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## Evolution of the (co)variances of quantitative traits in stage-structured populations.

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The speed of evolution of a phenotypic trait increases with the proportion of its variation that is transmitted to the next generation. The genetic variance for the trait is thus considered a good measure of evolutionary potential. The former can be computed from the joint distribution of the different gene copies that determine the trait value in the population. Evolutionary forces such as genetic drift, selection, recombination, mutation, and migration shape these distributions and thus the evolution of genetic variance. Many theoretical models for the evolution of quantitative traits, however, assume that genetic variance is constant through time and identical among different sub-groups of individuals in the population. Yet many populations are structured, with groups of individuals differing in sex, age, size, or developmental stage, which may differ in the amount of genetic variance they harbour for different traits. For instance, previous theory has shown that genetic variance for a trait subject to multiple selection episodes through the course of life decreases with age. Conversely, genetic variance for a trait expressed for the first time late in life is predicted to be higher than that for a trait first expressed when individuals are still young. However, we lack theoretical expectations for other types of structured populations, where individuals vary in the time they spend in different stages.

Here, we develop a set of general recursions to predict the change across time and stages of both the mean and the variance of a Gaussian-distributed trait affecting transitions between discrete stages in a structured population. We track the variation in the phenotypic trait value, the component of the trait that is transmitted to the next generation (the breeding value), and their covariation. We illustrate our predictions by parameterizing the model using demographic data on stage transitions for various plant species and exploring different scenarios of selection on the phenotypic trait. In particular, we show how genetic variance accumulates in some stages and is depleted in others, and how this affects the probability of escaping extinction while adapting to a new environment.

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