Opinion

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Spatial sorting promotes the spread of maladaptive hybridization

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Invasive hybridization is causing loss of biodiversity worldwide. The spread of such introgression can occur even when hybrids have reduced Darwinian fitness, which decreases the frequency of hybrids due to low survival or reproduction through time. This paradox can be partially explained by spatial sorting, where genotypes associated with dispersal increase in frequency at the edge of expansion, fueling further expansion and allowing invasive hybrids to increase in frequency through space rather than time. Furthermore, because all progeny of a hybrid will be hybrids (i.e., will possess genes from both parental taxa), nonnative admixture in invaded populations can increase even when most hybrid progeny do not survive. Broader understanding of spatial sorting is needed to protect native biodiversity.

The invasive hybridization paradox

The increasing number of species introductions and continuing alteration of natural environments has promoted hybridization (see Glossary) between previously geographically isolated species worldwide [1–3]. This, in turn, opens the door to introgression, where genes from one species spread into another by hybridization and fertility of the hybrid progeny. Introgressive hybridization is a major threat to biodiversity by causing the loss of locally adapted populations and species, and by the indirect effects of these losses on communities of interacting species [1–5]. Introgressive hybridization occurs across a wide array of taxa, including plants, invertebrates, and vertebrates [1,5,6], underscoring the breadth of these direct and indirect effects on biological diversity.

Introgressive hybridization can spread rapidly even when hybrids have reduced Darwinian fitness (i.e., survival and reproductive success [7,8]). Understanding this paradox is crucial for controlling the spread of introgressive hybridization and protecting native species, but also for revealing the scope of evolutionary mechanisms at work in nature. Specifically, the spread of introgressive hybridization in the face of strong selection against hybrids (i.e., outbreeding depression) challenges widespread assumptions about the primacy of natural selection in regulating genetic and phenotypic variation in the wild and in shaping emergent patterns of species co-occurrence and diversity. It also forces us to assess the degree to which these assumptions influence current conservation strategies – whether for individual species or communities – and to consider how these strategies could be adjusted to accommodate novel evolutionary mechanisms.

We believe that spatial sorting can partially explain the paradoxical spread of introgressive hybridization despite strong selection against hybrids. Natural selection increases the frequency of genes associated with greater survival or reproductive success within populations over time [9]. Spatial sorting has been proposed as a separate evolutionary mechanism that allows genes to increase in frequency because of greater success through space rather than time [10,11]. In the case of an expanding range edge, those genotypes associated with greater probability or greater rate of dispersal will increase in frequency at

Glossary

Admixture: the production of new genetic combinations in hybrid populations through recombination.
Assortative mating: preferential mating between individuals with similar or different phenotypes, referred to as positive or negative assortative mating, respectively.
Darwinian fitness: contribution of an individual to the next generation's gene pool due to survival and reproduction over time.
Dispersal: permanent movement away from an origin and long-term settlement at a new location.
Genomic extinction: the permanent loss of a population's genome-wide combination of alleles and genotypes through introgression.
Hybrid: an individual resulting from interbreeding between individuals from genetically distinct populations, including both first-generation hybrids (F1s) and individuals derived from later-generation crosses (e.g., F2s, backcrosses).
Hybridization: interbreeding between individuals from genetically distinct populations.
Hybrid swarm: populations in which all individuals are hybrids by varying numbers of generations of backcrossing with parental types and mating among hybrids.
Hybrid zone: where two genetically distinct taxa are sympatric and hybridize to form at least partially fertile progeny.
Introgression: the incorporation of genes from one population into another through hybridization, resulting in fertile offspring that further hybridize and backcross to parental populations.
Invasive hybridization: the rapid spread of hybridization between an introduced, nonnative species and a native species.
Natural selection: process by which genes become more or less common in a population as a function of their effect on survival and reproductive success over time.
Self-organization: process where organization arises from local interactions among initially disorganized components, independent of the environment or external forces.
Spatial sorting: process by which genes change in frequency as a function of their effects on dispersal.

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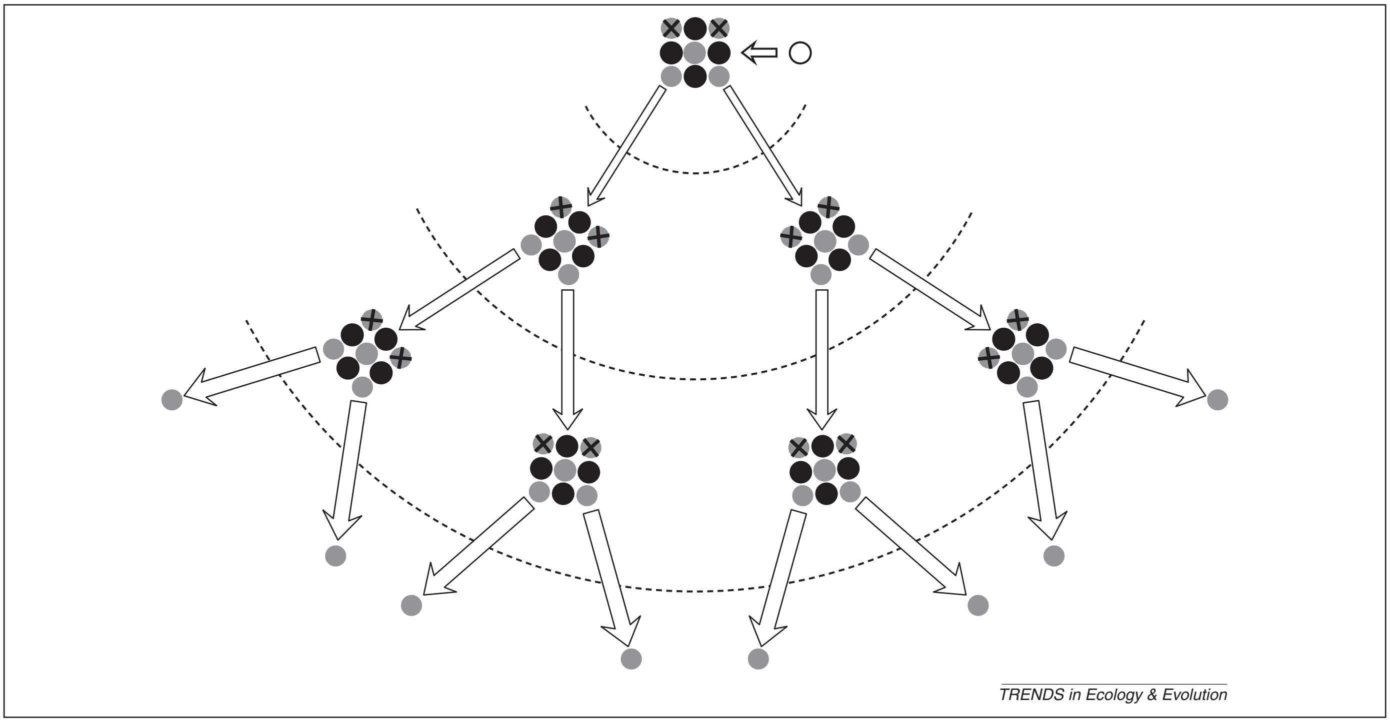

Figure 1. The spread of invasive hybridization by spatial sorting. Hybrids (gray circles) created by mating between the native species (black circles) and an introduced species (white circle) are disfavored by Darwinian natural selection within sites (×, mortality). However, hybrids are more likely to disperse to other sites than the native species, causing introgressive genes to increase in frequency due to spatial sorting: greater success through space rather than time. Over time, those hybrid genotypes associated with greater probability of dispersal or greater rate of dispersal will increase in frequency at the edge of expansion, fueling further expansion.

the edge of expansion, fueling further expansion (Figure 1). Shine *et al.* [10] have argued that spatial sorting should be recognized as a fundamentally different process than natural selection. Regardless of whether spatial sorting acts in conjunction with or independently of natural selection, it should be recognized to have important implications for conservation and is likely to be a general mechanism for the spread of invasive hybridization.

Here we argue that introgression from an introduced species into populations of a native species provides ideal conditions for spatial sorting to accelerate the spread of introgression, even when hybrids have reduced fitness. Understanding the conceptual basis and empirical signs of spatial sorting is, therefore, necessary to protect the genomic integrity, adaptations, and ecological roles of native species. Broader understanding of the principles and implications of spatial sorting will also strengthen research on basic spatial ecology and evolutionary processes, including metapopulation and metacommunity ecology, local adaptation, and range shifts.

We first review the conceptual basis of spatial sorting, emphasizing its relevance to invasive hybridization and links to the disciplines of evolutionary biology, population genetics, and ecology. We then describe recent research showing the influence of spatial sorting on the spread of invasive hybridization. Finally, drawing on both conceptual and empirical work, we highlight key implications of spatial sorting for efforts to protect native species and ecosystems, at the same time showing how current approaches to the study and conservation of native species rely on implicit – and potentially incorrect – assumptions about the influence of natural selection.

We hope this opinion article stimulates research on how spatial sorting influences the spread of invasive hybridization and other ecological and evolutionary processes (e.g., source–sink dynamics, local adaptation, species interactions). As importantly, we hope to improve conservation and management efforts for native species by encouraging explicit consideration of the effects of spatial sorting.

What is spatial sorting?

The term 'spatial sorting' was originated by Shine *et al.* [10], who provide an excellent description of the concept, empirical evidence, and dispersal-associated traits that allow spatial sorting to occur. They describe a species expanding into previously unoccupied territory, where individuals with the highest dispersal rates will be concentrated at the expanding edge of the range. These fast-dispersing individuals are then more likely to interbreed due to spatial aggregation, increasing the frequency of heritable traits conferring high dispersal rates at the range edge and fueling further increases in dispersal rates (and the frequency of associated genes) as successive generations of fast dispersers move across the landscape. Shine *et al.* [10] recognize that dispersal-associated traits can be diverse and multifaceted, including morphological, behavioral, or physiological traits influencing the pace, distance, frequency, or direction of movement.

Spatial sorting is rooted in evolutionary concepts that are not novel but have received less attention than classic, adaptive models of evolution. Spatial sorting represents a form of self-organization where the formation of new groups of individuals with shared traits is nonrandom in space, but instead concentrated at the periphery of an