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Hybridization as a facilitator of species range expansion

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Explaining the evolution of species geographical ranges is fundamental to understanding how biodiversity is distributed and maintained. The solution to this classic problem in ecology and evolution remains elusive: we still do not fully know how species geographical ranges evolve and what factors fuel range expansions. Resolving this problem is now more crucial than ever with increasing biodiversity loss, global change and movement of species by humans. Here, we describe and evaluate the hypothesis that hybridization between species can contribute to species range expansion. We discuss how such a process can occur and the empirical data that are needed to test this hypothesis. We also examine how species can expand into new environments via hybridization with a resident species, and yet remain distinct species. Generally, hybridization may play an underappreciated role in influencing the evolution of species ranges. Whether—and to what extent—hybridization has such an effect requires further study across more diverse taxa.

1. Introduction

A central challenge of ecology and evolutionary biology is to explain why species occur where they do [1–3]. Generally, the border of a species geographical range is set by the inability of populations at the margin to adapt to novel environments just beyond its present range [1–4]. Thus, adaptive evolution is a key component of range expansions [1,3,5–7]. Specifically, unless a species expands into a new region by occupying environments to which it has already adapted in its ancestral range (e.g. as can occur in some human-introduced species [8]), range expansion depends critically on populations at a range edge adapting to novel environments before they go extinct [1,3,5,7].

Populations at the range edge can be 'rescued' from extinction by the advent of alleles for traits that are adaptive in the new environment, and prevailing theory generally assumes that the sources of such rescue alleles are either *in situ* mutation or gene flow from other conspecific populations [1,3,5,7,9–12]. However, theory further predicts that local adaptation at a range edge is unlikely to result from novel mutations, because the wait time for favourable mutations is long [13–16]. Instead, local adaptation might more likely result from admixture (the mixing of genotypes from different populations [1,17–26]) creating novel allelic combinations. Empirical evidence is consistent with this possibility [27–33].

Although gene flow can contribute to adaptation and range expansion in this way, a further issue is that gene flow from conspecific populations frequently consists of alleles from within the *centre* of the range. Because alleles at the range centre are predicted to be maladaptive at the range edge [1,3,5,6,12], gene flow/admixture among conspecific populations can actually counter local adaptation. Thus, the outcomes of mutation and gene flow for range expansion are mixed in that they might not contribute new, beneficial genetic variants that allow species to adapt to the range edge.

An alternative source of adaptive allelic variants at the range edge is hybridization—interbreeding of distinct evolutionary groups or species [34–39]. Indeed, interspecific admixture has been shown to provide genetic variation that allows populations to adapt to selective pressures, either through an increase in overall genetic diversity or through the transfer of specific,

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adaptive alleles [39–42]. Moreover, hybridization can maintain or increase population sizes and counter extinction [43]. If hybridization allows for population persistence at the range edge, then this can provide more time and larger populations for new mutations to arise or genetic rescue via *intraspecific* admixture. Thus, hybridization can enhance the chances of local adaptation both directly by facilitating evolutionary innovation and indirectly by fostering the conditions in which mutation and gene flow among conspecifics generate local adaptation.

The potential for hybridization (as opposed to intraspecifc admixture or new mutations) to enable a species to expand its range comes with unique issues. Specifically, hybridization can lead to replacement of the resident species by the invading species or the breakdown of species boundaries [44,45]; both outcomes result in biodiversity loss. These issues are especially pressing, as climate change is associated with changes in community composition and spatial shifts in geographical distribution [46–48], and hybridization events will likely become more common [49,50]. Thus, studies are needed to evaluate the role of hybridization in the evolution of species ranges across diverse taxa.

The hypothesis that hybridization contributes to range expansion is not new and is often embedded in reviews on hybridization's role in adaptation and evolutionary innovation [36,40,51–53]. Here, we focus exclusively on the hypothesis that hybridization facilitates range expansion with the goals of: outlining how hybridization can enable a species to expand its range; describing predictions of the hypothesis and how to test them; and evaluating the limitations on hybridization's role in range expansions, especially hybridization's potential to collapse hybridizing lineages.

Before proceeding, we must clarify our terminology. First, 'hybridization' refers to interbreeding between evolutionarily distinct lineages, whereas 'introgression' refers to gene flow between species as a consequence of hybridization [34,38,54]. If hybrids are sterile or inviable, then introgression will not result. In this review, we refer only to cases where hybrids are viable and capable of at least some reproduction. We therefore use the terms hybridization and introgression interchangeably, even though they are not synonymous.

Second, we refer to range expansion as movement into a new environment that enlarges a focal species distribution. 'New' environments can refer to abiotic or biotic conditions that were previously not experienced by the focal species. 'New' can also represent environments with conditions similar to the ancestral environment but that vary in novel ways (e.g. same mean temperature, but different temperature ranges). Moreover, an 'enlarged distribution' refers to both the expansion of geographical boundaries within which a species occurs and the occupation of a greater diversity of habitats within existing geographical boundaries.

A further caveat to consider throughout is that range expansions occur not only when species adapt to new habitats, but also when they overcome dispersal barriers and occupy habitat resembling that in which they occurred previously [55]. We do not discuss this latter type of expansion. Nevertheless, even when organisms experience such shifts they are still likely to encounter novel conditions to which they must adapt. Moreover, it is worth noting that hybridization could play a role in such expansions if it makes overcoming dispersal barriers more likely (e.g. by modifying dispersal traits).

2. Hybridization's role in range expansion

Understanding whether and how hybridization enables a species to expand its range requires stepping back and describing what limits species ranges in the first place. In the absence of barriers to dispersal, the general theoretical explanation for species range limits is that populations at the geographical range limit (i.e. peripheral populations) are unable to adapt to novel, local environments that are encountered at the range edge [1,3,5,7]. By failing to adapt at the range edge, peripheral populations cannot be a source of dispersers beyond the existing boundary and are themselves likely to go extinct. In other words, these peripheral populations become population 'sinks' rather than become 'sources' of dispersers [3].

However, why might peripheral populations be unable to adapt to conditions at the range edge? One answer is that they lack the standing genetic variation that enables adaptation [15]. Populations at the range edge are potentially the product of serial founder effects that reduce genetic variation [55,56] and any such remaining variation consists of alleles that are adaptive in the ancestral, but not the novel range edge, habitat [1,3–6,12]. To the degree that peripheral populations receive an influx of alleles from other populations, they are most likely to receive alleles from the range centre (because such populations are sources of dispersal) and, again, these alleles are predicted to be maladaptive at the range edge [3,57].

Moreover, mutation, a source of novel genetic variation, is unlikely to contribute to adaptability in peripheral populations. The waiting time for adaptive new mutations is long, especially in small, declining populations such as those at the range edge [13–16]. Thus, peripheral populations can go extinct before such mutations arise and spread [18,36].

For a range expansion to occur, these limits on the adaptive potential of peripheral populations must be overcome by countervailing factors that foster adaptation. As indicated above, one such factor is admixture among conspecific populations, which can increase standing genetic variation and generate novel, adaptive combinations resulting in enhanced adaptability at the range edge [27,28,32,33,58]. Nevertheless, lack of genetic variation in peripheral populations and lack of new beneficial mutations can still restrict the extent to which genetic exchange among conspecific populations enhances their adaptability at the range edge [57,59].

Alternatively, hybridization by members of peripheral populations with an established resident species can enhance the adaptive potential of peripheral populations in two non-mutually exclusive ways. First, hybridization can sustain peripheral population sizes, so that new adaptive variants can arise via mutation before they go extinct [43]. For example, in many species, males and females hybridize rather than forgo mating altogether [60,61]. Provided hybrid offspring are at least partially fertile, rare dispersers can mate successfully, establish and subsequently sustain, new populations ([43]; but see [35,62] and §4 for discussion of how rare species can be overwhelmed by gene flow from the other species).

Second, introgression can transfer alleles from the resident species into the peripheral populations of the focal species [62–64]. This introgression has two possible consequences in the focal species: (i) it can result in the acquisition of alleles for key traits that are already adaptive in the new environment [35,36,39,51,52,65,66] and (ii) it could increase standing genetic variation and opportunities for the production of novel
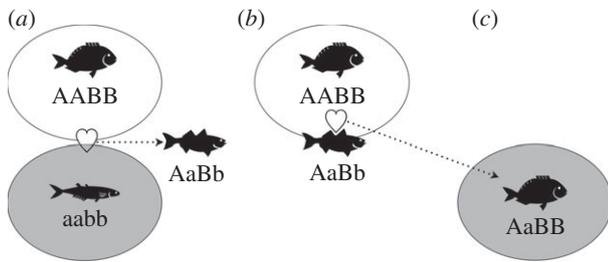
Figure 1. Hybridization can promote range expansion via its genetic effects. (*a*) Two species of fish (indicated by the different shapes and genotypes) that occupy different habitats (differential shading) hybridize and produce viable and fertile F_1 offspring, which (*b*) later backcross to one parental species. (*c*) As a result of introgression, one of the parental species acquires an allele (indicated as 'a') that enables adaptation and expansion into the other environment. Allele 'a' could encode for a key functional trait that is already adaptive in that environment. Alternatively, allele 'a' could represent additional genetic variation that interacts with other loci to take the species to a different adaptive optimum for that environment (see text).

genotypes/phenotypes on which selection can then act to facilitate adaptation [29,67–69] (figure 1).

In the case where hybridization transfers alleles for already adaptive traits, introgression enables an expanding species to 'adaptively capture' allelic variants that have already been tested, and confer adaptation, in the resident species ([39,42,63,64,67]; figure 1). Such transfer of key alleles or co-adapted sets of genes that code for already adaptive traits means that hybridizing populations can bypass unfavourable intermediate steps in adaptive evolution and thereby jump directly to the adaptive optimum in the new environment [34,39]. This scenario is most likely if key adaptive traits are underlain by major and/or linked loci or if selection on the key traits is strong. For instance, chromosomal inversions containing linked alleles for adaptive traits are prime candidates for adaptive introgression that facilitates range expansion [70,71]. Indeed, the spread of such co-adapted complexes can occur in a genome that is otherwise not introgressing because of the fitness costs or fitness trade-offs of hybridization [72,73].

In the case where hybridization increases genetic variation, hybridization might or might not result in adaptive evolution in peripheral populations; introgression simply serves as a source of new variation upon which selection can act (figure 1). Enhanced genetic variation derived from heterospecifics could counter inbreeding depression or even counter gene flow from central, maladaptive populations [62] if the influx of alleles from heterospecifics generates incompatibilities between conspecifics in peripheral, sympatric populations and central, allopatric populations (*sensu* [74]). Perhaps more critically, introgression of heterospecific alleles into the genetic background of the focal species can have significant impacts on population adaptability by increasing variation in existing phenotypes or by creating entirely new phenotypes (e.g. via heterosis or transgressive segregation; [51,75–79]). Thus, even the transfer of alleles that were previously neutral can increase adaptability once in the genetic background of the focal species.

3. Testing the hypothesis that hybridization facilitates species range expansion

Testing the hypothesis that hybridization facilitates a range expansion requires establishing that hybridization between

two species occurs (or has occurred) and that such hybridization is a causal factor in a range expansion by one or both species. In some cases, the spatio-temporal dynamics of a range expansion can provide evidence of whether hybridization contributes to range expansion (*sensu* [53,80]). Specifically, if a range expansion can be observed directly by comparing contemporary populations to historical populations (e.g. using museum specimens), then it could be possible to observe evolutionary shifts in: key functional traits (or their proxies) that confer adaptation; underlying genetic markers linked to those traits and frequency and biogeographic patterns of hybridization that are concordant with a range expansion (*sensu* [53,80]). As the impacts of invasive species and global change become more evident, such data might be obtainable [81,82]. In the absence of such data, indirect assessments of hybridization's role in range expansion require an integrated approach that combines ecological surveys, trait assays, fitness measures, and population and genetic analyses. In the following discussion, we highlight some of the major considerations to examine if—and how— hybridization enables a species to expand its range.

One of the key predictions of the hypothesis that hybridization enables a species to expand its range is that hybridizing populations or populations derived from them should occupy novel environments relative to ancestral environments. This prediction rules out the possibility that a species expanded its range geographically by occupying microenvironments to which it was already adapted in its ancestral range, as can occur when species overcome dispersal barriers or are human dispersed [8]. Satisfying this prediction also associates hybridization with occupation of the novel habitat, a pattern that would not necessarily be predicted if admixture among conspecific populations was enabling a species to expand its range.

However, although a positive association between hybridization and expansion into novel environments is consistent with the hypothesis that hybridization enables a species to expand its range, hybridization is often the *outcome* of range expansion [62,83,84]. Thus, associating hybridization with the occupation of new environments by a given species is insufficient to demonstrate that hybridization *enabled* the range expansion. Further evidence would be required to identify how, if at all, hybridization contributed to a range expansion.

(a) Introgression of adaptive alleles

If hybridization facilitates range expansion via introgression of already adaptive alleles, then hybridizing populations of the expanding focal species (or those derived from them) should possess adaptive traits that resemble those possessed by the resident species with which hybridization occurred (see also [29], e.g. [85]). These traits should differ from ancestral, allopatric traits in the focal species. Moreover, hybridizing populations of the focal species (or those derived from them) should occur in environments that are the same or similar to those of the resident species and these should differ from the focal species ancestral environment [39,86].

Critically, introgression should have occurred, with loci underlying the adaptive traits showing evidence of allelic transfer from the resident species to the focal species [39]. Specifically, peripheral populations should carry haplotypes of the resident species from the regions where they initially hybridized; the two species should exhibit greater genetic similarity in sympatric populations than in allopatric populations and introgression

should be evident at those loci for traits conferring success in the new environment [35,39,42,51,64,66,67,87,88]. In other words, there should be direct evidence that the expanding species acquired adaptive alleles from the resident species via hybridization. This final critical prediction rules out the possibility that the focal species converged on an adaptive trait via new mutations and/or gene flow among conspecifics.

An example in which this series of predictions appear satisfied comes from *Anopheles* mosquitoes. Specifically, *A. gambiae* expanded beyond its ancestral range in the rainforests of central Africa into arid environments of sub-Saharan Africa 3000–11 000 years ago. Adaptation to the arid environment is associated with a chromosomal inversion, *2La*, which is ancestral to the arid-adapted species *A. arabeinsis* [89]. Critically, genetic analyses have revealed that introgression from *A. arabeinsis* into *A. gambiae* resulted in the transfer of the *2La* inversion [63,65,66]. Thus, transfer of a key genomic region via introgression appears to have enabled *A. gambiae* to expand beyond its ancestral range by conferring adaptive traits in the novel habitat.

(b) Increased genetic variation

An alternative route by which hybridization enables range expansion is by increasing genetic variance that potentially generates novel types in populations of the expanding species [29,67,69,90]. Numerous reviews (and empirical studies cited therein) highlight hybridization's role in generating entirely new phenotypes that were previously not present in either parental species, making this scenario distinct from the introgression of adaptive alleles described above [32,35,38,39,51, 77,78,87,88,91–95]. This new variation can provide the substrate on which selection acts to promote adaptation [67] to environments at the range periphery or such variants can 'pre-adapt' hybridizing populations to invade new niches [96]. In such situations, the novel environment occupied by the expanding, focal species could differ from the ancestral environment of either parental species (although this need not be the case). Indeed, hybridization has long been known to produce hybrid lineages that invade entirely new environments that are distinct from those of the parent species [35,92,93,95,97–99].

If hybridization facilitates range expansion by increasing genetic variation, then populations that hybridize should show enhanced population fitness relative to populations that do not hybridize. Such populations should reveal novel traits, especially relative to ancestral populations of the focal species, and such novelty should stem from introgression at the loci involved in the production of those traits. Moreover, the particular traits (and underlying loci) involved might differ among different populations depending on the standing genetic variation in both the focal species and the resident species with which it hybridizes.

Whether hybridization facilitates range expansion via introgression of already adaptive traits versus an increase in genetic variation will likely depend on the nature and genetic architecture of traits that are adaptive. Generally, hybridization might be more likely to facilitate range expansion if a single functional trait (e.g. heat tolerance, desiccation resistance) confers adaptation to a new environment. If such traits are underlain by few or tightly linked loci (as in inversions [66]), then introgression of alleles at these loci could more readily occur [70,71]. Thus, hybridization might be

most likely to facilitate range expansions through the introgression of already adaptive alleles, and this would suggest that hybridization's impacts on evolutionary range expansions are narrowly restricted to such special cases. However, hybridization's imprint on range expansion might simply be more easily detected in those situations where loci for functional traits are known and introgression can be more readily identified. By contrast, hybridization's more subtle effect of enhancing genetic variation might go undetected [34]. Historically, identifying hybridization's subtle effects and tying them to range expansion was difficult, if not impossible. Emerging technologies now make it possible to ascertain hybridization's impacts across the genome [76,100] and to evaluate how introgressed alleles may interact with a new genetic background. Additional studies are needed to discern if, and how, hybridization affects genetic variation and adaptation during range expansion.

Regardless of whether hybridization results in introgression of already adaptive alleles or simply enhances genetic variation, descendants of hybrid populations can spread once they have adapted to the new environments. Population phylogeographic patterns could therefore reveal if and how hybridization facilitated a range expansion. A single hybridization event or region of contact (or a relatively small number of parallel events) might be sufficient to fuel subsequent spread of a focal species, especially if the acquisition of a key adaptive trait propels further expansion into the novel habitat. Thus, populations of the focal species within a new habitat might show no evidence of ongoing hybridization but they should be derived from those populations or regions where hybridization occurred. Alternatively, range expansions could be fuelled by repeated hybridization across different regions of contact between two species. In the case of adaptive introgression, such replicate hybridization should generate parallel instances of the acquisition of specific alleles at the loci underlying these traits and the subsequent spread of the focal species as a result [101]. By contrast, if hybridization fosters range expansion via enhanced genetic variation, then the population sources for range expansion would depend on standing genetic variation in those populations and historical context that shaped that variation (*sensu* [102]).

(c) Population maintenance

Hybridization could foster range expansion by enhancing population sizes in peripheral populations and preventing their extinction before adaptation occurs [103,104]. In this scenario, hybridization rates should be relatively high, especially when peripheral population sizes of a focal species are low [105]. Specifically, hybridization should be negatively associated with peripheral population size [105], and hybridizing populations should be larger and more likely to persist than populations without hybridization. Moreover, hybridization by the expanding species might be associated with particular mating behaviours such as mating with heterospecifics in the absence of conspecifics, forced copulations and harassment of heterospecific females, or competitive aggression against heterospecific males [60,61,106].

This prediction that hybridization rates should be high differs from what might be expected under the scenarios involving hybridization's genetic effects. If hybridization enhances range expansion via its genetic effects, then rates of hybridization need not be high, especially for the adaptive transfer of key loci

[34,87]. Moreover, unlike the above scenarios, the genetic signature of population maintenance by hybridization should be neutral patterns of introgression across the genome as opposed to enhanced introgression at adaptive loci. To the extent that peripheral populations locally adapt to the new environment, such adaptation should be driven by admixture among conspecific lineages or de novo mutations that arise in populations that are simply stable or persistent because of hybridization.

The notion that hybridization enables a species to expand its range by enhancing population sizes is not mutually exclusive of hybridization's genetic effects. Introgression that enhances adaptation and population fitness can contribute to higher rates of population increase [40]. However, even if hybridization does not lead to local adaptation, hybridization can generate transient fitness benefits that enhance population growth. Indeed, Drake [43] postulates a 'catapult effect' in which heterosis in the initial stages of contact between two species results in only transient fitness benefits to the hybridizing population; although transient, such benefits increase population sizes (i.e. 'catapult them') high enough to buffer them against extinction. This process was supported in ring-necked pheasant establishment in the USA [43] and in laboratory experiments [107].

4. Limitations on hybridization's role in range expansions

Whether hybridization has the above-mentioned effects potentially depends on the fitness consequences of hybridization. Generally, hybridization is deleterious, because hybrid offspring are often less fit than pure-species types [108–110]. Theory suggests that such deleterious hybridization can actually *limit* species geographical ranges, because hybridization depresses fitness in peripheral populations that are already vulnerable to extinction [1,5,111]. Essentially, hybrid zones become sinks, rather than sources, of dispersal. Indeed, deleterious hybridization can result in local extinction of rare species (and therefore cause range reduction), a possibility that can occur in conjunction with range expansion by the other species [35,112].

Yet, even when hybrids are viable and capable of interbreeding with each other or parentals, two problems remain. First, if hybrids are superior to parents in a particular habitat and capable of interbreeding with each other, they might become reproductively isolated (i.e. hybrids breed only with hybrids) from, and even competitively exclude, parental types [113]. Hybrid lineages might therefore occupy a restricted geographical area that is bounded by the parentals' ranges or they might actually displace parentals from a given habitat [35]. Thus, although hybrid speciation enhances species richness and the diversity of niches occupied by a taxonomic group, they do not necessarily result in the evolutionary range expansion of a focal species.

A second problem arises when hybridization generates introgression: species (or other distinct evolutionary groups) could potentially collapse [114,115]. The collapse of two distinct lineages (including what might be considered 'good species') into a single admixed population might result in a single species with an overall larger range than before, but at the cost of biodiversity loss. Moreover, for rare species, hybridization with a more common species can lead to their extinction via genome swamping from the common species [35]. Given

that an expanding species is likely to be rare at the range periphery, this extinction risk could be significant [35,62] so that, as when hybrid fitness is low, hybridization could actually limit—rather than expand—a species range.

Therefore, hybridization will generate a range expansion in a focal species when sufficient introgression confers genetic benefits in the peripheral populations, but introgression is not so great as to break down species integrity. At least three resolutions to the problem of maintaining species boundaries in the face of introgression exist. First, hybridization might carry high costs but be a relatively rare event. If costly hybridization is rare, then it would not likely depress peripheral population fitness to the point of enhancing extinction risk or generate swamping effects on the genome of the focal species. Yet, such hybridization could still generate sufficient gene exchange of novel allelic variants [38,73]. Indeed, if an introgressed allele or haplotype is adaptive, then it could spread relatively quickly throughout a population [116]. For example, in human evolutionary history, hybridization might have been both costly and rare [117,118]. Nevertheless, despite its costs, rare hybridization might have facilitated the spread of adaptive loci that contributed to range expansion by modern humans into novel habitats [64].

A second, related solution is that gene exchange could occur only in the early stages of contact between two species (i.e. when a species first moves into a new environment) [29]. When hybridization is costly, natural selection is expected to favour the evolution of traits that minimize the likelihood of hybridization [110,119–122]. Thus, in the early stages of contact, hybridization rates can be high but then subsequently decline, especially if the two species initially mate indiscriminately [29,123,124]. The influx of genes from the resident species into the expanding species during this initial period could be sufficient to facilitate local adaptation, even if hybrids are disfavoured (note that population fitness could concomitantly increase with declining hybridization).

A final solution to the problem of gene exchange is the potential for hybridization to generate fitness trade-offs. In particular, hybridization might be beneficial in some contexts but not in others [125]. Alternatively, it might represent the 'best of a bad situation' (as when hybridizing is better than not reproducing at all [60]). In systems where hybridization involves fitness trade-offs, hybridization will contribute to gene exchange at those loci underlying traits that are either neutral or adaptive. Yet, in that same system, genes underlying the traits that confer low hybrid fitness will not introgress [73]. Moreover, in those contexts where hybridization is disfavoured, selection will favour traits that maintain species boundaries [126]. Such trade-offs can thereby contribute to semipermeable species boundaries where ongoing hybridization fosters gene exchange between species without the complete breakdown of species boundaries (*sensu* [73]).

5. Conclusion

Hybridization is increasingly recognized as a potentially important contributor to the origins of evolutionary novelty and niche-width expansion [38,40,51,73,77,90]. Nevertheless, whether and how hybridization impacts species range dynamics remains largely unknown.

Evaluating hybridization's role in species range dynamics is important, because the evolution of species ranges remains

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an enduring problem in ecology and evolutionary biology [1,5,127] with critical downstream consequences. Species that undergo range expansions will encounter new species and thereby generate novel ecological and evolutionary dynamics that can impact trait evolution and population dynamics of the resident species [112], as well as alter ecosystem and community dynamics [90,127–129]. In the light of global biodiversity threats and movement of species, hybridization is not merely a question of academic interest, but one that impinges on issues of conservation and public policy [130,131]. Thus, evaluating the factors that drive range expansions is not only crucial for explaining the distribution of biodiversity, but also for understanding biodiversity's origins, maintenance and conservation. Ironically, hybridization—a process that can collapse species and limit species distributions—might be a factor that enhances a species' potential for expanding into and adapting to, new environments. Whether hybridization's effects are broadly important or applicable only to relatively few species or taxonomic groups remains an open empirical question.

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