Evolution of Cooperation through Niche Construction Feedback

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

Several factors can defer this potential *tragedy of the commons*[1–4]. For example, cooperators must benefit more from the cooperative act than others. This can occur when cooperators are clustered together in spatially-structured populations[5–7] or when cooperators use communication[8,9] or other cues[10–12] to cooperate conditionally with kin. Interestingly, cooperation can also be bolstered by genetic linkage with self-benefitting traits[13–15], setting the stage for an "adaptive race" in which cooperators and defectors vie for the first highly-beneficial non-social adaptation[16,17]. We recently showed that cooperators can gain a substantial leg up on defectors in an adaptive race when the cooperative behavior increases local population density, thus increasing the likelihood of acquiring beneficial non-social mutations (in prep.). Nevertheless, this advantage is fleeting (Fig. 1A). As soon as the opportunities for adaptation are exhausted, cooperators are once again at a disadvantage against defectors. As shown in Fig. 1B, however, cooperation can be maintained indefinitely when frequent environmental changes produce a stream of non-social adaptive opportunities. Although natural organisms typically find themselves in changing environments, cooperators may not be able to rely on the the environment to provide sufficient adaptive opportunities for their long-term survival.

Previous studies on the evolution of cooperation have have typically neglected one potentially major determinant of evolutionary outcomes: environmental change brought about by the organisms themselves. Through their metabolism, their interactions with others, and even through their deaths, organisms constantly modify their environment. These changes can produce evolutionary feedback loops in which environmental change alters selection, which, in turn, alters phenotypes and their corresponding effects on the environment[18]. **This research will reveal how environmental change brought about by organisms, or *niche construction*, affects the evolution of cooperation.** First, we will explore how selective feedbacks influence evolution as populations construct their environment. We then widen our scope to include scenarios where the environment itself is biotic, such as when symbiont populations modify their host.

Because this research requires a level of control over both population and environment that would be difficult to attain even with well-characterized systems, we employ computational modeling for these initial studies. However, we expect that the results gained through this project will be instrumental in designing future microbial experiments. We first describe the model that will be developed and then detail how it will be used to study the effects of niche construction on the evolution of cooperation in two contexts.

Model Description In our proposed agent-based model, 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. The remaining L loci are *stress loci*, and are each occupied by a 0 or an integer from the set $A = \{1, \ldots, a_{max}\}$, 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 δ. 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 allele a at locus i increases with the proportion of the population that has allele $a - 1$ (modulo A) at locus $i - 1$. The slope of this increase is ϵ (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 populations.

We observe the evolutionary process in a metapopulation of N populations, which are initiated with non-adapted
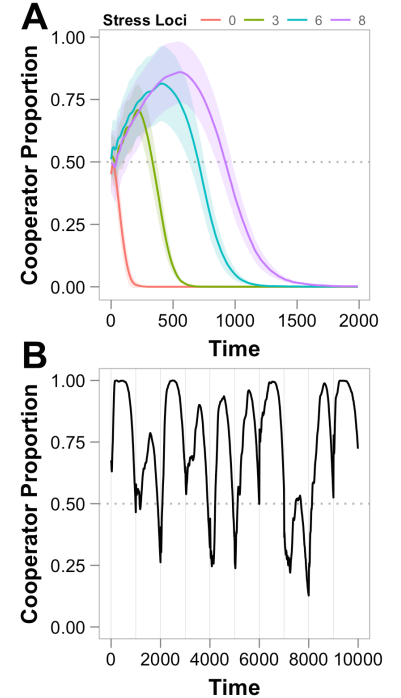

Fig. 1: (**A**) Through "genetic niche hiking", cooperators outrun defectors by association with non-social adaptations that compensate for the cost of cooperation. Colored lines represent different opportunities for adaptation (or "stress loci" in our model). Once defectors become equally adapted, however, they quickly drive cooperators to extinction. (**B**) When environmental change is frequent (here every 1,000 cycles), the continual potential for adaptation allows cooperators to persist indefinitely.

individuals and cooperator proportion p_0. Each population grows to capacity $S_{min} + p(S_{max} - S_{min})$, where p is the proportion of cooperators in that population. After growth, mutations alter the allelic state at stress loci and the cooperation locus with probabilities μ_s and μ_c, respectively. Individuals then migrate to a randomly chosen neighbor patch at rate m. Finally, populations are thinned to proportion d to accommodate the next cycle of growth.

Can Niche Construction Feedbacks Sustain the Evolution of Cooperation?

As illustrated in Fig. 2, we will first explore how selective feedbacks affect the evolution of cooperative public goods production. In our model, public goods enable populations to reach greater densities ($S_{max} > S_{min}$). This increase in growth provides larger populations with more mutational opportunities to gain non-social adaptations. Importantly, as populations adapt, they alter selection at their patch. Using our model (varying parameters ϵ and a_{max}), we will explore how the degree to which individuals construct their environments affects evolutionary trajectories and outcomes. Aside from providing adaptive opportunity, niche construction may diminish the threat of invasion by immigrant defectors (Fig. 3). We also hope to gain an understanding of how emigration allows populations to effectively export their environment, and whether this benefits cooperators, whose larger populations produce more migrants.

How do Selective Feedbacks affect Host-Symbiont Co-Evolution?

For our first aim, the state of the environment is implicit, depending entirely on the composition of the population. However, the environment is often itself a biological entity, which can produce additional evolutionary feedbacks. These feedbacks are certainly present in infections and the human microbiome, where bacterial behaviors greatly affect host fitness. 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. Conversely, cooperative light production by *A. fischeri* is vital for the survival of its host, the Hawaiian bobtail squid.

To address how feedbacks from niche construction affect social evolution in host-symbiont systems, we will extend our model to include selection and replication at the host level. Here, patches will be replaced by replicating hosts. Each host will have a genotype, and their fitness will depend both on this genotype and the genotypes in their symbiont populations. We can control this relationship by altering the symmetry of the fitness effects of a match between host and symbiont genotypes. If a match improves the fitness of both players simultaneously, the relationship is mutualistic. If a match improves fitness of the symbiont, but not the host, then the relationship is antagonistic (e.g., the symbiont is a parasite). By altering such features, we will be able to observe how host-symbiont co-evolution differs with *positive* and *negative niche construction*. Using this model, we can also explore how co-evolution differs when symbiont populations are transferred vertically or horizontally.

Summary

Using a model of public goods production, this project will explore how the selective feedbacks that result from niche construction affect the evolution of cooperative behaviors from both a population-level and a host-symbiont perspective. Both investigators are currently studying the relationship between ecology and evolution, and the results from this study will inform future microbial experiments in their labs. It was recently suggested that this niche construction perspective will be critical for improving our understanding of viral evolution[19] and evolution in co-infecting parasites[20]. We believe it may play the same role in understanding the evolution of cooperative behaviors.
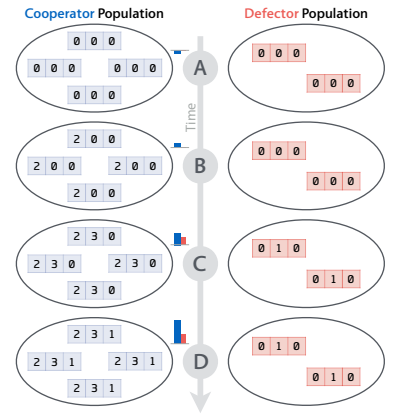

Fig. 2: Model Overview: For simplicity, we consider two clonal populations. (**A**) Because public good production is costly, the cooperator population has lower fitness relative to the defector population, as shown in the bar graph. However, these public goods enable the cooperator population to be larger. (**B**) As a result, the cooperator population acquires beneficial mutations more quickly, allowing cooperator fitness to surpasses that of the ancestral defector (bar graph baseline). (**C**) Selection favors alleles at adjacent loci that form sequences, offering a further boost to cooperators. Here, there 3 possible alleles, so allelic state 1 follows 3. (**D**) The cooperator patch now favors individuals with allelic state 2, 3, 1.
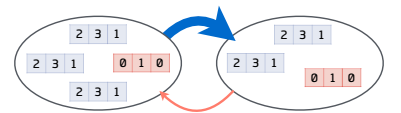

Fig. 3: Migration reveals two key effects of niche construction. First, when immigrating to the cooperator patch (left), defectors will be at a disadvantage against cooperators, which are more adapted to their environment (2, 3, 1). Second, the larger group of co-operators that emigrate to the defector population (right) will strongly affect selection at the defector patch, effectively "exporting" their niche.

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