

Digest: Frequent hybridization in *Darevskia* rarely leads to the evolution of asexuality

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Asexuality in vertebrates is often generated via hybridization, but is it a rare product of pervasive hybridization or a common product of rare hybridization? Freitas et al. show that hybridization is frequent among the sexual species of *Darevskia*, although the crossings between parents of the asexual hybrids are undetected. This study illustrates that hybridization is not extraordinary in nature, and thus scalable phylogenetic network inference methods, rather than phylogenetic trees, are needed to accurately represent the true evolutionary history.

Hybridization is an important evolutionary phenomenon that generates genetic and phenotypic diversity in nature, providing conditions for evolution to occur. Hybridization includes hybrid speciation and introgression, both of which involve interbreeding between individuals from distinct species that differ in one or more heritable traits (Anderson 1953). Hybrid speciation results in the production of a stabilized evolutionary lineage that persists over evolutionary time, whereas introgression results in the horizontal transfer of genes between two parental species via backcrossing of the hybrid daughter (see Fig. 1). The distinction between introgression and gene flow is vague and somewhat arbitrary; however, in practice, the former often refers to unidirectional genetic exchange, whereas the latter explains bidirectional exchange.

Freitas et al. (2022) investigate the rock lizard genus *Darevskia*, which contains 25 sexual and seven parthenogenetic (i.e., able to reproduce asexually from ovum) species, where the latter are the products of hybridization among four sexual species. The study explores the pattern of occurrence of introgression (or gene flow) among the sexual species using a combination of phylogenetic and introgression detection analyses, computed from a multilocus genomic dataset. The three phylogenetic trees esti-

mated using *BEAST2, BUCKy, and SVDQuartets were generally congruent except for the branching of *Darevskia parvula*, possibly due to extensive historical hybridization events. Results from four introgression tests (BUCKy, *D*-statistic, *f*₄ test, and TreeMix) consistently showed that hybridization is pervasive throughout the genus; however, no significant introgression among the putative parental species of parthenogenetic hybrids was detected.

Investigating hybridization requires a multi-locus genomic dataset, because hybridization results in discordance among gene genealogies. Such discordance is explained by the “historical mosaicism” that describes the genomic constitution of a hybrid as a patchwork of parental genes (Folk et al. 2018), each of which individually evolved under a single phylogenetic tree and is drawn from a different gene tree distribution (Meng and Kubatko 2009). Therefore, a phylogenetic tree is inadequate to represent the true evolutionary history of species if hybridization played a role in their past, even when the gene tree discordance is considered in their reconstruction, because the bifurcating branching pattern represents only vertical evolution (i.e., speciation), not horizontal evolution (e.g., hybridization). In this case, a phylogenetic network, a modification of a phylogenetic tree that allows two branches to merge into a single node to create a structure called a reticulation, is a more appropriate representation of the true evolutionary history (Fig. 1).

Although phylogenetic networks have critical value in biology and beyond (Kong et al. 2022), their widespread use has been

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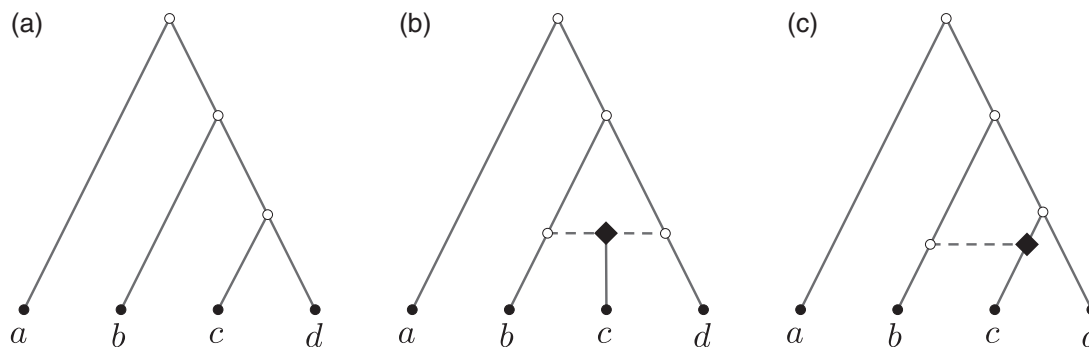


Figure 1. An example of (a) phylogenetic tree and (b, c) phylogenetic network of four taxa a, b, c, and d. In (b) and (c), filled diamonds represent reticulation nodes and dotted lines directed toward the reticulation node are reticulation edges, which create a reticulation that represents a hybridization event. The phylogenetic network represented in (b) depicts a hybrid speciation scenario, where c is the hybrid daughter of parental species b and d, whereas the scenario depicted in (c) represents an introgression event where the genes are transferred from b to c via backcrossing of the hybrid daughter (not shown in the diagram) with its parent c. In the case of the *Darevskia*, the generation of parthenogenetic species is expected to be represented in the network (b), whereas the rest of genetic transfer between species can be depicted using the network (c).

hindered by computational challenges that arise when using data to estimate them (Hejase and Liu 2016). In brief, the performance of current methods degrades as dataset size or the complexity of the network increases (i.e., lacks scalability). Freitas et al. (2022) contribute to the increasing evidence of interspecific hybridization as a common natural phenomenon that must not be overlooked in evolutionary studies, but more importantly, they clearly illustrate the urgent need for scalable phylogenetic network inference methods that can be applied to genomic datasets.

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