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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

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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.
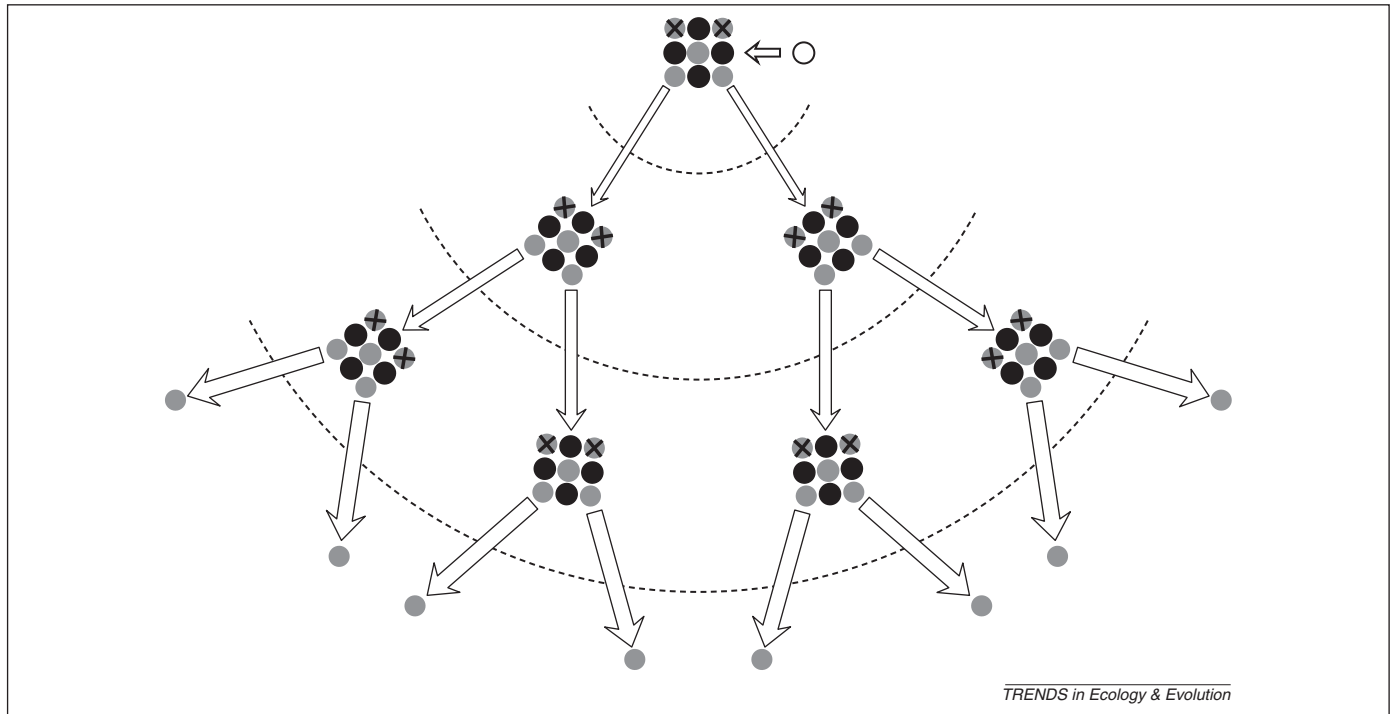
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Figure 1. The spread of invasive hybridization by spatial sorting. Hybrids (gray circles) created by mating between the native species (black circles) and an introduced species (white circle) are disfavored by Darwinian natural selection within sites ($\times$, 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

expanding range [11]. Similarly, its emphasis on the evolutionary influence of dispersal can be traced back to group selection models showing that groups producing many dispersive propagules can have strong genetic effects at the metapopulation level, even when individuals within the group experience low average fitness [12].

Spatial sorting is a nonequilibrium process because it requires colonization of space previously unoccupied by the expanding species, whether that unoccupied space is beyond the historic range edge of a native species or – in the case of an expanding introduced species – currently occupied by a closely related native species (Figure 1) [13]. However, Lee [13] notes that despite this nonequilibrium assumption, spatial sorting can generate long-term evolutionary effects when combined with natural selection. He suggests that spatial sorting will increase variance in dispersal-associated traits throughout the range of a species (e.g., by increasing the upper limit of dispersal rate), potentially setting the species on a new evolutionary trajectory when natural selection acts on these novel phenotypes.

The principles of spatial sorting also align with studies of evolutionary and population genetic processes during range expansion. For example, simulation studies have shown that the spread of novel mutations can be accelerated by demographic conditions experienced during range expansion and by the dispersal traits of the expanding species. The concept of 'gene surfing' predicts that strong founder effects during range expansion allow novel mutations to reach high frequencies in populations at the expanding edge [14,15]. Although gene surfing can occur under any dispersal pattern, we also know that rates of spread of novel mutations (and species) accelerate nonlinearly with increasing dispersal rates and distances [16]. Recently, Hallatschek and Fisher [17] showed that long-distance jumps not only increase the frequency of novel mutations at the range edge, but can also lead to very fast ('metastatic') growth of the mutant population throughout the colonized range. These findings underscore the influence of nonequilibrium demographic conditions and dispersal traits on evolutionary dynamics during range expansion.

Invasive hybridization
Sorting and selection during invasions
Nonnative species are spreading throughout the globe due to human activities [18]. Many of these nonnative invasions have harmful effects on native biodiversity through direct ecological interactions (e.g., competition, predation) [19]. Likewise, weak effects of nonnative invasions are often attributed to competition and predation by native species [20,21] and resistance to invasion of diverse native communities [22,23]. In these cases, harmful effects of the nonnative species are reduced or eliminated by fitness advantages of the native species, which may be conferred by abiotic or biotic aspects of the 'home' environment (e.g., thermal regime, coexistence with multiple native competitors).

Clearly, spatial sorting will exacerbate ecological effects of an invasion when the nonnative experiences greater fitness relative to native species. However, when the invader experiences reduced fitness relative to native species, and hybridization does not occur, spatial sorting is likely to be a transient phenomenon [13]. In this case, we would expect an initial phase of rapid expansion followed by elimination of the nonnative species from colonized sites by mechanisms of ecological selection. This scenario does not preclude negative ecological effects of the invasion, such as mass effects on native communities [24]. However, provided that mechanisms of ecological selection act in few generations, the short timescale should prevent strong evolutionary effects and allow post-invasion recovery.

The dark power of the genomic ratchet
When spatial sorting occurs in invasive hybrids (Figure 1), genetic and ecological effects on native biodiversity are likely to be long lasting and significant. These long-term effects are enhanced by the poor effectiveness of natural selection at removing introgressive genes from populations. Population models indicate that admixture within a breeding population can increase in frequency even when up to 90% of the hybrid progeny do not survive [7]. This is a consequence of the unidirectional production of hybrids: all of the progeny of a hybrid will be hybrids (i.e., will possess genes from both parental taxa), creating a genomic ratchet effect where the presence of even a few hybrids in the breeding population is enough to ensure the retention and proliferation of nonnative genes [25]. For example, consider a population comprising 90% native individuals and 10% hybrids between the native and an introduced species. If this population mates at random, there will be only 81% (0.9^2) native individuals in the next generation. Therefore, the proportion of hybrids will nearly double from 10% to 19%. Ongoing immigration of hybrids, as is predicted under the spatial sorting model, will further accelerate this process.

Consequently, spatial sorting can allow the rapid, widespread, and irreversible infiltration of nonnative genes and phenotypes (with associated ecological effects) throughout the invaded range, even when hybrids or the nonnative species experience reduced fitness relative to native species. Ecological constraints (biotic or abiotic) will matter only if they are strong enough to block colonization of new sites or mating with the native species [26,27].

Ecological escalation of invasive hybridization
In addition to intrinsic traits that promote hybrid dispersal – the focus of the original spatial sorting model – ecological mechanisms can further accelerate the spread of invasive hybridization. According to the Shine *et al.* [10] model of spatial sorting, increased dispersal rates at the range edge are a consequence of the expansion process itself, requiring only that the expanding species possess additive genetic variation for traits that affect dispersal rate or dispersal distance [28]. The same model will apply when invasive hybrids retain genetically based traits making them more likely to disperse than native individuals [29,30], but the ecology of hybrids can also play a role in spatial sorting.

Habitat quality is widely recognized to influence emigration rates in animals, where habitat quality may be a function of biotic or abiotic conditions [31,32]. If these conditions underlie the low Darwinian fitness of invasive

hybrids – partially or entirely – we would expect high rates of hybrid emigration from colonized sites as a response to habitat quality alone. These 'conditional' emigrants should increase the pool of individuals available to colonize new sites, adding to the number expected based on spatial sorting of dispersal phenotypes [10].

Landscape disturbances can also favor dispersal by nonnative species and their hybrids, accelerating the rate of spread of invasive hybridization. In undisturbed ecosystems, reproductive isolation is maintained primarily by spatial and temporal isolation. These barriers to interbreeding can be lost as habitats become degraded and fragmented by human activities, creating secondary contact between previously isolated species [33]. Additionally, both localized habitat disturbances and large-scale climate change can promote the spread of invasive plants and animals by creating environmental conditions that favor the invader. In western North America, logging has allowed the encroachment of barred owls (*Strix varia*) into the native range of the northern spotted owl (*Strix occidentalis caurina*), leading to hybridization between the two species [34,35]. At much larger scales, climate change can facilitate the dispersal of nonnative species or their hybrids and the spread of invasive hybridization [36].

Box 1. The spread of invasive hybridization into native trout

Over 20 million nonnative rainbow trout were released into the upper Flathead River drainage, USA and Canada, beginning in the late 1800s and ending in 1969 [40] (Figure I). In 1984, we detected hybridization in only two of 13 sites (15%) distributed throughout our study area [40]. However, 24 of 42 sites (57%) sampled between 1998 and 2001 across the same area contained introgressive hybridization. Moreover, seven of the 11 sites that did not show evidence of hybridization in 1984 were hybridized when sampled 15 years later.

Both laboratory [65] and field [8,29] studies have shown that hybrids have greatly reduced fitness compared with the native westslope cutthroat trout. Muhlfeld *et al.* [8] used parentage analysis to measure the effect of introgression on reproductive success in Langford Creek. Small amounts of admixture markedly reduced the fitness of male and female trout; the number of progeny produced declined by approximately 50% with only 20% admixture. Using multiyear cohort analysis of genotyped fish, Kovach *et al.* [29] found strong selection against nonnative admixture in two streams [mean selection coefficient against genotypes with nonnative alleles (s) = 0.60; standard error (SE) = 0.10].

The rapid spread of rainbow trout introgression is surprising given the greatly reduced fitness of hybrids. However, this system provides ideal circumstances for spatial sorting to accelerate the rate of spread of hybridization. Boyer *et al.* [42] showed that hybrid invasion was facilitated by both long-distance and stepping-stone dispersal from hybrid swarms. Similarly, Kovach *et al.* [29] found that hybridization was maintained in two streams by continuous immigration of individuals with high levels of nonnative admixture. Direct evidence for these patterns of dispersal by rainbow trout and highly admixed individuals has also been reported using radiotelemetry [66].

In contrast to the high dispersal rates observed in hybrids, strong allele frequency divergence has been found among nonhybridized populations of native westslope cutthroat trout [65,67]. These genetic data are consistent with other studies showing low dispersal in the native species [68]. Thus, although hybrids experience low reproductive success locally, their offspring are more likely to disperse to other streams than offspring of the native species. This mechanism of spatial sorting is increasing the frequency of hybridization throughout the entire drainage and eroding hope that native westslope cutthroat trout will persist in the wild.
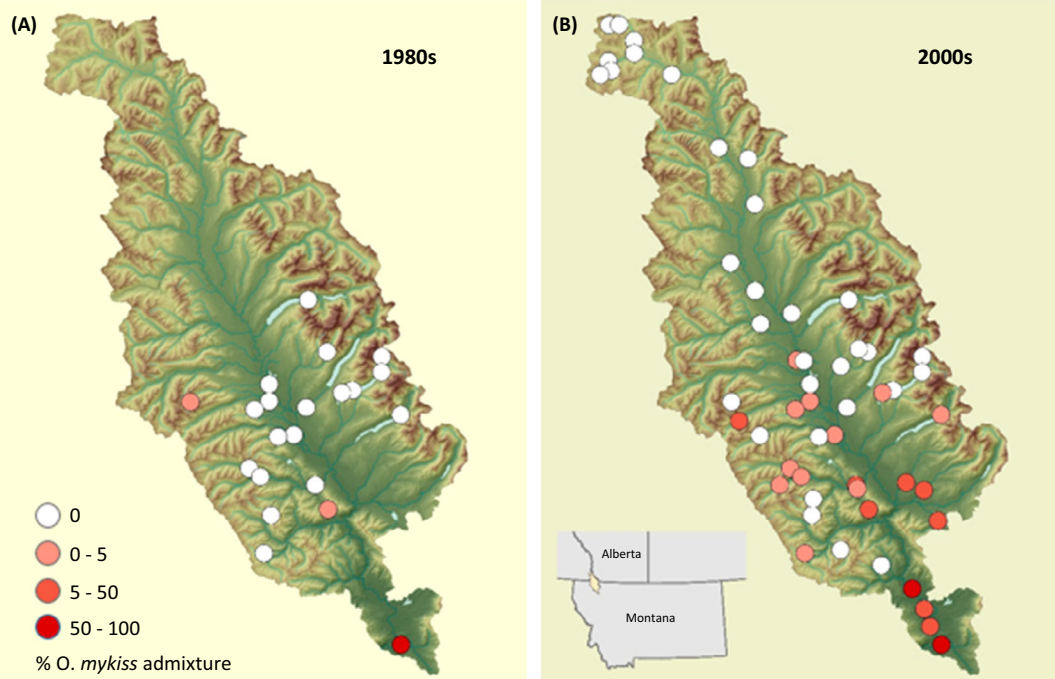

Figure I. Map showing the spread of invasive hybridization from nonnative rainbow trout into native populations of westslope cutthroat trout in the upper Flathead River system, USA and Canada. Maps illustrate the proportion of rainbow trout admixture present in samples collected during the early 1980s and early 2000s. The entire upper Flathead River system encompasses 7730 km^2 in northwest Montana, USA and 1580 km^2 in southwest British Columbia, Canada.

Evidence of spatial sorting

Invasive hybridization is more common in fish than in any other vertebrate taxon [37]. Many fishes have external fertilization, similar mating behaviors, and genomic compatibilities – all traits that facilitate interbreeding. This is particularly true in salmonids, where widespread stocking of hatchery-raised fish has led to extensive introgression within and between species [1,38].

Spatial sorting appears to be the evolutionary mechanism fueling the rapid spread of invasive hybridization between introduced rainbow trout (*Oncorhynchus mykiss*) and native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) in western North America (Box 1). The rainbow trout is the most widely introduced invasive fish in the Northern Hemisphere [39], first introduced by fisheries managers into the native range of westslope cutthroat trout in the later 19th century [40]. By 2005, a review of native westslope cutthroat trout found that most populations contained introgression from nonnative rainbow trout [41].

Despite strong selection against nonnative genetic admixture, hybridization between rainbow trout and westslope cutthroat trout has increased rapidly in populations inhabiting a wide range of abiotic and biotic conditions [42]. Continuous immigration of dispersing hybrids appears to be the primary mechanism promoting the spread of hybridization [29]. Candidate superinvasive alleles from rainbow trout may also be increasing in frequency at the leading edge of the hybrid zone [43], suggesting that these alleles might have phenotypic effects on dispersal. Notably, intraspecific hybrid pink salmon (*Oncorhynchus gorbuscha*) also show increased rates of straying compared with native fish [44].

Spatial sorting might also promote hybridization between native and introduced salamanders, although fitness effects appear to be environment specific. Introductions of nonnative barred tiger salamanders (*Ambystoma tigrinum mavortium*) and subsequent dispersal of individuals have led to widespread admixture across at least 20% of the range of the native California tiger salamander (*Ambystoma californiense*) over the past 60 years [45]. Landscape patterns of introgression within the hybrid zone showed higher frequencies of nonnative alleles in modified perennial breeding ponds, whereas higher proportions of native alleles were found in unmodified ephemeral breeding sites [46]. Similarly, controlled experiments revealed hybrid fitness advantages in perennial mesocosms and native-genotype fitness advantages in rapidly drying mesocosms [47]. Given the rapid expansion and patterns of hybridization in this system, hybrid dispersal – facilitated by pond and wetland modification – could be an important mechanism driving hybrid zone expansion.

Hybridization has been recognized as a stimulus for rapid invasiveness in plants [30,48,49]. There are also numerous examples in plants of invasive populations that have traits in the new range that suggest greater dispersal than in the home range. For example, Cwynar and MacDonald [50] showed that wind-dispersed seeds of lodgepole pine (*Pinus contorta*) have a higher ratio of wing to seed mass on the expanding front. Weeds directly descended from crops (sometimes from hybridization with wild types)

frequently have increased seed dispersal via the evolution of 'shattering', where seeds are forcefully projected from the fruit [51]. Here again, however, the degree to which dispersal compensates for – or complements – hybrid fitness to promote expansion is likely to vary among hybridizing species and environments.

Conservation and management

Recognizing the potential influence of spatial sorting is crucial for managing native species threatened by invasive hybridization. Management agencies have often assumed that greater fitness of native individuals would act to prevent the spread of invasive hybridization [52,53]. Consequently, a great deal of effort has been spent assessing the genetic status of imperiled species and the relative fitness of hybrids to predict and manage the spread of hybridization. We argue that understanding the effects of hybridization on dispersal is just as important. That is, empirical understanding of dispersal of hybrids is as valuable as understanding the fitness of hybrids in predicting and preventing the harmful effects of introgressive hybridization. To improve conservation and management programs, we suggest investing as much effort in quantifying dispersal as quantifying the fitness of invasive hybrids.

Detecting the occurrence of spatial sorting is crucial for taking management actions to mitigate its effects. The most direct approach is to measure the relative dispersal of the parental species and their hybrids. When such direct measures are not possible, detection of spatial sorting must rely on interpreting spatiotemporal patterns of hybridization spread. A central prediction of spatial sorting is that the rate of spread will accelerate over time as the fastest dispersers are progressively sorted into range-edge populations (Figure 1). Managers could detect this pattern by monitoring native populations arrayed at consistent distance intervals away from a putative site of introduction. Incremental reductions in the time until hybridization appears in successive native populations would support the occurrence of spatial sorting. A less quantitative signal of accelerating spread would be observation of little or no spread within multiple generations after initial detection of hybridization, followed by a period where hybridization spreads rapidly. However, other mechanisms could produce these spatiotemporal patterns (e.g., the assembly of high-fitness multilocus hybrid phenotypes over multiple generations), reinforcing the value of direct data on hybrid dispersal (and fitness) for detecting spatial sorting. Also, detecting these patterns relies on rigorous monitoring of hybridization in native populations to estimate the time at which hybridization initially appears in a study area, the rate of spread away from that initial introduction point, and interactions with environmental changes.

What management actions would be helpful if we do detect or suspect the effects of spatial sorting? Perhaps most fundamentally, any conservation or management strategy aimed at preventing invasive hybridization must recognize the power of the genomic ratchet, which makes even low-admixture populations important threats in the continued expansion of hybridization. It also underscores the value of protecting nonhybridized native populations and preventing initial colonization by hybrids [54] – even

when the costs are high. Any actions that decrease the probability of hybrid dispersal would also be extremely useful. These might include changes in large-scale land use regulations for cases where human disturbance favors hybrid spread (e.g., [35]), containment of hybridized source populations, especially in the early stages of spread [55], or even targeted removal of hybrid dispersers in systems where it is feasible [56]. These efforts could affect native populations directly or disrupt gene flow and dispersal in the native species, thus necessitating careful consideration of the risks and benefits of stopping hybrid spread. Clearly, however, simply relying on the greater fitness of native species to withstand the spread of invasive hybridization – both across the landscape and within native genomes – is not a sound conservation strategy.

Concluding remarks

Spatial sorting can only occur when there is a genetic basis for individual variation in dispersal traits [10]. Therefore, any empirical test of spatial sorting requires untangling how extrinsic ecological conditions and intrinsic phenotypes influence rates and spatial patterns of dispersal [57,58]. Although such comprehensive analyses of the ecological and genetic basis of dispersal have been conducted for a few species (e.g., [59–62]), we are not aware of any work of similar intensity targeting hybrids. Nevertheless, conceptual and methodological tools for these analyses are expanding rapidly [57,63,64], suggesting that we are on the verge of a rapid expansion of insight on the evolutionary and ecological drivers of dispersal in diverse systems and taxa, including invasive hybrids.

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