




Digest: Stable phenotypes, fluid genotypes: how stochasticity impacts network evolution and speciation

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A longstanding goal of evolutionary biology is to understand the relationship between genotype and phenotype. Schiffman and Ralph use mathematical modeling to theoretically examine how the genetic network underlying a conserved phenotype can change over time. They found that when phenotypically identical populations with different gene network configurations interbreed, hybrid incompatibilities can arise. These results suggest that neutral processes could play a major role in driving speciation.

The evolutionary process often results in morphological diversity, yet there are some instances where we observe morphological stasis throughout time or space. For example, geographically separated populations of African butterfly fish in the Niger and Congo basins remain morphologically similar despite diverging 57 million years ago (Lavoué et al. 2011). Furthermore, similar phenotypes in separate lineages may repeatedly arise in systems of replicated evolution, as seen in stickleback fish (Deagle et al. 2012). However, the “stable” nature of these phenotypes is not necessarily due to the continuous maintenance of underlying genetic mechanisms. Rather, the genetic mechanisms within a single lineage can be “fluid” over time, despite the phenotype remaining unchanged. These complex dynamics highlight the need to explore how genotypic variation modulates phenotypic variation.

In this article, Schiffman and Ralph (2021) combine linear systems theory with quantitative genetics to explore how pheno-

types can be maintained despite change in their underlying gene regulatory networks. The authors model a single quantitative trait under stabilizing selection (Fig. 1a). They quantify how structurally different gene networks with identical phenotypes and fitness (functional equivalency) can arise. They found that the number of unconstrained directions in genotype space increases at least with the square of the network’s size, indicating a large space of phenotypically identical networks. Species can traverse across these networks via genetic drift without incurring a fitness cost in a process called system drift. This can be visualized using a fitness landscape (Fig. 1b). Functionally equivalent networks form a “fitness ridge,” where populations can move along this ridge via drift while maintaining their phenotype.

Although additive models such as Fisher’s geometric model (Fisher 1930) similarly consider how a variety of genotypes can produce identical phenotypes, they lack a description of how different genetic combinations may not be equivalent when hybrid incompatibilities are considered. Here, the authors postulate that if two phenotypically identical but genotypically divergent populations hybridize (e.g., populations on either end of the ridge in Fig. 1b), it is likely that their offspring will harbor genetic incompatibilities (Fig. 1c). This is because the set

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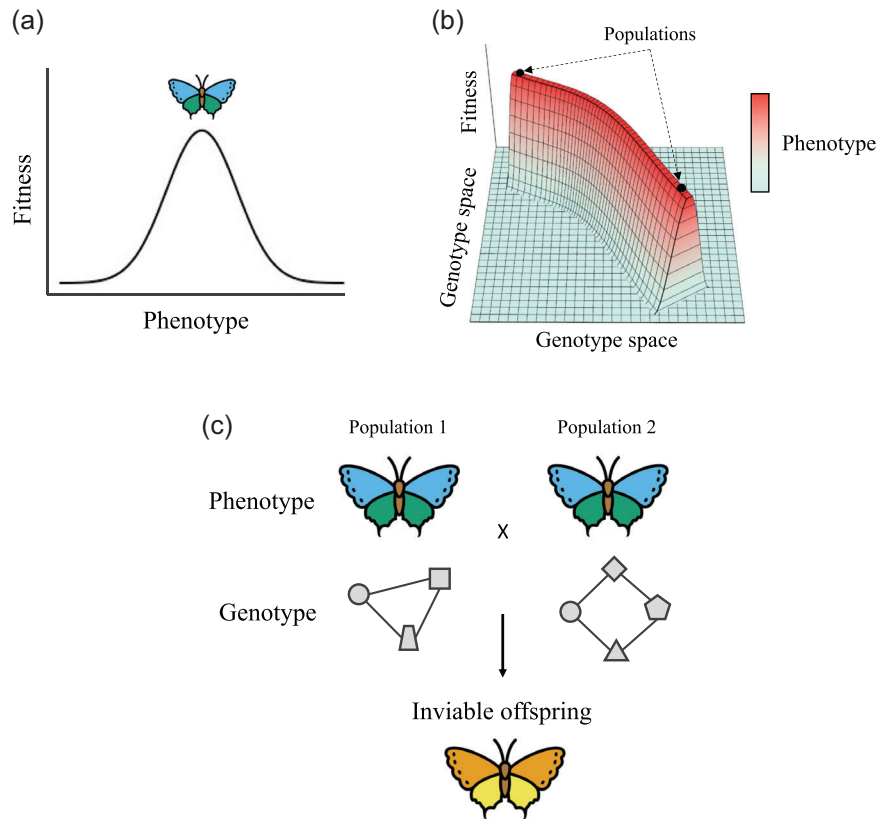


Figure 1. Relationship between the phenotype, genotype, and hybrid incompatibilities. Schematic diagram representing the model proposed by Schiffman and Ralph (2021). (a) A phenotype of a population, such as the color of a butterfly's wings, has an optimum value under stabilizing selection, at which fitness is maximized (given a particular set of environmental conditions). If multiple genotypic combinations can produce this optimal phenotype, we can represent the underlying genotypic fitness landscape as a ridge (b). Any point along the peak of the ridge produces the optimum trait value, and movement along this ridge can occur via genetic drift, where populations that reside in different positions along the ridge have the same phenotype, yet different genotypes. These genetic differences may be the result of changes to different genes from a single network, interconnected networks, or due to the use of entirely different networks. (c) If two populations (black dots in panel b) are on different locations of the genotypic ridge and hybridize together, even though each parent contains functionally equivalent phenotypes, the offspring will have a different phenotype and decreased fitness. This is because the independent movement of the two populations along the ridge is caused by a set of coordinated changes in the gene network of each population. When brought together, these changes are not compatible. The greater the distance between populations on the genotypic ridge, the more genetic incompatibilities they are likely to harbor.

of coordinated changes that have occurred in the gene network of each population are not compatible together. The speed at which this speciation occurs is a function of the effective population size and evolvability (i.e., the amount of heritable variation). In other words, the greater the distance between populations on the genotype-fitness ridge (Fig. 1b), the more genetic incompatibilities are expected to have arisen between the populations.

The relationship between a genotype and its phenotype is partly characterized by the number of genes that influence the phenotype in question. The likelihood of speciation from neutral processes is correlated with the number of genes influencing the trait under selection. In polygenic systems, where many alleles of small effect contribute to the phenotype, there is more potential for drift to change the configuration of the gene net-

work compared to systems where a single gene controls the phenotype (Barghi et al. 2020). Therefore, the appearance of genetic incompatibilities and the evolution of new species is more likely in polygenic systems. This is especially true when the population is small and has high genotypic variability.

In summary, this study shows how stochastic evolution of gene regulatory networks can lead to reproductive incompatibilities between separate lineages. Future work examining how genetic network modularity impacts robustness would be valuable to understand how the underlying architecture of genetic networks is under selection. Although the authors focus on a static fitness landscape, investigation of ecoevolutionary dynamics in a variable environment in which fitness optima are continually shifting will provide further insight into how neutral processes

impact evolution in natural systems. Such a dynamic environment might narrow the space of neutral networks, reducing the effect of system drift on speciation. Furthermore, extending the authors' work into multitrait space will give insights into how system drift can persist in the face of correlated selection (Lande and Arnold 1983) and pleiotropic constraints (Barghi et al. 2020). By synthesizing systems theory with quantitative and population genetics, future work can begin to understand the nature of adaptation through a strongly mechanistic and functional lens.

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