

# Digest: Revisiting morphology-derived hypotheses of hybridization in the light of genomics

Víctor Noguerales<sup>1,2</sup> 

<sup>1</sup>Island Ecology and Evolution Research Group, Institute of Natural Products and Agrobiolgy (IPNA-CSIC), CI Astrofísico Francisco Sánchez 3, 38206, San Cristóbal de La Laguna, Tenerife, Canary Islands, Spain

<sup>2</sup>E-mail: victor.noguerales@csic.es

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Genetic exchange between independently evolving lineages may give rise to the formation of new taxa, and hypotheses for this have been derived from species with intermediate phenotypes, when compared to potential parental species. Goulet-Scott and collaborators (2021) evaluate such a hypothesis in a wildflower species complex by integrating genomic and trait information. They find no support for hybrid speciation, despite detecting signatures of genetic admixture in some individuals resulting from interspecific gene flow in a hybrid zone.

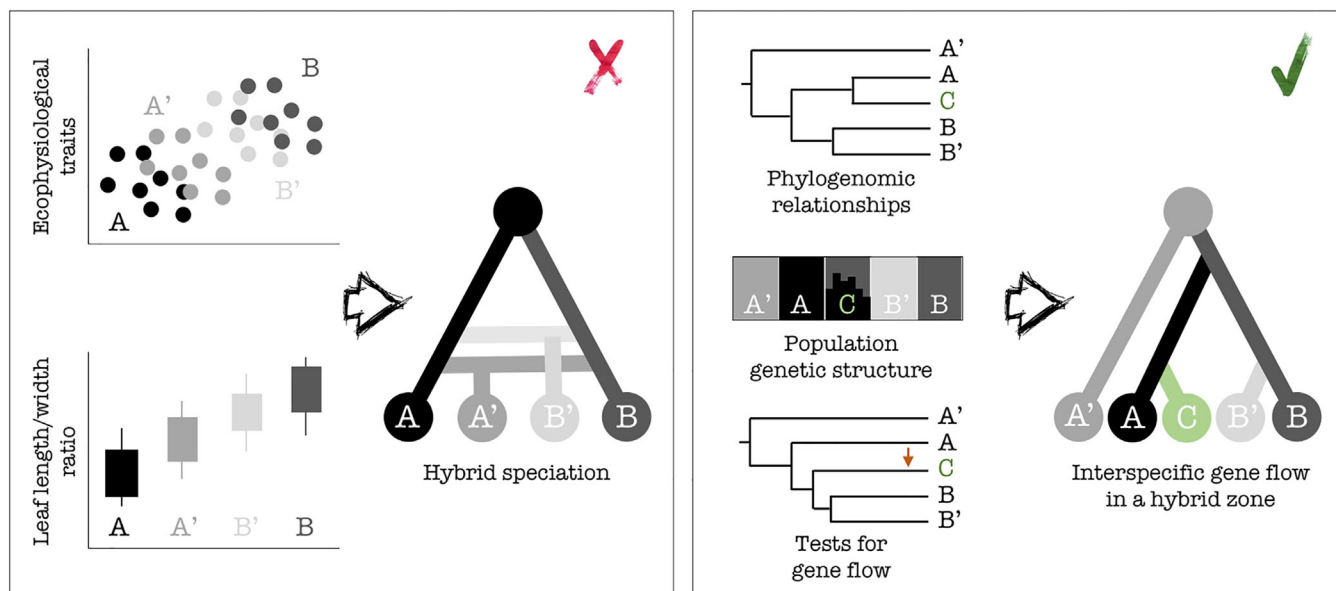
Hybridization may trigger opposite evolutionary consequences. These can be interpreted along a hybridization continuum, ranging from (i) coalescence and collapse of the genetic distinction between hybridizing lineages, to (ii) transfer of genomic regions into recipient populations with or without individual fitness consequences, and potentially (iii) the formation of new hybrid species, reproductively isolated from their progenitors, with or without change in ploidy (Abbott et al. 2013). The latter (i.e., homoploid hybrid speciation) has long attracted the interest of evolutionary biologists owing to its implications for understanding how interspecific gene flow can eventually generate species-level biodiversity. Yet the detection of hybrid taxa has typically been challenging, due to the often limited inferential power of small genetic datasets, and the paucity of adequate methodological approaches testing for gene flow.

To reconstruct the diversification and hybridization history of two wildflower species belonging to the *Phlox pilosa* complex (Fig. 1), Goulet-Scott et al. (2021) harness the potential of

integrating genome-wide data within a population genetic and phylogenetic framework. Specifically, they evaluate the hypothesis that *P. pilosa deamii* and *P. amoena lighthipei* are the results of hybrid speciation events, as previously posited based on microsatellite data and their intermediate morphology with regard to putative parental taxa (*P. pilosa pilosa* and *P. amoena amoena*). Using tests for introgression, which enable distinguishing between hybridization and ancestral shared variation, the authors found an absence of post-divergence gene flow between the hypothesized hybrid lineages (*P. p. deamii* and *P. a. lighthipei*) and any sister taxa. Indeed, phylogenomic analyses reveal: (i) *P. p. deamii* to be genetically distinct and distantly related to its putative parental forms, and that (ii) *P. a. lighthipei* is nested within the *P. amoena* clade. The clear lack of concordance between phenotype-based hypotheses and patterns of genetic relatedness rules out an explanation of hybrid speciation, while raising new questions concerning both the taxonomy of the species complex and the potential role of local adaptation and/or phenotypic plasticity in driving similarity in leaf traits between distantly related populations.

Despite finding no support for the hybrid-speciation hypothesis, Goulet-Scott et al. (2021) do detect genetically admixed individuals (*P. amoena* X *pilosa*) in a hybrid zone, likely resulting from genetic exchange between *P. pilosa pilosa* and

<sup>†</sup>This article corresponds to Goulet-Scott, B. E., A. G. Garner, and R. Hopkins. 2021. Genomic analyses overturn two long-standing homoploid hybrid speciation hypotheses. *Evolution* 75:1699–1710. <https://doi.org/10.1111/evo.14279>.



**Figure 1.** Schematic overview of the hypothetical and methodological framework of Goulet-Scott et al. (2021). Left panel represents the morphological-informed hypotheses of hybrid speciation, while right panel summarizes the genomic methods used and inferences obtained: (i) the lack of support for the hybrid-speciation hypothesis, and (ii) the detection of admixed individuals (new lineage C in this figure) compatible with interspecific gene flow in a hybrid zone. In the present figure, lineages A' and B' would represent the hypothesized hybrid lineages, while A and B represent the presumed parental taxa. For display purposes, some analyses, results, and details have been omitted from the figure.

*P. amoena* lineages. Hybrid zones provide a powerful framework to explore environmental factors that may facilitate or prevent the breakdown of boundaries between nascent species. Past landscape dynamics have been revealed to drive secondary contact between formerly isolated lineages, which may increase the chances for hybridization (Yamamoto et al. 2020) and the establishment of new hybrids (White et al. 2018). Additionally, contemporary processes linked to global change (climate-driven range shifts, habitat alteration, change in phenology, and pollination dynamics) are being increasingly reported to positively influence hybridization rates across numerous taxonomic groups (Vallejo-Marín and Hiscock 2016). However, untangling whether the observed patterns of genetic admixture are the result of past or recent hybridization, and their potential relationship to hybrid speciation, is challenging. In this context, demographic modeling using coalescent simulations provides an excellent and flexible framework to (i) simultaneously compare alternative demographic scenarios and estimate gene flow and divergence parameters (e.g., Barrera-Guzmán et al. 2018), and also (ii) validate inferences from tests for introgression, such as those used by Goulet-Scott et al. (2021). The decomposition of gene flow, by reconstructing its magnitude, direction, and timing, can provide relevant insights into hybridization dynamics, as well as the actual incidence of hybrid speciation in nature. Future studies on hybridization may benefit greatly from reconstructing the tempo, mode, and evolutionary outcome of gene

flow, and ultimately shed light on the relative contribution of past (e.g., Pleistocene) and contemporary (human-driven) environmental changes in shaping reticulate trajectories of natural populations.

In summary, Goulet-Scott et al. (2021) provide further support for the widespread incidence of interspecific gene flow in plants, while simultaneously ruling out prior hypotheses of hybrid speciation. Their work provides an elegant example of the power of genome-wide SNP data sets to confidently resolve species origins within recently evolved plant species complexes.

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