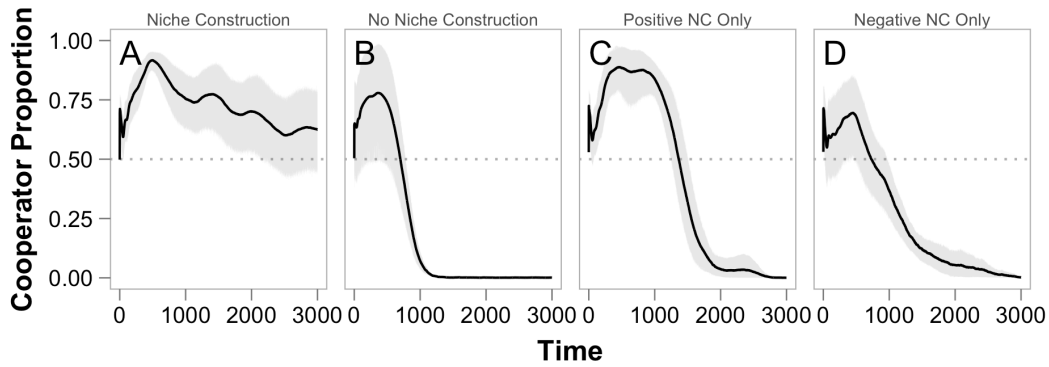


Figure 2: Niche Construction and the Evolution of Cooperation. The proportion of cooperators present in the population is shown for the duration of simulations. Curves show the average among replicates, and shaded areas indicate 95% confidence intervals. **(A)** Niche construction enables cooperation 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?)

319 **Figure 3**

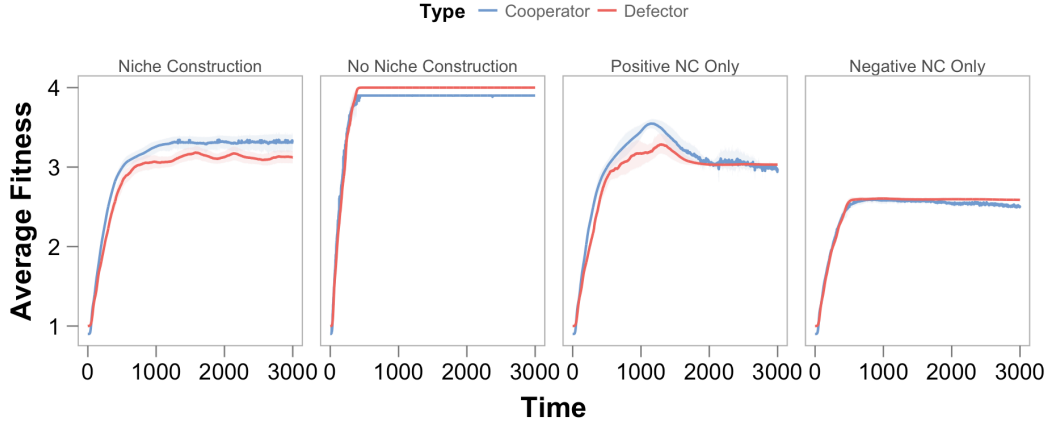


Figure 3: **Fitness Effects of Mutation Accumulation by Cooperators and Defectors.** Lines indicate the grand mean of cooperator (blue) and defector (red) fitness among replicate populations, while shaded areas indicate 95% confidence intervals. Upper and lower dotted lines indicate the maximum fitness 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.

320 **Figure 4**

321 Cooperators invade defector population. Fully adapted but mismatched. Neg-
322 ative NC.

323 **Figure 5**

324 Defectors invade cooperator population. Fully adapted and matched. Role of
325 Export.

326 **Figure 6**

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

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

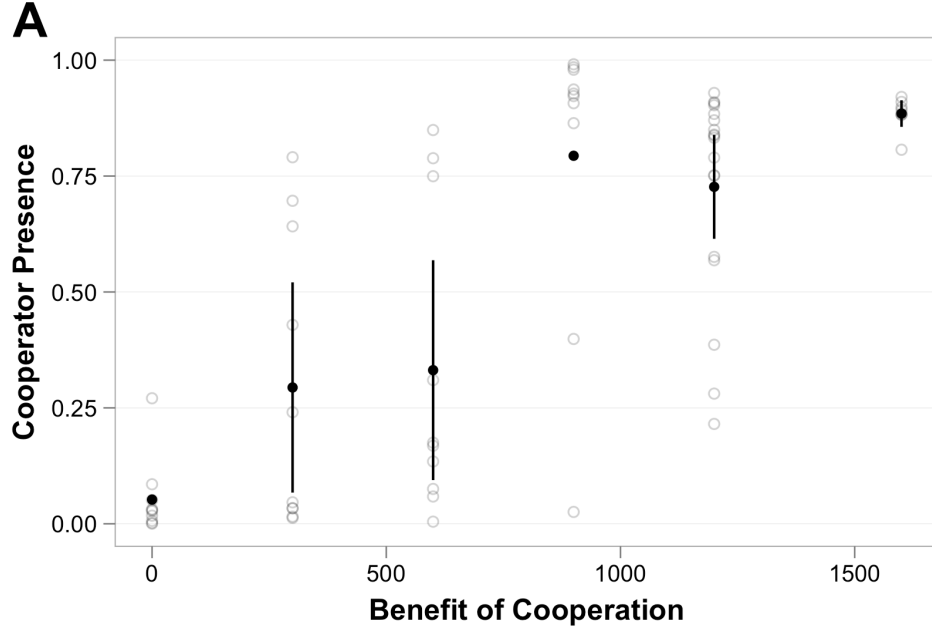


Figure 4: **Cooperator Presence as a Function of Population Size and Migration Rate.** Cooperator presence for each replicate population is shown as an open circle. The mean among these replicates is represented by a filled circle, and bars indicate 95% confidence intervals. **(A)** Cooperator presence 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 ϵ). **(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.

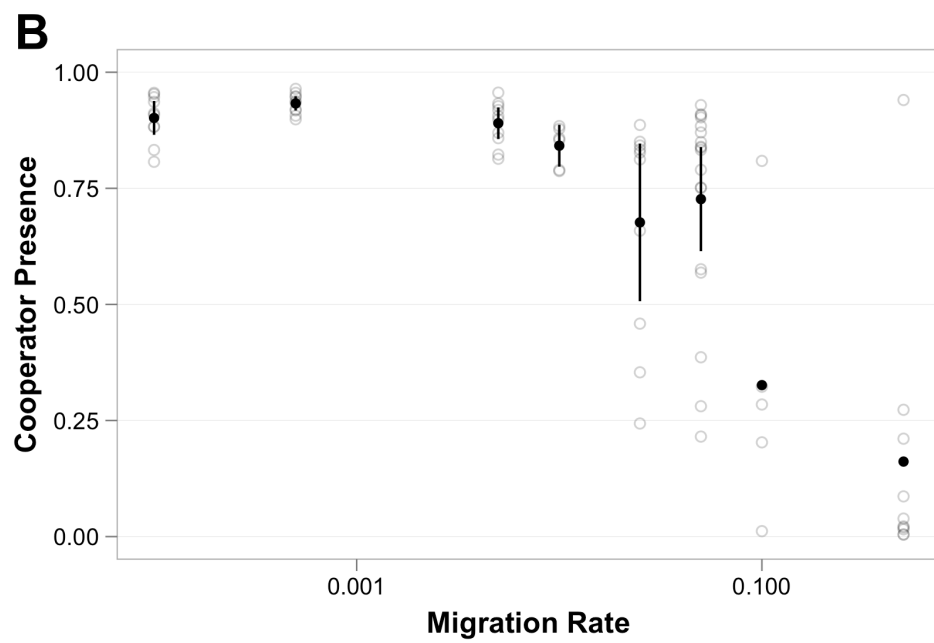


Figure 5: Will share caption with 6A

Table 1: Model parameters and their value

Parameter	Description	Base Value
N^2	Number of metapopulation sites	625
L	Number of adaptive loci	5
A	Number of alleles	6
δ	Fitness benefit, nonzero alleles	0.3
c	Production cost	0.1
ϵ	Fitness benefit, sequential alleles	0.00015
z	Baseline fitness	1
S_{min}	Minimum population size	800
S_{max}	Maximum population size	2000
μ_a	Mutation rate (adaptation)	10^{-5}
μ_c	Mutation rate (cooperation)	10^{-5}
m	Migration rate	0.05
p_0	Initial cooperator proportion	0.5
μ_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

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

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

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

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

360 Dumas, Z. and Kümmerli, R. 2012. Cost of cooperation rules selection for
361 cheats in bacterial metapopulations. *Journal of Evolutionary Biology*, **25**:
362 473–484.

363 Fletcher, J.A. and Doebeli, M. 2009. A simple and general explanation for the
364 evolution of altruism. *Proceedings of the Royal Society B: Biological Sciences*,
365 **276**: 13–19.

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

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

370 Ghoul, M., West, S.A., Diggle, S.P. and Griffin, A.S. 2014. An experimental
371 test of whether cheating is context dependent. *Journal of Evolutionary Biology*,
372 **27**: 551–556.

373 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-

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

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

400 Kümmerli, R., Griffin, A.S., West, S.A., Buckling, A. and Harrison, F.
401 2009. Viscous medium promotes cooperation in the pathogenic bacterium
402 *Pseudomonas aeruginosa*. *Proceedings of the Royal Society of London B:*
403 *Biological Sciences*, **282**.

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

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

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

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

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

418 Morgan, A.D., Quigley, B.J.Z., Brown, S.P. and Buckling, A. 2012. Selection
 419 on non-social traits limits the invasion of social cheats. *Ecology Letters*, **15**:
 420 841–846.

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

424 Nowak, M.A. 2006. Five rules for the evolution of cooperation. *Science*, **314**:
 425 1560–1563.

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

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

431 Sinervo, B., Chaine, A., Clobert, J., Calsbeek, R., Hazard, L. and Lancaster,
 432 L.*et al.* 2006. Self-recognition, color signals, and cycles of greenbeard mutu-
 433 alism and altruism. *Proceedings of the National Academy of Sciences*, **103**:
 434 7372–7377.

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

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

- 441 Waite, A.J. and Shou, W. 2012. Adaptation to a new environment allows coop-
442 erators to purge cheaters stochastically. *Proceedings of the National Academy*
443 *of Sciences*, **109**: 19079–19086.
- 444 West, S.A., Diggle, S.P., Buckling, A., Gardner, A. and Griffin, A.S. 2007a.
445 The social lives of microbes. *Annual Review of Ecology, Evolution, and Sys-*
446 *tematics*, **38**: 53–77.
- 447 West, S.A., Griffin, A.S. and Gardner, A. 2007b. Evolutionary explanations
448 for cooperation. *Current Biology*, **17**: R661–R672.
- 449 Zhang, X.-X. and Rainey, P.B. 2013. Exploring the sociobiology of pyoverdin-
450 producing *Pseudomonas*. *Evolution*, **67**: 3161–3174.