

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 pop-

43 ulations, cooperators gain a substantial leg up on defectors in an adaptive
44 race when the cooperative behavior increases local population density, thus
45 increasing the likelihood of acquiring beneficial non-social mutations. Never-
46 theless, this advantage is fleeting. As soon as the opportunities for adaptation
47 are exhausted, cooperators are once again at a disadvantage against defectors.
48 However, cooperation can be maintained indefinitely when frequent environ-
49 mental changes produce a stream of non-social adaptive opportunities (**If this**
50 **isn't included in Hankshaw paper, remove this sentence and re-write**
51 **next**). Although natural organisms typically find themselves in changing en-
52 vironments, cooperators may not be able to rely on the the environment to
53 provide sufficient adaptive opportunities for their long-term survival.

54 Here, we extend the model presented in Hankshaw and Kerr (2015) to address
55 whether the selective feedbacks generated by niche construction can act as a
56 source of adaptive opportunities that enables cooperators to persist. In the
57 model, cooperators produce a public good that increases the local carrying
58 capacity for their population. As in Hankshaw and Kerr (2015), populations
59 can also acquire non-social adaptations, which present an opportunity for co-
60 operation to hitchhike along. In our extended model, populations alter their
61 local environments based on the presence of these different non-social adap-
62 tations. As a result, selection for non-social alleles is altered, creating an
63 eco-evolutionary feedback. This has several potential benefits for cooperators.
64 First, because populations of cooperators are larger, they are more likely to
65 gain mutations that are beneficial in the changing environment. Similarly,
66 this difference in size means that larger cooperator populations “export” their

67 niche at a higher rate than defectors. Finally, because each population con-
68 structs a unique niche, the threat of immigrant defectors may be diminished
69 by maladaptation to a cooperator population’s niche.

70 Many instances of cooperatively-produced public goods benefit populations
71 by making the environment more hospitable. For example, bacteria produce
72 a wide variety of extracellular products such as iron-scavenging siderophores
73 (Griffin *et al.*, 2004), proteases for digesting protein sources (Diggle *et al.*,
74 2007; Darch *et al.*, 2012), and many more (West *et al.*, 2007a). While many
75 studies have explored how the environment affects the evolution of these behav-
76 iors, relatively few have examined how the behaviors affect the environment
77 or how that alters evolutionary trajectories. Lehmann (2007) demonstrated
78 analytically that when niche construction via a cooperative act benefits fu-
79 ture generations, cooperation is favored due to reduced competition among
80 kin. When rate-benefitting and yield-benefitting altruistic acts co-evolve, Van
81 Dyken and Wade (2012) showed that “reciprocal niche construction”, where
82 the feedbacks produced by one act benefitted the other, can lead to increased
83 selection for both traits. Finally, in a model of fire-prone ecosystems, Schwilk
84 and Kerr (2002) observed an increase in flammability when that altruistic trait
85 provided a clearing for offspring to grow and acquire adaptations to changing
86 environments.

87 Niche construction and cooperation * (Platt and Bever, 2009) * What’s unique
88 here—hitchhiking aspect

89 Here we explore how selective feedbacks from non-social phenotypes affect

90 TODO.

91 Niche construction and selective feedbacks

92 Niche construction and other social interactions

93 **Materials and Methods**

94 We develop a computational model to observe the evolution of public goods
95 cooperation in a spatially-structured metapopulation of populations. As de-
96 scribed below, populations grow to carrying capacity, mutate, and migrate
97 to neighboring patches. During this process, populations adapt to their lo-
98 cal environments. The environments are, in turn, modified by the presence
99 of these adapted individuals, allowing each population to construct a unique
100 niche along its evolutionary trajectory. Model parameters and their values are
101 listed in [Table 1](#).

102 **Individuals and Fitness**

103 Each individual has a genotype of length $L + 1$. A binary allele at the first
104 locus determines whether or not the individual is a cooperator, which carries
105 cost c . Note that we refer to all individuals with allelic state 0 at this locus as
106 a “defector”, regardless of origin. The remaining L loci are *stress loci*, and are
107 each occupied by a 0 or an integer from the set $A = \{1, \dots, a_{max}\}$, where a_{max}
108 is the number of possible alleles. These alleles represent adaptations to the
109 environment, and the number of loci determines the number of possible adap-

110 tations. All non-zero alleles carry fitness benefit δ . Organisms also influence
 111 their environment, which can feed back to influence selection. We model this
 112 as a form of frequency dependent selection. Specifically, the selective value
 113 of stress allele a at locus i increases with the proportion of the population
 114 that has allele $a - 1$ (modulo a_{max}) at locus $i - 1$. The slope of this increase
 115 is ϵ (which gauges the intensity of niche construction). As a consequence of
 116 this form of frequency dependence, genotypes with sequentially increasing al-
 117 lelic states will tend to evolve. Because mutations are random, as described
 118 below, each population will evolve sequences that start with different allelic
 119 states. These different sequences represent the unique niches constructed by
 120 populations. Under this model, the fitness of an individual with genotype g
 121 is:

$$W_g = z + a_{g,1}c + \delta \sum_{l=2}^{L+1} I_A(a_{g,l}) + \epsilon \sum_{h=1}^N I_{a_{h,1}}(a_{g,1}) + \epsilon \sum_{l=2}^L n(a_{g,l})$$

122 where $a_{g,l}$ represents the allelic state of genotype g at locus l , z is a baseline
 123 fitness, L is the number of stress loci, N is the population size at that patch,
 124 and c is the cost of the cooperative allele. $I_x(y)$ indicates whether the allelic
 125 state y matches allelic state x (1) or not (0). $n(a_{g,l})$ is the number of individuals
 126 in the population with allelic state at the previous locus equal to one less than
 127 that at the focal locus $a_{g,l}$, or:

$$n(a_{g,l}) = \sum_{h=1}^N I_{a_{g,l}}(1 + a_{h,l-1}(\text{mod } a_{max}))$$

128 **Population Growth**

129 If p is the proportion of cooperators in a population at the beginning of a
 130 growth cycle, then that population reaches the following size during the growth
 131 phase:

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

132 Therefore, a population composed entirely of defectors reaches size S_{min} , while
 133 one composed entirely of cooperators reaches size S_{max} (with $S_{max} \geq S_{min}$).
 134 The function $S(p)$ gauges the benefit of public good production, as popula-
 135 tion size increases linearly with the proportion of cooperators. During growth,
 136 competition occurs. Consider an arbitrary genotype g . Let n_g be the num-
 137 ber of individuals with genotype g , and let W_g be the fitness of genotype g
 138 (see equation [1]). The composition of genotypes after population growth is
 139 multinomial with parameters $S(p)$ and $\{\pi_1, \pi_2, \dots, \pi_{|G|}\}$, where:

$$\pi_g = \frac{n_g W_g}{\sum_{i=1}^G n_i W_i}$$

140 Thus, π_g is the probability that an individual in the population after growth
 141 has genotype g (such that $\sum \pi_g = 1$). G represents the set of all $(a_{max} + 1)^L$
 142 genotypes.

143 Mutation

144 For simplicity, we apply mutation after population growth. These mutations
 145 occur independently at each locus and result in an allelic state change. At the
 146 binary cooperation locus, mutations flip the allelic state at rate μ_c , causing
 147 cooperators to become defectors and vice versa. Mutations at a stress locus
 148 cause a new allelic state to be chosen at random from the set $\{0\} \cup A$. These
 149 mutation occur at each stress locus at rate μ_s . Therefore, the probability that
 150 genotype g mutates into genotype g' is given by:

$$\tau_{g \rightarrow g'} = \mu_s^{H_s(g, g')} (1 - \mu_s)^{\{L - H_s(g, g')\}} \mu_c^{H_p(g, g')} (1 - \mu_c)^{\{1 - H_p(g, g')\}}$$

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

156 Migration and Metapopulation Structure

157 The metapopulation consists of N^2 patches arranged in a $N \times N$ lattice. After
 158 mutation, individuals emigrate to an adjacent patch with probability m . This
 159 adjacent patch is randomly chosen with uniform probability from the source
 160 patch's Moore neighborhood, which is composed of the nearest 8 patches on the
 161 lattice. Because the metapopulation lattice has boundaries, patches located

162 on an edge have smaller neighborhoods.

163 Initialization and Simulation

164 Metapopulations are initiated in a state that follows the onset of an environ-
165 mental stress. First, populations are seeded at each patch with cooperator
166 proportion p_0 and grown to density $S(p_0)$. Stress is then introduced by sub-
167 jecting the population to a bottleneck. The number of survivors with each
168 genotype g is sampled from a binomial distribution, where the number of tri-
169 als is n_g . The probability of success is μ_t , which represents the likelihood that
170 a mutation occurs that enables survival. Because individuals have not yet
171 adapted to this new stress, the allelic state of each genotype is set to 0 at each
172 stress locus ($\forall g \in G, l \in \{2, \dots, L + 1\} : a_{g,l} = 0$). Following initialization,
173 simulations are run for T cycles, where each cycle consists of growth, mutation,
174 and migration. After migration, populations are thinned to allow for growth in
175 the next cycle. The number of survivors for each genotype g is sampled from
176 a binomial distribution, where the number of trials is n_g and the probability
177 of success is d .

178 Source Code and Software Environment

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

183 Results

184 results...

185 Discussion

- 186 • summary of results
- 187 • future primacy/recency
 - 188 – Laland et al. (1996)
 - 189 – Lehmann (2007)
- 190 • public goods as niche construction
- 191 • Host symbiont - many instances of cooperation occur among pathogens.
- 192 • future QS or other environmental sensing
- 193 • Facultative cooperation
 - 194 – Rodrigues (2012)
 - 195 – Dumas and Kümmerli (2010)
 - 196 – Kümmerli and Brown (2010)
 - 197 – Darch/Diggle
 - 198 – QS?
 - 199 – Environmental Sensing? # Acknowledgments
- 200 • PRFB
- 201 • BEACON
- 202 • Google

- Organizers?

204 **Figures**

Table 1: Model parameters and their value.

Parameter	Description	Base Value
L	Number of Stress Loci	3
a_{max}	Number of alleles	4
δ	Fitness benefit, nonzero alleles	0.5
ϵ	Fitness benefit, sequential alleles	TODO
c	Production Cost	0.1
z	Baseline fitness	1
S_{min}	Minimum Population Size	800
S_{max}	Maximum Population Size	2000
μ_s	Mutation Rate (Stress)	10^{-5}
μ_c	Mutation Rate (Cooperation)	10^{-5}
μ_t	Mutation Rate (Tolerance to New Stress)	10^{-5}
m	Migration Rate	0.05
d	Population Dilution Factor	0.1
N^2	Number of Metapopulation Sites	625
p_0	Initial Cooperator Proportion	0.5
T	Number of Simulation Cycles	TODO

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