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Hybrids Along a Natural-Anthropogenic Gradient: Improving Policy and Management Across All Levels of Biodiversity

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ABSTRACT

Hybridization has long been a central topic in evolution and conservation. Recent developments in genomics have increased the ability to detect hybridization, defined here as breeding between species, subspecies or distinct populations, and assess levels of introgression between taxa. For decades, hybrids directly or indirectly created and/or spread by humans have typically been considered as threats to conservation, reflected by current regional and national environmental policies that focus largely on potential negative effects. In the context of the latest global conservation policy goals, and increasing evidence of historic natural hybridization events, we call for science-based, reflective and context-dependent management of hybrids, applying a framework that shifts focus towards measuring the impact of hybrids, and assessing potential risks and benefits. Alongside demographic and ecological information, it is crucial for impact assessments to consider genetic information, and conservation management of hybrids needs to be more case-specific.

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1 | The Ambiguity of Hybrids

Hybrids are the result of mating between organisms of different species, subspecies and genetically distinct populations (Rhymer and Simberloff 1996), leading to the (genetic) admixture of these (hereafter called) taxa. Introgression occurs when hybrids breed (or backcross) with individuals from the parental groups. Natural, non-anthropogenic, hybridization is an important evolutionary process that can lead to new species as well as reverse speciation (e.g., Kearns et al. 2018). Hybridization can also occur in situ during domestication, stockbreeding, conservation management, or following the introduction of species that become invasive (e.g., Blackwell et al. 2021). In addition, humans may produce hybrids ex situ and release them into the wild, deliberately or unintentionally (e.g., Pogorevc et al. 2024). Whereas natural hybrids that occur without human influence have long been recognized for their important role in evolution (Allendorf et al. 2001), range expansion in wild species following human-induced environmental changes can lead to hybridization with both wild and domestic species that raises complex management challenges (e.g., Trouwborst et al. 2015). Because these human-induced changes are often indirect, there is not always a clear line between hybrids of natural and human-induced origin (Donfrancesco and Luque-Lora 2022; Figure 1). We acknowledge that hybridization can be problematic, and in many cases the costs will exceed any benefits. Nevertheless, our aim with this paper is to present a nuanced approach to encourage case-by-case management. One difficulty is finding the framework and language to effectively address this case-specificity in hybrid policy and management, and we seek to address these obstacles in a constructive and balanced manner.

Recent genomic and analytical methods have broadened our knowledge on hybridization and improved the detection of hybrids (Wang 2024; see Supplementary Information, SI1). Studies revealed both higher numbers of hybrid individuals, and hybrids occurring between a greater number of taxa, than previously thought (Taylor and Larson 2019; Brown et al. 2024). Additional undetected cases may also be discovered in the future, raising new conservation questions. Though likely representing only a small proportion of the population in most cases, hybrids were found in about 23% of all carnivore species (Tensen and Fischer 2024). Populations in areas altered by ever-growing global trade and international travel (Ottenburghs 2021), or at range edges affected by anthropogenic changes (Lobo et al. 2023), might in the future experience increased rates of hybridization. Hence, environmental policy makers and natural resource managers are increasingly challenged to handle and manage hybrids (Grobler et al. 2018) influenced to various extents by human activities, either directly (e.g., release of nonnative species) or indirectly, linked to climate or habitat changes (Allendorf et al. 2001; Figure 1).

In early conservation literature, hybrids between native and non-native taxa were primarily considered a threat (e.g., Simberloff 1996). Such hybrids could lead to loss of biodiversity by replacing resident taxa through introgression and genetic swamping (Todesco et al. 2016; Figure 1, Examples 11–15). Genetic swamping is the extensive displacement of alleles in a taxon by those from another taxon via hybridization (Figure 2, Examples 5 and 6). In other cases, native taxa may decline and disappear due to hybrid offspring being unviable ("demographic swamping", e.g., Mikkelsen and Irwin 2021; Figure 2, Examples 1 and 2) or sterile. Beyond overall loss of biodiversity, specific alleles that underlie local adaptation may disappear (Olden et al. 2004), or hybrids may introduce maladaptive alleles given local climates or pathogens (Banes et al. 2016), potentially reducing adaptation and viability (Stockwell et al. 2003). Hybrids can also reduce fitness (Todesco et al. 2016) via reduced fertility and outbreeding depression when the parent taxa are strongly differentiated (e.g., large geographic, phylogenetic and/or environmental distance) (Frankham et al. 2017). At the species level, few extinctions caused by hybrids have been documented (Draper et al. 2021; Tensen and Fischer 2024) but see Rhymer and Simberloff 1996. However, negative fitness consequences sometimes only become apparent after two or three generations (Bell et al. 2019). Importantly, the effect of heterosis, the enhanced fitness sometimes observed in hybrid offspring, is often only temporary (Bell et al. 2019).

Recent studies have shown that hybrids are omnipresent and can, at times, play a key role in evolutionary processes (vonHoldt et al. 2018; Runemark et al. 2019; Hirashiki et al. 2021; Ottenburghs 2021). Some potentially positive impacts of hybridization that have been highlighted, despite a degree of human influence, are:

1. For taxa at the brink of extinction and displaying negative growth rates, mixing of different gene pools can improve and restore genetic variation (Lucena-Perez et al. 2024), often to the benefit of those taxa (e.g., through heterosis ("hybrid vigor"); Jackiw et al. 2015; Frankham et al. 2017; Ralls et al. 2018; Rodger et al. 2024).
2. Hybrids may provide important genetic diversity to certain taxa that otherwise would not survive new challenges. As climate change causes spatial shifts in the suitable habitat or niche of taxa, introgression could allow them to more rapidly adapt to changing conditions (Bell et al. 2019; de Jong et al. 2023; Taylor and Larson 2019). For example, recent genomic evidence in snow sheep showed that past hybridization with Dall and Argali sheep has contributed to adaptation to snow conditions (Figure 1, Example 5/SI2). In forestry, hybrids may help numerous tree species currently suffering from introduced pests and diseases (e.g., butternut case in SI3). Also, in crop species, novel traits introduced from wild relatives provide critical agronomic characteristics or human-valued attributes (e.g., SI4).
3. Hybrids might harbor genetic diversity of species that are extinct, extirpated, or at risk, as exemplified in Galapagos tortoises (Quinzin et al. 2019). The alleles from the lost or at-risk species might also be "revived" through controlled breeding (e.g., Lawson et al. 2024), genetic rescue or reintroduction efforts (e.g., Quinzin et al. 2019).
4. Hybrids may also fulfill an important role in an ecosystem, maintaining certain processes (e.g., predator–prey relationships, Stronen and Paquet 2013). Hybrid salt marsh grasses play a crucial role in ecosystem functioning. They help stabilize coastal environments, prevent erosion, and enhance biodiversity (Rezek et al. 2017). Potentially important functional variation needs to be investigated in the future (vonHoldt et al. 2022).

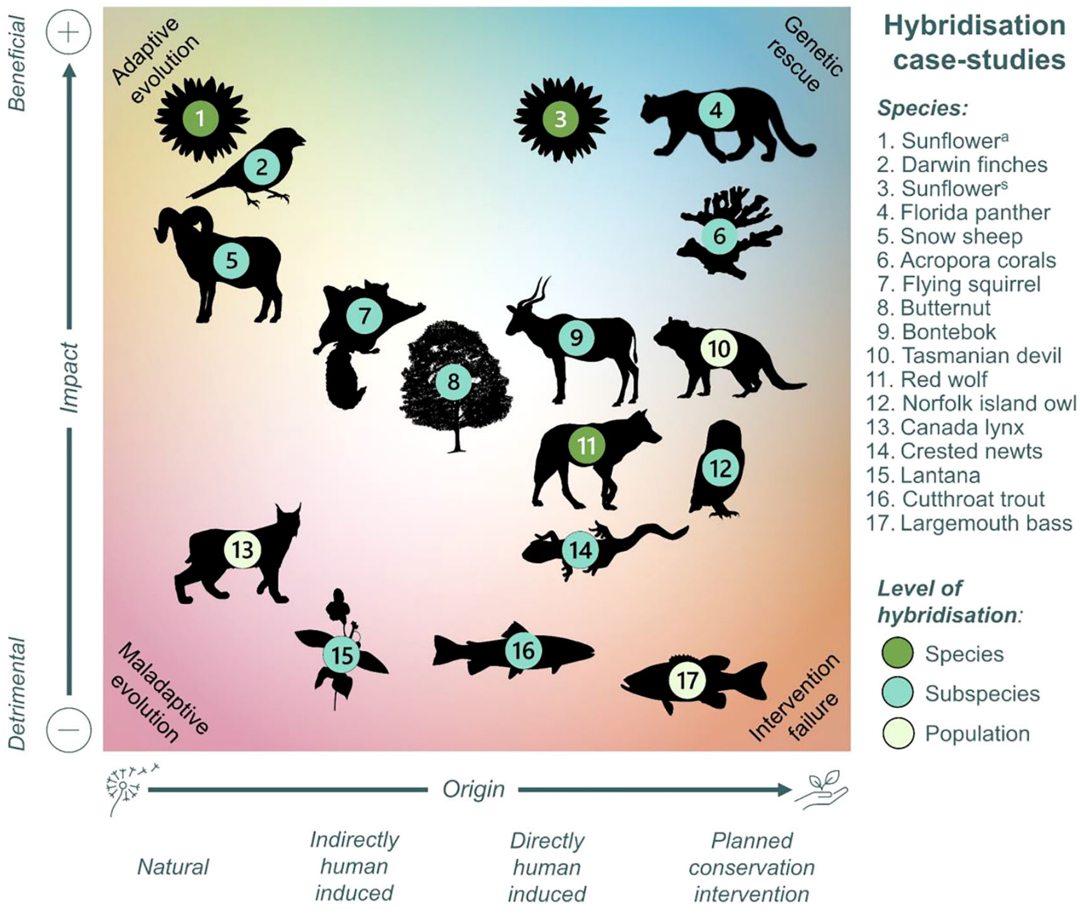

FIGURE 1 | Selection of 17 case-studies and examples of beneficial or detrimental (known or suspected) impacts (on an approximate gradient on the *y*-axis) from hybridization at the species, subspecies or population level. Intermixing by natural and artificial, human (intentional and unintentional) interference is placed approximately along a stylized gradient of natural-anthropogenic origin (*x*-axis). Detrimental impacts are those that are considered to have likely negative consequences for the taxa, i.e., lower fitness, depressed survival or reproduction, loss of unique gene variants, whereas (potential) beneficial impacts are considered to promote survival capabilities and restore genetic diversity. The sunflower examples (1 and 3) contain ancient[a] and human-mediated[s] hybridization. Every case of hybridization should be examined within its specific context (see Table S1 in SI2 for more details).

More data will likely emerge on negative consequences of hybridization for wild taxa, including risks to survival and long-term conservation. If none have been reported to date for a specific taxon, this can also reflect limited research efforts on hybrid organisms, which are often difficult to study. One recent example is wolf-dog hybridization, where new findings indicate behavioral differences between wolves and admixed individuals, with potential long-term implications for evolution and conservation (Amici et al. 2024). More research is thus essential to help quantify the ecological and evolutionary consequences of hybridization. Knowledge gaps and examples of taxa where these issues have been investigated or where further research has been identified as a priority, are listed in SI4.

2 | The Challenge of Managing Hybrids in the Wild

The International Union for Conservation of Nature (IUCN) Red Listing process generally considers hybrids as a threat to biodiversity conservation (IUCN 2021). Additionally, hybrids often lack legal status and are disregarded during conservation planning and actions, for example, with a goal to maintain the current status of a species gene pool (O'Brien et al. 2022). However, disregarding the potential of hybrids may, at times, impede conservation, for example, by limiting genetic diversity (Lucena-Perez et al. 2024). Reduced genetic diversity results in lower ecosystem resilience and impedes long-term survival (Frankham 2005; Figure 4; Kettenring et al. 2014). High genetic diversity often correlates with higher fitness. For example, Holzmann et al. (2023) found that montane lizard populations that survived climate changes had higher levels of genomic diversity than extinct populations. Conservation policy and nature management have therefore been encouraged to focus on maintaining genetic diversity for the future, as recently agreed at the 15th meeting of the Conference of Parties to the United Nations Convention on Biological Diversity (Kunming-Montreal GBF 2022). Although detrimental effects of human-induced hybridization need continued attention, further recognition of scenarios where hybrids might help maintain, restore, or enhance adaptive genetic variation can support effective conservation legislation and actions. A major challenge is to integrate traditional, species-focused conservation approaches with the current understanding of hybrids (but see also SI4

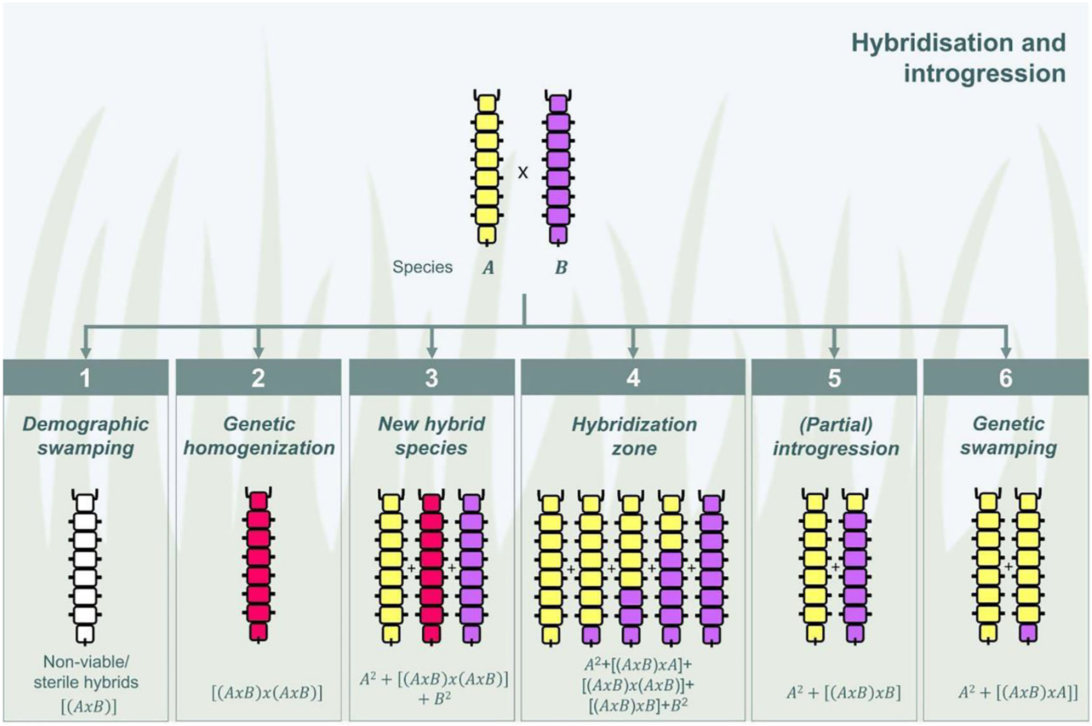

FIGURE 2 | Six possible (multi-generational) outcomes, on genetic composition, of hybridization (1–4) and introgression (4–6) between hypothetical, simplified arthropod species A (yellow) and B (purple). Hybrid zones, outcome 4, occur when these events are spatially restricted. Colors represent the (proportion of) species-specific genetic characteristics (after figure 1 in Runemark et al. 2019) and formulas represent the parental composition(s) of the outcomes (parental A or B, and/or hybrid (A × B)).

and Table S2) in conservation policy and management (see e.g., Quilodrán et al. 2020).

Intentional anthropogenic hybridization of a wild population is, at times, a tool in conservation management, in the form of genetic rescue and/or demographic rescue, or to improve adaptive diversity (but for further discussion on these topics, see e.g., DeMay et al. 2017; Van Oppen et al. 2015). In addition, unintentional anthropogenic hybridization (Ottenburghs 2021) can occur because of the inadvertent introduction of an invasive or domesticated species and may result in hybrids that are eligible for protection, if this can improve the conservation of a parent species at risk (Stoskopf et al. 2005 and SI3.B). Building on earlier frameworks for hybrid assessment (e.g., Allendorf et al. 2001; Jackiw et al. 2015; Wayne and Schaffer 2016; Ottenburghs 2021; Tensen and Fischer 2024), we propose a tailored approach to deal with hybrids on a case by case basis. We reconsider existing policy and management in light of ongoing challenges in biodiversity conservation, of new scientific developments and the increased recognition of the importance of genetic diversity (Hoban et al. 2021; Tensen and Fischer 2024; Norderhaug et al. 2024).

Because most assessments have previously centered on risks, we also address possible benefits that hybrids might yield in specific conservation cases. Importantly, these points should not be seen as promoting anthropogenic hybrids or ignoring their known or potential conservation impacts. Instead, we seek to discuss how to promote much-needed international coordination (e.g., Salvatori et al. 2020) while still permitting flexible, context-dependent decision-making. We outline recommendations to policy makers and managers with examples across taxa in various contexts. We reflect on the distinction between natural and human-induced hybridization, and advocate that policy makers and managers need to consider the origin of hybrids, their role in the ecosystem and their (observed or expected) impact (Quilodrán et al. 2020) on the fitness and gene pool of the taxa in question. The decision of whether to remove or accept hybrids or to prioritize certain populations, ultimately depends on (i) the conservation status of taxa involved, (ii) the level of anthropogenic influence, (iii) the impact on the taxa of interest (see Figure 3), (iv) political will and (v) the relevant spatiotemporal scale. As such, we recommend careful case-by-case assessments, analyzing possible positive and negative outcomes (in terms of ecological, demographic, and genetic parameters). We advocate for policies that strive for nuanced conservation management with the possibility of including hybrid organisms, if beneficial, and provide practical guidelines for (individual) management (in Section 5).

3 | Current Policies, Legislations, Regulations, and Practice

Hybrid management in practice can take on many forms, but often it is a question of whether to ignore or remove hybrids (e.g., see bontebok case study in SI3). However, removal of hybrids may, at times, undermine long-term restoration efforts, especially for taxa that naturally experience a high frequency of hybridization (vonHoldt et al. 2018). At the global scale, hybrids (and backcrosses up to the fourth generation) are protected by CITES and the EU Wildlife Trade Regulations when at least one of the two "parents" is (CITES) listed in Appendix I or II (Fossati 2024). Other international legal instruments (i.e., the Habitats Directive and the Bern Convention) also allow for the protection or removal of hybrids. However, this approach is currently not followed by the IUCN. As such, the IUCN, with the exception of apomictic hybrid plants, excludes interspecific hybrids from the Red List of Threatened Species (IUCN 2021), which limits the ability to evaluate the status of hybrids (Bauer et al. 2021).

Moreover, there is a discrepancy between international policy and agreements versus national rules or laws and their application. In general, there is a lack of formal policies on the status or value of hybrids for the agencies responsible for managing endangered taxa (Rees 2002), although hybrids have been discussed extensively in the United States and Canada (USFWS 1996; Allendorf et al. 2001; Haig and Allendorf 2006, Jackiw et al. 2015, Wayne and Schaffer 2016, COSEWIC 2018, Hirashiki et al. 2021). To our knowledge, evidence-based legislation regarding hybrids is lacking in many countries, often resulting in ad hoc decision-making. Although some guidance to control hybrids is provided, its implementation in management is not guaranteed. For example, wolf-dog hybrids have been reported in all nine extant European wolf populations (Salvatori et al. 2020). In the absence of international policies on hybrid management, national interpretations of standing guidelines could lead to conflicting strategies even in neighboring countries (Salvatori et al. 2020), highlighting the need for clearer policies and more international coordination, including standardized genetic methods for the detection of hybrids. Trouwborst (2014) previously recommended for the Standing Committee of the Bern Convention and the European Commission to adopt a common and scientifically-based understanding of what hybrids are and to promote a uniform application of the legal instruments concerning hybrids. However, we recognize the challenge in achieving a balance between international harmonization and flexibility. Hence, in the next section we propose a common framework to advance evidence-based decision-making.

4 | Framework for Future Conservation Policy and Management Including Hybrids

We present a process-based framework (Figure 3) that can help national and subnational entities to build legal schemes for evidence-based decision-making regarding hybrids. This framework includes elements of the IUCN-SSC's "Assess-Plan-Act" framework in the IUCN Species Strategic Plan for 2021–2025. Our framework does not consider hybrids to be a threat or benefit a priori, but states that hybrids should not by default be excluded from protection, as avoiding hybrids can result in the loss of genetic diversity and adaptive potential (see e.g. Coleman et al. 2013).

It focuses on measuring the impact of hybrids and introgression, before considering management actions, and takes into account the specific context (e.g., natural vs. human-induced hybrids).

4.1 | Analyze

Here, we focus on gathering knowledge regarding all three levels of biodiversity (ecosystem, species and genetic diversity) with specific focus on the available genetic/genomic information (The IUCN SSC Conservation Genetics Specialist Group, CGSG focus), as genetic diversity is the basis for future selection and adaptation (Powell 2023). Hence, a first step in this framework is to obtain,

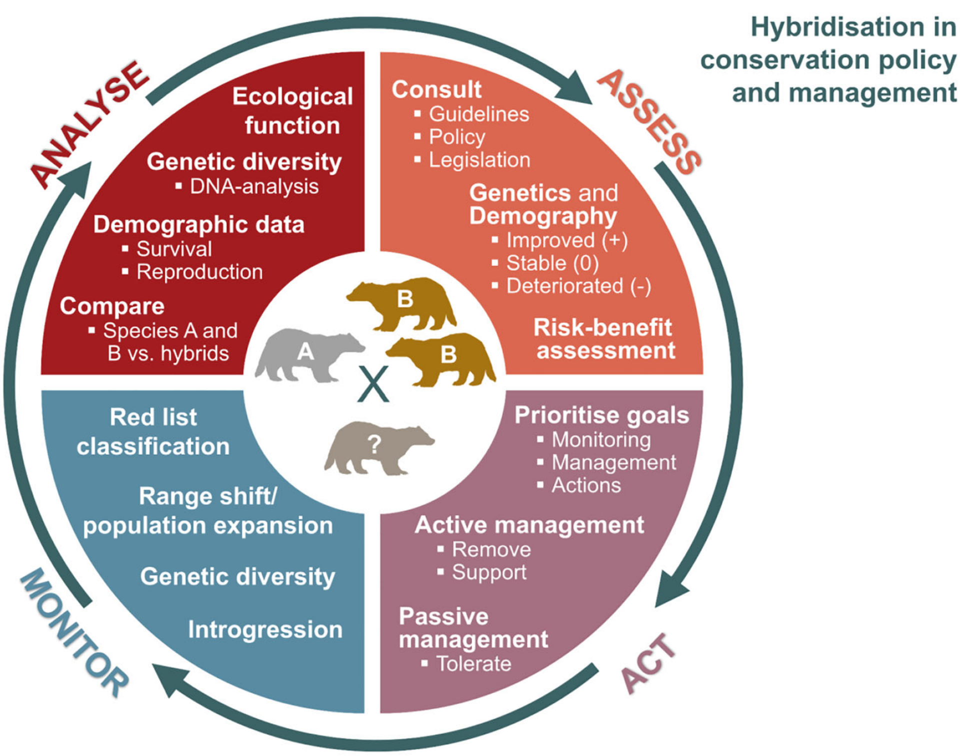

FIGURE 3 | Proposed framework for guidance in evidence-based management and decision-making of hybrids with parental taxa (A and B).

analyze and compare genetic, demographic and ecological data of the hybrid and the parental taxa. Managers and scientists need to address questions such as: How long have the taxa been separated (naturally or by e.g., domestication)? Is the hybridization of anthropogenic origin? How many known hybrids and individual parents of each taxon exist in the wild, and how are they distributed over populations and the landscape? Do the parental taxa and hybrids have different traits and/or preferences in terms of habitat, species (predator–prey) interactions? What are the levels of genetic diversity? Are there indications of inbreeding and/or outbreeding depression?

4.2 | Assess

Risk assessments looking at both negative and positive effects on long-term survival have been put forward as an appropriate tool. Management decisions and actions to either remove or protect hybrids need to be based on these assessments, considering other guidelines (e.g., see Section 5), available time, expertise, budgets, and legislation. A review indicated that such overarching risk assessments increase the probability of the recommendation of mixing gene pools (Liddell et al. 2021). Managers, in collaboration with scientists, need to address questions such as: If hybridization increased, how will genetic and demographic parameters change? What impacts will this have on other taxa and the ecosystem (e.g., change in diet)? These can be categorized into (likely) positive and negative impacts by consulting a range of experts and knowledge holders, and by carefully designed research. Conservation planning could then proceed, resources depending, in either qualitative (scenario planning, in which general possible futures are described in a storytelling fashion) and/or quantitative analyses (modelling, in which simulations are used to predict different outcomes based on certain assumptions).

4.3 | Act

If an assessment leads to the insight that some populations are at higher risk for hybridization than others or, to the contrary, that they have minimal nonnative ancestry (Kovach et al. 2025), those could be prioritized for monitoring, management and possible action. Further assessment outcomes include passive management, where hybrids are tolerated and monitored to study long-term impacts, and active management (see also Sections 2 and 3). The latter might consider the removal of hybrids when the relative risks are outweighing the benefits. For example, the Assess stage may show that hybrids pose a serious threat to endemic endangered taxa when simulations suggest that hybrids will continue to displace alleles of these taxa (Tensen and Fischer 2024). On the other hand, simulations may show that hybrids prevent the loss of an endangered taxon while maintaining much of its genetic integrity (Miller et al. 2003; Stoskopf et al. 2005, see red wolf case study SI3.B). Once an overall decision on a specific case is made, managers can decide on the fate of (groups of) individuals (see Section 5).

4.4 | Monitor

Given that the effects caused by hybridization can span over several generations, it is advised to monitor genetic diversity and introgression across time and space, for example, using genetic indicators (Hoban et al. 2021) and/or changes in Red List classification (but see Norderhaug et al. 2024). In many cases there may be insufficient data to make a well-informed decision. For example, it may be that the relative fitness of hybrids needs to be evaluated in an experiment, or the diet and aggressiveness of hybrids needs to be determined. Here, researchers and managers can benefit from close collaboration in designing research that includes specific, applied conservation questions relative to hybridization.

5 | Managing Individual Hybrids in Practice: Setting Thresholds

Practical conservation management at the individual level needs clear definitions to prescribe designated actions (e.g., on live-captured individuals): Is a potential hybrid to be euthanized, sterilized, or permitted to reproduce? However, proposing an unequivocal, operational definition of hybrids for conservation management is not straight-forward (see SI3), especially when hybridization is followed by introgression (Figure 2). This process leads to a genetic continuum spanning from parental to introgressed individuals. If managers decide to remove hybrids, they must set a threshold of hybrid ancestry somewhere on this continuum (Stoskopf et al. 2005; Senn et al. 2019; Donfrancesco and Luque-Lora 2022; Kovach et al. 2025). Most hybridization management case studies seem to accept 1%–25% introgression (Wayne and Shaffer 2016), depending on available resources (reference data, samples and funds) and the conservation objectives (demographics, genetics and ecology).

In addition, the “introgression-threshold” in the management of hybrids is partially determined by their detection reliability. For instance, it is not practical to recommend the removal of hybrids with very low, undetectable levels of introgression. Developing a reliable hybridization test depends on the availability of good quality samples and reference data for the parental taxa (see SI1). Furthermore, the selected genetic markers need to detect hybrids with high accuracy (Miller et al. 2003). However, several questions have to be answered before determining the precise introgression-threshold value (Figure 4). Over time, broader application of these questions across jurisdictions and populations, for example, standardizing markers for hybrid detection, can help balance international harmonization and flexibility.

If hybridization is advanced and the measures taken to eradicate hybrids are stringent (low introgression-threshold value), population numbers could go down severely (Miller et al. 2003). Also, such management decisions could unintentionally reduce historic genetic diversity found in threatened taxa (e.g., Kovach et al. 2025), which will be disadvantageous for their survival on an evolutionary timescale (Hoban et al. 2021; see also bontebok case study in SI3). Conversely, if the measures taken to eliminate hybrids are too weak, and individuals with substantially introgressed genomes are allowed to breed, then even elaborate conservation actions might have little impact. Furthermore, the risk-benefit assessment on whether or not to remove introgressed individuals (and how stringent a threshold to apply) may change with the severity of the conservation crisis (Stoskopf et al. 2005; Senn et al. 2019). Hence, we suggest

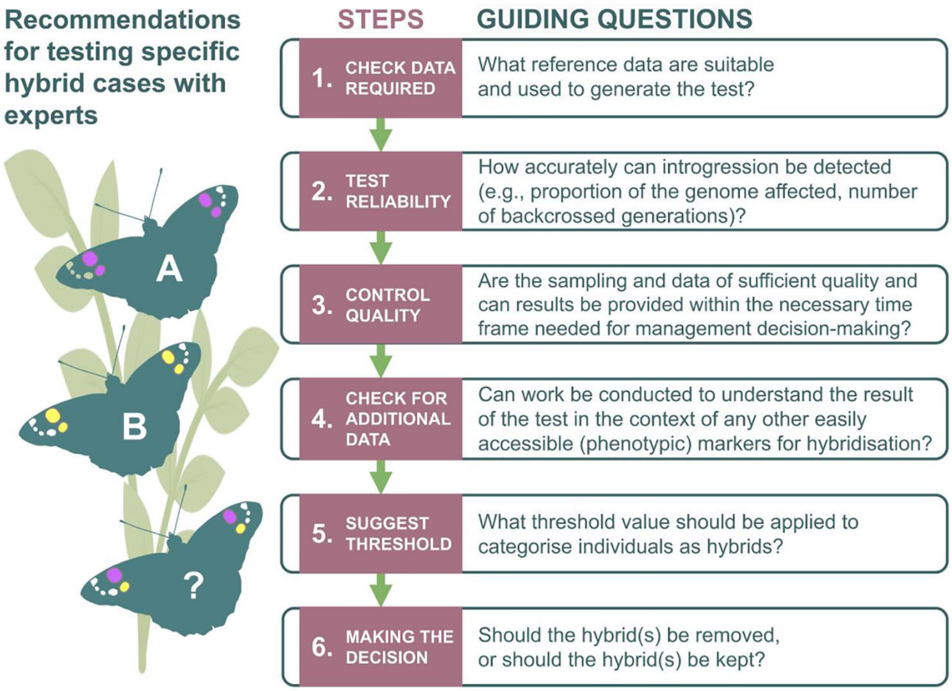

FIGURE 4 | Recommended steps with guiding questions for hybrid testing when categorizing individuals for management actions. The answers to these questions can be highly species, habitat, and context specific. Therefore collaboration with species experts and conservation geneticists is required. Managers may commission genetic testing in order to make management decisions on individuals, based on commonly-agreed introgression-threshold value (between taxa A and B).

that introgression-thresholds need to be decided (i) on a case-by-case basis, as part of the "Assess" step (Allendorf et al. 2001), (ii) in discussion with experts and stakeholders (using e.g., Population Viability Analysis simulations), (iii) with a clear understanding of the conservation objectives, and (iv) followed by regular review that allows for nuanced management (e.g., by integrating new information from high-resolution data and evolving taxonomies). Accordingly, it is important that scientists, policy makers and natural resource managers strive toward openness and develop/agree on terminology, avoiding loaded labels such as "pure" which can be misleading or even misused for a political agenda, when describing individuals or taxa (see e.g., Donfrancesco and Luque-Lora 2022; Hirashiki et al. 2021).

6 | Conclusions

Hybrids require and deserve more attention. Because genomics is a rapidly evolving field and management of wild hybrids is relatively new, further efforts are needed to improve conservation management and develop policy and legislation for hybrids influenced to various extents by human activities. So far, hybrids have been largely ignored in conservation management planning because of their complexity, variable impact, the science-policy gap and the fact that they often lack legal status. Here, we recommend carefully evaluating hybrids with focus on the evolutionary consequences, including overall genetic diversity, adaptive variants, and ecological function, on a case-by-case basis.

Author Contributions

Conceptualization: All authors. Investigation: All authors. Visualization: PG, LDB, AS, AK. Project administration: PG, AK. Writing—original draft: PG, MWB, AK, EvW, LDB, IMR, AVS. Writing—review and editing: All authors

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

Supplementary Material: conl13158-sup-0001-SuppMat.docx