

# 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 Using a model of public goods production, Hankshaw and Kerr (2015) recently

43 showed that in spatially-structured populations, cooperators gain a substan-  
44 tial leg up on defectors in an adaptive race when the cooperative behavior  
45 increases local population density, thus increasing the likelihood of acquiring  
46 beneficial non-social mutations. By hitchhiking along with these adaptations,  
47 cooperators can rapidly become more abundant. Nevertheless, this advantage  
48 is fleeting. As soon as the opportunities for adaptation are exhausted, coopera-  
49 tors are once again at a disadvantage against defectors. However, cooperation  
50 can be maintained indefinitely when frequent periodic environmental changes  
51 produce a stream of non-social adaptive opportunities. Although natural or-  
52 ganisms typically find themselves in changing environments, cooperators may  
53 not be able to rely on the the environment to provide sufficient adaptive op-  
54 portunities for their long-term survival.

55 Here, we extend the model presented in Hankshaw and Kerr (2015) to ex-  
56 plore whether niche construction feedbacks can act as a continual source of  
57 adaptive opportunity that allows cooperation to persist. Populations alter  
58 their local environment based on the the presence of different non-social adap-  
59 tations. Frequency-dependent selection on these adaptations creates an eco-  
60 evolutionary feedback, which increasingly favors the adaptations present in  
61 each population. This has several potential benefits for cooperators. First,  
62 because populations of cooperators are larger, they are more likely to gain  
63 mutations that enable them to track their changing environment. Similarly,  
64 this difference in size means that larger cooperator populations “export” their  
65 niche at a higher rate than defectors. Finally, because each population con-  
66 structs a unique niche, the threat of immigrant defectors may be diminished

67 by maladaptation to a cooperator population’s niche.

68 By their very nature, public goods benefit populations by making their environ-  
69 ment more hospitable. For example, bacteria produce extracellular products  
70 that find soluble iron (Griffin *et al.*, 2004), digest large proteins (Diggle *et al.*,  
71 2007; Darch *et al.*, 2012), and reduce the risk of predation (Cosson *et al.*, 2002),  
72 among many others (West *et al.*, 2007a). While many studies have explored  
73 how the environment affects the evolution of cooperative behaviors, relatively  
74 few have examined how those behaviors affect the environment and the result-  
75 ing change in evolutionary trajectories. Lehmann (2007) demonstrated analyti-  
76 cally that when niche construction act benefits future generations, cooperation  
77 is favored due to reduced competition among kin. When rate-benefitting and  
78 yield-benefitting altruistic acts co-evolve, Van Dyken and Wade (2012) showed  
79 that “reciprocal niche construction”, where the feedbacks produced by one act  
80 benefitted the other, can lead to increased selection for both traits. While  
81 these studies have focused on the niche constructing effects of cooperation, we  
82 instead focus our attention here on how niche construction enables cooperators  
83 to escape defection by hitchhiking along with non-social traits.

## 84 **Materials and Methods**

85 We develop a computational model to observe the evolution of public goods  
86 cooperation in a spatially-structured metapopulation of populations. As de-  
87 scribed below, populations grow to carrying capacity, mutate, and migrate  
88 to neighboring patches. During this process, populations adapt to their lo-

cal environments. The environments are, in turn, modified by the presence of these adapted individuals, allowing each population to construct a unique niche along its evolutionary trajectory. Model parameters and their values are listed in [Table 1](#).

## Individuals and Fitness

Each individual has a genotype of length  $L + 1$ . A binary allele at the first locus determines whether or not the individual is a cooperator, which carries cost  $c$ . Note that we refer to all individuals with allelic state 0 at this locus as a “defector”, regardless of origin. The remaining  $L$  loci are *stress loci*, and are each occupied by a 0 or an integer from the set  $A = \{1, \dots, a_{max}\}$ , where  $a_{max}$  is the number of possible alleles. These alleles represent adaptations to the environment, and the number of loci determines the number of possible adaptations. All non-zero alleles carry fitness benefit  $\delta$ . Organisms also influence their environment, which can feed back to influence selection. We model this as a form of frequency dependent selection. Specifically, the selective value of stress allele  $a$  at locus  $i$  increases with the proportion of the population that has allele  $a - 1$  (modulo  $a_{max}$ ) at locus  $i - 1$ . The slope of this increase is  $\epsilon$  (which gauges the intensity of niche construction). As a consequence of this form of frequency dependence, genotypes with sequentially increasing allelic states will tend to evolve. Because mutations are random, as described below, each population will evolve sequences that start with different allelic states. These different sequences represent the unique niches constructed by

111 populations. Under this model, the fitness of an individual with genotype  $g$   
 112 is:

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

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

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

## 119 Population Growth

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

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

123 Therefore, a population composed entirely of defectors reaches size  $S_{\min}$ , while  
 124 one composed entirely of cooperators reaches size  $S_{\max}$  (with  $S_{\max} \geq S_{\min}$ ).

125 The function  $S(p)$  gauges the benefit of public good production, as popula-  
 126 tion size increases linearly with the proportion of cooperators. During growth,  
 127 competition occurs. Consider an arbitrary genotype  $g$ . Let  $n_g$  be the num-  
 128 ber of individuals with genotype  $g$ , and let  $W_g$  be the fitness of genotype  $g$   
 129 (see equation [1]). The composition of genotypes after population growth is  
 130 multinomial with parameters  $S(p)$  and  $\{\pi_1, \pi_2, \dots, \pi_{|G|}\}$ , where:

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

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

## 134 Mutation

135 For simplicity, we apply mutation after population growth. These mutations  
 136 occur independently at each locus and result in an allelic state change. At the  
 137 binary cooperation locus, mutations flip the allelic state at rate  $\mu_c$ , causing  
 138 cooperators to become defectors and vice versa. Mutations at a stress locus  
 139 cause a new allelic state to be chosen at random from the set  $\{0\} \cup A$ . These  
 140 mutation occur at each stress locus at rate  $\mu_s$ . Therefore, the probability that  
 141 genotype  $g$  mutates into genotype  $g'$  is given by:

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

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

## 147 **Migration and Metapopulation Structure**

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

## 154 **Initialization and Simulation**

155 Metapopulations are initiated in a state that follows the onset of an environ-  
156 mental stress. First, populations are seeded at each patch with cooperator  
157 proportion  $p_0$  and grown to density  $S(p_0)$ . Stress is then introduced by sub-  
158 jecting the population to a bottleneck. The number of survivors with each  
159 genotype  $g$  is sampled from a binomial distribution, where the number of tri-  
160 als is  $n_g$ . The probability of success is  $\mu_t$ , which represents the likelihood that  
161 a mutation occurs that enables survival. Because individuals have not yet  
162 adapted to this new stress, the allelic state of each genotype is set to 0 at each



163 stress locus ( $\forall g \in G, l \in \{2, \dots, L + 1\} : a_{g,l} = 0$ ). Following initialization,  
 164 simulations are run for  $T$  cycles, where each cycle consists of growth, mutation,  
 165 and migration. After migration, populations are thinned to allow for growth in  
 166 the next cycle. The number of survivors for each genotype  $g$  is sampled from  
 167 a binomial distribution, where the number of trials is  $n_g$  and the probability  
 168 of success is  $d$ .

## 169 Source Code and Software Environment

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

## 174 Results

175 results...

## 176 Discussion

- 177 • summary of results
- 178 • similarities/differences from previous work
  - 179 – Schwilk and Kerr (2002)

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

193 Niche construction and selective feedbacks

194 Niche construction and other social interactions # Acknowledgments

- 195 • PRFB
- 196 • BEACON
- 197 • Google
- 198 • Organizers?

199 **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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