

# TODO title

## TODO

### **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 future  
79 generations, cooperation is favored due to reduced competition among kin.

80 Niche construction and cooperation \* (Van Dyken and Wade, 2012) \*  
81 (Platt and Bever, 2009) \* (Schwilk and Kerr, 2002) \* What’s unique  
82 here—hitchhiking aspect

83 Here we explore how selective feedbacks from non-social phenotypes affect  
84 TODO.

85 Niche construction and selective feedbacks

86 Niche construction and other social interactions

## 87 **Materials and Methods**

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

## 96 **Individuals and Fitness**

97 Each individual has a genotype of length  $L + 1$ . A binary allele at the first  
98 locus determines whether or not the individual is a cooperator, which carries  
99 cost  $c$ . Note that we refer to all individuals with allelic state 0 at this locus as  
100 a “defector”, regardless of origin. The remaining  $L$  loci are *stress loci*, and are  
101 each occupied by a 0 or an integer from the set  $A = \{1, \dots, a_{max}\}$ , where  $a_{max}$   
102 is the number of possible alleles. These alleles represent adaptations to the  
103 environment, and the number of loci determines the number of possible adap-  
104 tations. All non-zero alleles carry fitness benefit  $\delta$ . Organisms also influence  
105 their environment, which can feed back to influence selection. We model this  
106 as a form of frequency dependent selection. Specifically, the selective value  
107 of stress allele  $a$  at locus  $i$  increases with the proportion of the population  
108 that has allele  $a - 1$  (modulo  $a_{max}$ ) at locus  $i - 1$ . The slope of this increase

109 is  $\epsilon$  (which gauges the intensity of niche construction). As a consequence of  
 110 this form of frequency dependence, genotypes with sequentially increasing al-  
 111 lelic states will tend to evolve. Because mutations are random, as described  
 112 below, each population will evolve sequences that start with different allelic  
 113 states. These different sequences represent the unique niches constructed by  
 114 populations. Under this model, the fitness of an individual with genotype  $g$   
 115 is:

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

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

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

## 122 Population Growth

123 If  $p$  is the proportion of cooperators in a population at the beginning of a  
 124 growth cycle, then that population reaches the following size during the growth  
 125 phase:

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

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

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

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

## Mutation

For simplicity, we apply mutation after population growth. These mutations occur independently at each locus and result in an allelic state change. At the binary cooperation locus, mutations flip the allelic state at rate  $\mu_c$ , causing cooperators to become defectors and vice versa. Mutations at a stress locus cause a new allelic state to be chosen at random from the set  $\{0\} \cup A$ . These

143 mutation occur at each stress locus at rate  $\mu_s$ . Therefore, the probability that  
 144 genotype  $g$  mutates into genotype  $g'$  is given by:

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

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

## 150 Migration and Metapopulation Structure

151 The metapopulation consists of  $N^2$  patches arranged in a  $N \times N$  lattice. After  
 152 mutation, individuals emigrate to an adjacent patch with probability  $m$ . This  
 153 adjacent patch is randomly chosen with uniform probability from the source  
 154 patch's Moore neighborhood, which is composed of the nearest 8 patches on the  
 155 lattice. Because the metapopulation lattice has boundaries, patches located  
 156 on an edge have smaller neighborhoods.

## 157 Initialization and Simulation

158 Metapopulations are initiated in a state that follows the onset of an environ-  
 159 mental stress. First, populations are seeded at each patch with cooperator  
 160 proportion  $p_0$  and grown to density  $S(p_0)$ . Stress is then introduced by sub-



jecting the population to a bottleneck. The number of survivors with each genotype  $g$  is sampled from a binomial distribution, where the number of trials is  $n_g$ . The probability of success is  $\mu_t$ , which represents the likelihood that a mutation occurs that enables survival. Because individuals have not yet adapted to this new stress, the allelic state of each genotype is set to 0 at each stress locus ( $\forall g \in G, l \in \{2, \dots, L + 1\} : a_{g,l} = 0$ ). Following initialization, simulations are run for  $T$  cycles, where each cycle consists of growth, mutation, and migration. After migration, populations are thinned to allow for growth in the next cycle. The number of survivors for each genotype  $g$  is sampled from a binomial distribution, where the number of trials is  $n_g$  and the probability of success is  $d$ .

## 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), NetworkX 1.9.1 (Hagberg *et al.*, 2008). Data analyses were performed with R 3.1.3 (R Core Team, 2015).

## Results

results...

## 179 Discussion

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

198 **Figures**

Table 1: Model parameters and their value.

Parameter	Description	Base Value
$L$	Number of Stress Loci	3
$a_{max}$	Number of alleles	4
$\delta$	Fitness benefit, nonzero alleles	0.5
$\epsilon$	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
$\mu_s$	Mutation Rate (Stress)	$10^{-5}$
$\mu_c$	Mutation Rate (Cooperation)	$10^{-5}$
$\mu_t$	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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