

TODO title

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Abstract

Through their interactions, their activities, and even their mere presence, organisms change the environment for themselves and others. This “niche construction” process becomes particularly interesting when it creates evolutionary feedback, whereby selective pressures are altered in response to environmental change. Here we consider how niche construction influences the evolution of cooperation, which has been a long-standing challenge to evolutionary theory. We simulate populations of individuals that cooperatively produce a public good that permits increased growth in a stressful environment and investigate how local- and global-scale niche construction affects the ability of these populations to resist invasion by non-producing cheats. We find that niche construction profoundly impacts the evolution of cooperation by creating new opportunities for adaptation. Cooperators are able to escape subversion by cheats as long as niche construction clears these paths of adaptation. This work provides a crucial step towards understanding how evolution occurs in complex environments like those found in nature.

20 Introduction

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

30 Several factors can defer this potential *tragedy of the commons* (Hamilton,
31 1964; Hardin, 1968; Nowak, 2006; West *et al.*, 2007b). For example, coopera-
32 tors must benefit more from the cooperative act than others. This can occur
33 when cooperators are clustered together in spatially-structured populations
34 (Fletcher and Doebeli, 2009; Nadell *et al.*, 2010; Kuzdzal-Fick *et al.*, 2011) or
35 when cooperators use communication (Brown and Johnstone, 2001; Darch *et*
36 *al.*, 2012) or other cues (Sinervo *et al.*, 2006; Gardner and West, 2010; Veelders
37 *et al.*, 2010) to cooperate conditionally with kin. Interestingly, cooperation can
38 also be bolstered by genetic linkage with self-benefitting traits (Foster *et al.*,
39 2004; Dandekar *et al.*, 2012; Asfahl *et al.*, 2015), setting the stage for an “adap-
40 tive race” in which cooperators and defectors vie for the first highly-beneficial
41 non-social adaptation (Waite and Shou, 2012; Morgan *et al.*, 2012).

42 Hankshaw and Kerr (2015) recently showed that in spatially-structured popu-

43 lations, cooperators can gain a substantial leg up on defectors in an adaptive
44 race when the cooperative behavior increases local population density, thus in-
45 creasing the likelihood of acquiring beneficial non-social mutations. By hitch-
46 hiking along with these adaptations, the cooperative trait can rapidly rise in
47 abundance. Nevertheless, this advantage is fleeting. As soon as the opportu-
48 nities for adaptation are exhausted, cooperators are once again at a disadvan-
49 tage against defectors, particularly those that arise from within via mutations
50 that disable cooperation. However, Hankshaw and Kerr (2015) demonstrated
51 that cooperation can be maintained indefinitely when frequent environmental
52 changes produce a steady stream of non-social adaptive opportunities. Al-
53 though organisms typically find themselves in dynamic environments, change
54 might not occur at a rate that provides sufficient adaptive opportunities to
55 ensure long-term cooperator survival.

56 In this work, we examine whether the changes in selection that arise as organ-
57 isms modify their environment can create opportunities that allow cooperators
58 to be maintained by hitchhiking. We expand upon the model presented in Han-
59 kshaw and Kerr (2015), by allowing populations to alter their local environ-
60 ment based on the the presence of different non-social adaptations. Frequency-
61 dependent selection on these adaptations creates an eco-evolutionary feedback
62 that increasingly favors the adaptations present in each population. We first
63 examine how the intensity of these feedbacks affects the hitchhiking process.
64 Because the production of public goods increases population density, popula-
65 tions containing cooperators will exert a greater influence on their environment.
66 As a result, these environments will be more quickly brought to states where

67 fitness is higher.

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

79 Finally, we demonstrate how *negative* niche construction, where populations
80 change their environment in ways that reduce fitness, can further support
81 cooperation. Even though the niche construction process creates selective
82 feedbacks, we would expect the magnitude of these feedbacks to decrease as
83 populations evolve. Once individuals can no longer gain adaptations that
84 compensate for the costs of cooperation, they are then outcompeted by non-
85 cooperators. However if populations construct their environment in a way
86 which decreases fitness, cooperation can still hitchhike when this change also
87 creates the opportunity to gain compensatory adaptations.

88 **Materials and Methods**

89 We build upon the model described in Hankshaw and Kerr (2015), in which co-
90 operators and defectors compete and evolve in a spatially-structured metapop-
91 ulation of populations. Each of these populations grows to carrying capacity,
92 mutates, and migrates to neighboring patches. During this process, popula-
93 tions adapt to their local environments. In our extended model, we allow
94 these individuals to modify their local environment, and these modifications
95 feed back to affect selection.

96 **Model Description**

97 Our simulated environment consists of N^2 patches arranged as an $N \times N$
98 lattice (see [Table 1](#) for model parameters and their values), where each patch
99 supports a population of zero or more individuals. Each individual in the
100 population has a genotype, which is an ordered list of $L + 1$ integers (loci).
101 The first L loci are *adaptive loci*, and are each occupied by a 0 or an integer
102 from the set $A = \{1, \dots, a_{max}\}$, where a_{max} is the number of potential alleles.
103 At each of these loci, the presence of a non-zero allele represents an adaptation
104 to the environment that confers fitness benefit δ . A binary allele at locus $L + 1$
105 determines whether or not that individual is a cooperator. Individuals with
106 allelic state 1 at this locus are cooperators, carrying a cost c , while individuals
107 with allelic state 0 are defectors. When $\delta \geq c$, an adapted cooperator recoups
108 the cost of cooperation.

109 Organisms also influence their environment, which can feed back to influence

110 selection. We model this as a form of frequency dependent selection. Specif-
 111 ically, the selective value of adaptive allele a at locus l increases with the
 112 number of individuals in the population that have allele $a - 1$ (modulo a_{max})
 113 at locus $l - 1$ (modulo L). The slope of this increase is ϵ , which specifies the
 114 intensity of niche construction. As a consequence of this form of frequency
 115 dependence, genotypes with sequentially-increasing allelic states will tend to
 116 evolve. Because mutations are random, as described later, each population
 117 will evolve sequences that start with different allelic states. These different
 118 sequences represent the unique niches constructed by populations. Under this
 119 model, the fitness of an individual with genotype g in population P is:

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

120 where z is a baseline fitness, $a_{g,l}$ represents the allelic state of genotype g at
 121 locus l , L is the number of adaptive loci, and c is the cost of the cooperative
 122 allele. The function I_A indicates whether allelic state y is in A (i.e., it is non-
 123 zero). The function $n(a_{g,l})$ gives the number of individuals in the population
 124 with allelic state at the previous locus equal to one less than that at the focal
 125 locus $a_{g,l}$, or:

$$n(a_{g,l}) = \sum_{i \in P} I_{a_{g,l}}(1 + a_{\gamma(i), \{1+(l-2 \pmod L)\} \pmod{a_{max}}}) \quad (2)$$

126 Here, $I_x(y)$ indicates whether the allelic state y matches allelic state x (1) or
 127 not (0), and $\gamma(j)$ is the genotype of individual j . Note that the selective value

128 of an allele at the first locus is affected by the allelic state at locus L .
 129 Cooperators produce a public good that is equally accessible to all members
 130 of the population. This public good increases the carrying capacity at that
 131 patch, allowing the population to reach greater density. This benefit increases
 132 linearly with the proportion of cooperators. Thus, if p is the proportion of
 133 cooperators in a population at the beginning of a growth cycle, then that
 134 population reaches the following size during the growth phase:

$$S(p) = S_{min} + p(S_{max} - S_{min}) \quad (3)$$

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

$$\pi_i = \frac{W_{\gamma(i)}}{\sum_{j \in P} W_{\gamma(j)}} \quad (4)$$

141 Here, $\gamma(i)$ is the genotype of individual i , and $W_{\gamma(i)}$ is its fitness (see Equation
 142 1). π_i therefore reflects that an individual's ability to persist is proportional
 143 to its fitness relative to others'.

144 For simplicity, we apply mutations after population growth. Mutations occur
 145 independently at each locus and cause the allelic state to change. Mutations

146 occur at each adaptive locus at rate μ_a , and cause a new allelic state to be
 147 chosen at random from the set $\{0\} \cup A$. At the binary cooperation locus,
 148 mutations occur at rate μ_c . These mutations flip the allelic state, causing
 149 cooperators to become defectors and vice versa. Therefore, the probability
 150 that genotype g mutates into genotype g' is given by:

$$\tau_{g \rightarrow g'} = \mu_a^{H_a(g, g')} (1 - \mu_a)^{\{L - H_a(g, g')\}} \mu_c^{H_c(g, g')} (1 - \mu_c)^{\{1 - H_c(g, g')\}} \quad (5)$$

151 where $H_a(g, g')$ and $H_c(g, g')$ are the Hamming distances between genotypes g
 152 and g' at the cooperation locus and adaptive loci, respectively. The Hamming
 153 distance is the number of loci at which allelic states differ (Hamming, 1950).
 154 Because we define no inherent relationship among alleles, each of the $a_{max} + 1$
 155 allelic states is equally likely to arise via mutation at a given locus.

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

161 Metapopulations are initiated in a state that follows an environmental change.
 162 First, populations are seeded at all patches with cooperator proportion p_0 and
 163 grown to density $S(p_0)$. An environmental challenge is then introduced, which
 164 subjects the population to a bottleneck. For each individual, the probability
 165 of survival is μ_t , which represents the likelihood that a mutation occurs that
 166 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 ($\forall i \in P, l \in \{1, \dots, L\} : a_{\gamma(i),l} = 0$). Following initialization, simulations are run for T cycles, where each discrete cycle consists of growth, mutation, and migration. At the end of each cycle, populations are thinned to allow for growth in the next cycle. The individuals that remain are chosen by binomial sampling, where each individual persists with probability d , regardless of allelic state.

Source Code and Software Environment

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

Results

Niche construction prolongs cooperator survival

“cooperator presence” greater in NC runs than with no-NC (GNH)

Negative Niche construction helps

Runs with wraparound persist indefinitely, while those without do not.

184 **NC Prevents/Limits Defector invasion**

185 **NC Enables Cooperator Spread by “exporting” environ-**
186 **ment**

187 **Discussion**

- 188 • summary of results
- 189 • similarities/differences from previous work
 - 190 – Schwilk and Kerr (2002)
 - 191 – 10.1073/pnas.0812644106
- 192 • public goods as niche construction
- 193 • future QS or other environmental sensing
- 194 • Facultative cooperation
 - 195 – Rodrigues (2012)
 - 196 – Dumas and Kümmerli (2010)
 - 197 – Kümmerli and Brown (2010)
 - 198 – Darch/Diggle
 - 199 – QS?
 - 200 – Environmental Sensing? - (Koestler and Waters, 2014, Bernier et
 - 201 al. (2011))
- 202 • Negative Niche construction as a strategy? - would those that create this
- 203 constant pressure (L=5, A=6) do better than those that do not (L=5,

204 A=5)?

205 Niche construction and selective feedbacks Niche construction and other social
206 interactions

207 **Public Goods**

208 TODO: merge this in with the “Cooperative Niche Construction” section
209 **TEST**

210 By their very nature, public goods benefit populations by making their environ-
211 ment more hospitable. For example, bacteria produce extracellular products
212 that find soluble iron (Griffin *et al.*, 2004), digest large proteins (Diggle *et al.*,
213 2007; Darch *et al.*, 2012), and reduce the risk of predation (Cosson *et al.*, 2002),
214 among many others (West *et al.*, 2007a). While many studies have explored
215 how the environment affects the evolution of cooperative behaviors, relatively
216 few have examined how those behaviors affect the environment and the result-
217 ing change in evolutionary trajectories. Lehmann (2007) demonstrated analyti-
218 cally that when niche construction act benefits future generations, cooperation
219 is favored due to reduced competition among kin. When rate-benefitting and
220 yield-benefitting altruistic acts co-evolve, Van Dyken and Wade (2012) showed
221 that “reciprocal niche construction”, where the selective feedbacks produced
222 by one act benefitted the other, can lead to increased selection for both traits.
223 While these studies have focused on the niche constructing effects of cooper-
224 ation, we instead focus our attention here on how niche construction enables
225 cooperators to escape defection by hitchhiking along with non-social traits.

226 Primacy/Recency

227 In our model, alterations to the environment were immediately echoed by
228 changes in selection. However, decoupling the timescales on which these pro-
229 cesses occur can have substantial effects (Laland *et al.*, 1996). By integrating
230 past allelic states into Equation 1, we can begin to explore how the cumulative
231 effects of niche construction affect the creation of non-social adaptive oppor-
232 tunities and the benefits that they offer cooperation. Here, how these past
233 allelic states are integrated will play an important role. For example, when
234 the effects of earlier generations are weighted more heavily, the influence of
235 migration may be diminished. While this will reduce the threat of emigration
236 by defectors, cooperator populations will also be less effective at exporting
237 their niche.

238 Cooperative Niche Construction

239 While our focus for this work has been on the eco-evolutionary feedbacks cre-
240 ated by non-social traits, it would also be interesting to explore how this system
241 is affected by the timescale at which carrying capacity at a given patch is in-
242 creased by public goods. In natural settings, a multitude of factors including
243 protein durability (Brown, 2007; Kümmerli and Brown, 2010), diffusion (Al-
244 lison, 2005; Driscoll and Pepper, 2010), and resource availability (Zhang and
245 Rainey, 2013; Ghoul *et al.*, 2014) influence both the rate and the degree to
246 which public goods alter the environment (and thereby selection). Lehmann
247 (2007) demonstrated that a cooperative, niche constructing behavior can be fa-

vored 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 remain competitive (Kümmerli and Brown, 2010).
TODO: wrap up. Facultative cooperation requires sensing.

Host-Symbiont

In many instances of cooperation, the environment is itself a biological entity, which can produce additional evolutionary feedbacks. As the host population changes, so too will selection on their symbiont populations. Here, evolutionary outcomes depend greatly on the degree of shared interest between the host and symbiont. For example, the cooperative production of virulence factors by the human pathogen *P. aeruginosa* in lung infections is harmful to those with cystic fibrosis (Harrison, 2007). Conversely, cooperative light production by *A. 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.

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- 270 • TODO: Organizers?
- 271 • TODO: lab comments

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280 **Figures**

281 **Figure 1**

282 **Figure 1A**

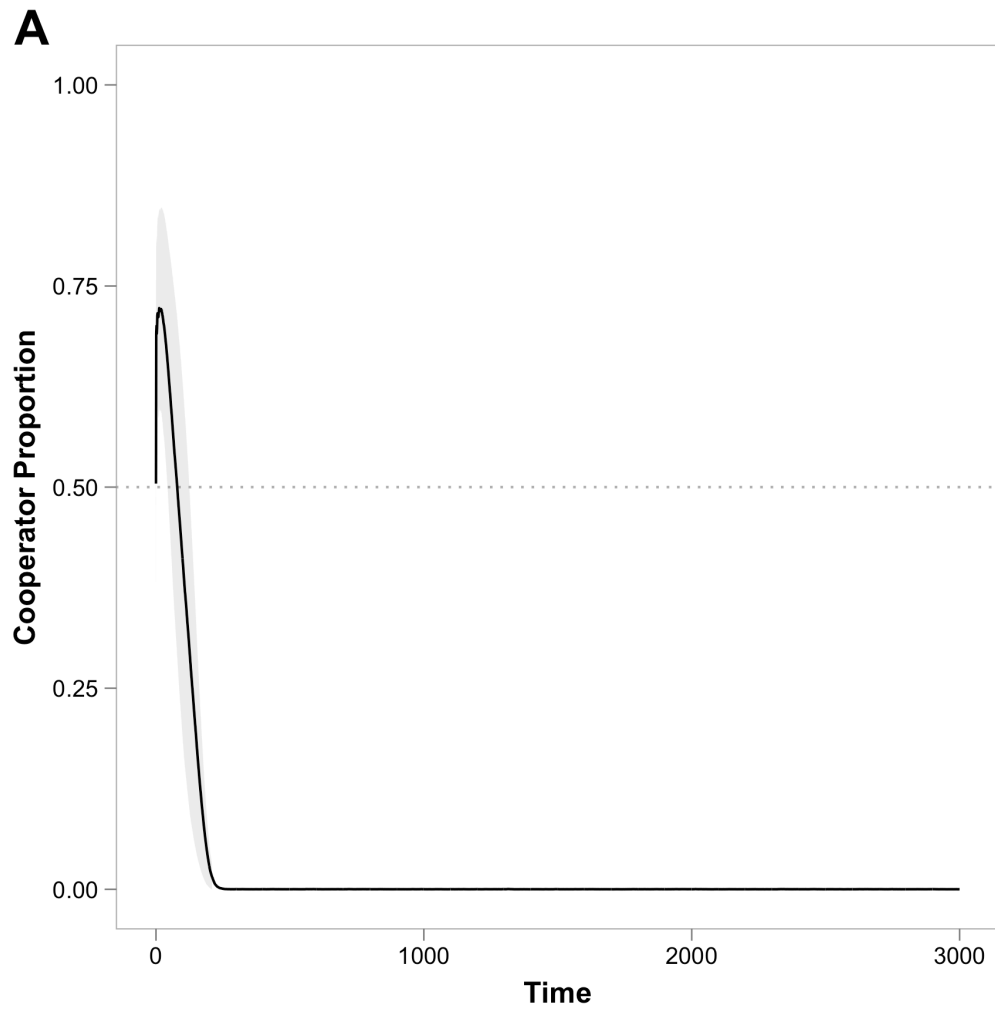


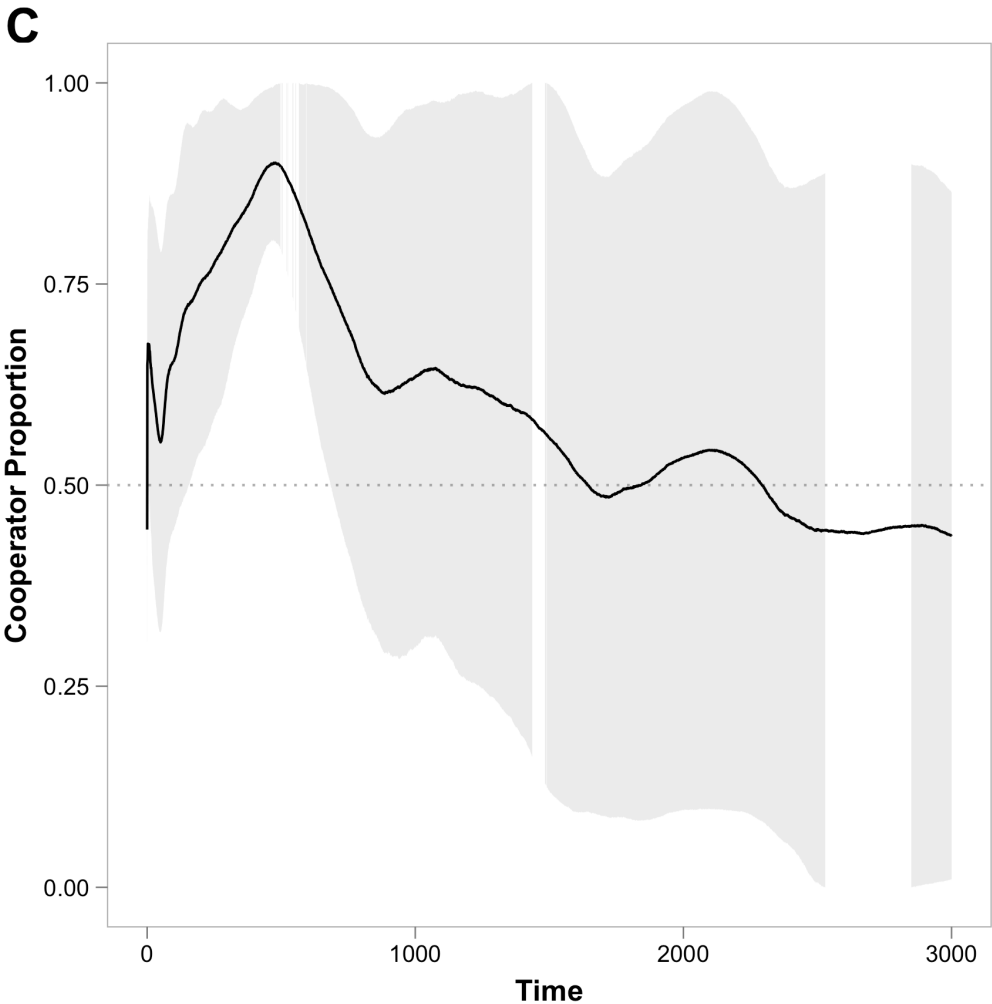
Figure 1: Proportion of cooperators over time when there are no opportunities for non-social adaptation

283 **Figure 1B**

284 Proportion of cooperators over time with non-social adaptation

285 **Figure 1C**

286 Proportion of cooperators over time with non-social adaptation and niche con-



287 struction

288 {#fig:fig1c}

289 **Figure 2**

290 Plot showing integral for baseline values, double adaptive benefit (no NC,
291 epsilon=0), no negative NC (L=5, A=5), Extreme negative niche construction
292 (L=1, A=6)

293 **Figure 3**

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

295 **Figure 4**

296 Cooperators invade from single population

297 **Figure 5**

298 Defectors are kept at bay

299 **Figure 6**

300 **Figure 6A - Effect of Migration Rate (m)**

301 **Figure 6B - Effect of Public Good Benefit (Smax-Smin)**

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_c	Mutation rate (cooperation)	10^{-5}
μ_a	Mutation rate (adaptation)	10^{-5}
m	Migration rate	0.05
p_0	Initial cooperator proportion	0.5
μ_t	Mutation rate (tolerance to new stress)	10^{-5}
T	Number of simulation cycles	1000
d	Population dilution factor	0.1

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