



# Conservation and Hybridization in a Time of Global Change



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Human activities have caused a number of profound changes to global-scale earth systems. One important impact of these changes on the biosphere has been the breakdown of geographic and ecological reproductive barriers. This has resulted in novel hybridization events between previously separated species. Contact between these species is driven primarily by the movement of species to new locations through direct human activity, by the decline of ecological barriers, usually maintained by reproductive phenology (timing) and pollinator specialization or, increasingly, as a result of species' range shifts in response to climate change. Hybridization has been identified as a potential threat to biodiversity due to its role in the evolution of invasiveness and the impacts of genetic and demographic swamping. However, an increasingly nuanced understanding of hybridization as an evolutionary force has led some to propose that it may also represent a pathway for rapid species adaptation to climate change. This paper reviews the literature on the causes, impacts and conservation implications of hybridization and their relation to global change, with a particular focus on plants. Additionally, the paper discusses recent debates on both natural and human-assisted hybridization as possible pathways for species to adapt to climate change and argues for a nuanced approach, rooted in the precautionary principle, to be considered for both possibilities. Future research on this topic should investigate more cases of both past and novel hybridization events. This should be done in order to clarify the ecological impacts of hybridization and to inform the development of explanatory and decision-making frameworks that account for variability.

## AUTHOR SUMMARY

Over the past few centuries, human activities have driven a number of changes to the earth's ecosystems, some of which have resulted in the collapse breaking down of reproductive barriers between species long considered to be separate, thus leading to the formation of hybrid organisms. In this article, I review the current literature on ways in which invasive species and climate change drive hybridization events in plants and how these events impact both the species directly involved directly and the larger ecosystems in which they live. I then explore examine some of the implications that these events have for species conservation and argue for the importance of developing

a flexible research and policy framework for responding to these events when they happen.

## INTRODUCTION

Over the last several centuries, humanity has become an increasingly important force in shaping the character of global-scale earth systems. As human societies have industrialized and globalized, they have triggered significant changes to the biosphere and the climate system, which have, in turn, resulted in changes to the global distribution of species (Steffen et al., 2007; Vitousek, 1994). Revolutions in transportation technology and the establishment of global trade networks have led to both intentional and unintentional introductions of exotic species to new locations, as well as the ecologically damaging proliferation of certain invasive species (Westphal et al. 2008; Hulme 2009). At the same time, the widespread use of fossil fuels is driving a global warming event, which is forcing the migration of a number of species in order to live within their preferred climate conditions (Thomas 2010; Chen et al. 2011; Román-Palacios and Wiens 2020).

One important impact of these human-driven changes in species distribution is the breakdown of geographic and ecological reproductive barriers between certain species, resulting in contact and hybridization that would not have otherwise occurred. Interspecies hybridization occurs when two individuals from different species mate and produce offspring (Soltis and Soltis 2009). In most species, there are biological barriers to hybridization that prevent the production

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of viable hybrid offspring. For others, however, the only barriers to hybridization are geographic isolation or differing ecological niches. When human activities cause changes to a species' geographic distribution or ecology, it can lead to novel hybridization events.

In many cases, these events appear to result in negative ecological outcomes, such as the creation of new invasive species or a loss of biodiversity (Rhymer and Simberloff 1996; Schierenbeck and Ellstrand 2009; Todesco et al. 2016). However, in recent decades, biologists have also come to understand hybridization as an important evolutionary force for many taxa, potentially allowing them to adapt quickly to new conditions (Rieseberg 1995; Mallet 2007; Soltis and Soltis 2009). These competing interpretations of the significance of hybridization have produced a unique tension in the debate over how conservationists should respond to the trend of novel, human-driven hybridization events.

## HYBRIDIZATION IN EXOTIC AND INVASIVE SPECIES

### Breaking Down Barriers

Hybridization occurs when the reproductive barriers between two or more species are in some way broken down, allowing for potential reproductive contact between those species. As human society becomes increasingly globalized, the resulting movement of species, both intentional and unintentional, provides many more opportunities for this kind of contact. Indeed, while a global increase in hybridization due to human-mediated species movement has not yet been conclusively demonstrated, many examples of exotic-native and exotic-exotic hybrids have been documented. In a few well-studied regions, such hybrids have been found to make up a substantial portion of the total hybrid flora (Vallejo-Marín and Hiscock 2016). For example, in a survey of plant species in Britain and Ireland, Preston and Pearman (2015) found that about 15% of known hybrid taxa were formed as a result of in situ hybridization events between a native and an exotic species or between two exotics. Guo (2014) found similar numbers of exotic-native and exotic-exotic plant hybrids (185 out of 941 documented hybrids or 16.43%) in the United States.

Exotic species introduction can break down reproductive barriers and elicit contact between formally isolated species in a few different ways. Perhaps the most obvious of these is by bringing together species that have been geographically separated but are still capable of producing viable hybrid offspring. Additionally, human-mediated movement of species can break down reproductive barriers between species already sharing the same habitat in ways that are much less obvious. For example, species of the genus *Tragopogon* that have been introduced into North America appear to hybridize much more often with each other than in their native European ranges. This may be

because in Europe, each species is serviced by a more specialized set of pollinators, while in North America, they are visited by generalist species that are more likely to visit other *Tragopogon* species, thus increasing the likelihood of hybridization events (Soltis and Soltis 2009). Similar breakdowns of ecological barriers may also occur if species are introduced into new climates that disrupt flowering or growth phenology (timing). This can cause a reproductive overlap between species.

### Hybridization as a Cause of Invasion

In a then controversial review paper published in 2000, Ellstrand and Schierenbeck suggested that hybridization may be an important factor contributing to the evolution of invasiveness in plants. This claim has since become much more widely accepted as more evidence has been collected and as the possibility of invasiveness “evolving” has itself become more widely accepted. In a 2009 follow-up to their original review, Schierenbeck and Ellstrand found 35 examples of invasive plant taxa from 16 different families that formed through a hybridization event. This was a 30% increase from the number of taxa found in their 2000 review. Although such examples are still relatively rare, several more have since been documented, further supporting a link between hybridization and invasiveness (LaRue et al. 2013; Li et al. 2016; Welles and Ellstrand 2020). For instance, the knotweed *Fallopia x bohémica*, a hybrid of the common invasive knotweeds *F. japonica* and *F. sachalinensis* appears to be much more invasive than either parental species (Parepa et al. 2013; Figure 1a).

Over the past few centuries, human activities have driven a number of changes to the earth's ecosystems, some of which have resulted in the collapse breaking down of reproductive barriers between species long considered to be separate, thus leading to the formation of hybrid organisms. In this article, I review the current literature on ways in which invasive species and climate change drive hybridization events in plants and how these events impact both the species directly involved directly and the larger ecosystems in which they live. I then explore examine some of the implications that these events have for species conservation and argue for the importance of developing a flexible research and policy framework for responding to these events when they happen.

Several possible explanations for the apparent connection between hybridization and invasiveness have been proposed. In the case of *Fallopia x bohémica*, the cause may lie at least partially in the high phenotypic variability of the hybrid relative to either parent (Parepa et al. 2013). Such variation is a common feature of hybrid taxa, and by producing individuals with a variety of combinations of characteristics, including some outside the range of either parent, it may increase invasiveness by allowing hybrids to better colonize



**Figure 1.** Invasive species and hybridization: (a) *Fallopia x bohémica*<sup>1</sup>, (b) *Typha angustifolia*<sup>2</sup>, (c) *Spartina alterniflora*<sup>3</sup> and (d) *Senecio madagascariensis*<sup>4</sup>

varied and disturbed habitats (Rieseberg 1995; Dittrich-Reed and Fitzpatrick 2013; Figure 2a). Interestingly, hybridization may facilitate invasion even in cases where adaptive traits are not manifested. This occurs when hybridization with a more established species allows a density dependent exotic species (species in which individual fitness is connected to population density) to survive the early stages of colonization when their numbers are still low (Mesgaran et al. 2016). Other possible explanations include “hybrid vigor,” a phenomenon in which increased fitness occurs in early generations following a hybrid event, and the purging of non-lethal deleterious genes during the process of hybridization (Schierenbeck and Ellstrand 2009).

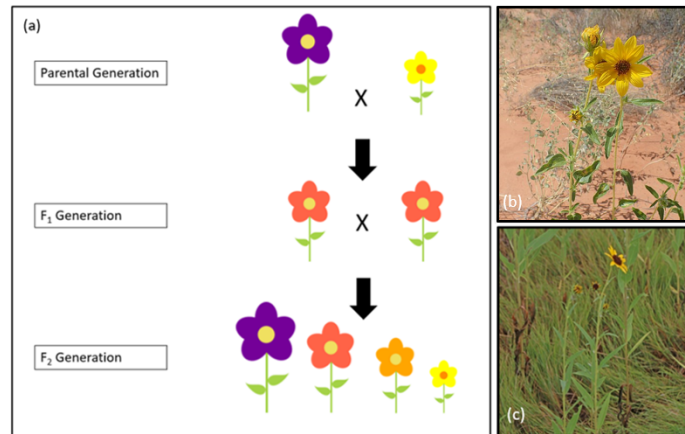
Like most factors that have been implicated in the evolution of invasiveness, hybridization should not be seen as a guarantee of invasive status across all contexts, and indeed, may constitute a relatively weak factor. If hybridization were a major cause of invasiveness, plant families that are more hybridization-prone would likely contain more invasive species. This, however, does not appear to be the case, possibly due to reproductive and ecological barriers connected to the genetic and phenotypic similarity between members of these families (Whitney et al. 2009). Still, the number of hybrid taxa that have become invasive does seem to demonstrate a link between hybridization and invasiveness, one that may prove useful in predicting future outbreaks of new invasive species and in managing current ones (Schierenbeck and Ellstrand 2009; Whitney et al. 2009).

### Hybridization as an Impact of Invasion

In addition to being a potential factor in the evolution of plant invasiveness, hybridization can also be a source of ecosystem damage caused by existing invasives when they interbreed with native species (Vilà et al. 2000; Todesco et al. 2016). This is especially the case when the native species is rare or threatened. In these situations, hybridization can lead to further decline, local extirpation or even extinction.

Depending on the viability of the hybrid offspring produced, hybridization with an invasive species can cause native species to decline, be extirpated or go extinct in a few different ways. The first is through ecological competition with a viable hybrid offspring that is fitter than one or both parents. The invasive cattail hybrid *Typha x glauca*, for example, grows to be much taller than either its exotic parent *T. angustifolia* or its native parent *T. latifolia* (Zapfe et al. 2015; Figure 1b). As a result, it tends to outcompete both parents, along with most native species, and forms monospecific stands along the shores of midwestern lakes (Bunbury-Blanchette et al. 2015).

Another way in which invasive hybridization impacts native plant species is through genetic swamping, a process by which native genotypes are replaced by hybrid individuals (Todesco et al. 2016). In the salt marshes around San Francisco, for example, the common native cordgrass species *Spartina foliosa* hybridizes with the exotic *S. alterniflora* (Daehler and Strong 1997; Figure 1c). Even though *S. alterniflora* populations are relatively small, they have higher male fitness than *S. foliosa*. Individual *S. foliosa* plants with eggs fertilized by *S. alterniflora* pollen thus have



**Figure 2.** (a) Transgressive segregation in plant hybrids. When two species hybridize, they produce offspring in the F<sub>1</sub> generation that possess characteristics that are intermediate between those of the two parents. When members of the F<sub>1</sub> generation mate with each other, however, segregation results in individuals from the F<sub>2</sub> generation that possess a wide range of allelic combinations, including some that result in phenotypes outside the range of either parental species. These individuals, if they are viable, may be able to take advantage of extreme conditions that neither parent species would be able to survive. The hybrid sunflowers *Helianthus anomalus*<sup>5</sup> (b) and *Helianthus paradoxus*<sup>6</sup>(c), for example, are able to live on dry dunes and in salt marshes that would be inhospitable to either of their parent species.

much larger seed sets than those fertilized by their own species (Anttila et al. 1998). As a result, hybridization is common and there is a high risk of local extirpation for *S. foliosa* due to the dilution of its genome. Fortunately, widespread restoration efforts have done much to address the issue (Ayres et al. 2004; Ort and Thornton 2016).

Finally, invasive hybridization can result in demographic swamping. This occurs when the population growth rate of a native species is reduced as a result of widespread, non-viable hybridization with another species (Todesco et al. 2016). Although demographic swamping seems to be much less common than genetic swamping, it may contribute in some cases to local extinctions or declines, especially in rarer species. The native Australian ragwort *Senecio pinnatifolius*, for example, can produce offspring with the invader *S. madagascariensis*, but these hybrid individuals rarely survive to adulthood. This wasted reproductive effort by *S. pinnatifolius* may eventually lead to demographic swamping if populations of *S. madagascariensis* grow large enough (Prentis et al. 2007; Figure 1d).

Compared to other impacts that invasive species can have on native taxa, the actual risk associated with hybridization may be relatively low. In a recent review of 870 species in the IUCN's Global Invasive Species Database, Hirashiki et al. (2021) found that while 35 species are cited as potential threats to native taxa through hybridization, direct evidence of hybridization occurring between these species and native taxa is only provided for 16. This should not undermine the importance of hybridization in cases where it

does represent a well-documented threat to native species nor discourage future attempts to document risk in cases where in-depth research is currently lacking.

### HYBRIDIZATION AND CLIMATE CHANGE

Although research into the impacts of climate change on species hybridization is not nearly as well-developed as research into the impacts of invasive species, the work that has been done points towards a possible positive relationship. A few studies have implicated the geographic and climatic changes associated with past glaciations as potential drivers of hybridization and hybrid speciation, either through physical habitat disturbance or through species migration in response to the advance and retreat of ice sheets (Becker et al. 2013; Guo 2014; Marques et al. 2016). The extent to which modern climate change results in hybridization will likely depend substantially on the extent to which species' range shifts result in novel overlap in the ranges of closely related species. Recent studies of the overall impacts of climate change on ecosystems suggest that many species may struggle to track changes geographically, suggesting a low risk of hybridization (Román-Palacios and Wiens 2020; Krosby et al. 2015). The documentation of a few novel hybrid zones that have formed as a result of climate change, however, indicate that a relationship between climate change and hybridization does exist, even if its strength is not yet clear (Chunco 2014; Gómez et al. 2015).



### Climate Change as a Cause of Hybridization

As with direct anthropogenic movement of species, climate change is expected to cause hybridization when it leads to the breakdown of reproductive barriers between species. This could happen in a few different ways, the most obvious being through species' range shifts. Both contemporary observation and studies of the responses of biological systems to past climate change have established range shifts as an important response to climate changes and that these shifts can result in the formation of novel species assemblages (William and Jackson 2007; Thomas 2010). According to a 2011 meta-analysis by Chen et al., recent range shifts towards higher latitudes in response to climate change were occurring at a median rate of ~16.9 km per decade, while range shifts towards higher elevations were occurring at ~11.0 m per decade. More recent studies have suggested, however, that many species will not be able to track favorable climate conditions in the long term, with Román-Palacios and Wiens (2020) suggesting that 57-70% of the 538 species they studied could face this problem. For those species that are able to shift their ranges, the likelihood of widespread hybridization will depend on factors such as the commonality and ecological success of the species involved, as well as the number of species in the new range with which hybridization can occur (Krosby et al. 2015).

Phenology shifts – changes in the timing of life history events – may be another cause of climate change-induced hybridization events (Chunco 2014; Vallejo-Marín and Hiscock 2016). Phenology has been demonstrated to be a limiting factor for gene flow between species, subspecies and individuals that share the same habitat, but time their life cycles according to different stimuli (Martin et al. 2007; Bonner et al. 2019). Because different species appear to change their phenology in response to different climatic or non-climatic stimuli, it is possible that climate change will result in the reproductive overlap between certain species that formally relied at least in part on differences in phenology to prevent hybridization (Visser and Both 2005; Donnelly et al. 2011). Gérard et al. (2006), for example, predicted that hybridization between the ash species *Fraxinus excelsior* and *F. angustifolia* may increase at their hybrid zone since their primary reproductive barrier appears to be their differing flowering phenologies.

Climate change may lower reproduction barriers and encourage hybridization in other ways as well. Besides the timing of life cycles, changing climatic conditions drive hybridization by impacting other factors related to reproduction, such as pollen production (Gallego-Tévar et al. 2019). There is also some evidence that climate change may increase the fitness of certain invasive plant species or allow certain exotic species that were previously limited by climatic conditions to become invasive or at least survive

in places where they are currently unable to (Hellman et al. 2008; Mainka and Howard 2010). This, in turn, could lead to more contact between native and exotic species and more opportunities for hybridization (Vallejo-Marín and Hiscock 2016; Klonner et al. 2017). Warming temperatures may also contribute to the lowering of the gametic barrier known as “triploid block.” This phenomenon occurs when a diploid species and a tetraploid species hybridize, usually resulting in endosperm failure (Bretagnolle & Thompson 1995; Köhler et al. 2010). This outcome can be circumvented, however, in cases where the hybrid is formed from gametes that have failed to complete meiosis, a phenomenon which occurs more frequently in plants experiencing the sorts of extreme temperature conditions that may result from climate change (De Storme and Mason 2014; Vallejo-Marín and Hiscock 2016).

### Impacts of Climate-Induced Hybridization

Since very few cases of climate change-induced hybridization have been documented, it is difficult to generalize its impact and, in fact, it may continue to be difficult, even if more cases are documented. On one hand, climate change may result in more situations like those described above, in which hybridization represents a conservation concern. Of the thirteen novel climate change-induced hybrid zones identified by Chunco (2014), seven are thought to represent possible or definite threats to at least one of the hybridizing species. In a study of the impacts of encroachment by lower-altitude species on the habitat of rare, alpine plants in the Sierra Nevada mountains of southeastern Spain, Gómez et al. (2015) found that around 25% of endemic flora were already beginning to hybridize with lowland invaders, suggesting that hybridization, along with competition, may represent a real threat to alpine species as the climate warms. The possibility of climate change increasing the fitness of invasive species or creating new ones, as well as breaking down barriers between them and native species, may increase the risks associated with invasive species hybridization as well. Gallego-Tévar et al. (2019), for example, found that higher temperatures during the breeding season increased the likelihood of the formation of *Spartina maritima* x *densiflora* hybrids, which represent an important competitive threat to the endangered *S. maritima* on the coast of the Iberian Peninsula. Theoretical work by Klonner et al. (2017), on the other hand, suggests that climate change will not necessarily cause an increase in native-exotic hybridization across all taxa, at least in Europe.

At the same time, hybridization has also been proposed as a potential path of rapid evolution by which some species may be able to adapt to climate change. While it is important to note that no current cases of this have been documented, a study by Becker et al. (2013) suggests that hybridization between plants in the New Zealand endemic



genus *Pachycladon* may have helped them survive the last glaciation. Connections between hybrid speciation and glaciation in North America identified by Guo (2014) also suggest a potential correlation between climate change events and hybridization. When first generation ( $F_1$ ) hybrids mate with each other, some of their offspring in the second generation ( $F_2$ ) may possess phenotypes outside the range of either parent species due to transgressive segregation (Soltis and Soltis 2009; see Figure 2). As a result, these individuals may be better adapted to certain extreme conditions than either parent. Multiple hybridization events between the sunflower species *Helianthus annuus* and *H. petiolaris*, for example, have resulted in the evolution of at least three separate species which are able to live in dry dune and salty marsh environments that neither parent is able to colonize (Rieseberg et al. 2007). It has therefore been suggested that hybridization may allow certain species to rapidly adapt to extreme conditions resulting from climate change, either through transgressive segregation or increased genetic and phenotypic diversity from the mixing of parental genomes (Hamilton and Miller 2016; Janes and Hamilton 2017; Charles and Stehlik 2021).

Interestingly, a hybrid may not need to be especially fit relative to its environment in order to contribute positively to its parent species' response to climate change. Pfeilsticker et al. (2022), for example, suggest that as the rare Tasmanian *Eucalyptus risdonii* and the more common *E. amygdalina* both shift their ranges in response to climate change, hybridization events may help the slow-dispersing *E. risdonii*, despite the reduced fitness of the resulting hybrid. This is because fitness can be restored in later generations by backcrossing – events in which a hybrid individual reproduces with a purebred member of one of its parent species. Because *E. risdonii* pollen can travel relatively far, it can produce hybrids with *E. amygdalina* along the border of its range and then quickly backcross with those hybrids. As *E. amygdalina* continues to decline in this area, backcrossing between *E. risdonii* and its hybrids would become more likely and eventually result in the “resurrection” of *E. risdonii* as its phenotypes come to dominate the population. This may represent a way for *E. risdonii* to track changes in the climate faster than it otherwise would, due to its seed's poor dispersal abilities.

## DISCUSSION

Factors contributing to contemporary global change – anthropogenic climate warming and the transplanting of species to new locations as a result of human activities – represent a source of new and possibly increasingly common hybridization events. Through the breakdown of reproductive barriers, these phenomena have led to contact and hybridization between species previously separated by geography, climate, phenology and pollinator preference,

among other factors. There is some controversy over how these hybridization events should be viewed from a biodiversity and conservation perspective. On one hand, a myriad of documented cases of the negative impacts that hybrid taxa can have on parental species and on other species in an ecosystem suggest that hybridization is yet another threat to biodiversity driven by global change. On the other hand, the increasingly clear understanding of hybridization as an evolutionary pathway, and thus a potential source of biodiversity, has caused others to suggest that, in some cases, it may represent a source of rapid adaptation to these very changes.

Arguing for this latter position, some have even gone as far as to suggest that human-enabled interspecific hybridization may represent a possible management strategy for increasing evolutionary potential in the face of climate change (Hamilton and Miller 2016; Janes and Hamilton 2017; Charles and Stehlik 2021). While certainly interesting, these ideas should be carefully vetted in the spirit of the precautionary principle. As Kovach et al. (2016) point out, the difficulty that invasive species ecologists have had in determining the factors that contribute to invasiveness and predicting which species will become invasive does not bode well for our capacity to predict how a new hybrid will behave in whatever ecosystem it gets released into. While hybridization is no longer seen as an absolute evolutionary dead end, there remains a danger of the new hybrid experiencing outbreeding depression – a collapse of fitness that can occur in hybrid lineages. Finally, taking a chance with such uncertainty may not even be necessary – it is possible that many species will be able to adapt to climate change (at least up to a certain point) through phenotypic plasticity and niche shifting alone (Merilä and Hendry 2014; Román-Palacios and Wiens 2020). Yet, it should be noted that recent attempts to provide proof-of-concept for the efficacy of deliberate hybridization have had some success. A study of two pairs of lab-crossed hybrids between species of *Acropora* coral found that at least some members of the  $F_1$  generation were more resilient in the face of higher temperatures and elevated levels of dissolved  $CO_2$  (Chan et al. 2018). The authors of the study note that the fitness of the hybrids in the wild and over multiple generations remains unknown, but nonetheless provide an important example of research that would be needed to reduce the uncertainties involved in this type of intervention.

Separate from the question of deliberate, human-enabled hybridization is that which concerns the conservation response to the possibility of “naturally” forming hybrids that are well-adapted to climate change. Given the documented cases of hybrid taxa responding well to other anthropogenic sources of disturbance (Abbot et al. 2000; Kays et al. 2010), there is little reason to suspect that this could not also be the case with climate change. One frequently raised criticism of embracing taxa that adapt well to human-



modified conditions (as signs of nature's ability to go on even in spite of human activity, for example) is that doing so allows people to avoid responsibility for changing those conditions (Hiltner 2018). Another way of thinking about this criticism is through the concept of feasibility. In the field of restoration ecology, feasibility broadly refers to how easily a restoration project can be completed (Hopfensperger et al. 2007). A project can have higher or lower feasibility depending on a number of ecological, technical, economic and social justice factors, as well as the weight that those executing the project give to these factors. In emphasizing taxa (hybrid or otherwise) that are able to adapt easily to modified conditions, one might be able to imagine an argument against a particularly expensive (less economically feasible) restoration project because there are species that are able to adapt to these conditions anyway. This argument can be countered, however, by pointing out the tendency for these highly modified conditions to result in homogenized, less biodiverse communities, a phenomenon which hybridization may further exacerbate (Olden et al. 2004; McKinney 2006). It is also unclear whether more adaptable taxa will be able to ecologically replace certain eliminated species by acting in the important functional roles they once filled (Bensen et al. 2017; Ottenburghs 2021). Therefore, assuming one's goal is maximum biodiversity and the more resilient ecosystems that come with it, it makes little sense to over-embrace highly adaptable or hybrid taxa until one has taken every possible step to bring about conditions that encourage existing, native species and functional diversity.

Climate change may well adjust the outcome of these sorts of deliberations. Unlike habitat destruction, the impacts of climate change may turn out to be effectively irreversible, meaning that restoration of previous climate conditions in a particular location would be impossible, at least for a very long time. It is also likely that some areas will develop novel climate conditions unlike those currently existing anywhere on the planet (Williams et al. 2007; Burke et al. 2018). Under such conditions, riskier conservation interventions such as human-assisted species relocation or hybridization may become significantly more attractive, along with embracing a more gene-focused outlook on conservation in general. Such an outlook would likely place much more value on hybrids or other taxa that are able to easily adapt to new conditions as potential sources of future diversification, while also deemphasizing more species-centric threats, such as genetic swamping (Chan et al. 2019; Hirashiki et al. 2020). At the very least, natural hybridization may well end up as an occasional ally for conservationists working to maximize adaptive capacity in existing taxa through less risky tactics, such as preserving climate refugia, building habitat connectivity and managing for compounding threats to vulnerable species. Meanwhile, riskier interventions, such as human-mediated hybridization, should continue to be

evaluated according to the success of these less risky tactics, the innate abilities of species to move or adapt and the results of research similar to that performed by Chan et al. (2018) into the efficacy of human-mediated hybridization as an intervention for specific threatened taxa.

### **CONCLUSION AND FUTURE DIRECTIONS**

The above discussion attempts to examine the implications of a few of the most important questions involved in the relationship between hybridization and biodiversity conservation. However, since much is still unknown about the relationship between hybridization and global change, it remains difficult to formulate a general conservation response to the patterns described in this review. Today, very few conservation laws and agencies offer guidance on how hybrids should be treated from a conservation perspective (Hill 1993; Ellstrand et al. 2010), leaving them open to inconsistent application (Pieltt et al. 2015) and, in some cases, political attack (Fears 2019). The filling of this gap with well-informed, flexible policy guidelines represents an important goal that conservation biologists should pursue, especially if cases of novel hybridization are indeed becoming more common. In light of both its positive and negative impacts, future work on hybridization should focus on studying as many cases as possible, with the goal of developing explanatory and decision-making frameworks that make use of what generalizations can be identified while also taking variability into account (Allendorf 2001; Chan et al. 2019).

Care should be taken in studying hybrids to search out cases of harmful, benign and adaptive hybridization in order to determine the relative frequency of all three, as well as how factors such as the rarity of parental species, the presence of an exotic parent and the fitness of the hybrid offspring affect its eventual status. Studying this latter factor, in particular, may help to answer the question of what sorts of ecological impacts a theoretical climate-adaptive hybrid may have and whether or not it would be likely to display invasive behavior. Studying hybrids on the genetic level may also allow conservationists to better detect and characterize hybrid populations, as well as understand how factors such as the amount and identity of exchanged genetic material may contribute to negative impacts, such as genetic or demographic swamping, or positive, adaptive outcomes of hybridization (Ottenburghs 2021).

A particular focus should be placed on seeking out and studying cases of contemporary, climate change-induced hybridization events, as very few have thus far been documented in spite of the high probability that they will at least occasionally occur. As suggested by Chunco (2014), existing datasets that seek to track species' range shifts and phenology changes in response to climate change can be used to predict future breakdowns in



geographical and ecological reproductive barriers or to look for existing areas of contact that may have already produced novel hybrids. Examining possible cases of hybridization resulting from past climate change events may also help to inform predictions of the extent and ecological impacts of contemporary hybridization. Finally, further research ought to be done into specific taxa that may benefit from human-mediated hybridization as a conservation intervention. Carefully controlled experiments might then be performed to investigate the invasive potential of hybrids, their long-term fitness and other dimensions related to the risk and efficacy of these proposals.

### PHOTO CREDITS

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### CONFLICTS OF INTEREST/DISCLOSURE

The author declares no conflicts of interest.

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