

The genic view of hybridization in the Anthropocene

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Abstract

Human impact is noticeable around the globe, indicating that a new era might have begun: the Anthropocene. Continuing human activities, including land-use changes, introduction of non-native species and rapid climate change, are altering the distributions of countless species, often giving rise to human-mediated hybridization events. While the interbreeding of different populations or species can have detrimental effects, such as genetic extinction, it can be beneficial in terms of adaptive introgression or an increase in genetic diversity. In this paper, I first review the different mechanisms and outcomes of anthropogenic hybridization based on literature from the last five years (2016–2020). The most common mechanisms leading to the interbreeding of previously isolated taxa include habitat change (51% of the studies) and introduction of non-native species (34% intentional and 19% unintentional). These human-induced hybridization events most often result in introgression (80%). The high incidence of genetic exchange between the hybridizing taxa indicates that the application of a genic view of speciation (and introgression) can provide crucial insights on how to address hybridization events in the Anthropocene. This perspective considers the genome as a dynamic collection of genetic loci with distinct evolutionary histories, giving rise to a heterogeneous genomic landscape in terms of genetic differentiation and introgression. First, understanding this genomic landscape can lead to a better selection of diagnostic genetic markers to characterize hybrid populations. Second, describing how introgression patterns vary across the genome can help to predict the likelihood of negative processes, such as demographic and genetic swamping, as well as positive outcomes, such as adaptive introgression. It is especially important to not only quantify how much genetic material introgressed, but also what has been exchanged. Third, comparing introgression patterns in pre-Anthropocene hybridization events with current human-induced cases might provide novel insights into the likelihood of genetic swamping or species collapse during an anthropogenic hybridization event. However, this comparative approach remains to be tested before it can be applied in practice. Finally, the genic view of introgression can be combined with conservation genomic studies to determine the legal status of hybrids and take appropriate measures to manage anthropogenic hybridization events. The interplay between evolutionary and conservation genomics will result

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in the constant exchange of ideas between these fields which will not only improve our knowledge on the origin of species, but also how to conserve and protect them.

KEYWORDS

climate change, conservation, genomics, hybrid zones, introgression, speciation

1 | INTRODUCTION

Human activities are affecting global environmental processes and patterns, from rapid climate change and radical land-use changes to the introduction of exotic species, prompting some scientists to declare that we have entered a new era: the Anthropocene. The exact start of the Anthropocene has been a matter of debate and its onset has been connected to different events, such as the rise of deforestation and agriculture (Ruddiman, 2003), the Columbian Exchange of species between the Old World and the New World (Lewis & Maslin, 2015), the Industrial Revolution in the 1800s (Crutzen, 2002), and the population growth and industrialization during the mid-20th century (Steffen et al., 2015). Based on the increase in the use of certain materials (e.g., aluminum, plastics, concrete), the nuclear fallout of atomic bomb testing, the geochemical signatures of particular compounds (e.g., polyaromatic hydrocarbons and pesticides), and the atmospheric rise in carbon concentrations, Waters et al., (2016) proposed a lower boundary for the Anthropocene during the mid-20th century. In this review, I will follow this definition to provide a clear distinction between hybridization events that occurred before or during the Anthropocene.

Anthropogenic developments affect the distribution of numerous species, often resulting in secondary contact between previously allopatric taxa. If these taxa are closely related and reproductive isolation is incomplete, hybridization might occur. In this review, I will define hybridization following Arnold (1997), namely the situation in which “two populations of individuals that are distinguishable on the basis of one or more heritable characters overlap spatially and temporally and cross to form viable and at least partially fertile offspring.” These hybrid interactions can have detrimental consequences for the interbreeding populations, such as genetic swamping or extinction by hybridization (Rhymer & Simberloff, 1996; Todesco et al., 2016). This is why conservationists have established guidelines to deal with such cases of human-induced hybridization (Allendorf et al., 2001). However, hybridization can also provide ecological and evolutionary opportunities, such as the origin of new hybrid species (Mallet, 2007; Ottenburghs, 2018) or the exchange of adaptive genetic variation (Arnold & Kunte, 2017; Hedrick, 2013). It is thus important to determine the balance between these potential detrimental and beneficial consequences when devising effective conservation strategies.

In the following sections, I first review the literature on anthropogenic hybridization from the last five years (2016–2020) to identify the most common mechanisms and outcomes of human-mediated hybridization events (see Table 1, extending the search strategy from Grabenstein & Taylor, 2018). Next, I introduce the “genic view

of speciation,” a concept that has shaped recent research agendas in speciation genomics (Campbell et al., 2018; Ravinet et al., 2017; Wu, 2001). This viewpoint focuses on the heterogeneous nature of genetic differentiation and introgression across the genome. The insight that different genomic regions tell different evolutionary stories needs to be taken into account when dealing with anthropogenic hybridization events. Specifically, it has important consequences for (1) the development of molecular markers, (2) the quantification of (adaptive) introgression patterns, and (3) the legal status of hybrids.

2 | MECHANISMS OF ANTHROPOGENIC HYBRIDIZATION

There are three main mechanisms of anthropogenic hybridization (Figure 1), namely human-assisted translocations, habitat modifications, and climate change (Crispo et al., 2011; Grabenstein & Taylor, 2018). Translocations or introductions of certain taxa can be intentional, such as in genetic rescue programs. This strategy is used to restore genetic diversity and reduce the extinction risk of small, isolated, and often inbred populations. About 90 percent of these genetic rescue attempts have been successful, indicating that human-mediated hybridization can be an important tool in conservation (Frankham, 2015). In this review, however, I focus on species translocations and introductions that are unrelated to conservation efforts. My literature search uncovered 31 papers (out of 59 studies, 53%) that involved the introduction of non-native species (Figure 2a). Some of these cases involved intentional movement of organisms, such as the release of game-farm birds for hunting purposes (Forcina et al., 2020), the stocking of fish populations with captive-bred animals (Beheregaray et al., 2017; Bruce et al., 2020), or the translocation of large mammals between African game reserves (Grobler et al., 2018; Miller et al., 2020; van Wyk et al., 2019). Other human-assisted translocations were unintentional, such as the transport of aquatic organisms in ship hulls (Oziol et al., 2019) or plant seeds by cargo or passenger transport, sometimes resulting in cryptic invasions and hybridization events (Morais & Reichard, 2018). In addition, domestic animals that escape from captivity often interbreed with their wild relatives (Anderson et al., 2019; Salvatori et al., 2019; Tiesmeyer et al., 2020). Species translocations or introductions—both intentional and unintentional—leading to hybridization events have thus been documented in a variety of taxa and are expected to increase as humans continue to move species across the globe (Crispo et al., 2011).

Anthropogenic hybridization can also be the outcome of habitat modifications (Grabenstein & Taylor, 2018). Edgar Anderson (1948)

TABLE 1 Overview of studies on anthropogenic hybridization events published in the last five years (2016–2020)

Species	Location	Mechanism	Outcome	Molecular markers	Reference
Plants					
<i>Centaurea seridis</i> <i>Centaurea aspera</i>	Spain	Habitat Change	F1 hybrids (triploids)	NA	Garmendia et al., (2018)
<i>Eucalyptus tetrapleura</i>	Australia	Habitat Change	Introgression	RADseq	Rutherford et al., (2018)
<i>Odontarrhena</i> spp.	Albania	Habitat Change	Introgression	AFLP-fingerprinting	Coppi et al., (2020)
<i>Phragmites australis</i> <i>Phragmites mauritanicus</i>	Southern Africa	Habitat Change	Introgression	Chloroplast DNA Microsatellites	Canavan et al., (2018)
	Nevada, USA	Introduction	F1 hybrids		Saltonstall et al., (2016)
<i>Quercus durata</i> <i>Quercus berberidifolia</i>	California, USA	Habitat Change (fire frequency)	Introgression	Microsatellites	Ortego et al., (2017)
<i>Rhododendron ferrugineum</i> <i>Rhododendron hirsutum</i>	Italy	Habitat Change	Introgression	Chloroplast DNA Microsatellites	Bruni et al., (2016)
<i>Taraxacum calanthodium</i> <i>Taraxacum lugubre</i>	China	Pollination by introduced bees	Introgression	Microsatellites	Peng et al., (2018)
Insects					
<i>Bactrocera tryoni</i> <i>Bactrocera aquilonis</i>	Australia	Habitat Change (horticulture)	Introgression	RADseq	Popa-Báez et al., (2020)
<i>Helicoverpa armigera</i> <i>Helicoverpa zea</i>	Brazil	Introduction (invasive species)	Introgression * (adaptive)	Whole Genome	Valencia-Montoya et al., (2020)
<i>Phaulacridium marginale</i> <i>Phaulacridium otagoense</i>	New Zealand	Habitat Change (deforestation)	Introgression	Mitochondrial and nuclear loci	Sivyer et al., (2018)
Amphibians					
<i>Bufo woodhousii</i> <i>Bufo microscaphus</i>	Southwest USA	Habitat Change	Introgression	Microsatellites	Wooten et al., (2019)
<i>Hyperolius thomensis</i> <i>Hyperolius malleri</i>	Sao Tomé Island	Habitat Change (deforestation)	Introgression	mtDNA RADseq	Bell and Irian (2019)
<i>Lissotriton vulgaris meridionalis</i> <i>Lissotriton vulgaris vulgaris</i>	Italy	Introduction	F1 hybrids	Mitochondrial and nuclear loci	Dubey et al., (2019)
<i>Pelophylax</i> spp.	Switzerland	Introduction	F1 hybrids	mtDNA Microsatellites	Dufresnes et al., (2018)
<i>Rana pipiens</i>	Southern USA	Introduction	Introgression	mtDNA Microsatellites	O'Donnell et al., (2017)
<i>Triturus cristatus</i> <i>Triturus carnifex</i>	The Netherlands	Introduction	Introgression	Mitochondrial and nuclear loci	Wielstra et al., (2016)
Reptiles					
<i>Pelodiscus</i> spp.	China	Introduction (farmed turtles)	Introgression	Mitochondrial and nuclear loci	Gong et al., (2018)
<i>Sternotherus depressus</i> <i>Sternotherus peltifer</i>	Alabama, USA	Habitat Change	Introgression (unidirectional)	RADseq	Scott et al., (2019)
Fish					
<i>Archosargus probatocephalus</i> <i>Archosargus rhomboidalis</i>	Florida, USA	Habitat Change	F1 hybrids	mtDNA & nDNA microsatellites	Seyoum et al., (2020)
<i>Alosa alosa</i> <i>Alosa fallax</i>	France	Habitat Change	Introgression	Mitochondrial and nuclear loci	Taillebois et al., (2020)
<i>Alosa pseudoharengu</i>	Connecticut, USA	Introduction	Introgression	RADseq	Reid et al., (2020)
<i>Catostomus discobolus</i> <i>Catostomus ardens</i>	USA	Habitat Change	F1 hybrids	Mitochondrial and nuclear loci	Bangs et al., (2017)
<i>Cobitis magnostrata</i> <i>Cobitis minamorii oumiensis</i>	Japan	Habitat Change	Reproductive Interference	mtDNA	Morii et al., (2018)

(Continues)

TABLE 1 (Continued)

Species	Location	Mechanism	Outcome	Molecular markers	Reference
<i>Colpichthys regis</i> <i>Colpichthys hubbsi</i>	California, USA	Habitat Change	Introgression (unidirectional)	mtDNA Microsatellites	Lau and Jacobs (2017)
<i>Coregonus lavaretus</i> (wild and stocked)	Finland	Introduction & Habitat Change	Introgression	Microsatellites	Huuskonen et al., (2017)
<i>Coregonus</i> spp.	Switzerland	Habitat Change (eutrophication)	Introgression	RADseq	Feulner and Seehausen (2019)
<i>Cottus</i> sp. <i>Cottus cognatus</i>	Canada	Habitat Change	Introgression	mtDNA Microsatellites	Rudolfson et al., (2019)
<i>Etheostoma osburni</i> <i>Etheostoma variatum</i>	West Virginia, USA	Habitat Change	Introgression	Microsatellites	Gibson et al., (2019)
<i>Fundulus grandis</i> <i>Fundulus heteroclitus</i>	Mexico	Habitat Change	Introgression * (adaptive)	Whole Genome	Oziolor et al., (2019)
<i>Gila cypha</i> <i>Gila robusta</i>	Colorado, USA	Habitat Change	Introgression	RADseq	Chafin et al., (2019)
<i>Macquaria ambigua</i> (wild and stocked)	Australia	Introduction	Introgression	RADseq	Beheregaray et al., (2017)
<i>Micropterus</i> spp.	Southern USA	Introduction	Introgression	Mitochondrial and nuclear loci	Bangs et al., (2018)
<i>Oncorhynchus chrysogaster</i> <i>Oncorhynchus mykiss</i>	Mexico	Introduction (aquaculture)	Introgression	RADseq	Escalante et al., (2020)
<i>Oncorhynchus clarkii</i> <i>Oncorhynchus mykiss</i>	USA	Introduction	Introgression	Allozymes, SNPs and microsatellites	Muhlfeld et al., (2017)
<i>Oncorhynchus tshawytscha</i>	Washington, USA	Habitat Change	F1 hybrids	SNP markers	Fraser et al., (2020)
<i>Oreochromis niloticus</i>	Ethiopia	Introduction	Introgression	Microsatellites	Tibihika et al., (2020)
<i>Parachondrostoma toxostoma</i> <i>Chondrostoma nasus</i>	France	Habitat Change	Introgression	mtDNA Microsatellites	Guivier et al., (2019)
<i>Salvelinus alpinus</i> <i>Salvelinus fontinalis</i>	Sweden	Introduction	Introgression	mtDNA Microsatellites	Faulks and Östman (2016)
<i>Salvelinus fontinalis</i> (wild and stocked)	New York, USA	Introduction	Introgression	Microsatellites	Bruce et al., (2020)
<i>Salvelinus fontinalis</i> <i>Salvelinus confluentus</i>	Oregon, USA	Introduction & Habitat Change	F1 hybrids (morphology)	NA	Howell (2018)
<i>Sander vitreus</i> <i>Sander Canadensis</i>	Canada	Introduction & Habitat Change	Introgression	RADseq	Graham et al., (2020)
<i>Tropheus moorii</i> (two lineages)	Lake Tanganyika	Habitat Change (lake levels)	Introgression	mtDNA, AFLP, and Microsatellites	Sefc et al., (2017)
Birds					
<i>Alectoris rufa</i> <i>Alectoris chukar</i>	Italy	Introduction (hunting)	Introgression	mtDNA	Forcina et al., (2020)
<i>Francolinus francolinus</i> (subspecies)	Pakistan	Introduction	Introgression	mtDNA Microsatellites	Forcina et al., (2018)
<i>Mycteria cinerea</i> <i>Mycteria leucocephala</i>	Singapore	Introduction (captive hybrids)	Introgression	RADseq	Baveja et al., (2019)
<i>Vermivora chrysoptera</i> <i>Vermivora cyanoptera</i>	Canada	Habitat Change	F1 Hybrids	mtDNA	Moulton et al., (2017)
Mammals					
<i>Aepyceros melampus petersi</i> <i>Aepyceros melampus melampus</i>	Namibia & South Africa	Introduction	Introgression	Microsatellites	Miller et al., (2020)
<i>Callithrix</i> spp.	Brazil	Introduction	Introgression	NA	Malukiewicz (2019)

(Continues)

TABLE 1 (Continued)

Species	Location	Mechanism	Outcome	Molecular markers	Reference
<i>Canis lupus</i> <i>Canis lupus familiaris</i>	Italy	Introduction (domestic dogs)	Introgression	Nuclear loci	Salvatori et al., (2019)
<i>Cervus elaphus</i> <i>Cervus nippon</i>	Scotland	Introduction	Introgression	SNP genotyping	McFarlane et al., (2020)
<i>Cervus elaphus</i>	Spain & Portugal	Introduction (non-native deer)	Introgression	mtDNA Microsatellites	Queirós et al., (2020)
<i>Damaliscus pygargus pygargus</i> <i>Damaliscus pygargus phillipsi</i>	South Africa	Introduction	F1 hybrids	Microsatellites	Van Wyk et al., (2017)
<i>Felis silvestris</i> <i>Felis catus</i>	Europe	Introduction (domestic cats)	Introgression	SNP genotyping Microsatellites	Tiesmeyer et al., (2020)
<i>Gazella bennettii</i> <i>Gazella subgutturosa</i>	Iran	Introduction	F1 Hybrids	Mitochondrial and nuclear loci	Fadakar et al., (2020)
<i>Sus scrofa</i> (wild and domesticated)	Japan	Introduction (escaped animals)	Introgression	mtDNA	Anderson et al., (2019)
Other taxa					
<i>Daphnia pulex</i> (different lineages)	Canada	Habitat Change	Introgression	mtDNA Microsatellites	Millette et al., (2020)
<i>Daphnia longispina</i> <i>Daphnia galeata</i>	Switzerland	Habitat Change (eutrophication)	Introgression	mtDNA Microsatellites	Alric et al., (2016)
<i>Pomacea canaliculata</i> <i>Pomacea maculata</i>	Brazil & Uruguay	Introduction	Introgression	Nuclear markers	Glasheen et al., (2020)

Note: These studies were found in a systematic literature search of Google Scholar and the Web of Science, using the combined search terms: 'anthropogenic AND disturb* AND hybrid*' OR 'habitat AND chang* AND hybrid*' OR 'human AND chang* AND hybrid*' OR 'environment* AND chang* AND hybrid*' NOT climate NOT introduc* NOT zone* (following Grabenstein & Taylor).

coined the phrase "hybridization of the habitat" to indicate that human disturbances of the environment can lead to the production of hybrid offspring. Indeed, 30 studies (51%) attributed hybridization events to human-induced habitat changes (Figure 2a). In several plant species, the rate of hybridization increased with the level of disturbance in the area, such as the concentration of heavy metals (Coppi et al., 2020) or the frequency of wildfires (Ortego et al., 2017). Hybridization can also be the outcome of homogenization of the habitat or the construction of landscape features that facilitate dispersal (e.g., roads and verges), culminating in contact between previously isolated populations (Bangs et al., 2017; Carantón-Ayala et al., 2018; van Hengstum et al., 2012). For instance, deforestation has led to hybridization between certain insect (Sivyer et al., 2018) and amphibian populations (Bell & Irian, 2019). Moreover, habitat disturbances can affect selective pressures, allowing hybrids to thrive in new environments that are not accessible for the parental populations (Arnold et al., 2012; Arnold & Martin, 2010). For example, hybrids between cave salamanders (*Hydromantes ambrosii* and *Hydromantes italicus*) with transgressive phenotypes could expand into more harsh environments with higher food availability (Ficetola et al., 2019). Human-mediated actions can also influence the sensory environment in a number of ways, such as pollutants that alter chemical signaling (Smadja & Butlin, 2009) or anthropogenic noise that interferes with auditory communication (Slabbekoorn et al., 2010; Slabbekoorn & Ripmeester, 2008). A well-studied example concerns

the effect of increased lake eutrophication on species recognition in fish (Alexander et al., 2017; Vonlanthen et al., 2012). Eutrophication decreases water clarity, leading to a breakdown of prezygotic barriers because individuals cannot discriminate between conspecifics and heterospecifics in the turbid waters (Seehausen et al., 1997). As human-mediated habitat modifications continue to change the environmental and sensory conditions for numerous taxa, more hybridization events are expected to arise in the near future (Crispo et al., 2011; Grabenstein & Taylor, 2018).

Climate change can be seen as a special case of habitat change and can affect hybridization dynamics in a myriad of ways (Chunco, 2014). Both latitudinal and altitudinal range shifts are expected to occur, leading to secondary contact between previously isolated species (Larson et al., 2019; Parmesan, 2006; Taylor et al., 2015). Such distributional shifts and consequent hybridization events have already been documented, for instance between polar bears (*Ursus maritimus*) and grizzly bears (*U. arctos*) in the Arctic (Kelly et al., 2010) and between species of *Glaucomys* flying squirrels (Garroway et al., 2010), and will be observed more often in the future (Chunco, 2014; Taylor et al., 2015). Apart from distributional changes, climate change might also result in the breakdown of reproductive isolation mechanisms between sympatric species, such as the disappearance of temporal isolation due to phenological changes (Vallejo-Marín & Hiscock, 2016). Climate change will thus alter population dynamics in time and space, culminating in more hybridization events.

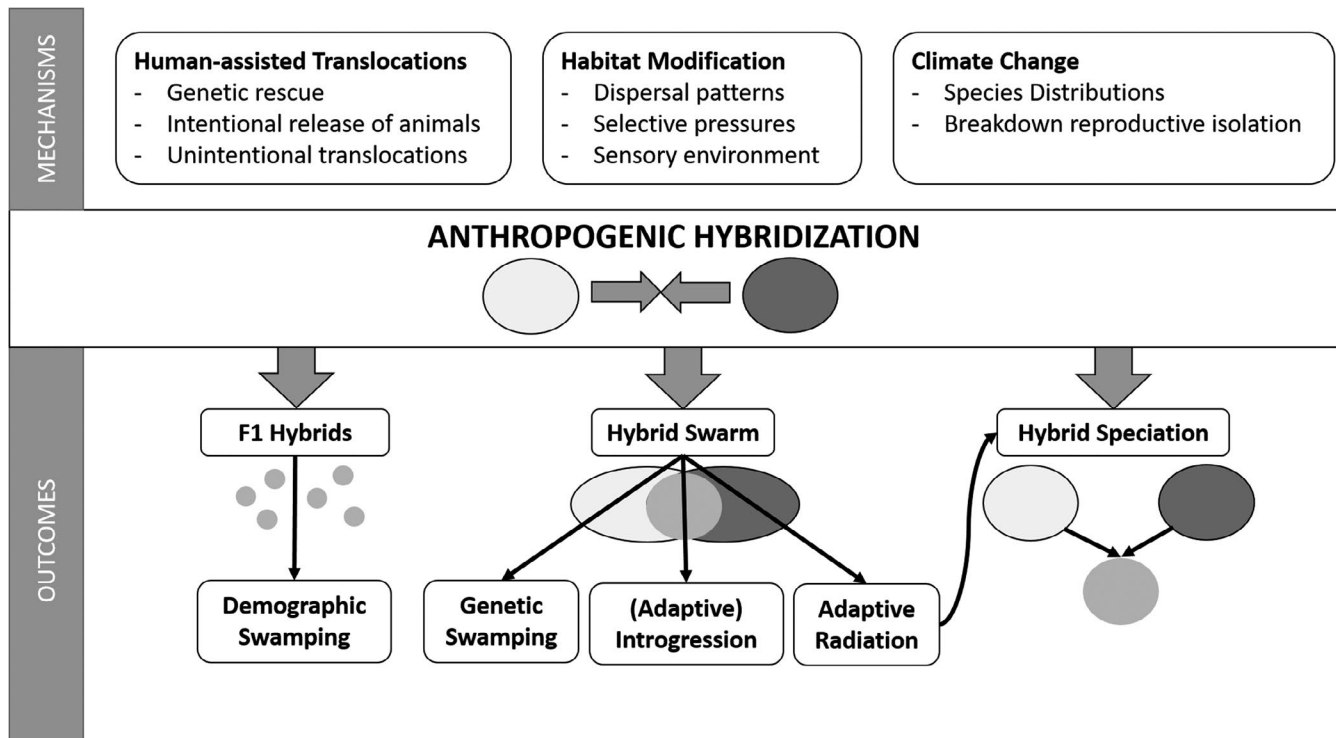


FIGURE 1 Mechanisms and outcomes of anthropogenic hybridization. Mechanisms that can result in hybridization include human-assisted translocations (both intentional and unintentional), habitat modification and climate change. Anthropogenic hybridization events can result in the formation of first-generation (F1) hybrids, a hybrid swarm or a hybrid species. If the production of F1 hybrids interferes with the reproductive output of the parental species, demographic swamping can occur. A hybrid swarm can lead to (adaptive) introgression, genetic swamping or provide the raw material for an adaptive radiation (potentially including the origin of a hybrid species)

3 | OUTCOMES OF ANTHROPOGENIC HYBRIDIZATION

Regardless of the underlying mechanism, anthropogenic hybridization can have several outcomes, which are mainly determined by the level of genetic divergence and the nature of reproductive isolation between the interacting species (Figure 1). In some cases, the hybridization event is limited to first-generation (F1) hybrids (11 studies, 19%, Figure 2b), such as the production of triploid hybrids between diploid and tetraploid *Centaurea* species in Spain (Garmendia et al., 2018) or the occasional hybrid between subspecies of the smooth newt (*Lissotriton vulgaris*) in Italy (Dubey et al., 2019). The absence of second-generation hybrids or backcrosses might be due to the lower fitness of F1 hybrids (e.g., decreased fertility) or the lower sensitivity of certain molecular markers that fail to identify later-generation hybrids. Another possible outcome of human-induced hybridization is a hybrid swarm: a population of fertile hybrids that survived past the first hybrid generation, followed by interbreeding between hybrid individuals and backcrossing with their parental populations. Hybrid swarms generally form within a hybrid zone, an area where two populations overlap spatially and temporally and produce viable and at least partially fertile offspring within a restricted area (e.g., Carney et al., 2000; Fisher et al., 2006). In the majority of studies (47 studies, 80%), the production of hybrids resulted in the exchange of genetic material through backcrossing with parental species (i.e.,

introgression, Figure 2b). On a longer timeframe, the fate of these hybrid swarms is difficult to predict. The mixing of different genetic lineages might lead to the extinction of particular lineages through species collapse (Zhang et al., 2019) or it might provide the raw material for an adaptive radiation (Marques et al., 2019; Seehausen, 2004). In theory, hybrid species can emerge from hybrid swarms, but this speciation process is typically too slow to observe on a short timescale (Lamichhaney et al., 2018; Ottenburghs, 2018; Seehausen, 2004). There are, however, some exceptions, such as the Oxford ragwort (*Senecio squalidus*) that originated from the interbreeding of two Italian species (*S. aethnensis* and *S. chrysanthemifolius*) in British gardens at the turn of the 18th century (Nevado et al., 2020).

On a population level, different combinations of hybrid fitness and hybridization rate can lead to drastically different outcomes in an anthropogenic hybridization event. First, if hybrid fitness is comparable to the fitness of parents (i.e., outbreeding depression is low) and hybrids show higher population growth rates than the parental taxa, genetic swamping might occur in which the parental taxa are replaced by hybrids (Rhymer & Simberloff, 1996). This might be occurring in West Virginia (USA) where hybrids between candy darters (*Etheostoma osburni*) and variegated darters (*E. variatum*) are replacing the now endangered candy darter (Gibson et al., 2019). A special case of potential genetic swamping concerns the release of actively managed species, such as fish stocks and game birds (Randi, 2008). These artificially selected organisms often differ genetically from

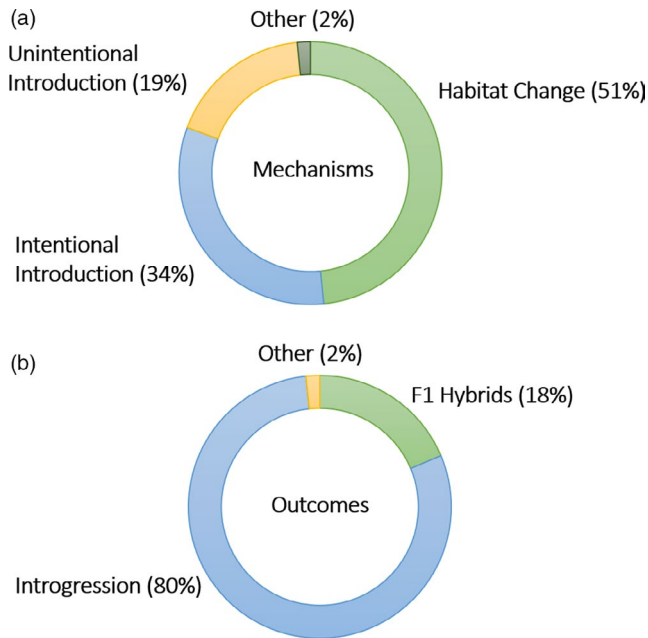


FIGURE 2 The most common mechanisms and outcomes of anthropogenic hybridization, based on a literature review of the last five years (2016–2020). Habitat change is the most prevalent mechanism behind human-induced hybridization events, followed by intentional and unintentional translocations of organisms. The vast majority of anthropogenic hybridization events results in introgression

their wild conspecifics which can result in outbreeding depression when they interbreed (Muhlfeld et al., 2009). Moreover, the strong selection pressures in captivity might lead to low genetic diversity and inbreeding depression (Willoughby et al., 2015). Hybridization with these maladapted individuals can lower the average fitness of wild populations. Although most studies documented introgression and warn for the possibility of genetic swamping, few studies directly quantified the likelihood of genetic swamping in their study system. This important knowledge gap should be addressed with more detailed analyses, complemented with modeling studies, to determine crucial tipping points in introgression levels that can lead to genetic swamping.

If hybrid fitness is strongly reduced compared to the parental taxa (i.e., outbreeding depression is high) and hybridization rates are high, parental taxa will waste reproductive effort when hybridizing. This situation can lead to demographic swamping where parental taxa decline due to decreased population growth rates (Wolf et al., 2001). This situation has been described for the Australian native variable groundsel (*Senecio pinnatifolius*) and the invasive Madagascar ragwort (*S. madagascariensis*). Hybridization rates between these species are very high, but hybrids are not viable. As the invasive plant increases in abundance, the native plant continues to waste reproductive effort and will start declining in numbers (Prentis et al., 2007). Another example concerns reproductive interference between two spined loaches (*Cobitis magnostriata* and *C. minamorii oumiensis*) that could lead to the decline of the latter species (Morii et al., 2018). Between the extremes of genetic and demographic

swamping, there is a continuum of introgression patterns that are neutral or benefit one or both hybridizing taxa.

4 | THE GENIC VIEW OF SPECIATION AND INTROGRESSION

This overview of the different mechanisms and outcomes of anthropogenic hybridization highlights the difficulty in predicting the future developments of hybrid interactions and devising appropriate conservation measures. Recent developments in genomic tools have led to more accurate detection of hybrids and the quantification of introgression patterns (McFarlane & Pemberton, 2019), but an overarching framework is needed to interpret these findings and translate them to successful conservation strategies. Here, speciation genomics and the study of pre-Anthropocene hybridization events can provide additional insights (Campbell et al., 2018; Taylor et al., 2015). In particular, the genic view of speciation has drastically changed the way evolutionary biologists study the process of speciation (Bazykin, 1969; Key, 1968; Wu, 2001) and this perspective can be applied to several conservation genomic questions.

Speciation research has long been dominated by the Biological Species Concept (BSC) which focuses on reproductive isolation between diverging lineages (Mayr, 1963). This concept assumed that species differentiation is controlled by a large number of genetic loci and that the whole genome functions as an integrated and cohesive genetic unit. Hybridization and consequent genetic exchange were thought to destroy this integrity and break up “co-adapted gene complexes.” This perspective is still widely followed by conservationists that describe introgressive hybridization as “genetic erosion” (Chafin et al., 2019) or “genetic pollution” (Wielstra et al., 2016). However, genomic studies have overturned the idea of the genome as a cohesive genetic unit that can be destroyed by hybridization. Instead, the genome can better be regarded as a dynamic collection of genetic loci with separate, but entangled evolutionary histories. Moreover, reproductive isolation is often controlled by epistatic interactions between a few genetic loci (Ravinet et al., 2017; Wu, 2001).

This new perspective is nicely illustrated by recent studies that showed how genetic differentiation between diverging lineages is heterogeneously distributed across the genome, often concentrated in a few genomic regions, so-called “islands of differentiation” (Wolf & Ellegren, 2017). The genomic islands may harbor loci that contribute to reproductive isolation, and these so-called barrier loci are thus less likely to introgress compared to neutral loci. Consequently, barrier loci and closely linked genomic regions will diverge while introgression homogenizes the rest of the genome (Ravinet et al., 2017). An alternative explanation for the origin of genomic islands concerns linked selection, which comprises two processes: background selection and genetic hitchhiking (Burri, 2017). Background selection refers to purifying selection against recurring deleterious mutations, while genetic hitchhiking occurs when positive selection on a variant result in the selection for the genomic region in which this advantageous variant resides. As the advantageous variant increases in

frequency, the loci linked to this variant hitchhike along (Sendell-Price et al., 2020). Regardless of the underlying process—barrier loci or linked selection—the end result is a heterogenous genomic landscape of differentiation, which affects several aspects of conservation genomics, including (1) the development of molecular markers, (2) the study of introgression, and (3) the legal status of hybrids.

5 | DEVELOPMENT OF MOLECULAR MARKERS

A first step in the assessment of an anthropogenic hybridization event involves determining the composition of the hybrid population in terms of parental individuals, first-generation hybrids (F1), second-generation hybrids (F2), backcrosses, etc. For example, a mixture of different generational hybrids indicates the formation of a hybrid swarm, whereas the absence of backcrosses and second-generation hybrids suggests selection against hybrids. Most conservation genetic studies use a set of variable genetic markers (e.g., microsatellites) to quantify the genetic make-up of different individuals using software packages such as *STRUCTURE* (Pritchard et al., 2000) or *ADMIXTURE* (Alexander et al., 2009). Next, this genetic make-up can be compared with simulated data to test the power of discriminating between different levels of admixture (Anderson, 2008). The resulting composition of the hybrid population provides the basis for subsequent analyses and potential conservation measures.

The use of a few genetic markers works well to identify early-generation hybrids and backcrosses, but can run into several issues (McFarlane & Pemberton, 2019). First, the determination of a threshold to discriminate between hybrid and parental species can be problematic. Population assignment algorithms calculate an admixture score (*Q*) for individuals where a score of 0 or 1 indicates a purebred individual from one of the parental populations. However, due to errors in genotyping or the presence of nondiagnostic markers, most individuals will have a score that is not exactly 0 or 1. But how does one discriminate between these errors and actual hybrids (which have a score between 0 and 1)? Generally, a threshold is used to delimit the parental classes, but this threshold varies between studies, ranging from 0.8 (Schulte et al., 2012) to 0.99 (Galaverni et al., 2017), and the choice of the threshold depends on the number of hybrid classes one recognizes. Using a threshold of 0.8 would, for instance, assign some later-generation backcrosses to a parental class. A second issue of using few genetic markers for hybrid detection concerns homozygous loci. By chance, several generations of backcrossing can result in homozygous genetic markers for some individuals, which will consequently not be recognized as hybrids or backcrosses (Boecklen & Howard, 1997).

These two issues—setting a realistic admixture threshold and the presence of homozygous markers—can often be solved by adding more markers. Indeed, genomic studies can more confidently identify hybrids and later-generation backcrosses, leading to more sound conclusions about the hybridization dynamics (Lemopoulos et al.,

2019; McFarlane et al., 2020; McFarlane & Pemberton, 2019). For instance, analyses based on microsatellite markers suggested that hybridization between mallards (*Anas platyrhynchos*) and American black ducks (*Anas rubripes*) might lead to genetic extinction of the latter species (Mank et al., 2004). However, genomic studies of this system revealed little gene flow between the species, indicating that hybridization is not threatening the genetic integrity of the American black duck (Lavretsky et al., 2019, 2020). Similarly, McFarlane et al., (2020) investigated the sensitivity of microsatellites and RADseq (restriction site-associated DNA sequencing) to discriminate between different hybrid classes of red deer (*Cervus elaphus*) and Japanese sika (*C. nippon*). The RADseq data were able to identify more advanced backcrosses compared to the microsatellites, leading to a more fine-grained picture of introgression dynamics between these species.

The discrepancy between microsatellite markers and genomic data can partly be explained by the underlying genomic landscape of differentiation. The random selection of a few genetic markers might result in a marker set that only captures the undifferentiated section of the genome, missing the genomic islands of differentiation. Genomic sequencing methods, such as RADseq, cover a larger proportion of the genome compared to microsatellites and can be used to develop diagnostic markers. For instance, Taillebois et al., (2020) developed 77 species-specific SNPs (single nucleotide polymorphisms) that could detect hybrids and backcrosses between allis shad (*Alosa alosa*) and twaite shad (*A. fallax*) up to the third generation. Similar marker sets and sequencing protocols have been developed for other study systems (Feulner & Seehausen, 2019; Vaux et al., 2021; Wielstra et al., 2016) and show that conservationists do not always need whole genome sequencing data to reconstruct the entire genomic landscape. This conclusion is further supported by evolutionary studies that used less powerful sequencing methods (e.g., RADseq or ultraconserved elements) to explore the genomic landscape of differentiation (Battey, 2019; Bourgeois et al., 2020; Oswald et al., 2019; Plomion et al., 2018). There are, however, certain situations where these methods do not provide the necessary resolution to investigate genetic differentiation across the genome, such as polyploids (Bourke et al., 2018; Clark et al., 2019), large genome sizes (Lowry et al., 2016), or populations with large-scale demographic changes (Arnold et al., 2013). It is thus important to be conscious about the potential biases of reduced representation methods, such as RADseq (reviewed in Andrews et al., 2016). Nonetheless, being aware of the heterogenous nature of the underlying genomic landscape will already lead to a more conscious selection of diagnostic markers, even if not using whole genome sequencing.

6 | PATTERNS OF ANTHROPOGENIC INTROGRESSION

Hybridization often results in introgression: the exchange of genetic material between populations through backcrossing (Ottenburghs,

Kraus, et al., 2017; Ottenburgs, Megens, et al., 2017; Taylor & Larson, 2019). Introgression can have detrimental effects, such as loss of genetic integrity, speciation reversal (Seehausen et al., 2008), and the genetic extinction of certain taxa (Rhymer & Simberloff, 1996). However, introgression can be beneficial by facilitating the exchange of adaptive loci and increasing genetic diversity (Arnold & Kunte, 2017; Hedrick, 2013), possibly improving the adaptive potential of a population or species (Funk et al., 2019; Milot et al., 2020). Indeed, several authors have suggested that hybridization can be used as an effective conservation measure (Chan et al., 2019; vonHoldt et al., 2018). From a conservation point of view, we are thus faced with a difficult dilemma when assessing a human-induced hybridization event: should we prevent potential genetic extinction with conservation measures (e.g., culling hybrids) or should we not intervene to provide the opportunity for adaptive introgression and an increase in genetic diversity?

The positive effects of introgressive hybridization have been well-documented in several genetic rescue programs (Frankham, 2015; Whiteley et al., 2015), but does it also occur in unintentional anthropogenic hybridization events? A literature survey reported that the majority of human-induced hybridization events led to an increased extinction risk of the parental species (Todesco et al., 2016), indicating that introgression was mainly detrimental. The discrepancy between the success of intentional genetic rescue programs and the detrimental effects of unintentional anthropogenic hybridization events can be partly explained by the genetic divergence between the hybridizing taxa (Whiteley et al., 2015). Genetic rescue involves the carefully planned supplementation of a small inbred population with individuals from other populations that belong to the same (Heber et al., 2013; Miller et al., 2012) or a closely related subspecies (Harrisson et al., 2016; Pimm et al., 2006) in order to restore genetic diversity. Because the genetic distance between the local and supplemented individuals is low, it is unlikely that the resulting hybrids will suffer from outbreeding depression (i.e., decreased fitness of hybrids relative to their parents). In fact, hybrids in genetic rescue programs often exhibit a temporary increase in fitness due to the masking of rare deleterious alleles (Pickup et al., 2013; Weeks et al., 2017). In contrast to genetic rescue interventions, anthropogenic hybridization events often occur between more distantly related taxa, increasing the likelihood of outbreeding depression due to negative epistatic interactions between divergent loci (Edmands, 1999). Indeed, the majority of studies in my literature search (43 out of 59 studies, 73%) involved different species.

Speciation genomics—particularly the study of pre-Anthropocene hybrid zones—has shown that introgression varies across the genome (Payseur, 2010). Genetic loci can roughly be divided into three categories: (1) neutral loci that flow freely between taxa, (2) deleterious loci that contribute to reduced fitness in hybrids and inhibit introgression, and (3) beneficial loci that confer an adaptive advantage and increase in frequency following introgression. Admixed genomes can be seen as a mosaic of these three categories, shaped by genetic drift, recombination, and selection (Runemark et al., 2019). This genic view of introgression illustrates that the dichotomy

between the deleterious and beneficial effects of introgression on the population level becomes more nuanced on the genomic level (Wu, 2001). Both effects can be acting simultaneously within a collection of genomes: some genomic regions will be homogenized by (adaptive) introgression, while other regions will remain species-specific due to strong negative selection against introgressed loci.

The majority of conservation genetic studies only quantified the level of introgression between interacting populations, but they did not assess which genomic loci are being exchanged or not. Genomic regions that contribute to reproductive isolation, either because they contain barrier loci or because they are involved in local adaptation, do not introgress and will thus preserve species integrity, even in the face of high levels of hybridization. A study only quantifying introgression might thus warn for genetic swamping or species collapse, even though species-specific loci will prevent this from happening. For instance, extensive introgression between taiga bean goose (*Anser fabalis fabalis*) and tundra bean goose (*A. f. serrirostris*) resulted in a largely homogeneous genomic landscape, but a few genomic islands of differentiation seem to prevent these taxa from merging (Ottenburgs et al., 2020). However, if reproductive isolation mechanisms break down completely, such as the loss of species recognition between fish species due to eutrophication (Vonlanthen et al., 2012), the genomic barriers preventing species from merging have been broken and the underlying loci can also introgress. Hence, the threat of genetic swamping might increase and conservation measures will be warranted. It is thus important to investigate the functional role of introgressed regions. If the genes at the exchanged genomic locations are important in adaptation to rapidly changing environments (e.g., immune genes), a local increase in genetic diversity can provide the necessary adaptive potential to deal with these challenges (Chan et al., 2019; Derry et al., 2019). The development of more powerful techniques to detect introgression (Hibbins & Hahn, 2021) and the increasing completeness and better annotation of genome assemblies (Peona et al., 2018) suggest that these types of analyses will be possible for nonmodel organisms in the near future.

The genic view of introgression also becomes apparent in studies that documented the exchange of adaptive traits between taxa. In most cases, these traits can be traced back to one or a few genetic loci, such as polymorphisms in the gene *vkorc1* that causes resistance to rodenticides and introgressed between European and Algerian mouse populations (Song et al., 2011). Similarly, adaptive changes in coat color have been linked to particular introgressed loci in wolves (Anderson et al., 2009) and snowshoe hares (Jones et al., 2018). Examples of adaptive introgression in plants include the transfer of herbivore resistance traits between *Helianthus* sunflowers (Whitney et al., 2006) and regulatory genes for certain ecological traits between *Senecio* plants (Kim et al., 2008). Two recent studies on anthropogenic hybridization documented adaptive introgression. Oziolor et al., (2019) showed that Gulf killifish (*Fundulus grandis*) adapted to high levels of water pollution through introgressive hybridization with the non-native Atlantic killifish (*F. heteroclitus*). And a study on hybridization between the local moth species *Helicoverpa zea* and the invasive *H. armigera* revealed that an insecticide-resistant

locus introgressed into the local species and increased in frequency (Valencia-Montoya et al., 2020). Interestingly, both studies relied on whole genome sequencing data, suggesting that it is difficult to detect adaptive introgression with less powerful sequencing methods. However, the methods for detecting adaptive introgression are improving (Moest et al., 2020; Setter et al., 2020; Zhang et al., 2020) and it will only be a matter of time before these methods can be applied more widely, as exemplified by the increasing availability of test statistics to detect introgression (Hibbins & Hahn, 2021). However, not intervening in anthropogenic hybridization events to provide the opportunity for adaptive introgression is generally not advisable and requires a thorough understanding of the study system (Allendorf et al., 2001). In summary, it is not only important to quantify how much genetic material introgressed, but also what has been exchanged.

7 | INSIGHTS FROM PRE-ANTHROPOCENE HYBRIDIZATION EVENTS?

Several anthropogenic hybridization events occur between species that have previously not overlapped in range. For example, hybridization between *Corbicula* clams in the European river Rhine probably started with the introduction of American lineages through cargo ships (Pfenninger et al., 2002). When two previously allopatric taxa interact for the first time prezygotic isolation mechanisms are often not well developed, resulting in high level of interbreeding and possibly introgression. Indeed, reproductive isolation is often weaker between allopatric taxa compared to sympatric taxa (Coyne & Orr, 1989; Presgraves, 2002), probably because reproductive isolation between sympatric taxa has been strengthened by reinforcement (Calabrese & Pfennig, 2020; Coughlan & Matute, 2020). Alternatively, some hybridizing taxa might have a history of hybridization with previous periods of secondary contact. For instance, polar bears and grizzly bears, that are currently interbreeding in the Arctic due to recent climate change (Kelly et al., 2010), have an extensive history of pre-Anthropocene hybridization events (Kumar et al., 2017; Kutschera et al., 2014). This raises the question whether conservationists can apply insights from these past hybridization events to inform current policy.

One could compare past introgression patterns with the current dynamics of the human-mediated hybridization event, potentially allowing researchers to assess different outcomes with greater confidence. For example, according to one theoretical model of genome evolution during speciation, genomic islands of differentiation that house barrier loci are expected to increase in size as genomic regions are linked together. This process—known as genome hitchhiking—leads to an average genome-wide reduction in introgression, ultimately culminating in complete reproductive isolation (Feder et al., 2012; Flaxman et al., 2013). Comparing the genomic landscape between pre- and post-Anthropocene hybridization events might reveal this expansion of genomic islands over time, suggesting that reproductive isolation has been strengthened and genetic swamping

is less likely to occur. It is also possible that some taxa are in merging-and-diverging cycles where periods of geographic isolation are punctuated by introgression events (Grant & Grant, 2008; McKay & Zink, 2015). During each allopatric phase, more genetic divergence builds up between the taxa, resulting in lower levels of introgression during the subsequent merging phase. Human-mediated changes might have sped up the occurrence of a merging event, such as the interbreeding of polar bears and grizzly bears. Reconstructing the dynamics during these merging-and-diverging cycles might provide insights into the likelihood of genetic swamping or species collapse during the anthropogenic introgression event. However, the environmental and genetic context of pre-Anthropocene hybridization events might not be comparable with the dynamics in current hybrid zones (Gompert et al., 2017). To my knowledge, no study has explicitly compared pre-Anthropocene hybridization events with current human-induced cases. This knowledge gap provides an exciting avenue for further research that could lead to better conservation measures.

8 | RETICULATION AND CONSERVATION

The genetic legacy of past hybridization events is still detectable in present-day genomes (Lombal et al., 2020; Ottenburghs, 2020; Taylor & Larson, 2019). These genetic patterns can be especially apparent in phylogenomic studies where phylogenetic analyses of different genomic regions point to distinct evolutionary histories—as one would expect based on the genic view of introgression (Edelman et al., 2019; Li et al., 2019; Ottenburghs, Kraus, et al., 2017; Ottenburghs, Megens, et al., 2017). For instance, phylogenomic analyses of the cat family (Felidae) revealed that the phylogenetic signal for the species tree was concentrated within genomic regions of low recombination, whereas regions of high recombination were heavily influenced by past introgression (Li et al., 2019). Apart from introgressive hybridization, this phylogenetic incongruence between different genomic regions—known as gene tree discordance—can also be the outcome of other evolutionary processes, such as incomplete lineage sorting or gene duplications (Degnan & Rosenberg, 2009; Maddison, 1997). Several methods have been developed to discriminate between these processes and to deal with high levels phylogenetic incongruence (Kapli et al., 2020; Ottenburghs, Kraus, et al., 2017; Ottenburghs, Megens, et al., 2017; Zhou et al., 2020). One promising approach is the application of phylogenetic networks to highlight the reticulated nature of evolution (Blair & Ané, 2019; Ottenburghs et al., 2016).

Conservation efforts are still mainly focused on a tree-like pattern of evolution in which distinct evolutionary lineages warrant protection. This perspective is reflected in the Endangered Species Act (ESA) in the United States which lists and protects vulnerable species and subspecies of plants and animals (Ellstrand et al., 2010). At the moment, interspecific hybrids are generally denied protection under ESA (although some hybrid plant species might be considered). Similarly, the IUCN Red list does not consider hybrids (IUCN,

2020). Other organizations do take hybrids into account or provide guidelines on how to deal with hybridization (Jackiw et al., 2015). For example, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) has included some hybrids in Appendices I and II (i.e., species threatened with extinction or species that will become threatened without controlling trade). These examples clearly indicate that there are still large discrepancies in conservation efforts regarding hybrids between different countries and organizations. Acknowledging the reticulated nature of the evolutionary process by reconstructing past hybridization events and adopting a phylogenetic network approach can help to design better guidelines for hybrids (vonHoldt et al., 2018).

Jackiw et al., (2015) proposed an elaborate framework to implement conservation efforts for hybrids, taking into account ethical and ecological considerations. We can incorporate insights from speciation genomics into this framework to deal with hybridization events in the Anthropocene (Figure 3). First, consider human-mediated hybridization events (e.g., due to land-use changes or the release of particular species). The release of individuals can be intentional as part of a genetic rescue program. If this program is closely monitored and there are no negative effects of hybridization, the hybrids are eligible for legal protection (Frankham, 2015). However, if the genetic rescue program leads to unforeseen issues, such as outbreeding depression or maladaptive introgression, and the hybrids threaten the endangered population, conservation efforts are needed (Frankham et al., 2011; Mills & Allendorf, 1996). This scenario also applies to the intentional release of game birds or fish that might negatively

affect local populations through interbreeding (Randi, 2008). When the introduction of a particular species is unintentional—either due to individuals escaping from captivity or the spread of populations due to land-use changes—the legal status of the hybrids depends on the native distribution of hybridizing species. If one parental species is non-native, the hybrids cannot be legally protected and conservation measures should be implemented. For example, the introduction of North American *Corbicula* clams in the European river Rhine (Pfenninger et al., 2002). However, some studies documented adaptive introgression between a native and an exotic species (Oziolor et al., 2019; Valencia-Montoya et al., 2020), indicating this possibility should be taken into account when setting the legal status of hybrids. When both parental species are native, the hybridization event can be treated as a natural phenomenon and the conservation status of the interbreeding species should be taken into account. If one or both species are threatened by genetic or demographic swamping, then legal protection of the resulting hybrids is not advisable and conservation efforts should be implemented. If the parental species are not threatened by hybridization, the situation needs to be assessed to determine whether hybridization could be beneficial (e.g., adaptive introgression or increasing genetic diversity). Here, insights from speciation genomics can be useful. However, be aware that this decision tree only provides a rough framework and each hybridization event—anthropogenic or natural—should be assessed individually (Allendorf et al., 2001).

An aspect that is currently missing from this framework is how anthropogenic hybridization affects ecosystem functioning. Most

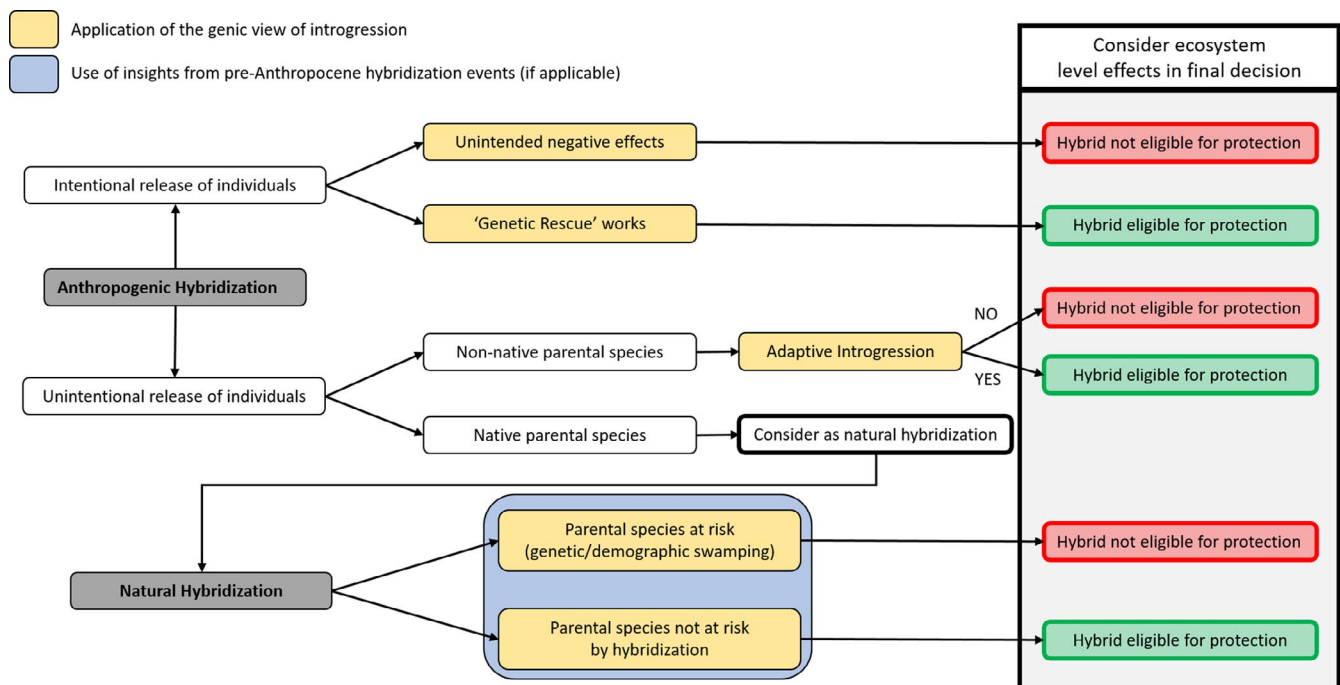


FIGURE 3 A decision tree to guide conservationists in determining the legal status of hybrids (based on Jackiw et al., 2015). Insights from speciation genomics (yellow) and past hybridization (blue) events are especially relevant in determining the risk for parental populations and the likelihood of adaptive introgression. In the final legal decision, it is important to also take into account potential ecosystem-level effects of the hybrids. Please note that this decision tree only provides a rough framework and each hybridization event—anthropogenic or natural—should be assessed individually

research on hybridization has focused on the interactions and genetic consequences between two or several taxa (Ottenburghs, 2019; Schwenk et al., 2008; Taylor & Larson, 2019). However, the production of hybrids not only affects the interbreeding taxa, it can also have far-reaching consequences on an ecosystem level, altering food webs or nutrient cycles (Brennan et al., 2014). Some of these consequences are clearly negative, such as the spread of invasive pests (Corrêa et al., 2019) and the emergence of novel pathogens (Stukenbrock, 2016). But hybrids can also have a positive effect on other species in the ecosystem. For example, the spread of invasive *Spartina* hybrids provided extra habitat for the endangered California Ridgway's Rail (*Rallus obsoletus*) in the San Francisco Estuary (Ort & Thornton, 2016). Should the positive effect of these hybrids be taken into account in conservation efforts? The ecosystem perspective on anthropogenic hybridization adds another layer of complexity to the implementation of conservation measures.

9 | CONCLUSION

As humans continue to change the environment and alter species distributions, more anthropogenic hybridization events will definitely occur. This will pose challenges for the conservation of endangered species, but also provide unique opportunities for evolutionary biologists. The interplay between conservation genomics and speciation genomics provides an exciting avenue for further research to gain important insights into the origin of species and how to protect them. In this review, I have illustrated this exchange of ideas by showing how insights from speciation genomics can guide the management of anthropogenic hybridization events. These insights range from practical issues (e.g., the development of diagnostic markers) to theoretical considerations, such as patterns of introgression, ancient hybridization events, and the reticulated nature of evolution.

From a conservation perspective, the unpredictability of (adaptive) introgression dynamics (Taylor & Larson, 2019) in combination with the strong link between anthropogenic hybridization and extinction risk (Todesco et al., 2016) suggests that the default course of action for human-induced hybridization events should be the implementation of conservation measures to prevent hybridization. However, some studies documented the exchange of adaptive traits between native and non-native species (Oziol et al., 2019; Valencia-Montoya et al., 2020), indicating that anthropogenic hybridization can result in adaptive introgression. The removal of introduced species and hybrids might have prevented the local species from adapting to the changing environment. These examples illustrate that each case of human-induced hybridization should be judged separately (Allendorf et al., 2001). In addition, speciation genomic studies have shown that species can remain distinct in the face of high levels of introgression when species-specific loci are not exchanged. Hence, high levels of introgression do not necessarily imply genetic swamping. It is not only important to quantify how

much genetic material introgressed, but also what genomic regions have been exchanged. Finally, comparing current introgression dynamics with pre-Anthropocene hybridization events might lead to novel insights on how to manage human-mediated hybridization events, although this idea remains to be tested. Taking all these perspectives into account, in combination with the conservation status of the hybridizing taxa, thoughtful and evidence-based conservation measures can be implemented.

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CONFLICT OF INTEREST

None declared.

DATA AVAILABILITY STATEMENT

There are not data associated with this manuscript, which is solely based on literature.

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