

1 Negative Niche Construction Favors the  
2 Evolution of Cooperation

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4 Brian D. Connelly<sup>1</sup>, Katherine J. Dickinson<sup>1</sup>, Sarah P. Hammarlund<sup>1,2</sup>, and  
5 Benjamin Kerr<sup>1,3</sup>

6 <sup>1</sup>Department of Biology and BEACON Center for the Study of Evolution in  
7 Action, University of Washington, Seattle, Washington, 98195, USA

8 <sup>2</sup>Current Address: Department of Zoology, University of Oxford, Oxford OX1  
9 3PS, United Kingdom

10 <sup>3</sup>E-mail: kerrb@uw.edu

## 11 Abstract

12 By benefitting others at a cost to themselves, cooperators face an ever present  
13 threat from defectors, or individuals that avail themselves of the cooperative  
14 benefit without contributing. A longstanding challenge to evolutionary biology  
15 is to understand the mechanisms that support the many instances of cooper-  
16 ation that nevertheless exist. Hammarlund et al. recently demonstrated that  
17 cooperation can persist by hitchhiking along with beneficial non-social adapta-  
18 tions. Importantly, cooperators play an active role in this process. In spatially-  
19 structured environments, clustered cooperator populations reach greater densi-  
20 ties, which creates more mutational opportunities to gain beneficial non-social  
21 adaptations. Cooperation rises in abundance by association with these adap-  
22 tations. However once adaptive opportunities have been exhausted, the ride  
23 abruptly ends as cooperators are displaced by adapted defectors. Using an  
24 agent-based model, we demonstrate that the selective feedback that is created  
25 as populations alter their environments can maintain cooperation indefinitely.  
26 We show that cooperator success depends specifically on negative niche con-  
27 struction. Here, negative niche construction acts as a perpetual source of  
28 adaptive opportunities. As populations adapt, they further alter their envi-  
29 ronment in ways that reveal additional opportunities for adaptation. Despite  
30 being independent of niche construction in our model, cooperation feeds this  
31 cycle. We show that by reaching larger densities, populations of cooperators  
32 are better able to adapt to changes in their constructed niche and successfully  
33 respond to the constant threat posed by defectors. We relate these findings to

34 previous studies from the niche construction literature and discuss how this  
35 model could be extended to provide a greater understanding of how coopera-  
36 tion evolves in the complex environments in which it is found.

## 37 Introduction

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

47 Several factors can prevent this *tragedy of the commons* (Hamilton, 1964;  
48 Nowak, 2006; West *et al.*, 2007b). One such factor involves non-random so-  
49 cial interaction, in which cooperators benefit more from the cooperative act  
50 than defectors. This can occur when cooperators are clustered together in  
51 spatially-structured populations (Fletcher and Doebeli, 2009; Nadell *et al.*,  
52 2010; Kuzdzal-Fick *et al.*, 2011) or when cooperators use communication  
53 (Brown and Johnstone, 2001; Darch *et al.*, 2012) or other cues (Sinervo *et*  
54 *al.*, 2006; Gardner and West, 2010; Veelders *et al.*, 2010) to cooperate condi-  
55 tionally with kin. Cooperation can also be bolstered by pleiotropic connections  
56 to personal benefits (Foster *et al.*, 2004; Dandekar *et al.*, 2012) or through as-  
57 sociation with alleles encoding self-benefitting traits (Asfahl *et al.*, 2015). In  
58 the latter case, the associated alleles may provide private benefits that are  
59 completely independent from the public benefits of cooperation. In asexual

60 populations of cooperators and defectors, this sets the stage for an “adaptive  
61 race” in which both types vie for the first highly beneficial adaptation (Waite  
62 and Shou, 2012; Morgan *et al.*, 2012). The tragedy of the commons can be  
63 deferred if a cooperator, by chance, wins the adaptive race.

64 Hammarlund et al. (2015) recently showed that in spatially-structured pop-  
65 ulations, the “Hankshaw effect” can give cooperators a substantial leg up on  
66 defectors in an adaptive race. This advantage is reminiscent of Sissy Han-  
67 kshaw, a fictional character in Tom Robbins’ *Even Cowgirls Get the Blues*,  
68 whose oversized thumbs—which were otherwise an impairment—made her a  
69 prolific hitchhiker. Similarly, cooperation is costly, but it increases local pop-  
70 ulation density. As a result, cooperators are more likely to acquire benefi-  
71 cial mutations. By hitchhiking along with these adaptations, cooperation can  
72 rise in abundance. Nevertheless, this advantage is fleeting. As soon as the  
73 opportunities for adaptation are exhausted, cooperators are once again at a  
74 selective disadvantage against adapted defectors that arise via mutation. How-  
75 ever, Hammarlund et al. (2015) also demonstrated that cooperation can be  
76 maintained when frequent environmental changes produce a steady stream of  
77 new adaptive opportunities. Although organisms typically find themselves in  
78 dynamic environments, the nature and frequency of these changes might not  
79 ensure long-term cooperator survival.

80 However, organisms do more than simply experience changing environments  
81 passively. Through their activities, their interactions with others, and even  
82 their deaths, organisms constantly modify their environment. This *niche con-*  
83 *struction* process can produce evolutionary feedback loops in which environ-

84 mental change alters selection, which, in turn, alters the distribution of types  
85 and their corresponding influence on the environment (Odling-Smee *et al.*,  
86 2003). The nature of this feedback can have dramatic evolutionary conse-  
87 quences. One critical distinction is whether the constructing type is favored in  
88 the resulting environment. Under positive niche construction, selection favors  
89 the constructor, and evolution stagnates as this type fixes. Under negative  
90 niche construction, selection favors a type other than the constructor, which  
91 creates an opportunity for novel adaptation. If the resulting adapted type also  
92 engages in negative niche construction, cycles of construction and adaptation  
93 can ensue, such that populations find themselves continually chasing beneficial  
94 mutations as their adaptive landscape perpetually shifts.

95 Here, we show that the selective feedbacks that result from niche construction  
96 can maintain cooperation indefinitely. We find that it is specifically negative  
97 niche construction that is responsible for this result because of the endless  
98 opportunities for adaptation that it produces. These results indicate that  
99 cooperators can ensure their survival when they play an active role in their  
100 own evolution.

## 101 **Methods**

102 Building upon Hammarlund et al. (2015), we describe an individual-based  
103 model in which cooperators and defectors evolve and compete in a population  
104 of subpopulations (i.e., a metapopulation). Through mutations, individuals  
105 gain adaptations to their environment, which increase reproductive fitness,

106 and allow those lineages to rise in abundance. More successful lineages spread  
107 to neighboring subpopulations by migration.

108 In this expanded model, subpopulations additionally modify their local envi-  
109 ronment. As this process occurs, environmental changes feed back to affect  
110 selection. We explore how niche construction affects the evolution of cooper-  
111 ation; specifically, how cooperative behavior can hitchhike along with adapta-  
112 tions to modified environments. Box 1 provides additional information about  
113 the model.

## 114 **Model Description**

### 115 **Individual Genotypes and Adaptation**

116 Each individual has a haploid genome with  $L + 1$  loci (see [Table 1](#) for model  
117 parameters and their values). Different alleles at each locus are represented  
118 by different integers. A binary allele at the *cooperation locus* (locus zero)  
119 determines whether that individual is a cooperator (1), which carries fitness  
120 cost  $c$ , or a defector (0). The remaining  $L$  loci are *adaptive loci*, and are each  
121 occupied by 0 or a value from the set  $\{1, 2, \dots, A\}$ . Allele 0 represents a lack of  
122 adaptation, while a non-zero allele represents one of the  $A$  possible adaptations  
123 at that locus.

124 These non-zero alleles signify two types of adaptations, both of which increase  
125 fitness. First, adaptations to the external environment confer a fitness benefit  $\delta$ .  
126 This selective value is the same regardless of which non-zero allele is present  
127 and is not affected by other individuals. We assume  $\delta > c$ , which allows a

128 minimally adapted cooperator to recoup the cost of cooperation and gain a  
129 fitness advantage.

## 130 **Niche Construction and Selective Feedbacks**

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

136 In our model, the feedback from niche construction takes the form of density  
137 dependent selection, and individuals evolve to better match their constructed  
138 niche. Specifically, the selective value of non-zero allele  $a$  at adaptive locus  
139  $l$ —and consequently the fitness of an individual carrying that allele—increases  
140 with the number of individuals in the subpopulation that have allele  $a - 1$  at  
141 locus  $l - 1$ . For example, if  $L = 5$  and  $A = 6$ , and allele 4 has fixed at locus  
142 2, then a genotype with allele 5 at locus 3 is favored. And as allele 5 fixes at  
143 locus 3, the niche that this population constructs will favor allele 6 at locus 4  
144 (see Box 1). As a consequence, genotypes with sequentially increasing allelic  
145 states will tend to evolve. We treat both adaptive loci and their non-zero allelic  
146 states as “circular”: the selective value of an allele at locus 1 is affected by the  
147 allelic composition of the subpopulation at locus  $L$ . Similarly, the selective  
148 value of allele 1 at any locus increases with the number of individuals carrying  
149 allele  $A$  at the previous locus. This circularity is represented by the function



150  $\beta(x, X)$ , which gives the integer that is below an arbitrary value  $x$  in the set  
 151  $\{1, 2, \dots, X\}$ :

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

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

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

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

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

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

161 Thus, an individual's fitness is determined both by adaptations to the exter-  
 162 nal environment and by adaptations to its constructed environment. **Box 1**

163 illustrates the process of adaptation to the constructed environment. While  
 164 cooperation is costly, we assume its effects are independent of the external and  
 165 constructed components of the environment.

## 166 **Subpopulation Growth and the Benefit of Cooperation**

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

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

172 During subpopulation growth, individuals compete through differential repro-  
 173 duction. Each individual's probability of success is determined by its fitness.  
 174 The composition of a subpopulation with size  $P$  and cooperator proportion  $p$   
 175 after growth is multinomial with parameters  $S(p)$  and  $\{\pi_1, \pi_2, \dots, \pi_P\}$ , where  
 176  $\pi_i$  represents the reproductive fitness of individual  $i$  relative to others in the  
 177 subpopulation (using Equation 2).

## 178 **Mutation**

179 For simplicity, we apply mutations after subpopulation growth. Mutations  
 180 occur independently at each locus and cause an allelic state change. At the

181 binary cooperation locus, mutations occur at rate  $\mu_c$ . These mutations flip  
182 the allelic state, causing cooperators to become defectors and vice versa. Mu-  
183 tations occur at rate  $\mu_a$  at each adaptive locus. These mutations replace the  
184 existing allele with a random selection from the set  $\{0\} \cup \{1, 2, \dots, A\}$ . Be-  
185 cause mutations are stochastic, the allelic sequences that evolve depend on  
186 which allele arises first and at which locus.

## 187 **Migration**

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

## 195 **Population Initialization and Simulation**

196 Following Hammarlund et al. (2015), we begin simulations with sparse pop-  
197 ulations. Subpopulations are first seeded at all patches with size  $S(p_0)$  and  
198 cooperator proportion  $p_0$ . The population is then thinned. Each individual  
199 survives this bottleneck with probability  $\sigma$ . Starting from this initial state,  
200 simulations then proceed for  $T$  cycles, where each discrete cycle consists of  
201 subpopulation growth, mutation, migration, and dilution. Dilution reduces

202 each subpopulation to support growth in the next cycle. Each individual re-  
203 mains with probability  $d$ , regardless of its genotype.

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

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

## 210 **Results**

211 Using the model described in the previous section, we perform simulations that  
212 follow the evolution of cooperation in a population of subpopulations that are  
213 connected by spatially-limited migration. Individuals increase their compet-  
214 itiveness by gaining adaptations. While cooperation does not directly affect  
215 the fitness benefits that these adaptations confer, cooperation has indirect  
216 effects on the adaptive process. Specifically, cooperation increases subpopula-  
217 tion density. As a result, larger subpopulations of cooperators experience more  
218 mutational opportunities. Cooperation can rise in abundance by hitchhiking  
219 along with beneficial mutations, which compensate for the cost of cooperation.  
220 Importantly, subpopulations alter their local environments, which feeds back

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

221 to influence selection. Here, we explore how such niche construction affects  
222 the evolution of cooperation.

## 223 Cooperation Persists with Niche Construction

224 Without any opportunity for adaptation ( $L = 0$ ), cooperators are swiftly elim-  
225 inated from populations (Figure 1A). Despite an initial lift in cooperator abun-  
226 dance due to increased productivity, the cost of cooperation becomes disad-  
227 vantageous as migration mixes the initially isolated subpopulations. When  
228 populations can adapt to the external environment ( $L > 0$  and  $\delta > 0$ ), but  
229 niche construction is absent ( $\epsilon = 0$ ), cooperators are maintained only tran-  
230 siently (Figure 1B). Here, larger cooperator subpopulations can more quickly  
231 adapt to their external environment. However, as previously described by  
232 Hammarlund et al. (2015), cooperation is subsequently lost once populations  
233 become fully adapted. This occurs when isogenic defectors (i.e., defectors with  
234 identical adaptive loci) arise via mutation and displace cooperators due to their  
235 selective advantage. However, when niche construction feeds back to influence  
236 selection ( $\epsilon > 0$ ), cooperation persists in the majority of the replicate popula-  
237 tions (Figure 1C). We see in Figure 2A that despite oscillations, cooperation  
238 is maintained at high levels in these populations.

## **Fitness Increases Alone do not Support Persisting Cooperation**

In the model, adaptations to both the external environment and the constructed environment contribute to an individual's fitness. To determine whether cooperation is maintained solely due to the larger selective values that result from the contributions of niche construction, we performed simulations in which these contributions were removed ( $\epsilon = 0$ ). We instead increased the fitness benefits conferred by adaptation to the external, non-constructed environment ( $\delta = 0.6$ ). In doing so, we conservatively estimate the selective effects of niche construction by supplementing the selective benefits of adaptations to the external environment by the maximum possible selective benefit that results from niche construction. Nevertheless, we find that simply increasing selective values does not enable cooperators to persist (Figure 2B). Niche construction, therefore, plays a decisive role here.

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

In our model, an adaptation to the constructed environment initiates a new instance of niche construction, leading to sequentially increasing allelic states across the adaptive loci. Under certain conditions, this construction always makes the constructor sub-optimal for the niche it creates (see Box 1). This negative niche construction occurs when the number of adaptive alleles ( $A$ )

260 does not divide evenly into the number of adaptive loci ( $L$ ). In such a case,  
 261 any sequence of integers on the circular genome will always contain a break  
 262 in the sequence; that is, one locus will have an allele that is not one  
 263 less than the allele at the next locus. Given this unavoidable mismatch, any  
 264 type that has fixed will always construct a niche that favors selection for a  
 265 new type. When negative niche construction is removed (by setting  $L = 5$ ,  
 266  $A = 5$ ), cooperators are again driven extinct after an initial lift in abundance  
 267 (Figure 2C). These results indicate that the type of niche construction matters.  
 268 Specifically, negative niche construction is crucial for maintaining cooperation.

## 269 **Selective Feedbacks Limit Defector Invasion**

270 The adaptation resulting from selective feedbacks can limit invasion by de-  
 271 fectors, which arise either through immigration from neighboring patches or  
 272 through mutation at the cooperation locus. The latter challenge is particularly  
 273 threatening, as these isogenic defectors are equally adapted, yet do not incur  
 274 the cost of cooperation. As demonstrated in Figure 3A, isogenic defectors  
 275 rapidly spread when introduced at a single patch in the center of a population  
 276 of cooperators if mutations do not occur. However, when cooperators can gain  
 277 adaptations via mutation, cooperators resist defector invasion in over half of  
 278 the replicate populations (Figure 3B). Figure 4 depicts one such instance. In  
 279 that population, isogenic defectors are seeded at a single patch in an otherwise  
 280 all-cooperator population. These defectors quickly begin to spread. However,  
 281 a neighboring cooperator population gains an adaptation, which increases its

282 fitness above that of the defector. This type spreads more quickly, stopping  
283 the spread of defectors and eventually driving them to extinction. Because this  
284 adaption occurs in a cooperator population, cooperation is able to hitchhike  
285 to safety. Importantly, this new cooperator is favored because of the niche  
286 that its ancestral type created. Here, cooperators can find safety in numbers—  
287 because their larger populations have more mutational opportunities, they are  
288 more likely to gain adaptations that rescue them from invasion. Further, these  
289 larger cooperators exert a greater influence on their niche, which increases se-  
290 lection for an adapted type. This allows that type to appear and to spread  
291 more quickly in the population. **Figure 3C** shows how quickly an adapted coop-  
292 erator type can invade a population of defectors. Importantly, this cooperator  
293 type is adapted to the niche constructed by the defector.

## 294 Discussion

295 Despite their negative effects, deleterious traits can rise in abundance due to ge-  
296 netic linkage with other traits that are strongly favored by selection (Maynard  
297 Smith and Haigh, 1974). In a process termed the “Hankshaw effect”, Ham-  
298 marlund et al. (2015) recently demonstrated that cooperation can actively  
299 prolong its existence by increasing its likelihood of hitchhiking with a benefi-  
300 cial trait. In that work and in ours, subpopulations of cooperators grow to a  
301 higher density than those of defectors. These larger cooperator subpopulations  
302 therefore experience more mutations and are consequently more likely to gain  
303 adaptations. While this process does favor cooperation in the short term, it



304 eventually reaches a dead end: When the opportunities for adaptation are ex-  
305 hausted, and cooperators can no longer hitchhike, they face extinction. Here,  
306 we have investigated whether niche construction might serve to perpetually  
307 generate new adaptive opportunities and thus favor cooperation indefinitely.

308 When niche construction occurs, cooperation can indeed persist (Figures 1C  
309 and 2A). In our model, niche construction introduces additional selective ef-  
310 fects that influence the evolutionary process, leading to a more pronounced  
311 Hankshaw effect. However, these fitness benefits alone do not maintain co-  
312 operation (Figure 2B). Niche construction and the selective feedbacks that it  
313 produces play a crucial role.

314 We find that it is specifically *negative* niche construction that maintains coop-  
315 eration (Figure 2C). As cooperator and defector types gain adaptations, they  
316 alter their environment in ways that favor other types. Thus, negative niche  
317 construction serves as a perpetual source of adaptation. Here we observe an-  
318 other facet of the Hankshaw effect: Because subpopulations of cooperators  
319 are larger, they are better able to respond to the adaptive opportunities that  
320 follow from negative niche construction. By gaining adaptations more quickly,  
321 cooperators resist invasion by defectors (Figure 3B). Even in the presence of  
322 an equally-adapted defector type, cooperator subpopulations are more likely  
323 to produce the mutant most adapted to the current niche, which can then dis-  
324 place the slower-adapting defectors. These recurring cycles of defector invasion  
325 and cooperator adaptation underlie the oscillations in cooperator proportion  
326 seen in Figure 2A. When mutations do not confer these adaptations, coopera-  
327 tors lose the adaptive race and are driven to extinction by the defector. This

328 is something that we see occur stochastically in Figures 2A and 3B.

## 329 Cooperation as Niche Construction

330 In our model, niche construction and adaptation are independent of cooper-  
331 ation, which allows us to focus on hitchhiking. However, by increasing the  
332 size of the subpopulation, this form of cooperation can itself be seen as a kind  
333 of niche construction. Cooperative benefits often take similar forms in natu-  
334 ral systems. For example, bacteria produce a host of extracellular products  
335 that scavenge soluble iron (Griffin *et al.*, 2004), digest large proteins (Diggle  
336 *et al.*, 2007; Darch *et al.*, 2012), and reduce the risk of predation (Cosson *et*  
337 *al.*, 2002), among many others (West *et al.*, 2007a). As in our model, these  
338 forms of cooperation are likely to increase local subpopulation density. While  
339 many studies have focused on how the environment affects the evolution of  
340 these cooperative traits, relatively few have addressed how the environmental  
341 changes created by these products feed back to influence evolution.

342 Perhaps most similar to this study, Van Dyken and Wade (2012) demon-  
343 strated that when two negative niche constructing, cooperative behaviors co-  
344 evolve, selection can increasingly favor these traits, which are disfavored when  
345 alone. In that model, “reciprocal niche construction” occurred when the neg-  
346 ative feedback resulting from one strategy positively influenced selection for  
347 the other, creating a perpetual cycle that maintained both forms of coopera-  
348 tion. Arguably, this can be seen as an instance of hitchhiking: the currently-  
349 maladaptive form of cooperation is maintained by association with the adap-

350 tive form.

351 When dispersal is limited, competition among kin can undermine cooperation.  
352 To separate kin competition from kin selection, Lehmann (2007) developed  
353 a model in which a cooperative, niche-constructing behavior only benefitted  
354 future generations. Kin competition was thereby reduced, and cooperation  
355 instead benefitted descendants. This work highlights an important aspect of  
356 niche construction: Often, the rate of selective feedback from niche construc-  
357 tion is different from the rate at which populations grow.

## 358 **Evolution at Multiple Timescales**

359 In our work, the niche is modeled implicitly by the composition of the sub-  
360 population. Any changes in the subpopulation, therefore, produce immediate  
361 effects on the constructed environment and the resulting selective feedbacks.  
362 However, timescales in our model could be de-coupled in two ways. First, co-  
363 operators modify their niche by enabling their subpopulation to reach larger  
364 density (Equation 4). These increased subpopulation sizes play a critical role  
365 by effectively increasing the rate of evolution in these subpopulations. Because  
366 of the importance of this process, it would be very informative to explore how  
367 sensitive our results are to the rate at which cooperators increase population  
368 sizes and the rate at which this benefit decays in the absence of cooperators.  
369 Similarly, our results could be substantially affected by alterations in the rate  
370 at which the constructed environment changes in response to changes in the  
371 subpopulation. First, such changes in timescale would affect the selective val-

ues of alleles as the population changed. Changes in timescale would also influence whether or not populations were able to evolve adapted types and if so, how well those adapted types can propagate through the population to address the threat of a defector.

Other studies, while not focused on cooperation, have similarly shown that the timescales at which niche construction feedbacks occur can strongly influence evolutionary outcomes (Laland *et al.*, 1996, 1999). This perspective is likely to be crucial for understanding the evolution of cooperative behaviors like the production of public goods. In these instances, environmental changes are likely to occur on different timescales than growth, which can have profound effects. For example, a multitude of factors, including protein durability (Brown and Taddei, 2007; Kümmerli and Brown, 2010), diffusion (Allison, 2005; Driscoll and Pepper, 2010), and resource availability (Zhang and Rainey, 2013; Ghoul *et al.*, 2014) influence both the rate and the degree to which public goods alter the environment. While Lehmann (2007) showed that cooperation was favored when selective feedbacks act over longer timescales, niche construction may in fact hinder cooperation when selection is more quickly altered. For example, when public goods accumulate in the environment, cooperators must decrease production to remain competitive (Kümmerli and Brown, 2010; Dumas and Kümmerli, 2012). This favors cooperation that occurs facultatively, perhaps by sensing the abiotic (Bernier *et al.*, 2011; Koestler and Waters, 2014) or biotic environment (Brown and Johnstone, 2001; Darch *et al.*, 2012). In order to study how regulatory traits such as these evolve, we could instead represent the niche explicitly, allowing it to have its own dynamics.

## 396 Cooperation and Niche Construction in Host-Symbiont

## 397 Co-Evolution

398 In many biological systems, the environments modified by organisms are other  
399 organisms. In these instances, the “niche” becomes a biological entity with its  
400 own evolutionary process. A logical extension to our model, would be to treat  
401 the environment as a biological entity. As the host population changes, either  
402 in response to symbiont cooperation or other factors, so too does selection on  
403 their symbiont populations. Here, evolutionary outcomes depend greatly on  
404 the degree of shared interest between the host and symbiont. Future models  
405 could explicitly capture the environment as a biological entity to explore the  
406 rich co-evolutionary dynamics that these systems might offer. In our model,  
407 each patch could become hosts with their own genotypes, and death and re-  
408 production at the host level could be defined in ways that are sensitive to  
409 both host and symbiont genotypes. Such a model could be used to explore the  
410 evolution of cooperation in host-symbiont systems, where cooperation among  
411 symbionts affects host fitness.

412 For example, the cooperative production of virulence factors by the human  
413 pathogen *P. aeruginosa* is harmful to hosts with cystic fibrosis (Harrison,  
414 2007). Following what we have shown in this work, these antagonistic, neg-  
415 ative niche constructing behaviors may work to maintain these infections. If  
416 these populations do indeed benefit from adaptations that are created by niche  
417 construction, a case could perhaps be made for developing treatments that tar-  
418 get the selective feedback loop that provides adaptive opportunities in these

419 spatial environments. While the idea of removing negative selective feedbacks  
420 and supporting stability may seem counterintuitive, if it leaves the infecting  
421 population more susceptible, then perhaps pairing such a treatment with the  
422 introduction of defector mutants (see e.g., Rumbaugh et al. (2009)), could  
423 significantly improve host fitness. Expanding models such as ours to address  
424 the additional dynamics present in host-symbiont systems such as these could  
425 be quite productive.

426 It was recently argued that incorporating the effects of niche construction is  
427 critical for improving our understanding of viral evolution (Hamblin *et al.*,  
428 2014) and evolution in co-infecting parasites (Hafer and Milinski, 2015). In-  
429 corporating host dynamics, co-evolution, and the feedbacks that they produce  
430 is likely to be equally important for gaining a greater understanding of how  
431 cooperative behaviors evolve in these host-symbiont settings.

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## Box 1: Description of niche construction in our model

See [Figure B1](#)

**(A) Individuals.** The genome of each individual consists of a single *cooperation locus* and  $L$  *adaptive loci* (here,  $L = 5$ ). At the cooperation locus (labeled 0), this individual has allele 1, making it a cooperator. The adaptive loci (labeled 1-5) are arranged as a circular chromosome, where each locus has an integer allele between 0 and  $A$ , inclusive. In the description that follows, we focus exclusively on these adaptive loci. Genotypes are given by their allelic states starting with locus 1. For instance, the genotype shown here is [2,0,5,2,1]. Because of their circular structure, allele 2 at the first locus follows allele 1 at the fifth locus.

**(B) Niche Construction.** Consider a subpopulation fixed for genotype [1,2,0,0,0]. This subpopulation constructs environment  $E_{[1,2,0,0,0]}$ . Every non-zero allele influences selection at the next locus, favoring sequential allelic states. In this constructed environment, allele 3 at locus 3 would be favored. If genotype [1,2,3,0,0] arises via mutation, it is expected to fix. However, genotype [1,2,3,0,0] affects the environment differently. As [1,2,3,0,0] rises in abundance, the constructed environment changes to  $E_{[1,2,3,0,0]}$ , which favors [1,2,3,4,0].

**(C) Niche Construction and Adaptation.** The evolutionary transition shown in Part B is indicated in the dashed box. Here, we depict entire sub-

462 populations fixed for a genotype using a single instance of that genotype. Simi-  
 463 larly, an arrow represents niche construction and adaptation to the constructed  
 464 environment. We start with a case in which there are five alleles ( $A = 5$ ). Sub-  
 465 populations begin with the non-adapted genotype  $[0,0,0,0,0]$ , shown on the far  
 466 left. A non-zero allele is introduced via mutation, which represents an adapta-  
 467 tion to external aspects of the environment. Here, allele 1 arises and fixes at  
 468 locus 1. The remainder of this figure focuses on adaptation to the constructed  
 469 aspects of the environment. This genotype has a “mismatch” (shown by the  
 470 red sector), because  $E_{[1,0,0,0,0]}$  favors  $[1,2,0,0,0]$ . Assuming allele 2 arises at the  
 471 second locus, it will be selected, creating a “match” at the first and second  
 472 loci (green sector). Now there is a mismatch between the second and third  
 473 loci in the resulting environment, which a new round of mutation and selection  
 474 corrects, and so on. The green sector grows as the red sector shifts clockwise.  
 475 When the population reaches  $[1,2,3,4,5]$ , it constructs  $E_{[1,2,3,4,5]}$ . Here, since  
 476 allele 1 follows allele 5, there is no longer a mismatch, so no further adaptation  
 477 occurs.

478 **(D) Negative Niche Construction.** A different case emerges when the  
 479 number of alleles does not evenly divide into the number of loci. Here, we  
 480 change the number of alleles to six ( $A = 6$ ). As shown on the far left, we  
 481 begin with a subpopulation fixed for genotype  $[1,2,3,4,5]$ . This genotype has a  
 482 mismatch, because the niche constructed by allele 5 favors allele 6 (not 1) at the  
 483 next locus (locus 1). A mutant with genotype  $[6,2,3,4,5]$  has a fitness advantage  
 484 and can fix in  $E_{[1,2,3,4,5]}$ . However, as this type constructs  $E_{[6,2,3,4,5]}$ , a new  
 485 mismatch appears. In this instance of negative niche construction, adapting



486 to correct one mismatch generates a new mismatch. This system can never  
487 escape its mismatches—the red sector just shifts clockwise around the genome  
488 perpetually.

## 489 Figures

### 490 Figure 1

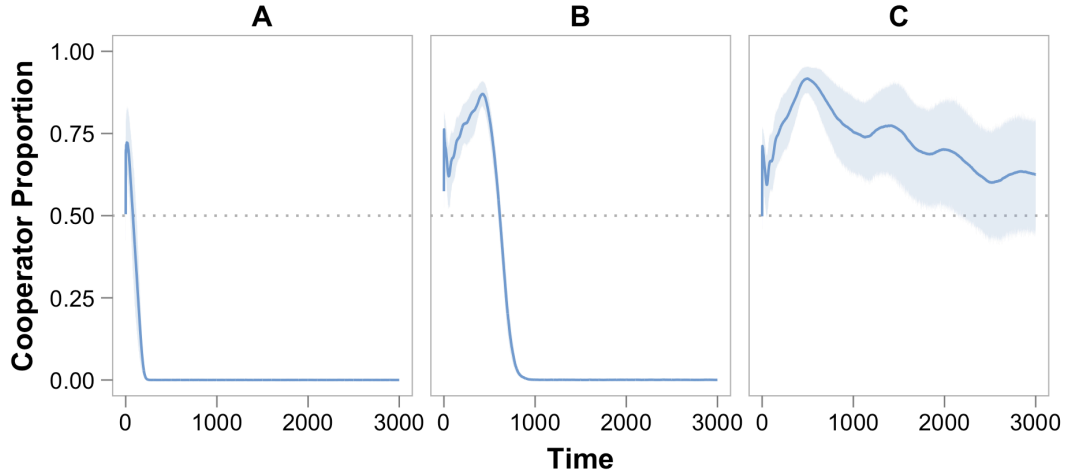
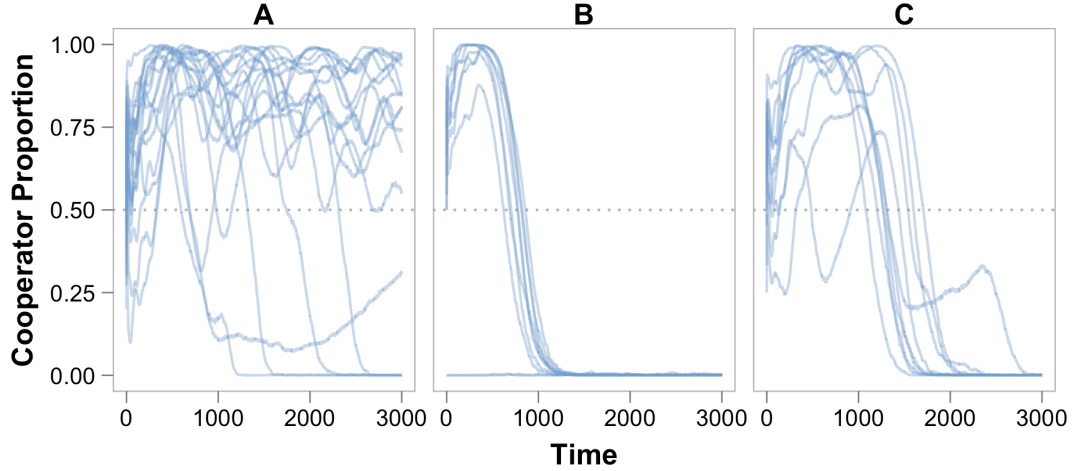


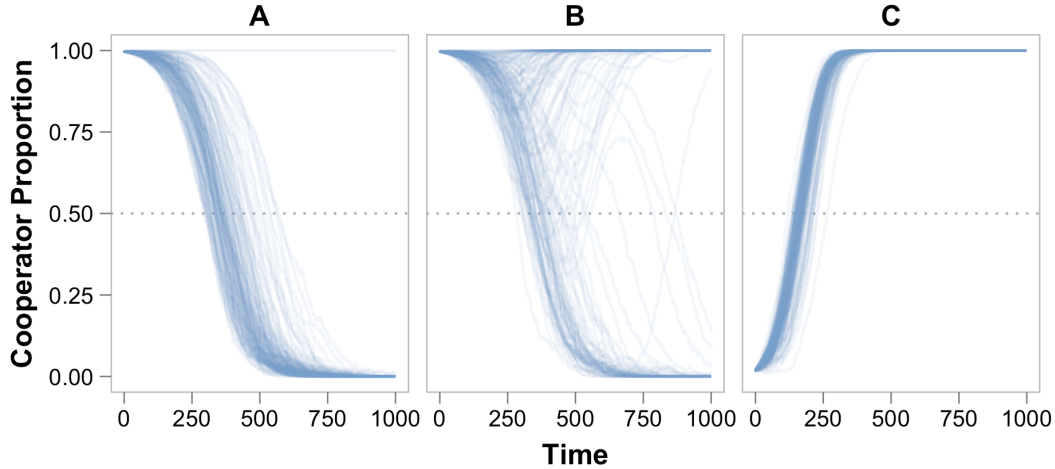
Figure 1: **Adaptation, Hitchhiking, and the Evolution of Cooperation.** Curves show the average cooperator proportion among replicate populations for the duration of simulations, and shaded areas indicate 95% confidence intervals. Unless otherwise noted, parameter values are listed in [Table 1](#). **(A)** Without any opportunity to adapt ( $L = 0$ ), cooperation is quickly lost. **(B)** When adaptation can occur ( $L = 5$ ), but niche construction does not affect selection ( $\epsilon = 0$ ), cooperators rise in abundance by hitchhiking along with adaptations to the external environment. Nevertheless, this effect is transient, and cooperators eventually become extinct. **(C)** Niche construction enables cooperation to be maintained indefinitely. In the majority of populations, cooperation remained the dominant strategy. The trajectories of individual populations are shown in Figure 2A.

491 **Figure 2**



**Figure 2: Niche Construction and the Evolution of Cooperation.** The proportion of cooperators present in each replicate population is shown for the duration of simulations. **(A)** Despite some oscillations, cooperation dominates in 13 of 18 populations when niche construction affects selection. **(B)** When the selective effects of niche construction ( $\epsilon$ ) are removed, and the selective benefit of adaptation to the external environment ( $\delta$ ) is increased to compensate, cooperators are driven to extinction by isogenic defectors that arise by mutation ( $\epsilon = 0$ ,  $\delta = 0.6$ ). Note that cooperation was not present after initialization in one replicate population. **(C)** Cooperators are also driven to extinction without negative niche construction ( $A = 5$ ).

492 **Figure 3**



**Figure 3: Niche Construction and Invasion.** Curves trace the proportion of cooperators present in each replicate population for the duration of simulations ( $T = 1000$ ). In each simulation, a rare type was initiated at a single patch in the center of the population lattice ( $N^2 = 121$ ). Unless otherwise noted, mutations are disabled in these ecological simulations to highlight the dynamics of invasion ( $\mu_a = 0, \mu_c = 0$ ). **(A)** When cooperators and defectors are isogenic (i.e., both types have stress alleles [1,2,3,4,5]), rare defectors quickly invade and drive cooperators to extinction due to the cost of cooperation. Defectors were stochastically eliminated in 2 replicate populations. **(B)** However, negative niche construction creates adaptive opportunities that enable cooperators to resist invasion by isogenic defectors. Here, cooperation remained the dominant in 91 of 160 populations ( $\mu_a = 0.00005$ ). Results from simulations where mutations also occurred at the cooperation locus are shown in Figure S1. **(C)** In fact, an adapted cooperator type (stress alleles [6,2,3,4,5], see Box 1) can swiftly displace defectors when isogenic defectors cannot arise or adapt via mutation.

493 **Figure 4**

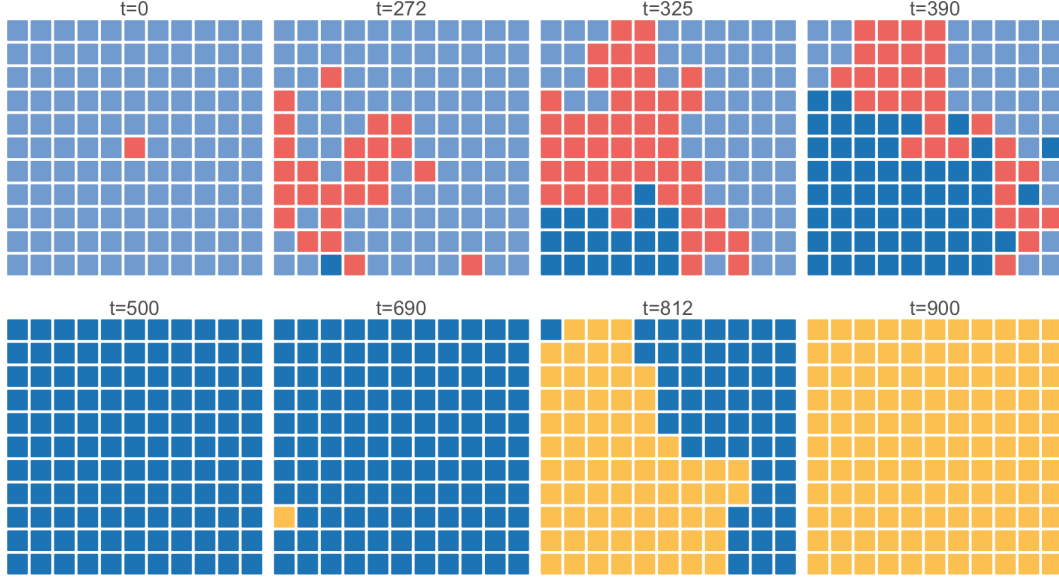


Figure 4: **Cooperator Adaptation Prevents Defector Invasion.** Here we depict the distribution of dominant types among subpopulations over time for one representative simulation in which isogenic defectors arise. To highlight the effects of adaptation, mutations did not occur at the cooperation locus ( $\mu_c = 0$ ). At time  $t = 0$  (upper left panel), a single isogenic defector population (red) is placed among cooperator populations (light blue). Because these defectors do not bear the costs of cooperation, they spread ( $t = 272$ ). However, cooperators in one population gain an adaptation that gives them a fitness advantage over defectors (second panel, dark blue, lower left). At  $t = 325$ , defectors continue to invade cooperator populations. However, the adapted cooperator type spreads more quickly due to its fitness advantage, invading both defector populations and ancestral cooperator populations ( $t = 390$ ), until it eventually fixes in the population ( $t = 500$ ). At  $t = 690$ , a new cooperator type emerges that is favored due to negative niche construction (orange). This new type spreads rapidly ( $t = 812$ ) until reaching fixation ( $t = 900$ ). At this point, it becomes susceptible to invasion by the next “adapted” cooperator type, and the cycle continues.

494 **Box 1 Figures**

495 **Figure B1**

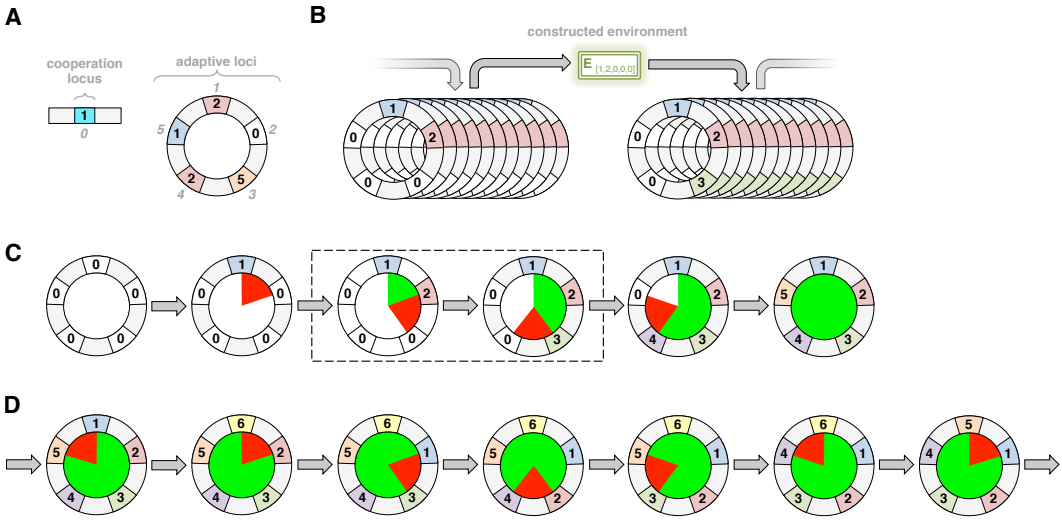


Figure B1: Figure for Box 1

<sup>496</sup> **Supplemental Figures**

<sup>497</sup> **Figure S1**



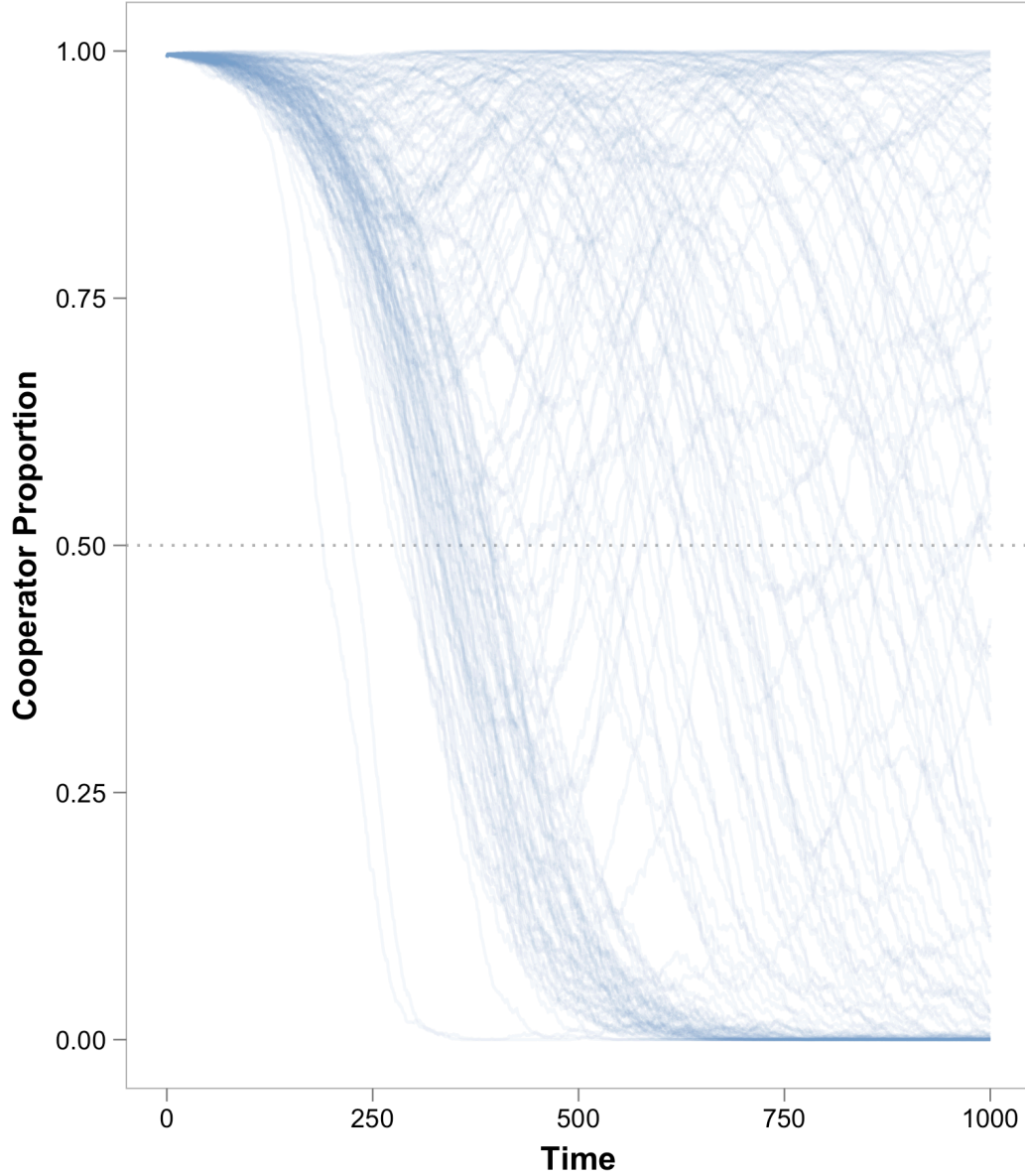


Figure S1: **Defector Invasion with Mutations.** The proportion of co-operators present in each replicate population is shown for the duration of simulations ( $T = 1000$ ). When mutations occur both at the adaptive loci and the cooperation locus ( $\mu_a = \mu_c = 0.00005$ ), cooperation remains dominant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

Table 1: Model parameters and their value

Parameter	Description	Base Value
$L$	Number of adaptive loci	5
$c$	Fitness cost of cooperation	0.1
$A$	Number of alleles	6
$\delta$	Fitness benefit, adaptation to external environment	0.3
$\epsilon$	Fitness benefit, adaptation to constructed environment	0.00015
$z$	Baseline fitness	1
$S_{min}$	Minimum subpopulation size	800
$S_{max}$	Maximum subpopulation size	2000
$\mu_a$	Mutation rate (adaptation)	$10^{-5}$
$\mu_c$	Mutation rate (cooperation)	$10^{-5}$
$N^2$	Number of patches	625
$m$	Migration rate	0.05
$p_0$	Initial cooperator proportion	0.5
$\sigma$	Survival rate at population initialization	$10^{-5}$
$T$	Number of simulation cycles	3000
$d$	Subpopulation dilution factor	0.1

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