

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

4 TODO

5 **Abstract**

6 Through their interactions, their activities, and even their mere pres-
7 ence, organisms change the environment for themselves and others. This
8 “niche construction” process becomes particularly interesting when it
9 creates evolutionary feedback, whereby selective pressures are altered
10 in response to environmental change. Here we consider how niche con-
11 struction influences the evolution of cooperation, which has been a long-
12 standing challenge to evolutionary theory. We simulate populations of
13 individuals that cooperatively produce a public good that permits in-
14 creased growth in a stressful environment and investigate how local- and
15 global-scale niche construction affects the ability of these populations
16 to resist invasion by non-producing cheats. We find that niche construc-
17 tion profoundly impacts the evolution of cooperation by creating new
18 opportunities for adaptation. Cooperators are able to escape subversion

19 by cheats as long as niche construction clears these paths of adaptation.
20 This work provides a crucial step towards understanding how evolution
21 occurs in complex environments like those found in nature.

22 Introduction

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

32 Several factors can prevent this *tragedy of the commons* (Hamilton, 1964;
33 Hardin, 1968; Nowak, 2006; West *et al.*, 2007b). For example, cooperators
34 must benefit more from the cooperative act than others. This can occur when
35 cooperators are clustered together in spatially structured populations (Fletcher
36 and Doebeli, 2009; Nadell *et al.*, 2010; Kuzdzal-Fick *et al.*, 2011) or when co-
37 operators use communication (Brown and Johnstone, 2001; Darch *et al.*, 2012)
38 or other cues (Sinervo *et al.*, 2006; Gardner and West, 2010; Veelders *et al.*,
39 2010) to cooperate conditionally with kin. Interestingly, cooperation can also
40 be bolstered by genetic linkage with self-benefitting traits (Foster *et al.*, 2004;

41 Dandekar *et al.*, 2012; Asfahl *et al.*, 2015), setting the stage for an “adap-
42 tive race” in which cooperators and defectors vie for the first highly-beneficial
43 adaptation (Waite and Shou, 2012; Morgan *et al.*, 2012).

44 Hammarlund et al. (2015) recently showed that in spatially structured popula-
45 tions, cooperators can gain a substantial leg up on defectors in an adaptive race.
46 Specifically, cooperative behavior increases local population density, thus in-
47 creasing the likelihood of acquiring beneficial mutations. By hitchhiking along
48 with these adaptations, the cooperative trait can rapidly rise in abundance.
49 Nevertheless, this advantage is fleeting. As soon as the opportunities for adap-
50 tation are exhausted, cooperators are once again at a disadvantage against
51 defectors. However, Hammarlund et al. (2015) demonstrated that coopera-
52 tion can be maintained indefinitely when frequent environmental changes pro-
53 duce a steady stream of adaptive opportunities. Although organisms typically
54 find themselves in dynamic environments, change might not occur at a rate
55 that provides sufficient adaptive opportunities to ensure long-term cooperator
56 persistence.

57 In this work, we demonstrate how cooperation can be maintained indefinitely
58 by niche construction. We expand upon the model presented in Hammarlund
59 et al. (2015) to allow populations to alter their local environment. As environ-
60 ments change, so too does selection. This creates an eco-evolutionary feedback
61 whereby selection is dependent on current genotypes, and the composition of
62 genotypes is dependent on selection. Niche construction can be positive or neg-
63 ative, depending on whether the environmental change increases or decreases
64 the fitness of the niche-constructing individual. Although niche construction

65 occurs independently of cooperation in our model, the increase in density that
66 results from cooperation has a profound effect on how populations evolve in
67 the presence of selective feedbacks. First, these populations exert greater in-
68 fluence on their environments, which better enables them to benefit from posi-
69 tive niche construction. And as environments change, either through negative
70 niche construction or external influences, these larger populations can adapt
71 more quickly. We show that it is the combination of these factors that allows
72 cooperation to persist.

73 **Stuff to be cut/integrated above**

74 As populations construct unique niches, they potentially decrease the threat
75 of invasion from neighboring patches. This occurs when the traits that were
76 advantageous in an immigrant’s home niche are maladaptive elsewhere. Be-
77 cause environmental change is influenced solely by non-social phenotypes in
78 this model, this change of invasibility affects cooperators and defectors equally.
79 Here again, however, populations containing a greater number of cooperators
80 may have an advantage. The greater number of individuals that emigrate from
81 these larger populations allow them to “export” their niche—and thus reduce
82 the fitness of neighboring competitors—at a higher rate. We explore whether
83 the range expansion that this process enables provides additional opportunities
84 for cooperation to hitchhike.

85 Finally, we demonstrate how *negative* niche construction, where populations
86 change their environment in ways that reduce fitness, can further support

87 cooperation. Even though the niche construction process creates selective
 88 feedbacks, we would expect the magnitude of these feedbacks to decrease as
 89 populations evolve. Once individuals can no longer gain adaptations that
 90 compensate for the costs of cooperation, they are then outcompeted by non-
 91 cooperators. However if populations construct their environment in a way
 92 which decreases fitness, cooperation can still hitchhike when this change also
 93 creates the opportunity to gain compensatory adaptations.

94 **Methods**

95 We build upon the model described in Hammarlund et al. (2015), in which co-
 96 operators and defectors compete and evolve in a metapopulation (a collection
 97 of populations). Individuals in each of the populations reproduce, mutate, and
 98 migrate to neighboring populations. Importantly, adaptation that is indepen-
 99 dent of cooperation can occur. In our model here, we further allow populations
 100 to modify their local environment, and these modifications feed back to affect
 101 selection.

102 **Model Description**

103 Our simulated environment consists of N^2 patches arranged as an $N \times N$
 104 lattice (see [Table 1](#) for model parameters and their values), where each patch
 105 can support a population. Each individual in a population has a genotype,
 106 which is an ordered list of $L + 1$ integers (loci). The first L loci are *adaptive*

107 *loci*, and are each occupied by 0 or an integer from the set $A \equiv \{1, 2, \dots, a_{max}\}$,
 108 where a_{max} is the number of alleles conferring a selective benefit. Specifically,
 109 the presence of a non-zero allele at any of these loci represents an adaptation
 110 that confers fitness benefit δ . A binary allele at locus $L+1$ determines whether
 111 or not that individual is a cooperator. Individuals with allelic state 1 at this
 112 locus are cooperators, carrying a cost c , while individuals with allelic state 0
 113 are defectors. When $\delta \geq c$, a minimally adapted cooperator recoups the cost
 114 of cooperation. Equation 1 defines function $n(a, l)$, which gives the number
 115 of individuals in the population with allelic state a at locus l . $I_x(y)$ indicates
 116 whether the allelic state y matches allelic state x (1) or not (0), and $\gamma(i)$ is
 117 the genotype of individual i .

$$n(a, l) = \sum_{i \in P} I_{a_{g,l}}(a_{\gamma(i),l}) \quad (1)$$

118 Organisms also influence their environment, which, in turn, influences selec-
 119 tion. We model this as a form of density dependent selection. Specifically,
 120 the selective value of adaptive allele a at locus l increases with the number
 121 of individuals in the population that have allele $a - 1$ at locus $l - 1$. We
 122 treat both adaptive loci and allelic states as “circular”, so the allelic state
 123 at locus 1 is affected by the allelic composition of the population at locus L ,
 124 and the selective value of allele 1 at any locus increases with the number of
 125 individuals carrying allele a_{max} at the previous locus. To make this circularity
 126 mathematically crisp, we define a function giving the integer below x in the
 127 set $\{1, 2, \dots, X\}$

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

Where $\text{mod}_Y(y)$ 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 $\beta(a, a_{max})$ 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:

$$W_g = z + \delta \sum_{l=1}^L I_A(a_{g,l}) + \epsilon \sum_{l=1}^L n(\beta(a_{g,l}, a_{max}), \beta(l, L)) - ca_{g,L+1} \quad (3)$$

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

$$I_A(a) = \begin{cases} 1 & \text{if } a \in A \\ 0 & \text{otherwise} \end{cases} \quad (4)$$

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.

Cooperators produce a public good that is equally accessible to all members of the population. This public good increases the carrying capacity at that patch, allowing the population to reach greater density. This benefit increases

linearly with the proportion of cooperators. Thus, if p is the proportion of cooperators in a population at the beginning of a growth cycle, then that population reaches the following size during the growth phase:

$$S(p) = S_{min} + p(S_{max} - S_{min}) \quad (5)$$

The function $S(p)$ reflects the benefit of public good production. A population composed entirely of defectors reaches size S_{min} , while one composed entirely of cooperators reaches size S_{max} (with $S_{max} \geq S_{min}$). During growth, individuals compete for inclusion in the resulting population. The composition of population P with cooperator proportion p after growth is multinomial with parameters $S(p)$ and $\{\pi_1, \pi_2, \dots, \pi_{|P|}\}$, where:

$$\pi_i = \frac{W_{\gamma(i)}}{\sum_{j \in P} W_{\gamma(j)}} \quad (6)$$

Here, $W_{\gamma(i)}$ is the fitness of an individual i with genotype $\gamma(i)$ (see Equation 3). 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 $\{0\} \cup A$. 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. Therefore, the probability that genotype g mutates into genotype g' is given by:

$$\tau_{g \rightarrow g'} = \mu_a^{H_a(g, g')}(1 - \mu_a)^{\{L - H_a(g, g')\}} \mu_c^{H_c(g, g')}(1 - \mu_c)^{\{1 - H_c(g, g')\}} \quad (7)$$

161 where $H_a(g, g')$ and $H_c(g, g')$ are the Hamming distances between genotypes g
 162 and g' at the cooperation locus and adaptive loci, respectively. The Hamming
 163 distance is the number of loci at which allelic states differ (Hamming, 1950).

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

169 Metapopulations are initiated in a state that follows an environmental change.
 170 First, populations are seeded at all patches with cooperator proportion p_0 and
 171 grown to density $S(p_0)$. An environmental challenge is then introduced, which
 172 subjects the population to a bottleneck. For each individual, the probability
 173 of survival is μ_t , which represents the likelihood that a mutation occurs that
 174 confers tolerance. Survivors are chosen by binomial sampling. Because indi-
 175 viduals have not yet adapted to this new environment, the allelic state of each
 176 individual's genotype is set to 0 at each adaptive locus. Following initializa-
 177 tion, simulations are run for T cycles, where each discrete cycle consists of
 178 growth, mutation, and migration. At the end of each cycle, populations are
 179 thinned to allow for growth in the next cycle. The individuals that remain are
 180 chosen by binomial sampling, where each individual persists with probability
 181 d , regardless of allelic state.

182 Source Code and Software Environment

183 The simulation software and configurations for the experiments reported are
184 available online (Us, 2015). Simulations used Python 3.4.0, NumPy 1.9.1,
185 Pandas 0.15.2 (McKinney, 2010), and NetworkX 1.9.1 (Hagberg *et al.*, 2008).
186 Data analyses were performed with R 3.1.3 (R Core Team, 2015).

187 Results

188 Niche Construction Maintains Cooperation

189 Without the opportunity for adaptation ($L = 0$), cooperators are swiftly elim-
190 inated in competition with defectors (Figure 1). Despite an initial lift due to
191 increased productivity, the cost of cooperation becomes disadvantageous as
192 migration mixes the initially isolated populations. With adaptive opportuni-
193 ties ($L = 5$, $\epsilon = 0$), cooperators are maintained transiently (Figure 1B). Here,
194 the additional mutational abilities provided by their larger sizes allows coop-
195 erator populations to more quickly adapt to their environment. As previously
196 described by Hammarlund et al. (2015), however, this advantage diminishes
197 as defector populations become equally adapted, and cooperators are outcom-
198 peted. When populations affect their environment and these changes feed
199 back on selection, we find that cooperation can persist, perhaps indefinitely
200 (Figure 1C, 3A). In these environments, cooperators maintain higher fitness
201 than cooperators, which enables survival (Figure 3A).

202 **Fitness Increases do not Support Cooperation**

203 In our model, niche construction provides additional selective benefits. To
204 determine how these selective effects contribute to our results, we performed
205 simulations in which the selective effects of niche construction were removed
206 ($\epsilon = 0$). As compensation, we increased the fitness benefits conferred by adap-
207 tation ($\delta = 0.6$). Here, the selective effects of niche construction are exag-
208 gerated, as a fitness benefit of 0.3 (our increase in δ) is the maximum value
209 possible (see 3). To quantify cooperator success and permit comparison, we
210 use the area under the cooperator proportion curve. This measure of *coop-*
211 *erator presence* increases as cooperators rise in abundance or remain in the
212 population longer.

213 We find that higher selective values do not provide a significant increase in
214 cooperator presence (Figure 2, column C). As shown in Figure 3, cooperators
215 gain adaptations more quickly than defectors, which provides a fitness advan-
216 tage. However, the cost of cooperation puts defectors at an advantage once
217 these populations become fully adapted.

218 **Positive Niche Construction is not Sufficient**

219 Both positive and negative niche construction are present in our model. We
220 focus first on the effects of positive niche construction by removing the allelic
221 conflict that leads to negative niche construction ($L = 5$, $a_{max} = 5$). When
222 this conflict is removed, we see find that positive niche construction prolongs
223 the fitness advantage of cooperators (Figure 3C), which significantly increases

cooperator presence (Figure 2, column D). However, cooperation is eventually lost as gain an advantage (Figure 1D).

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WHERE SHOULD THIS GO??? Negative niche construction occurs in our model due to selection for sequentially-increasing allelic states and the circular arrangement of these alleles. When the genome length (L) is not evenly divided by the number of non-zero alleles (a_{max}), a conflict arises when the allelic state at locus 1 is not 1 larger than the allelic state at locus L . For example, consider genotype $(1, 2)$ when $L = 2$ and $a_{max} = 3$. Here, allelic state 2 at locus 2 will be 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, because it does not follow 2.

When this allelic conflict is removed ($L = 5$, $a_{max} = 5$), positive niche construction prolongs the fitness advantage of cooperators (Figure 3C), which significantly increases cooperator presence (Figure 2, column D). However, cooperation is eventually lost as gain an advantage (Figure 1D).

Negative Niche Construction is not Sufficient

TODO

In our model, an individual's fitness is the product of two processes. First, mutations engender environmental adaptations, which are represented by non-zero alleles. These adaptations create the transient lift in cooperation seen in Figure 1B. The second process that contributes to fitness is niche construc-

246 tion. Selection favors individuals with sequentially-increasing alleles. Because
 247 larger populations will have a greater effect on their environment, this bene-
 248 fit is density dependent. In our experiments, this positive niche construction
 249 contributed equally to fitness when all individuals shared the same allele in a
 250 population at maximum carrying capacity. To determine whether cooperation
 251 was maintained simply due to the higher selective values made possible by this
 252 second source of fitness, we compared our results against the results of exper-
 253 iments in which the ordering of alleles did not matter, and the fitness benefit
 254 provided by adaptation was doubled ($\epsilon = 0$, $\delta = 0.6$). That this doubling is an
 255 over estimate of the magnitude of fitness contributions that arise from niche
 256 construction, since these values would only occur in populations at maximum
 257 carrying capacity, which does not occur in the presence of defectors. Never-
 258 theless, Figure 2 shows that higher selective values have little effect (columns
 259 A and C) and do not explain the maintenance of cooperation that we observe
 260 when niche construction occurs (column B).

261 Although we have seen that maximum fitness does not substantially effect the
 262 maintenance of cooperation, perhaps the rate at which fitness accumulates in
 263 cooperator and defector populations matters. When we compare the accumu-
 264 lation of fitness via adaptation in the presence of niche construction (Figure
 265 3A) against simulations in which selective values are doubled (Figure 3B), two
 266 features emerge. In both scenarios, cooperators gain adaptations more quickly
 267 than defectors due to their size. When niche construction is not present, co-
 268 operator fitness is eventually surpassed by that of defectors (Figure 3B). As
 269 described by Hammarlund et al. (2015), this leads to the demise of cooperators.

270 In contrast, cooperator fitness is never surpassed when niche construction is
271 present (Figure 3A), which allows cooperation to persist.

272 **TODO: discuss time at which fitness plateaus?**

273 **TODO: describe how maximum fitness is calculated?**

274 **Negative Niche Construction Plays a Key Role (TODO** 275 **title)**

276 Figure 3A also shows that niche-constructing populations never reach max-
277 imum fitness. One major contributor to this is the density dependence of
278 the benefit provided by niche construction. Because defectors remain present
279 (Figure 1C), the smaller populations that result are unable to unlock the full
280 benefit of niche construction. The second contributor to the reduced fitness
281 that we observe is negative niche construction.

282 This occurs in our model due to selection for sequentially-increasing allelic
283 states and the circular arrangement of these alleles. When the genome length
284 (L) is not evenly divided by the number of non-zero alleles (a_{max}), a conflict
285 arises when the allelic state at locus 1 is not 1 larger than the allelic state
286 at locus L . For example, consider genotype $(1, 2)$ when $L = 2$ and $a_{max} = 3$.
287 Here, allelic state 2 at locus 2 will be be beneficial, because it follows allelic
288 state 1 at locus 1. However, due to the circular effects, allelic state 1 at locus
289 1 will be deleterious, because it does not follow 2.

290 To isolate the effect of negative niche construction, we compare our results

291 against those from simulations in which this allelic conflict was absent ($L = 5$,
292 $a_{max} = 5$). Figure 2 shows that although positive niche construction still led
293 to an increase in cooperation (column D), these populations were not able to
294 maintain the same level of cooperation seen in the presence of negative niche
295 construction (column B). We find that because this lack of conflict allows
296 populations to reach a fully-adapted state, cooperators once again acquire
297 these adaptations more quickly but are eventually driven from the population
298 (Figures 3C and 1X). These results indicate that both positive and negative
299 niche construction is required to maintain cooperation.

300 **(TODO: explain why defector fitness doesn't reach 4 (density de-**
301 **pendent fitness))** maybe better in figure caption?)

302 To further explore the influence of negative niche construction, we performed
303 experiments in which the positive effects of niche construction were removed.
304 Here, individuals had a single adaptive locus that was constantly in conflict
305 ($L = 1$, $a_{max} = 6$). As seen in Figures 2 (column E) and 3D, the constant
306 source of adaptation that is provided by negative niche construction is not
307 sufficient to maintain cooperation via hitchhiking, and cooperators are quickly
308 purged from the population. This offers further evidence that feedbacks from
309 both positive and negative niche construction are required for cooperation to
310 persist.

311 NC Enables Cooperator Spread

312 Figure 4

313 NC Prevents Defector Invasion

314 Figure 5

315 How Public Good Fuels all of this

316 The production of public goods has played a central role in all of the results that
317 we have presented. By enabling populations to reach larger sizes, these public
318 goods have effectively increased the rate of evolution for these populations. As
319 a result, larger populations are able to gain adaptations more quickly, both in
320 response to their environment and the environmental changes brought about
321 by niche construction. Additionally, these larger populations more effectively
322 “export” their niche. As more individuals migrate to neighboring patches, these
323 emigrants exert greater selective pressure. Here, we examine how population
324 size and migration rate influence these processes.

325 To directly explore how the increase in population size affects evolutionary
326 outcomes, we vary the maximum size that a population can reach (S_{max} , see
327 Equation 5). Figure 6A shows the result of these simulations. (TODO de-
328 scription of results)

329 To address how migration affects the evolutionary process in this system, we
330 vary the rate at which migration occurs (m). As seen in Figure 6B, cooperation
331 decreases as migration rate increases. This is likely because migration defines
332 the spatial structuring in this system. As migration increases, the population
333 becomes more like a well-mixed system, where defectors are better able to

334 exploit the benefits of cooperation (Griffin *et al.*, 2004; Kümmerli *et al.*, 2009).

335 # Discussion

336 • summary of results

337 – niche construction helps. but how?

338 – the extra fitness that it provides does not account for it

339 * in fact, cooperators never get to max fitness!

340 – negative niche construction plays a role

341 – negative niche construction alone does not help

342 • similarities/differences from previous work

343 – Schwilk and Kerr (2002)

344 – 10.1073/pnas.0812644106

345 • negative/positive NC

346 – laland1996evolutionary

347 • public goods as niche construction

348 • future QS or other environmental sensing

349 • Facultative cooperation

350 – Rodrigues (2012)

351 – Dumas and Kümmerli (2010)

352 – Kümmerli and Brown (2010)

353 – Darch/Diggle

354 – QS?

355 – Environmental Sensing? - (Koestler and Waters, 2014, Bernier et
356 al. (2011))

- 357 • Negative Niche construction as a strategy? - would those that create this
358 constant pressure (L=5, A=6) do better than those that do not (L=5,
359 A=5)?

360 Niche construction and selective feedbacks Niche construction and other social
361 interactions

362 **Public Goods**

363 TODO: merge this in with the “Cooperative Niche Construction” section
364 **TEST**

365 By their very nature, public goods benefit populations by making their environ-
366 ment more hospitable. For example, bacteria produce extracellular products
367 that find soluble iron (Griffin *et al.*, 2004), digest large proteins (Diggle *et al.*,
368 2007; Darch *et al.*, 2012), and reduce the risk of predation (Cosson *et al.*, 2002),
369 among many others (West *et al.*, 2007a). While many studies have explored
370 how the environment affects the evolution of cooperative behaviors, relatively
371 few have examined how those behaviors affect the environment and the result-
372 ing change in evolutionary trajectories. Lehmann (2007) demonstrated analyti-
373 cally that when niche construction act benefits future generations, cooperation
374 is favored due to reduced competition among kin. When rate-benefitting and
375 yield-benefitting altruistic acts co-evolve, Van Dyken and Wade (2012) showed

376 that “reciprocal niche construction”, where the selective feedbacks produced
377 by one act benefitted the other, can lead to increased selection for both traits.
378 While these studies have focused on the niche constructing effects of cooper-
379 ation, we instead focus our attention here on how niche construction enables
380 cooperators to escape defection by hitchhiking along with non-social traits.

381 **Primacy/Recency**

382 In our model, alterations to the environment were immediately echoed by
383 changes in selection. However, decoupling the timescales on which these pro-
384 cesses occur can have substantial effects (Laland *et al.*, 1996). By integrating
385 past allelic states into Equation 3, we can begin to explore how the cumulative
386 effects of niche construction affect the creation of non-social adaptive oppor-
387 tunities and the benefits that they offer cooperation. Here, how these past
388 allelic states are integrated will play an important role. For example, when
389 the effects of earlier generations are weighted more heavily, the influence of
390 migration may be diminished. While this will reduce the threat of emigration
391 by defectors, cooperator populations will also be less effective at exporting
392 their niche.

393 **Cooperative Niche Construction**

394 While our focus for this work has been on the eco-evolutionary feedbacks cre-
395 ated by non-social traits, it would also be interesting to explore how this
396 system is affected by the timescale at which carrying capacity at a given patch

397 is increased by public goods. In natural settings, a multitude of factors in-
 398 cluding protein durability (Brown and Taddei, 2007; Kümmerli and Brown,
 399 2010), diffusion (Allison, 2005; Driscoll and Pepper, 2010), and resource avail-
 400 ability (Zhang and Rainey, 2013; Ghoul *et al.*, 2014) influence both the rate
 401 and the degree to which public goods alter the environment (and thereby selec-
 402 tion). Lehmann (2007) demonstrated that a cooperative, niche constructing
 403 behavior can be favored when it only affected selection for future generations,
 404 thus reducing the potential for competition among contemporary kin. The
 405 evolutionary inertia that this creates, however, may ultimately work against
 406 cooperators. When public good accumulates in the environment, cooperators
 407 must reduce their investment in production to remain competitive (Kümmerli
 408 and Brown, 2010).

409 TODO: wrap up. Facultative cooperation requires sensing.

410 **Host-Symbiont**

411 In many instances of cooperation, the environment is itself a biological entity,
 412 which can produce additional evolutionary feedbacks. As the host population
 413 changes, so too will selection on their symbiont populations. Here, evolution-
 414 ary outcomes depend greatly on the degree of shared interest between the host
 415 and symbiont. For example, the cooperative production of virulence factors by
 416 the human pathogen *P. aeruginosa* in lung infections is harmful to those with
 417 cystic fibrosis (Harrison, 2007). Conversely, cooperative light production by *A.*
 418 *fischeri* is vital for the survival of its host, the Hawaiian bobtail squid (Ruby,

1996). It was recently argued that incorporating the effects of niche construction is critical for improving our understanding of viral evolution (Hamblin *et al.*, 2014) and evolution in co-infecting parasites (Hafer and Milinski, 2015). Incorporating host dynamics, co-evolution, and the feedbacks that they produce into models is likely to be equally important for gaining an understanding of how cooperative behaviors evolve in these host-symbiont settings.

Acknowledgments

- TODO: Organizers?
- TODO: lab comments

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436 **Figures**

437 **Figure 1**

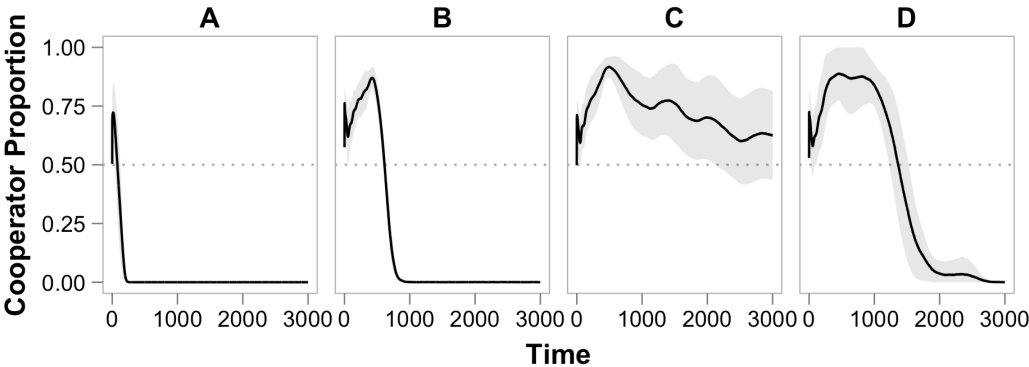


Figure 1: Proportion of cooperators over time TODO

438 **Figure 2**

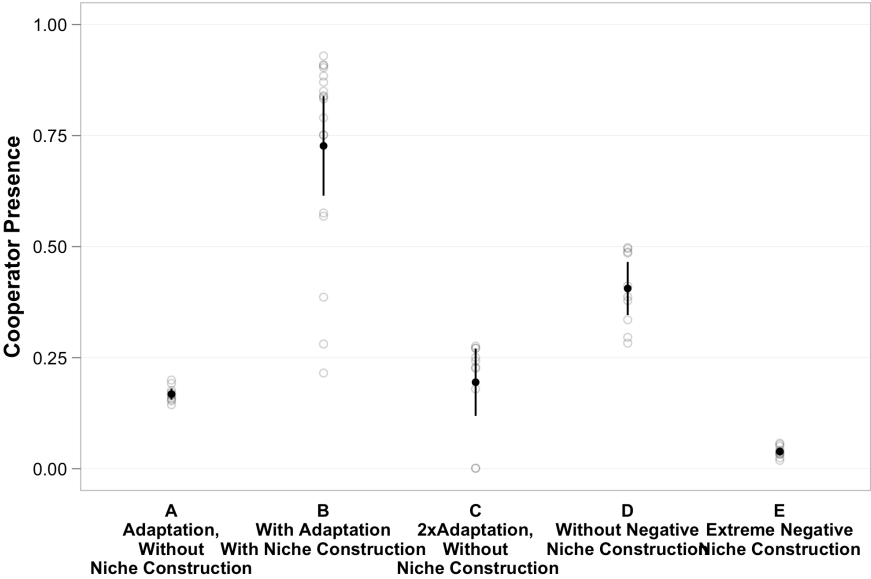


Figure 2: Cooperator Presence TODO

439 **Figure 3**

440 Mean fitness over time for the treatments shown in Figure 2

441 **Figure 3A - Fitness for base case: niche construction**

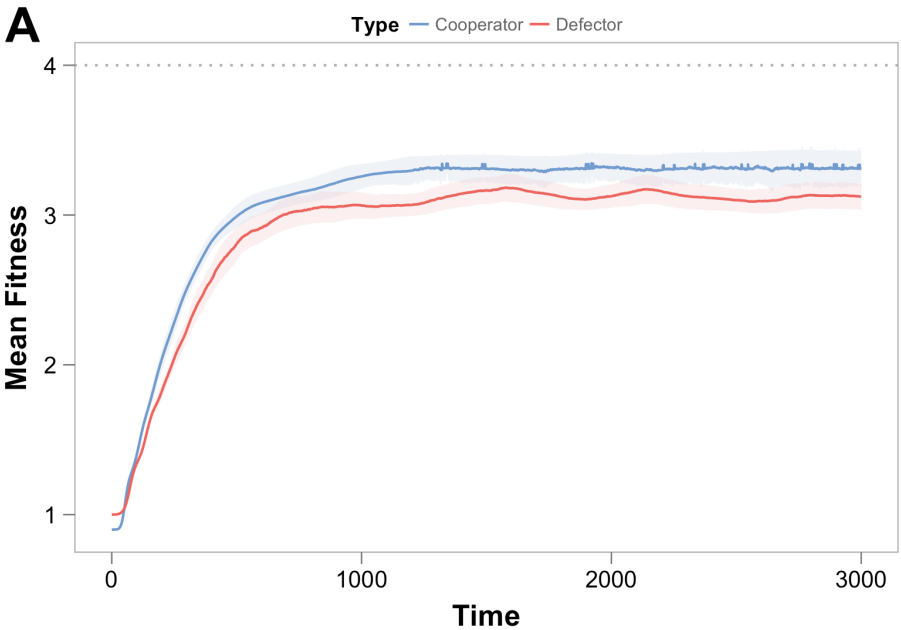


Figure 3: Grand mean Fitness of cooperators and defectors TODO

442 **Figure 3B - Fitness with double delta, no epsilon**

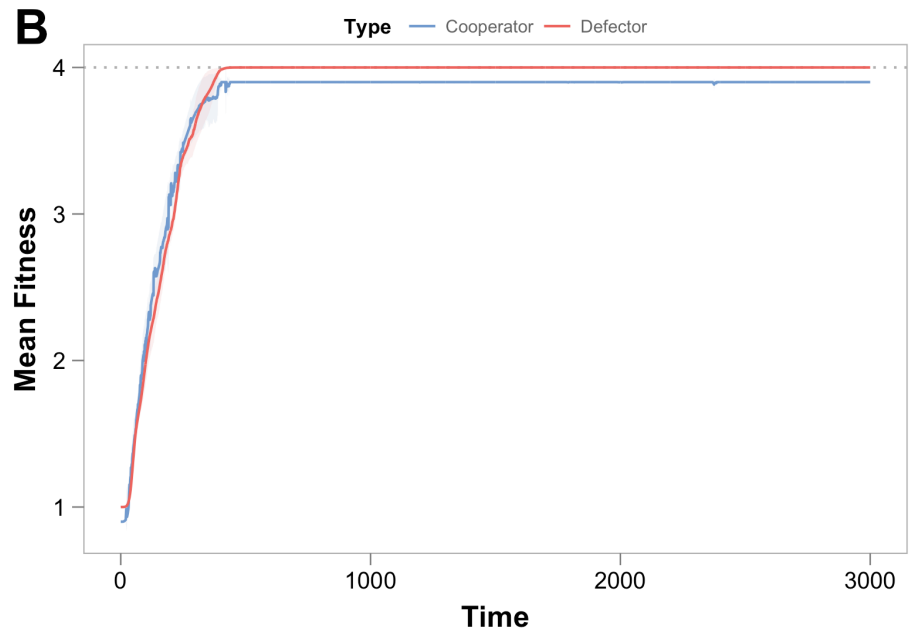


Figure 4: Grand mean Fitness of cooperators and defectors, double delta, no epsilon TODO

443 **Figure 3C - Fitness with no negative niche construction ($L=5$, $A=5$)**

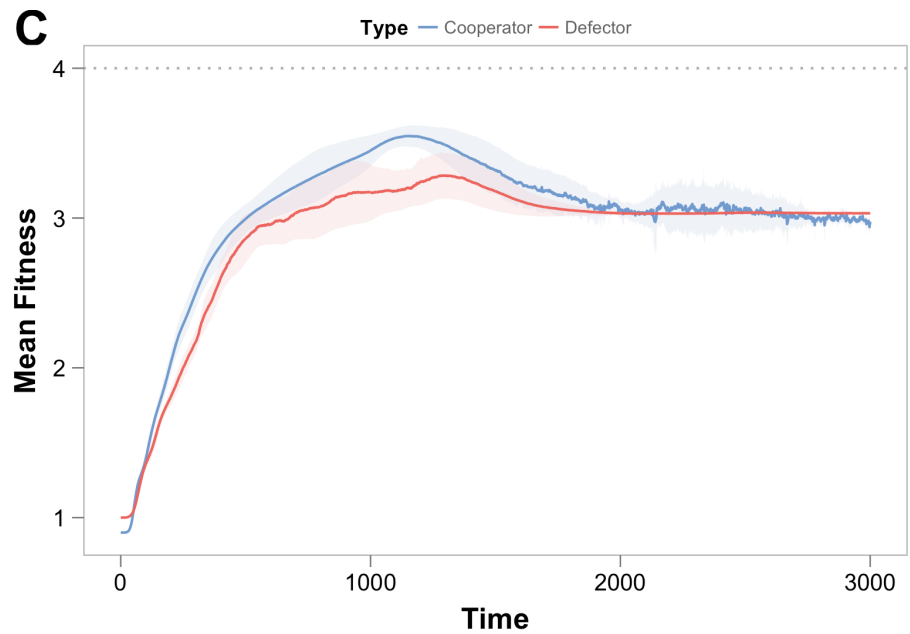


Figure 5: Grand mean Fitness of cooperators and defectors, no negative niche construction TODO

444 **Figure 3D - Fitness with extreme negative niche construction ($L=1$,**
445 **$A=6$)**

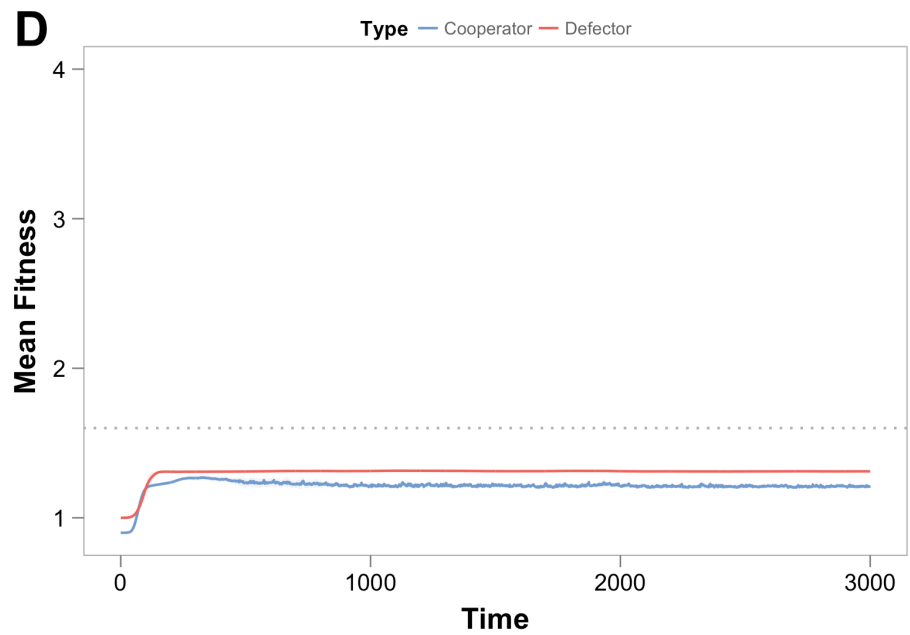


Figure 6: Grand mean Fitness of cooperators and defectors, extreme negative niche construction TODO

446 **Figure 4**

447 Cooperators invade from single population

448 **Figure 5**

449 Defectors are kept at bay

450 **Figure 6**

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

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

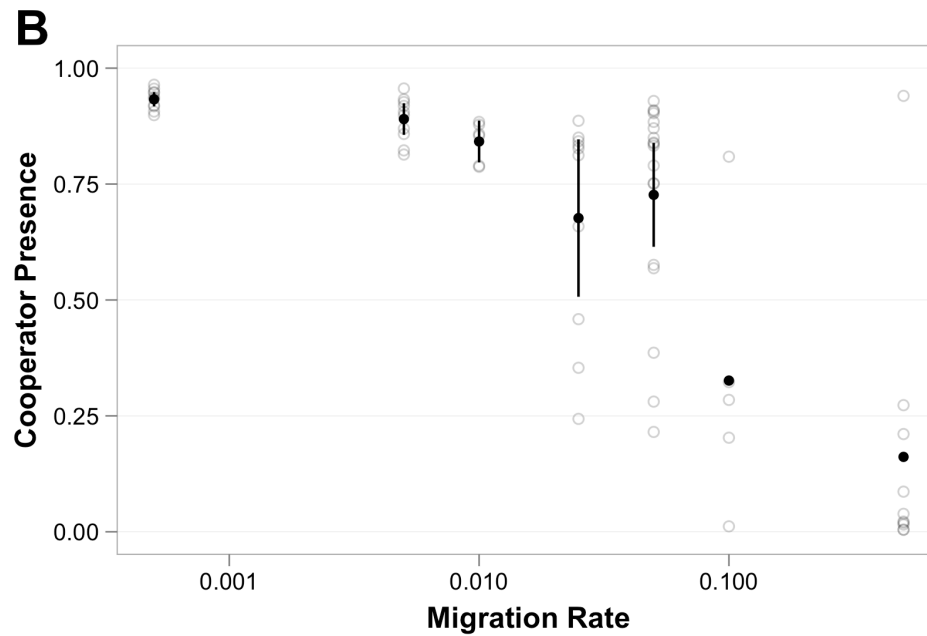


Figure 7: TODO Cooperator Presence for different migration rates

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_{max}	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

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