COMMENTARY

Hybridization helps colonizers become conquerors

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Species colonizing new environments face an uphill battle to become established. Because colonizing populations are often small, opportunities for sexual reproduction may be limited by availability of mates or viable pollen—an example of an Allee effect (1, 2). The presence of a more abundant related species with similar climatic, habitat, and nutritional needs can further reduce the odds of colonizer establishment (3, 4). Despite these hurdles, there are numerous examples of colonizing species increasing in number and range to the detriment of the recipient ecological and human communities. The field of invasion biology studies such species to further our understanding of the fundamental mechanisms that allow colonizing species to prosper (5), as well as the more applied goals of predicting, preventing, and controlling invasions (6). Mesgaran et al.'s study (7) contributes to these goals by illustrating how colonizing species can exploit the presence of congeners to overcome the problems associated with low numbers through hybridization and the subsequent reemergence of colonizer genotypes.

Hybridization between colonizing and resident species has been documented across diverse taxa including birds, fishes, and, particularly, plants (8). The consequences of such hybridization are varied: Both parental species may coexist through formation of a stable hybrid zone (9), a rare colonizer may be lost through genetic swamping by the more abundant resident (10), or both parental species may decline or disappear to be replaced by genetically diverse hybrid swarms (11) or a small number of hybrid genotypes with superior fitness to either parental species (12). Mathematical models, such as those developed by Mesgaran et al. (7), serve as a useful tool for understanding the ecological and genetic conditions under which these varied outcomes might arise (13).

Mesgaran et al. (7) built a model describing the population dynamics and genetics of a colonizing plant, an established sister species, and hybrid genotypes that interact through pollinator-mediated gene flow and density-dependent fecundity. In contrast to prior theoretical work (e.g., ref. 14), the model assumes no ecological fitness differences between genotypes. Instead,

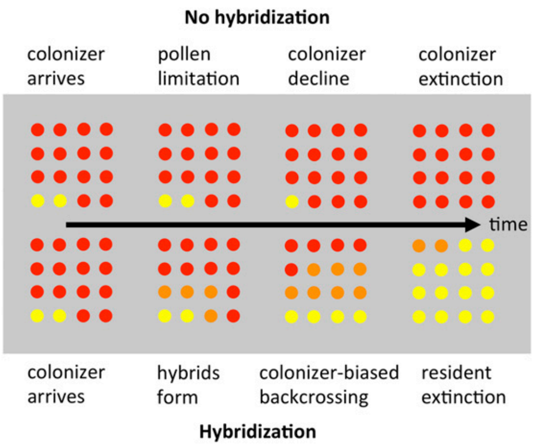

Fig. 1. **Schematic showing the fate of a small number of colonizers (yellow circles) interacting with a related resident species (red circles). In the absence of hybridization (*Upper*), the rare colonizer is swamped by incompatible pollen from the resident, resulting in low fecundity. Colonizers decline to vanishingly small frequency as they are replaced by resident seedlings. When hybridization occurs (*Lower*), colonizer genes persist in hybrids (orange circles) and colonizer genotypes reassemble through preferential backcrossing among colonizer-like individuals.**

the authors focus on how prezygotic (pollinator preference) and postzygotic (relative compatibility) forces determine genotype interactions. They explore how hybridization influences colonizer establishment by determining the minimum colonizer population size necessary to avoid population declines (the Allee threshold), and they examine the long-term fate of the colonizing and resident species by comparing how their relative frequencies change through time, with or without hybridization (Fig. 1).

Two noteworthy results arise. First, colonizers capable of hybridizing with a resident congener need fewer founding individuals to establish than when no hybridization occurs, provided hybrids are more likely to successfully backcross with the colonizer than with the resident. Pollinator preference for the colonizer and colonizer-like genotypes further lowers the Allee

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threshold. This result challenges conventional wisdom that hybridization can exacerbate Allee effects because small populations may be subject to outbreeding depression or face genetic extinction through swamping by genotypes of the more abundant species (10).

Second, hybridization can flip the outcome of ecological interactions from resident-dominated to takeover by the colonizer. In the absence of hybridization, the relative scarcity of the colonizer means it is unable to escape limited reproductive opportunities, even when preferred by pollinators. However, subject to colonizer-like backcrosses being favored, the colonizer is able to exclude the resident over ecologically relevant timescales. In striking contrast to previous studies (15, 16), colonizing genotypes do not need to convey a classical ecological fitness advantage over the resident in commonly measured life history traits such as seed set and survival.

By leveling the demographic playing field for the colonizing and resident species, this study (7) sheds light on how compatibility differences among genotypes alone can profoundly alter the outcome of newly interacting species. Compatibility biases are common among hybridizing plants (17) and may arise from epistatic effects on reproductive architecture, or from prezygotic processes such as pollinator preference. The results of the model should still hold in other plant and animal mating systems, for example, if there is a tendency for hybrids to more closely resemble colonizers in sexually selected characters or reproductive phenology (e.g., flowering times).

The authors (7) make a plausible case that ephemeral hybridization and subsequent reassembly of colonizer genotypes might explain the replacement of an exotic plant in the sea rocket family (*Cakile* spp.) by another invasive congener in western North America and Australasia. They further speculate that such hybridization might play a role more widely in facilitating colonization success, perhaps even in the displacement of Neanderthals by *Homo sapiens*. If this mechanism is indeed widespread, this work may yield additional insights into fundamental processes in invasion biology. For example, although the model is formulated for local species interactions, it may also inform basic theory on the factors governing the spread rate of expanding species. Classic theory suggests that the invasion speed of a spreading population is constrained by the population's growth rate at the leading edge of the invasion (18) and is slowed if the species experiences Allee effects (19). The findings of this study suggest that hybridization, rather than being simply a by-product of interspecies contact at the invasion front, may help speed up invasions by overcoming leading-edge Allee effects.

From an applied perspective, this work (7) could inform invasion management strategies aimed at prediction and prevention. Relatedness to known invaders is used as a predictor of invasiveness when assessing risk of importing commercially or horticulturally valuable plants (20), based on the underlying assumption that phylogenetically similar species may share ecological traits that predispose them to invasiveness. This study suggests that identifying the prior presence of compatible congeners in the recipient community may also serve as a red flag, and that controlling the densities of these congeners in likely introduction sites might further reduce the risk of invasion via hybridization.

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