Digest: Dispersal reduction drives rapid diversification in alpine grasshoppers

Jessica Fenker,^{1,2,3,*} Graham A. McCulloch,^{4,*} Mariana Mira Vasconcellos,⁵ Daiana Cardoso Silva,⁶ and Fabricius M. C. B. Domingos⁷

¹ Division of Ecology & Evolution, Research School of Biology, Australian National University, Canberra, Australia ² Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan, USA

³E-mail: jehfenker@gmail.com

⁴Department of Zoology, University of Otago, Dunedin, New Zealand

⁵Departamento de Ecologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

⁶Programa de Pós-Graduação em Ecologia e Conservação, Universidade do Estado de Mato Grosso, Nova Xavantina, Brazil ⁷Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil

Received April 27, 2021 Accepted June 14, 2021

Dispersal-associated traits —such as flight ability— influence how species move across the landscape, and can dramatically impact their distributions and patterns of genetic structure. Ortego et al. examine genomic data from two recently diverged alpine grasshopper lineages with distinct wing sizes to assess the demographic impacts of flight loss. The authors showed that flight loss may lead to asymmetric introgression during speciation, and can significantly increase rates of intraspecific diversification.

Dispersal is a key life-history component that can shape distribution patterns and influence diversification (Waters et al. 2020). Dispersal ability may vary significantly among species (even closely related ones), depending on a combination of factors, including environmental connectivity, biotic interactions (e.g., competition), and species-specific traits. Those dispersalassociated traits enable species' establishment and persistence in new areas by promoting gene flow across the landscape. Although such traits are apparently beneficial for population persistence over time, dispersal can be costly and maladaptive under many circumstances (Bonte et al. 2012).

Wings are the most obvious dispersal-associated trait in insects and are considered key to the evolutionary success of the class Insecta. However, this dispersal capacity has been lost repeatedly, within almost all insect orders (Roff 1990). Flight loss is particularly prominent in isolated habitats such as islands, mountain tops, and caves, as selection on morphological traits that favor survival in these environments can reduce dispersal potential (Roff 1990; Waters et al. 2020). Flight loss increases physical isolation among lineages and may increase the risk of extinction (Waters et al. 2020). Yet, broad-scale analyses suggest that it may also be a key driver of insect diversification (Salces-Castellano et al. 2021), though the demographic consequences of this evolutionary transition at the earliest stages of divergence remain poorly understood.

In this issue, Ortego et al. (2021) used genomic data to test the evolutionary impacts of wing size reduction on two sister lineages of alpine grasshoppers from Corsica, a mountainous Mediterranean island. *Chorthippus corsicus corsicus* and *C. c. pascuorum* have similar ecological preferences but distinct wing size phenotypes: *C. c. corsicus* is short-winged, while *C. c. pascuorum* is long-winged. The authors found no evidence of contemporary hybridization among sympatric populations of these two lineages, confirming they are distinct, independently evolving species, rather than a single polymorphic species. They also inferred a relatively recent speciation

^{*}Both authors contributed equally to this work.

[†]This article corresponds to Ortego, J., J. Gutiérrez-Rodríguez, and V. Noguerales. 2021. Demographic consequences of dispersal-related trait shift in two recently diverged taxa of montane grasshoppers. Evolution. https://doi.org/10.1111/evo.14205

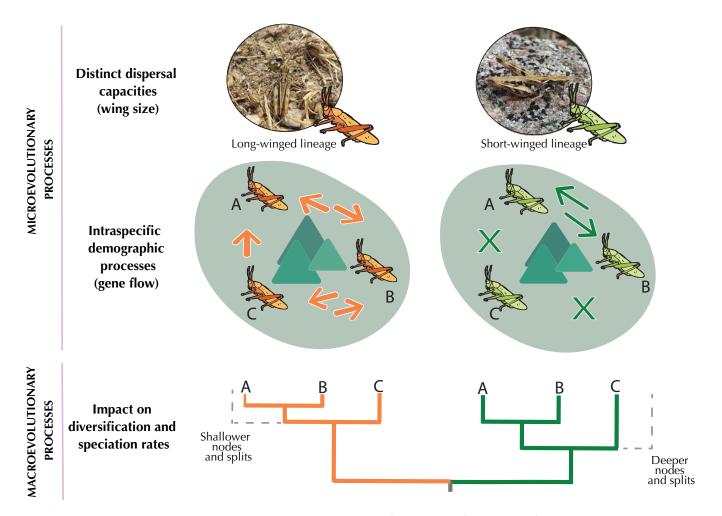


Figure 1. Dispersal-associated traits shape demographic processes and influence rates of insect diversification. Top panel: Short-winged Corsican grasshoppers have reduced dispersal abilities compared to their full-winged counterparts (Ortego et al. 2021). Middle panel: Dispersal capacity (as indicated by the thickness of the arrows) is reduced in the short-winged lineage compared to the long-winged lineage, leading to reduced levels of intraspecific gene flow. Bottom panel: Lower levels of intraspecific gene flow in the short-winged lineage increases diversification, which may ultimately result in higher speciation rates. Photos: Joaquín Ortego

event (less than 1.5 million years ago), with gene flow continuing between these two lineages until the late Pleistocene (ca. 30,000 years ago).

Interestingly, gene flow after speciation was asymmetric, occurring primarily from the more dispersive long-winged species to the short-winged species. The extent of introgression among these lineages following their initial divergence is somewhat surprising, as habitat isolation is often considered one of the key drivers of flight loss (Roff 1990). Despite this repeated introgression among lineages, the gene (or genes) conferring flight ability were not introgressed back into (or expressed) in the short-winged lineage. These results may suggest a strong selection against full-winged individuals across the distribution of the short-winged lineage, though further investigation is required to uncover the selective pressures driving flight loss in these environments. Ortego et al. (2021) also identified significantly deeper divergences among populations of the short-winged lineage compared to populations of the long-winged lineage, with almost no contemporary migration detected among the short-winged populations. Their results reflect the differences in dispersal ability of the lineages, with less dispersive organisms often showing marked genetic structure, reduced gene flow, and increased diversification rates (Harvey et al. 2019). By focusing on an evolutionarily young system, the authors were thus able to demonstrate that flight loss can drive rapid diversification in recently evolved species, even in the face of introgression from a flighted lineage.

In summary, Ortego et al. (2021) clearly demonstrated that shifts in dispersal-associated traits can directly influence geographic structuring and intraspecific diversification in a topographically complex habitat. Increased rate of intraspecific diversification in the short-winged lineages may ultimately lead to higher rates of speciation and interspecific diversification. Ortego et al. (2021) thus illustrate the links between dispersal traits and both microevolutionary and macroevolutionary processes (Figure 1; see also Harvey et al. 2019). In addition to dramatically influencing the demographic fate of individual lineages, it is possible that shifts in dispersal-related traits may even shape entire community assemblages. Similar coalescent approaches could also be used to examine the demographic consequences of dispersal reduction in other evolutionarily young lineages. Species complexes where flight has been lost repeatedly are potentially powerful model systems to further test the evolutionary impacts of dispersal reduction (e.g., Van Belleghem et al. 2018; McCulloch et al. 2021).

Estimates of gene flow and genetic diversity will particularly benefit from trait informed analytical methods. Such approaches may ultimately help explain why many comparative phylogeography studies often identify non-congruent patterns among different taxa (Zamudio et al. 2016). Testing trait-based hypotheses in a comparative context might even help to unveil how morphological evolution can shape community assembly in topographically less complex landscapes, as particular morphological traits are often needed to occupy and move through different habitats (Harvey et al. 2017). Using morphological-trait measurements as a predictor for dispersal may therefore provide crucial insights on long-standing questions of how gene flow and persistence shape contemporary ecological patterns.

LITERATURE CITED

- Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., et al. 2012. Costs of dispersal. Biol. Rev. 87(2): 290-312. https://doi.org/10.1111/j. 1469-185x.2011.00201.x.
- Harvey, M. G., Aleixo, A., Ribas, C. C., and Brumfield, R. T. 2017. Habitat association predicts genetic diversity and population divergence in Amazonian birds. Am. Nat. 190(5): 631-648. https://www.doi.org/10. 1086/693856.
- Harvey, M. G., Singhal, S., and Rabosky, D. 2019. Beyond reproductive isolation: Demographic controls on the speciation process.

Annu. Rev. Ecol. Evol. Syst. 50:75-95. https://doi.org/10.1146/ annurev-ecolsys-110218-024701.

- McCulloch, G. A., Foster, B. J., Dutoit, L., Harrop, T. W. R., Guhlin, J., Dearden, P. K., and Waters, J. M. 2021. Genomics reveals widespread ecological speciation in flightless insects. Syst. Biol. In Press. https://doi.org/10.1093/sysbio/syaa094.
- Ortego, J., Gutiérrez-Rodríguez, J., and Noguerales, V. 2021. Demographic consequences of dispersal-related trait shift in two recently diverged taxa of montane grasshoppers. Evolution. 75:1998– 2013.
- Roff, D. A. 1990. The evolution of flightlessness in insects. Ecol. Monogr. 60(4): 389-421. https://www.jstor.org/stable/1943013.
- Salces-Castellano, A., Andújar, C., López, H., Pérez-Delgado, A. J., Arribas, P., and Emerson, B. C. 2021. Flightlessness in insects enhances diversification and determines assemblage structure across whole communities. Proc. Royal Soc. B 288:20202646. https://doi.org/10.1098/rspb. 2020.2646.
- Van Belleghem, S. M., Vangestel, C., De Wolf, K., De Corte, Z., Möst, M., Rastas, P., De Meester, L., and Hendrickx, F. 2018. Evolution at two time frames: Polymorphisms from an ancient singular divergence event fuel contemporary parallel evolution. PLoS Genet. 14(11):e1007796. https://doi.org/10.1371/journal.pgen.1007796.
- Waters, J. M., Emerson, B. C., Arribas, P., and McCulloch, G. A. 2020. Dispersal reduction: Causes, genomic mechanisms, and evolutionary consequences. Trends Ecol. Evol. 35(6): 512-522. https://doi.org/10.1016/j.tree.2020.01.012.
- Zamudio, K. R., Bell, R. C., and Mason, N. A. 2016. Phenotypes in phylogeography: Species' traits, environmental variation, and vertebrate diversification. Proc. Natl. Acad. Sci. U.S.A. 113(29): 8041-8048. https://doi.org/10.1073/pnas.1602237113.

Associate Editor: K. Moore Handling Editor: T. Chapman

SUBMIT A DIGEST

Digests are short (\sim 500 word), news articles about selected original research included in the journal, written by students or postdocs. These digests are published online and linked to their corresponding original research articles. For instructions on Digests preparation and submission, please visit the following link: https://sites.duke.edu/evodigests/.