

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.*, 2007). 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 explore
55 whether the selective feedbacks generated by niche construction can act as a
56 source of adaptive opportunities that enables cooperators to persist. As pop-
57 ulations adapt to their environment, they alter selection of non-social alleles.
58 This has several potential benefits for cooperators. First, because populations
59 of cooperators are larger, they are more likely to gain mutations that are bene-
60 ficial in the changing environment. Similarly, this difference in size means that
61 larger cooperator populations “export” their niche at a higher rate than defec-
62 tors. Finally, because each population constructs a unique niche, the threat
63 of immigrant defectors may be diminished by maladaptation to a cooperator
64 population’s niche.

65 Niche construction and selective feedbacks

66 Niche construction and cooperation

67 Niche construction and other social interactions

68 **Materials and Methods**

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

77 **Individuals and Fitness**

78 Each individual has a genotype of length $L + 1$. A binary allele at the first
79 locus determines whether or not the individual is a cooperator, which carries
80 cost c . Note that we refer to all individuals with allelic state 0 at this locus as
81 a “defector”, regardless of origin. The remaining L loci are *stress loci*, and are
82 each occupied by a 0 or an integer from the set $A = \{1, \dots, a_{max}\}$, where a_{max}
83 is the number of possible alleles. These alleles represent adaptations to the
84 environment, and the number of loci determines the number of possible adap-
85 tations. All non-zero alleles carry fitness benefit δ . Organisms also influence

86 their environment, which can feed back to influence selection. We model this
 87 as a form of frequency dependent selection. Specifically, the selective value
 88 of stress allele a at locus i increases with the proportion of the population
 89 that has allele $a - 1$ (modulo a_{max}) at locus $i - 1$. The slope of this increase
 90 is ϵ (which gauges the intensity of niche construction). As a consequence of
 91 this form of frequency dependence, genotypes with sequentially increasing al-
 92 lelic states will tend to evolve. Because mutations are random, as described
 93 below, each population will evolve sequences that start with different allelic
 94 states. These different sequences represent the unique niches constructed by
 95 populations. Under this model, the fitness of an individual with genotype g
 96 is:

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

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

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

103 **Population Growth**

104 If p is the proportion of cooperators in a population at the beginning of a
 105 growth cycle, then that population reaches the following size during the growth
 106 phase:

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

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

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

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

118 **Mutation**

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

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

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

131 **Migration and Metapopulation Structure**

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

137 on an edge have smaller neighborhoods.

138 Initialization and Simulation

139 Metapopulations are initiated in a state that follows the onset of an environ-
140 mental stress. First, populations are seeded at each patch with cooperator
141 proportion p_0 and grown to density $S(p_0)$. Stress is then introduced by sub-
142 jecting the population to a bottleneck. The number of survivors with each
143 genotype g is sampled from a binomial distribution, where the number of tri-
144 als is n_g . The probability of success is μ_t , which represents the likelihood that
145 a mutation occurs that enables survival. Because individuals have not yet
146 adapted to this new stress, the allelic state of each genotype is set to 0 at each
147 stress locus ($\forall g \in G, l \in \{2, \dots, L + 1\} : a_{g,l} = 0$). Following initialization,
148 simulations are run for T cycles, where each cycle consists of growth, mutation,
149 and migration. After migration, populations are thinned to allow for growth in
150 the next cycle. The number of survivors for each genotype g is sampled from
151 a binomial distribution, where the number of trials is n_g and the probability
152 of success is d .

153 Source Code and Software Environment

154 The simulation software and configurations for the experiments reported are
155 available online (Us, 2015). Simulations used Python 3.4.0, NumPy 1.9.1,
156 Pandas 0.15.2 (McKinney, 2010), NetworkX 1.9.1 (Hagberg *et al.*, 2008). Data
157 analyses were performed with R 3.1.2 (R Core Team, 2014).

158 Results

159 results...

160 Discussion

- 161 • summary of results
- 162 • future primacy/recency
- 163 • public goods as niche construction
- 164 • Host symbiont - many instances of cooperation occur among pathogens.
- 165 • future QS or other environmental sensing # Acknowledgments
- 166 • PRFB
- 167 • BEACON
- 168 • Google
- 169 • Organizers?

170 **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 Producer Proportion	0.5
T	Number of Simulation Cycles	TODO

References

- Asfahl, K.L., Walsh, J., Gilbert, K. and Schuster, M. 2015. Non-social adaptation defers a tragedy of the commons in *Pseudomonas aeruginosa* quorum sensing. *The ISME Journal*, doi: [10.1038/ismej.2014.259](https://doi.org/10.1038/ismej.2014.259).
- Brown, S.P. and Johnstone, R.A. 2001. Cooperation in the dark: Signalling and collective action in quorum-sensing bacteria. *Proceedings of the Royal Society of London B: Biological Sciences*, **268**: 961–965.
- Dandekar, A.A., Chugani, S. and Greenberg, E.P. 2012. Bacterial quorum sensing and metabolic incentives to cooperate. *Science*, **338**: 264–266.
- Darch, S.E., West, S.A., Winzer, K. and Diggle, S.P. 2012. Density-dependent fitness benefits in quorum-sensing bacterial populations. *Proceedings of the National Academy of Sciences*, **109**: 8259–8263.
- Fletcher, J.A. and Doebeli, M. 2009. A simple and general explanation for the evolution of altruism. *Proceedings of the Royal Society B: Biological Sciences*, **276**: 13–19.
- Foster, K., Shaulsky, G., Strassmann, J., Queller, D. and Thompson, C. 2004. Pleiotropy as a mechanism to stabilize cooperation. *Nature*, **431**: 693–696.
- Nature Publishing Group.
- Gardner, A. and West, S.A. 2010. Greenbeards. *Evolution*, **64**: 25–38.
- Hagberg, A.A., Schult, D.A. and Swart, P.J. 2008. Exploring network structure, dynamics, and function using NetworkX. In: *Proceedings of the 7th Python in science conference (SciPy2008)*, pp. 11–15.

194 Hamilton, W.D. 1964. The genetical evolution of social behaviour I & II.
195 *Journal of Theoretical Biology*, **7**: 1–52.

196 Hankshaw, S. and Kerr, B. 2015. Hitching a ride on the evolutionary super-
197 highway. *Unknown Journal*, **0**: 0–0.

198 Hardin, G. 1968. The tragedy of the commons. *Science*, **162**: 1243–1248.

199 Kuzdzal-Fick, J.J., Fox, S.A., Strassmann, J.E. and Queller, D.C. 2011. High
200 relatedness is necessary and sufficient to maintain multicellularity in Dic-
201 tyostelium. *Science*, **334**: 1548–1551.

202 McKinney, W. 2010. Data structures for statistical computing in python. In:
203 *Proceedings of the 9th python in science conference* (S. van der Walt and J.
204 Millman, eds), pp. 51–56.

205 Morgan, A.D., Quigley, B.J.Z., Brown, S.P. and Buckling, A. 2012. Selection
206 on non-social traits limits the invasion of social cheats. *Ecology Letters*, **15**:
207 841–846.

208 Nadell, C.D., Foster, K.R. and Xavier, J.B. 2010. Emergence of spatial struc-
209 ture in cell groups and the evolution of cooperation. *PLoS Computational*
210 *Biology*, **6**: e1000716.

211 Nowak, M.A. 2006. Five rules for the evolution of cooperation. *Science*, **314**:
212 1560–1563.

213 R Core Team. 2014. *R: A language and environment for statistical computing*.
214 Vienna, Austria: R Foundation for Statistical Computing.

215 Sinervo, B., Chaine, A., Clobert, J., Calsbeek, R., Hazard, L. and Lancaster,

- 216 L.*et al.* 2006. Self-recognition, color signals, and cycles of greenbeard mutu-
217 alism and altruism. *Proceedings of the National Academy of Sciences*, **103**:
218 7372–7377.
- 219 Us. 2015. Name for data and code.
- 220 Veelders, M., Brückner, S., Ott, D., Unverzagt, C., Mösch, H.-U. and Essen,
221 L.-O. 2010. Structural basis of flocculin-mediated social behavior in yeast.
222 *Proceedings of the National Academy of Sciences*, **107**: 22511–22516.
- 223 Waite, A.J. and Shou, W. 2012. Adaptation to a new environment allows coop-
224 erators to purge cheaters stochastically. *Proceedings of the National Academy*
225 *of Sciences*, **109**: 19079–19086.
- 226 West, S.A., Griffin, A.S. and Gardner, A. 2007. Evolutionary explanations for
227 cooperation. *Current Biology*, **17**: R661–R672.