Title: System drift and speciation Running title: System drift and speciation

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September 14, 2021

Abstract

Even if a species' phenotype does not change over evolutionary time, the underlying mechanism may change, as distinct molecular pathways can realize identical phenotypes. Here we use linear system theory to explore the consequences of this idea, describing how a gene network underlying a conserved phenotype evolves, as the genetic drift of small changes to these molecular pathways cause a population to explore the set of mechanisms with identical phenotypes. To do this, we model an organism's internal state as a linear system of differential equations for which the environment provides input and the phenotype is the output, in which context there exists an exact characterization of the set of all mechanisms that give the same input-output relationship. This characterization implies that selectively neutral directions in genotype space should be common and that the evolutionary exploration of these distinct but equivalent mechanisms can lead to the reproductive incompatibility of independently evolving populations. This evolutionary exploration, or system drift, is expected to proceed at a rate proportional to the amount of intrapopulation genetic variation divided by the effective population size (N_e) . At biologically reasonable parameter values this could lead to substantial interpopulation incompatibility, and thus speciation, on a time scale of N_e generations. This model also naturally predicts Haldane's rule, thus providing a concrete explanation of why heterogametic hybrids tend to be disrupted more often than homogametes during the early stages of speciation.

Key words: Speciation, Models/Simulations, Genetic Drift

Acknowledgements

We would like to thank Sergey Nuzhdin, Stevan Arnold, Michael Turelli, Patrick Phillips, Erik Lundgren and Hossein Asgharian for valuable discussion. We would also like to thank Nick Barton, Sarah Signor, Todd Parsons, and Joachim Hermisson for very helpful comments on the manuscript. Work on this project was supported by funds from the Sloan Foundation and the NSF (under DBI-1262645) to PR.

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