



## Experimental test of the conditions of maintenance of polymorphism under hard and soft selection

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Theoretical work, initiated by Levene (1953) [1] and Dempster (1955) [2], suggests that within a given environment, the way populations are regulated and contribute to the next generation is a key factor for the maintenance of local adaptation polymorphism. In this theoretical context, hard selection describes the situation where the genetic composition of each population affects its contribution to the next generation whereas soft selection describes the case where the contribution of each population is fixed, whatever its genetic composition. Soft selection is able to maintain polymorphism, whereas hard selection invariably leads to the fixation of one of the alleles. Although the specific conditions (e.g. of migration between populations or drift level) in which this prediction holds have been studied in details by theoreticians, experimental tests have mainly failed, usually leading to the conclusion that the allele frequency dynamics was driven by other mechanisms in the experimental systems and conditions used.

Gallet, Froissart and Ravigné [3] have set up a bacterial experimental system which allowed them to convincingly demonstrate that soft selection generates the conditions for polymorphism maintenance when hard selection does not,

everything else being equal. The key ingredients of their experimental system are (1) the possibility to accurately produce hard and soft selection regimes when daily transferring the populations and (2) the ability to establish artificial well-characterized reproducible trade-offs. To do so, they used two genotypes resisting each one to one antibiotic and combined, across habitats, low antibiotic doses and difference in medium productivity. The experimental approach contains two complementary parts: the first one is looking at changes in the frequencies of two genotypes, initially introduced at around 50% each, over a small number of generations (ca 40) in different environments and selection regimes (soft/hard) and the second one is convincingly showing polymorphism protection by establishing that in soft selection regimes, the lowest fitness genotype is not eliminated even when introduced at low frequency.

In this manuscript, a key point is the dialog between theoretical and experimental approaches. The experiments have been thought and designed to be as close as possible to the situations analysed in theoretical work. For example, the experimental polymorphism protection test (experiment 2) closely matches the equivalent analysis classically performed in theoretical approaches. This close fit between theory and experiment is clearly a strength of this study. This said, the experimental system allowing them to realise this close match also has some limitations. For example, changes in allele frequencies could only be monitored over a quite low number of generations because a longer time-scale would have allowed the contribution of de novo mutations and the likely emergence of a generalist genotype resisting to both antibiotics used to generate the local adaptation trade-offs. These limitations, as well as the actual significance of the experimental tests, are discussed in deep details in the manuscript.

## References

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