



## Digest: Untangling the influence of soft and hard selection in experimental populations - from environment to genomics

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## Cover page

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### Title

Digest: Untangling the influence of soft and hard selection in experimental populations – from environment to genomics

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### Abstract

Gallet et al. (2018) studied the effect of two selection regimes on the maintenance of polymorphism in experimental populations. They took two strains of *Escherichia coli*, each resistant to a different antibiotic, evolved them in culture conditions representing “soft” or “hard” selective regimes, and measured polymorphism levels for three to five transfers. Their results supported theoretical predictions that only “soft” selection maintains polymorphism, highlighting the importance of experimental studies to understand maintenance of variation in nature.

### Main text

Genetic diversity is fundamental for the long-term persistence of species (e.g. Kenchington et al. 2003). A population with a diverse gene pool is better equipped to face environmental change. However, understanding the processes behind maintaining genetic diversity is not necessarily straightforward, since these processes result from complex interactions between genotypes and environments.

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Generally, external conditions change throughout species' distribution ranges, creating niches or micro-habitats. This environmental heterogeneity can lead to different selective pressures acting at the genotype level of individuals, thus influencing genetic polymorphism in a population. This process, local adaptation, is fundamental for shaping genetic diversity in natural populations.

A heterogeneous habitat is expected to maintain genetic polymorphisms if the environment does not influence the ability of an individual to survive and reproduce (individual fitness): all individuals are equally likely to transmit their genotypes (Levene 1953). On the contrary, if micro-habitats contribute differently to individual fitness and reproductive success, some genotypes will be preferentially transmitted, and overall polymorphisms will decrease (Dempster 1955). These two types of selection regimes, "soft" selection (Levene 1953) and "hard" selection (Dempster 1955), have been studied for decades, and the theoretical background is well established. However, these predictions have yet to be empirically tested.

In this issue, Gallet et al. (2018) proposed to evaluate these predictions using two strains of *Escherichia coli*, each resistant to a different antibiotic, placed in three habitats with differing concentrations of antibiotic and sugar (as a proxy for carrying capacity), representing soft or hard selective regimes (Figure 1). They looked for changes in genotype frequency across transfers ( $\approx 10$  generations per transfer). The findings corroborated the theoretical predictions, where soft selection led to maintenance of polymorphism through the generations.

Gallet et al. (2018) studied a single point in the genome, i.e. a locus that confers resistance to a specific antibiotic. However, we can now study the whole genome of a species to identify genome-wide effects of soft and hard selection. If we extended Gallet et al.'s work and looked at loci physically close to the locus under selection, we would see that their frequencies also change, even if they do not impact overall fitness. This phenomenon is called selection at linked sites, and is known to shape levels of polymorphisms along the genome in different ways (Cutter and Payseur 2013). For example, if there is a selective advantage in the locus (e.g. being resistant to antibiotics), the loci nearby will also increase in frequency (termed "genetic hitchhiking" by Smith and Haigh 1974), with an observed reduction of polymorphism proportional to the strength of the selection force.

Gallet et al. (2018) proposed an elegant system to study the relative importance of each selection regime in genetic polymorphism. Given the importance of standing genetic variation as a reservoir for adaptation in a population, we suggest that similar studies should now focus on whole genomes. These studies would help us better understand and predict the amount of variation that will remain in populations as a consequence of linked selection under different selection regimes in heterogeneous habitats.

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### Figure caption

Scheme of the experimental study carried out by Gallet et al. (2018). Inside the grey circle on the left, the figure shows different bacteria (squares) colored according to the antibiotic they are resistant to (grey and black). Those bacteria are living in a heterogeneous environment composed of two different habitats (represented by the blue and orange circles), where one of the two antibiotics is present. Inside the blue box on the right, each of the lines represents a portion of DNA from the individuals of the population under study in the grey circle on the left. The colored triangles represent a polymorphism at that locus (i.e. genetic variation).

