

Shape matters in cooperation

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Why do organisms cooperate with each other? This seemingly simple question has motivated a staggering amount of theoretical and experimental research. When cooperating with others carries a direct fitness cost for the individual, natural selection should act against such behavior. However, cooperation is widespread across natural systems, from birds and bees to bacteria. Past research has identified many factors favoring or disfavoring the evolution of cooperation. For example, we know that properties of public good molecules (Misevic et al. 2012) affect the evolution of cooperation. Here we summarize the results and provide additional discussion about the implications of our recently published work on the importance a previously overlooked factor, the population shape (Misevic et al. 2015).

In the past, we have studied different aspects of cooperation using a well established *in silico* system, Aevol (Frénoy et al. 2013). In Aevol, digital organisms with double-stranded binary genomes and complex genetic architecture mutate, compete, and evolve over thousands of generations. The ancestral organism is not a cooperator, but populations may evolve to secrete different amounts of public good. The secretor pays a cost proportional to the amount of public good it produces, and all neighboring individuals benefit equally from the secreted molecules. The secreted molecules diffuse to neighboring cells and degrade over time. Generations are synchronous, with nine individuals in the classical Moore neighborhood competing to populate the next generation. For the purpose of the study on the population shape, we have also introduced two new, simpler systems, Aevol-lite and CAevol. Aevol-lite has all the properties and simulation mechanics of Aevol, but instead of binary strings and non-trivial genotype to phenotype to fitness mapping, each Aevol-lite individual is represented by a single number, a binary gene identifying whether it secretes a public good or not. CAevol is a further simplification, a system without public good, in which individuals with pure cooperate/defect strategies play a classical Prisoner's dilemma.

Aevol individuals live on a quadrilateral grid with periodic boundary. All the locations on the grid are always full. We studied two different population shapes, a bulky 100x100 torus (akin to a fat doughnut) or a slender 4x2500 one (akin to a slender bicycle tire). It is interesting to note that we noticed the effect by accident, while studying a different population property and inadvertently modifying the shape as well. We corrected the mistake in the code, but the result remained: more secretion evolved in bulky than in slender populations (Figure 1A). This evolutionary outcome was highly robust and

not affected by changes in any of the other cooperation parameters, such as cost and benefit of secretion, or the diffusion and degradation rates.

The result was not intuitive and did not lend itself to an obvious explanation. We expected slender populations to facilitate separation between secretor and non-secretors, leading to fewer interactions, thus selecting for cooperation. In order to explain the prevalence of cooperation in populations of different shape, we closely examined the dynamics of cooperating patches, sub-populations. Additionally, we decided to simplify our model system, moving from Aevol onto first Aevol-lite and finally CAevol. This allowed us to rule out system idiosyncrasies, or plain bugs in the code, and test the generality of the results. Indeed, bulky populations evolved more cooperation no matter what particular simulation system or mode of cooperation (public good v. Prisoners' dilemma) we used (Figure 1).

Studying cooperation in Aevol-lite and CAevol, where there are only two types of individuals, made it much easier to visualize the population over time. We suspected that populations are not clonal, consisting of identical individuals, but instead a diverse assembly of cooperators and non-cooperators in a dynamic equilibrium. Indeed, by plotting Aevol-Lite populations we saw exactly that: populations are a collection of expanding and shrinking patches of cooperators and non-cooperators, constantly taking over one another. And it is in the dynamics of these patches that we found the answer for the population shape effect.

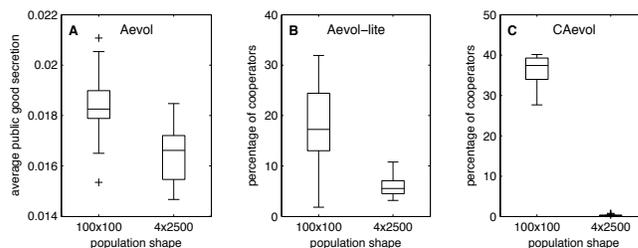


Figure 1. Average cooperation in bulky (100x100) and slender (4x2500) populations in (A) Aevol, (B) Aevol-lite, and (C) CAevol (from Misevic et al. 2015). Cooperation after 50,000 generations is quantified as the average amount of the public good secreted (A) or the percentage of cooperators (B and C). Line marks the median, the box edges are the 25th (q1) and the 75th (q3) percentile, the whiskers the most extreme data points still smaller than $q3 + w(q3 - q1)$ and larger than $q1 - w(q3 - q3)$, where $w = 1.5$.

In slender populations, the population shape constrained the expansion of cooperator patches. This can clearly be seen in Figure 2B, zooming in on a part of a single population over time, where after the first few generations, the cooperator patch (shown in gray) can increase only by eight individuals, four on the left and four on the right. In contrast, in the bulky population, such a patch can expand on all four sides, potentially by many more individuals in each generation. In Figure 2A, which focuses on a section of a bulky population over time, we exactly see such fast expansion. In both cases, the patches are eventually invaded from within by non-cooperators, which arise as mutants. However, before the cooperator patch gets completely overrun, it has a chance to expand to a greater size in bulky than in slender population. And that is precisely the reason for more cooperation in bulky than in slender populations: in all cases cooperator patches arise continuously, only to be taken over by no-cooperators, but in bulky populations they grow bigger, resulting in more cooperators present in the population at any given point in time. We quantified this difference by exhaustively simulating a single cooperator patch from its inception, through its ultimate demise. The results confirmed our verbal analysis of patch dynamics: no matter what the rate of mutation from cooperator to non-cooperators, over the entire lifetime of a patch, more cooperators existed in the bulky than slender population. This patch analysis was done in Aevol-lite, and was further confirmed in Aevol. By using Markov Cluster Algorithm we identified and measured the number and size of clusters formed by individuals based on the amount of public good secretion. We found that those clusters were smaller and more numerous in slender than in bulky populations, exactly in line with what we saw in Aevol-lite.

After hundreds of populations, millions of generations, and billions of individuals, we confirmed that shape does matter for cooperation and were able to explain the effect through the analysis of within-population patch dynamics. But what does our result mean for simulations of cooperation or for the study of evolution of cooperation in general? After all, population shape, as we defined it here, seems to be a rather peculiar parameter. However, it is not as obscure as it seems to be, since we can certainly think of cooperating populations living in complex 3D structures (soil, human lung), 2D plans (petri dish), or even effectively 1D (filamentous cyanobacteria). While we have not extended the simulation to different dimensions, our analysis indicates that the results would hold: more cooperation in populations of higher dimensions. Moreover, for some time there has been a push to consider different, more complex population structures, namely graphs (Ohtsuki et al. 2006). Our results make a strong argument that such treatment is useful and potentially necessary when considering the evolution and maintenance of cooperation, *in silico* or *in vivo*. The conclusions from the abstract bulky and slender populations directly extend to populations in which individuals have different number and strength of cooperative interactions, suggesting that graphs with higher connectivity will promote cooperation.

Finally, the heterogeneous and complex map of interactions between actors has already been studied in epidemiology (Salathé et al. 2010). A recent study using a microbial system established a connection between cooperation and information transfer (Dimitriu et al. 2014),

which allows us to make a connection between two fields here. In cooperation as well as epidemiology, all properties relating to the interactions between individuals, including the population shape and structure, should be considered because they may constrain and alter the maintenance and spread of (potentially infectious) cooperative trait.

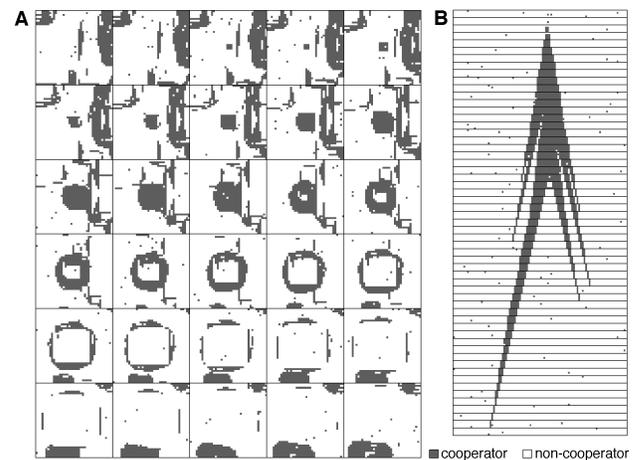


Figure 2. Example of a full lifecycle of a cooperator patch in (A) a bulky and (B) a slender Aevol-lite population (adapted from (Misevic et al. 2015)). Each square is either a cooperator (dark) or a non-cooperator (white cell). Each square in panel (A) and rectangle in panel (B) represents a snapshot of a population region from a single generation, with generations increasing from left to right, top to bottom.

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