Dispatch

Ecology: Tribal Warfare Maintains Microbial Diversity

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Summary

When two tribes of Myxococcus bacteria attack each other, the most numerous usually wins. Established colonies can therefore resist invaders by outnumbering them. This shows how positive frequency dependence can maintain diversity across spatially structured environments.

Main Text

The myxobacteria are ferocious predators of soil microbes [1]. They hunt in roving clonal tribes and overwhelm their quarry with a barrage of lethal compounds and lytic enzymes. Their victims' bodies burst open and the killers feast on the spilt innards of the dead [2]. When these predators run out of prey, they stop hunting and start building. Members of a tribe work together to construct a multicellular structure called a fruiting body, in which dispersive spores are made [2]. It is thought that the fruiting body helps some members escape as a group to re-establish the tribe in new hunting grounds, while others stay behind, making the ultimate sacrifice in aid of their comrades [3].

This remarkable cooperation between free-living, motile bacterial cells has made Myxococcus xanthus a model species for studying the evolution of social behaviour 3 and 4. But cooperation breaks down when genetically distinct tribes of M. xanthus from different areas are artificially mixed: the resulting chimeric fruiting bodies make fewer spores, and these spores carry an unequal proportion of one genotype over the other [4]. Just as natural selection favours alleles that benefit or assist other individuals carrying the same allele, as in clonal fruiting bodies, it also favours alleles that exploit or harm those lacking the same allele [5]. Spite is the evil twin of cooperation [6], and M. xanthus hunters are more than ready to use their formidable weapons against their own species. The antagonism between genetically diverged M. xanthus strains in mixed communities is often

extreme and decisive: when two tribes go to war, one can be completely obliterated by the other [4].

In natural soil, many different antagonistic tribes of M. xanthus co-exist just centimetres apart [2]. Given how readily one type annihilates another when they are mixed in the lab, how is this high diversity maintained? Why doesn't the most effective killer take over by force? A recent paper in Current Biology from Rendueles et al. [7] contains the results of careful experiments that address this interesting evolutionary problem.

Rendueles et al. [7] show that there is in fact no superior competitor overall, but that the fitnesses of M. xanthus genotypes depend on their initial frequencies. They first competed pairs of tribes containing equal numbers of fighters, to establish which tribe was fitter in one-to-one combat. Then they repeated the competitions but with unequal numbers, so that the tribe with the better fighters had far fewer of them. This time the fitnesses of the tribes were reversed, and the former losers emerged victorious from the experimental arena. In other words, the tribe with most fighters on the battlefield wins: regardless of the combat skills of an elite warrior, he or she can still be overwhelmed by a mob of less-able opponents. Thus, the competitive abilities of these bacteria are highly dependent upon their frequencies.

The idea that frequency-dependent selection affects diversity is well established [8]. The maintenance of diversity by negative frequency dependence is obvious: as one type becomes more frequent its fitness decreases until it matches that of other competitors, and thus multiple types may stably co-exist. A classical example of negative frequency dependence is Batesian mimicry [9], in which the morphologies of edible prey species evolve to resemble the warning patterns of toxic or unpalatable species, which predators avoid. Rare mimics will be protected despite being edible, but, as these edible mimics become common, predators are more likely to encounter them and thus learn those patterns are edible: thus, the fitness of the Batesian mimic decreases with its increasing frequency. This means an edible species may contain a diversity of rare Batesian mimics resembling different toxic model species [10]. But frequency dependence in M. xanthus is not negative but positive: here, fitness increases with increasing frequency. Theory predicts that positive frequency-dependent fitness should reduce diversity [8]. A related classical example is Mullerian mimicry [11], in which different unpalatable prey species are expected to evolve towards the same warning colours and patterns [8]. A rare morph is more likely to be killed, even though it is toxic, because predators have not learned to identify and avoid its pattern as effectively as a more common morph 12 and 13. Thus, variation in Mullerian mimicry patterns is expected to be unstable: rarer morphs are eliminated and all unpalatable prey species in a community converge on a single, best-recognised and best-protected phenotype [14]. Under positive frequency dependence, the most common phenotype reinforces its own abundance: even if pairs of M. xanthus genotypes were competed at frequencies at which their fitnesses were exactly equal, a small perturbation would be enough to give one or the other a tactical advantage from which it could make ever-increasing gains

until its enemy was eliminated. The system is thus bistable at frequencies of 1 and 0, eliminating diversity.

How, then, can positive frequency dependence maintain the great diversity of antagonistic M. xanthus tribes found in nature? As real-life warlords or armchair players of strategic wargames such as Risk™ will acknowledge, geography is key. Conquering new territories is harder than defending established territories because invaders tend to be outnumbered by local opponents and therefore tend to be defeated regardless of their prowess. Spatial structure therefore maintains global diversity by isolating antagonists geographically.

Rendueles et al. [7] demonstrate with a simple and elegant experiment how this principle applies to M. xanthus. A pair of strains was mixed in ratios of 99:1 and 1:99 and both mixtures were used to inoculate four patches, two each, on the surface on an agar plate, so that the initial overall frequency of strains on the plate was 50%. The cultures were then propagated for many generations and, although the majority strain outcompeted the minority strain within each patch, diversity on the plate was maintained because, although cells are motile, they were unable to invade neighbouring patches on the same plate, where they would be in the minority. Indeed, lines of 'no-man's-land' were visible between the patches. In contrast, when all four patches were inoculated with an equal mixture of the same two strains, one strain drove out the other across the whole plate, patches merged, and diversity was rapidly lost.

These experiments with antagonistic tribes of bacteria support recent theory showing that positive frequency dependence, by purging a local area of diversity, can actually help maintain variation across space, even when the initial spatial distribution of variation is a random mixture [15]. Positive frequency dependence should enable an initially random mixture of different types to self-organise into pure groups, separated by space and stabilised by within-group selection against invaders or immigrants [16], as observed in M. xanthus. This kind of spatial distribution of self-reinforcing local groups is exemplified most beautifully in butterflies. Whilst many unpalatable species within a local Mullerian mimicry ring converge on the same colour pattern, spatially separated mimicry rings evolve strikingly different patterns: the effect is so strong that different taxa within a local area resemble each other more than different geographic races of the same species do [14]. Neighbouring races are separated by narrow clines, comparable to Myxococcus inter-patch demarcation lines, in which strong selection limits migration between groups [13]. Clines can move rapidly and arbitrarily in space [17], indicating that the differences between neighbouring patches are not due to local adaptation to exogenous environmental factors, but are caused by endogenous selection, such as local positive frequency dependence [18]. Theory confirms the critical roles of spatial structure and positive frequency dependence in maintaining diversity among mimicry rings 19 and 20.

It is striking that positive frequency dependence produces such similar patterns of spatial variation in such different taxa as bacteria and butterflies, and it seems likely that these examples illustrate a general mechanism for maintaining diversity. Positive frequency dependence is probably common both within and between species: it occurs when fitness depends on signal recognition, when there are ecological priority effects favouring species arriving at a site first, or when Allee effects promote the growth of individuals in groups. Other destabilising evolutionary forces, such as selection against heterozygotes with intermediate phenotypes, or negative epistasis between mutations that are neutral alone but deleterious when combined, are also expected to produce similar patterns of diversity in space [17]. Elucidating how these processes scale across environments and species will be exciting areas of future research.

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