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PERSPECTIVE

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Human mediation should be a non-factor in hybridization and conservation

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Abstract
Hybridization by introgression ("hybridization") is a complex topic in conservation. Many conservation decision-makers are concerned about hybridization by introgression because it may threaten species persistence or local phenotypes, among other potential long-term problems. While attitudes have changed towards hybridization as a conservation threat, there are still concerns about hybridization as a problem, particularly if the hybridization was anthropogenically mediated. I propose that these concerns are overblown and that it is misguided to focus on whether hybridization is unintentionally human-mediated. I argue that practitioners should still consider the effects of hybridization on conservation, but the reasons should concern the long-term environmental consequences, such as ecological function and social and cultural that hybridization has, rather than whether humans "caused" the hybrid. I propose a series of steps to think differently about these cases.

KEYWORDS
conservation science, environmental ethics, hybridization, values

1 | INTRODUCTION

Hybridization by introgression (hereafter, "hybridization") is a complex topic in conservation and biology. Historically, many biologists—zoologists, primarily (Edelman & Mallet, 2021)—often thought hybridization was relatively rare and did not afford it much of an evolutionary role. Over time, mainly through genetic advancements, hybridization was found to be more common than previously thought, even if its prevalence varies across taxa (Arnold, 2015). Further complicating the topic, hybridization has many definitions depending on the biological field (Arnold, 2015; Harrison, 1993). That said, hybridization is often operationalized in terms of different species or lineages sexually reproducing and creating fertile offspring that can potentially backcross with parental species or lineages (Porretta & Canestrelli, 2023).[i]

Several foundational articles influenced attitudes toward viewing hybridization as a conservation threat (Allendorf et al., 2001; Rhymer & Simberloff, 1996). A concern raised in these papers is that hybridization may reduce or replace alleles in a species, population, or lineage, causing extirpation or extinction. Hybridization may result in deleterious alleles being passed onto future generations, reducing fitness in a population over time, such as replacing local phenotypes or ecotypes. This last point is important for conservation decision-makers in areas with ecological disturbance or novel environments, which appear to influence hybridization rates (Edelman & Mallet, 2021; Grabenstein & Taylor, 2018).

Overall, a primarily negative assessment of hybridization was and still is common in conservation literature. I highlight two examples to illustrate this.

Spotted owls (*Strix occidentalis*) and Barred owls (*Strix varia*) hybridize, and human activity, such as land-use changes and development over the last several hundred years, has facilitated the species interacting at higher rates than they probably would have otherwise (Long & Wolfe, 2019). Spotted owls have a lower population than Barred owls and, under some circumstances, may preferentially breed with the latter. This makes it likely that hybridization between the species will, over time, lead to more Barred owl alleles being present and fewer "pure" Spotted owls. Human-mediated land use changes facilitated the hybridization. This is often said to justify conservation interventions, such as killing hybrid owls and Barred owls (Odenbaugh, 2022).

In a second example, the Arizona toad (*Anaxyrus microscaphus*) and Woodhouse's toad (*Anaxyrus woodhousii*) have overlapping distributions across much of the American southwest. They are known to hybridize, especially in disturbed habitats (Schwaner & Sullivan, 2009). Regionally, this is a conservation concern; the Utah Wildlife Action Plan describes toad hybridization as a "common problem" that contributes to "unnatural mixing" (p. 151), and earlier work describing these species' hybridization even suggested the toads were "mismating" (Sullivan, 1995, p. 246).

Both cases identify hybridization as a threat to some species' persistence. This threat is used to justify conservation interventions such as culling or conserving particular habitats.

That said, the discussion around hybridization is changing; several recent articles propose reevaluating hybridization's purported conservation threat (Chan et al., 2019; Hirashiki et al., 2021; Jackiw et al., 2015; Quilodrán et al., 2020). A common thread in these papers is that hybridization is not necessarily a conservation concern, as hybridization may be a source of genetic resources or novelty in a changing world. Furthermore, recognizing the role of introgression and genetic exchange may be a more accurate biological perspective (vonHoldt et al., 2018). Rather than blanket concern about hybridization, there are particular contexts, such as when the hybridization is unintentionally human caused, that warrant priority. Older papers (Allendorf et al., 2001; Rhymer & Simberloff, 1996) also identify human caused hybridization as a conservation threat, but it takes on higher prominence in these reappraisals.

For example, martens (genus *Martes*) from Colorado were translocated to Alaska to shore up populations for furbearing and hunting purposes. However, subsequent investigation suggests that the Colorado and Alaskan populations were distinct lineages or species rather than one (Colella et al., 2018, 2019). Therefore, this case may be a conservation concern because the loss of specific alleles in the Alaskan population may affect mesopredator prey selection, which may have ecological consequences or affect genetic "purity." This may be salient because humans caused the hybridization through translocation.

2 | ANTHROPOGENIC

Whether or not the hybridization event is "natural" or "unintentionally caused" by humans ("human-mediated") is important in this literature: the former is at least sometimes good, and the latter is almost always bad (see Table 1 for other examples). I am concerned with this perspective, particularly the importance of "human-mediated hybridization." This term is sometimes used interchangeably with "anthropogenic hybridization," which is defined in several ways. For my purposes, I use the following definition: "the breakdown of reproductive isolation between two species as a result of human action, including but not limited to species introduction, habitat disturbance, or escape of domestic species" (McFarlane & Pemberton, 2019).

First, it is not clear how this definition should work in practice. Since humans have significantly altered the biosphere for tens of thousands of years, separating natural and human-mediated from one another is perhaps impossible. Plausibly, based on this definition, almost any case of hybridization will count as human-mediated, as habitat disturbance, species introduction, or the escape of domestic species have occurred across the world and may influence sympatry or other ecological processes (Rohwer & Marris, 2015). In addition, determining what caused a "breakdown" of reproductive isolation is not simple, either, as reconstructing the past is unlikely to be precise; answers will mostly come in terms of degree, which calls into question the distinction.[ii] Even if a matter of degree is taken as a criterion, why some degrees of human mediation are acceptable, and not others requires additional explanation.

Second, the ethical assumption that "natural" hybridization is morally preferable or better than human-mediated is unclear. Evolution by natural or artificial selection is not good or bad; it merely is (Rohwer, 2023). Evolution is a biological process that provides no practical guidance for whether intervention against hybridization should occur or why "natural" is preferred over human-mediated. Claiming otherwise reveals an unsteady ethical premise in environmental restoration and conservation biology. Favoring some biological processes over others requires explanation. Furthermore,

TABLE 1 Criteria for determining whether a case of hybridization is a conservation concern and any conservation actions performed or recommended.

Hybrid cases	Criteria for determining whether it is a conservation concern	Conservation actions performed or recommended
Spotted owls (*Strix occidentalis*) and Barred owls (*Strix varia*) Odenbaugh (2022)	Conservation of *S. occidentalis* under the Endangered Species Act; increased contact between taxa from human mediated land use changes	Culling hybrid owls; culling *S. varia* where there is or may be hybridization between the species
Woodhouse's toads (*Anaxyrus woodhousii*) and Arizona toads (*Anaxyrus microscaphus*) Utah (2015)	*A. microscaphus* is a conservation priority under the state wildlife action plan because of human mediated land use changes, which influence hybridization rates	Monitoring of "unnatural mixing" between the taxa
Martens (genus *Martes*) Colella et al. (2018) and Colella et al. (2019)	Translocation of individuals from Colorado and Alaska; prey selection and associated jaw changes that may occur from translocation	Monitor and further research
American crocodiles (*Crocodylus acutus*) and Cuban crocodiles (*Crocodylus rhombifer*) Milián-García et al. (2015) and Rossi et al. (2020)	Human mediation increased contact between the species despite historical introgression; conservation priority of conserving *C. rhombifer* "genetic integrity"	Captive breeding of *C. rhombifer* to conserve their "genetic integrity" and prevent increased hybridization
European orchids (*Orchis mascula*) and (*Orchis pauciflora*) Cozzolino et al. (2006)	The role natural hybridization plays in speciation and local genetic adaptation	Maintain existing hybrid zones
Red wolves (*Canis rufus*) and coyotes (*Canis latrans*) Gese et al. (2015) and Bohling and Waits (2015)	Hybridization occurs at an increased rate because of human activity, which makes it a problem for conservation of *C. rufus*	Removal, killing, and sterilization of coyotes and at least some hybrid individuals to maintain the relative integrity and persistence of *C. rufus*
Fishhook cacti (*Sclerocactus glaucus* and *Sclerocactus parviflorus*) Schwabe et al. (2015)	Hybridization between the species is acceptable so long as the rates do not increase; maintain distinct northern and southern populations of *S. glaucus* by preventing human-mediated movement	Prevent increased introgression and movement between populations
Bitterling hybridization between *Tanakia lanceolata* and *Tanakia limbata* Hata et al. (2019)	*T. limbata* is non-native and was transported by people	Recommend construction of sites to maintain distinct *T. lanceolata* populations

Note: While there are differences across the cases, a common theme is that human-mediated hybridization is a cause for conservation concern and intervention.

this potentially places human actions outside the natural world since human actions may not count as natural under some definitions (Arnold, 2015).

Overall, human mediation is not a clear criterion despite its commonality. Determining the proximal or ultimate cause of hybridization might be helpful for some scientific enterprises in some contexts (Ottenburghs, 2021) but may not matter for conservation. To avoid these concerns, I suggest alternative criteria that front-load ethical discussion and debate rather than relying on anthropogenic mediation.

3 | SUGGESTIONS

Let me propose a hypothetical case to frame my suggestions. Suppose American beavers (*Castor canadensis*) and Eurasian beavers (*Castor fiber*) hybridize, one consequence is that the hybrid offspring have increased fitness and, for some reason, no longer produce dams. Through long-term ecological and evolutionary modeling, there are good reasons to believe hybridization will merge the two species and that there will likely be no return to a previously non-hybridized state.

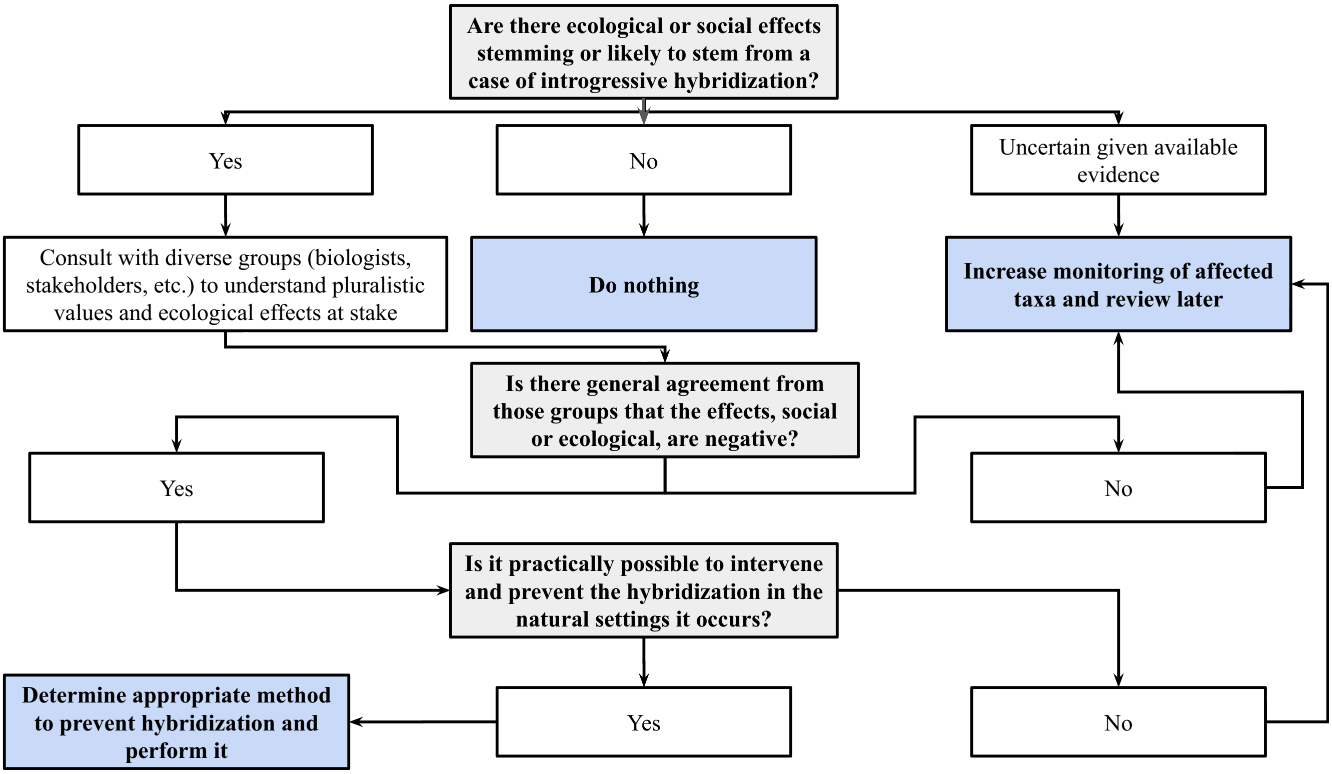

FIGURE 1 The figure visualizes my recommendations as a flowchart for conservation decision-making. Compare it with other flowcharts that discuss hybridization, such as Jackiw et al. (2015) and Quilodrán et al. (2020), and their usage of anthropogenic mediation as an important criterion for conservation. My recommendations are similar but diverge in not using that criterion. I recommend frontloading the ethical and social dimensions of conservation rather than relying on anthropogenic mediation.

Ecologically, a lack of dam-building behavior is pronounced. This behavioral change would have far-reaching consequences in watershed restoration, cultural and social practices, biodiversity conservation, and landscape management. Water flow patterns and riparian zones would dramatically change. In addition, these changes may significantly affect human activities near waterways, such as agriculture or development, or imperil other conservation efforts. Thinking about cases like this helps highlight an underlying worry about hybridization for conservation biologists. Namely, what ecological or human social changes may stem from hybridization.

I propose two criteria to determine whether it is worth intervening against a case of hybridization. First, what ecological effects does some particular hybridization event have (Porretta & Canestrelli, 2023; vonHoldt et al., 2018)? For example, this may take the form of ecosystem services or physical structure. Alternatively, these ecological effects might highlight changes in ecological function, meaning the movement and storage of energy or material in an ecological context (Bellwood et al., 2019; Jax, 2010). Other effects, such as the possible extinction of taxa should hybridization continue, are also salient considerations, but are not determinate.

Second, what social, economic, or cultural effects may hybridization have, particularly on local communities? I include human effects for pragmatic reasons, such as local buy-in, but also because conservation science has an obligation to include a diverse range of people's perspectives in the planning and execution of conservation decisions (Kareiva & Marvier, 2012).

These criteria frame my suggestions. Conservationists (managers, biologists, non-profits, or otherwise) should only intervene against hybridization when ecological or social effects occur or are likely to stem from some case of hybridization (Figure 1, flowchart). There are good reasons—managing landscapes, effects on ecological communities, social and cultural factors, predictability in water use—that maintaining dam-building organisms is worthwhile and has nothing to do with whatever "caused" the species to hybridize. I suggest thinking about effects is more direct than focusing on degrees of human mediation. I suggest this for several reasons.

First, I hope to have shown that natural and human-mediated, both common in the literature, are not clear criteria.

Second, hybridization is widespread. In conservation, I take it as a given that working contrary to common ecological or biological processes needs justification. This is for two sub-reasons. Practically, this is meant to direct limited resources. Conceptually, this is meant to shift the burden of justification to those who wish to intervene and prevent hybridization. Intervention is still possible, but a higher burden of evidence is necessary than appealing to anthropogenic mediated hybridization.

Third, these criteria help foster communication and understanding between different groups. While my criteria about ecological or social effects requires unpacking, these criteria are hopefully more tractable for discussion and clarify why intervention is sought. For example, attitudes about genetic "purity" may require explanation, particularly for those outside the conservation biology field.

That said, my criteria are process-oriented. People may still agree on large-scale removal of plants or animals, such as culling. However, my suggested standard is higher than focusing on human mediation. I am hopeful this shift dissuades some conservation actions, like indefinite suppression or appeals to "purity" to justify culling. Culling hybrids should be actively prevented and dissuaded, as it is a poor use of resources, has significant ethical questions, and may be ultimately ineffective, leading to perhaps endless killing. Intervention should focus on cases where intervention is justified and hybridization can be prevented, either through sterilization or culling, currently and in the future. I take for granted that there will be differences of opinion among professionals on this point (cf., Coghlan & Cardilini, 2022), which is partly why I frontload discussion and debate here. This is not to suggest that conservation scientists or managers do not currently have discussions. Rather, I am suggesting that relying on human mediation is a mistake and should be discarded from flowcharts and other decision-making tools managers may use.

To be clear, what is used as justification for intervention requires long-term thinking and envisioning what an ecological community may look like with hybridization occurring rather than relying on intuitions about human mediation and naturalness, which can come into conflict concerning hybrids (Marris, 2017). This perspective concerns discussions about hybrids rather than determining what must happen in any particular case.

4 | CRITICISMS

I hope my suggestions provide a more tractable way to consider conservation and hybridization. However, these suggestions may face resistance. Below, I address some of the potential criticisms that may arise.

First, would any hybridization constitute an ecological effect? Put another way, won't spotted owls being genetically swamped by barred owls automatically mean an ecological effect has occurred? On some level, there has been a potential loss of a species, which seems reasonable to chalk up to ecological change. However, I do not think it is necessarily a concern for this position. There are many species in any given environment, and sometimes those organisms are redundant or ecologically similar (Kareiva & Levin, 2003; Lawton & Brown, 1994; Rosenfeld, 2002).[iii] Granted, there are many unknowns (Reich et al., 2012), but redundancy or similarity can be the case, which means there should not necessarily be an assumption that there must be a problem with hybridization. This is not to say that ecological function (cf., Jax, 2010) or redundancy should be the sole criterion in decision-making. Rather, my position is that debate should focus on ecological effects like these rather than human-mediated hybridization.

Furthermore, maintaining a species count is different from thinking about organisms' ecological effects, such as ecosystem services, even if species richness may be an indicator of biodiversity. More investigation should occur if, for example, the hybrid owls behave quite differently post-hybridization. This shifts the burden of evidence to find a problem with a specific case of hybridization rather than assuming there must be a problem. If some species are eventually "replaced" by hybridization, this is not necessarily a problem on this account. Conserving species richness as the primary indicator for biodiversity may also be ill-advised for other reasons beyond this short comment (Santana, 2014).

Second, most examples of hybridization will be murky, so perhaps my standard is just too high a bar. What are the effects of marten hybridization? Will mesopredator prey selection have any significant effects? I accept and encourage this kind of inquiry. Part of conservation in an empirically informed manner is thinking about, modeling, and communicating with uncertainty. Each case is unique and should be approached with fresh eyes.

Third, a critic might say all this amounts to fiddling while the National forests burn: we must be more aggressive and intervene to protect genetic purity. By way of answer, there will be a lot more burning, and we ought to get used to it to some extent. This is not defeatism. Instead, it is acceptance of change and rethinking to what extent we ought to consider change a problem and what sort of circumstances it is worth spending limited capital, both literal and social, on. Some cases are worth reacting to and trying to prevent, but not all. Human-mediation does not serve a useful role here.

Fourth, what fate might befall local phenotypes, genes, or varieties if hybridization is not prevented? Or, consider cases such as domestic cats or dogs breeding with wild wolves or cats: what happens then? These concerns are met on a case-by-case basis and require multiple points of view for discussion, not relying on anthropogenic mediation to end or frame debate. This perspective is about framing discussion and showing problems with current approaches. Going forward, thinking about ecological and social effects is more fruitful, but it does not necessarily dictate what actions must follow.

Fifth, suppose someone is against hybridization in general or at least against human-mediated hybridization and I have not yet persuaded them. By way of response, I propose an alternative case. Suppose there are two trout (*Salmo* sp.) species that, independently, face certain extinction. However, evidence indicates that, should they hybridize, their offspring will be more fit than their parental lineages and can thrive in the disturbed habitat their parental lineages could not. Furthermore, suppose there are minimal ecological changes because of hybridization and people find little difference in the social aspects of this (i.e., they are of similar sporting quality). In this case, hybridizing the two lineages as a conservation intervention seems appropriate regardless of what caused the disturbance.[iv] This hopefully shows that at least some cases of hybridization are acceptable for a range of different reasons.

Finally, it might be suggested that cases like the spotted owls involve the Endangered Species Act and allow for broader conservation, such as conserving old-growth forests, and that the legal framework is at risk through hybridization. This is a fair concern, but it speaks more to the need to change laws, not continue working through problems with the existing ones (cf., Odenbaugh, 2022). Legislation sensitive to the reality of hybridization should be implemented rather than relying on old, even if well-intentioned, laws. This is difficult practically and conceptually but may be necessary going forward (Lind-Riehl et al., 2016; vonHoldt et al., 2018).

5 | CONCLUSION

My approach does not dissolve all difficulties; this is by design. There will be disagreement about what effects are worth avoiding and how social groups are affected. Conversation and coordination between many actors are both necessary for conservation to be effective. Human-mediation does not perform a useful role in these discussions.

I frame these points with some previously raised concerns (Arnold, 2015, pp. 142–144). However, I want to highlight further the necessity for pluralism about what people are involved in conservation decision-making. Arnold (2015) focuses on and frames his comments for scientists, conservationists, and managers, which is appropriate given the book's context. However, the pool of individuals should be further expanded. Looking at the ecological and social effects of hybridization requires more people brought to bear—non-scientists, policymakers, Indigenous communities, local people, stakeholders, and other groups—to discuss and debate cases worth intervening on. This is time-consuming and resource-intensive, but it avoids the pitfalls of relying on human mediation or some other simple solution to a complex and changing world.

Discussion about hybridization has changed and will continue to do so. The extent of admixture continues to show the complexity of life, which is ultimately part of the reappraisal of conservation and hybridization. This conceptual evolution should be taken in stride, as further insights into the tangled tree of life are undoubtedly forthcoming.

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ENDNOTES

[i] There are complications with plants (e.g., spontaneous polyploids), but generally animals are the locus of concern in conservation literature, which is why I use this definition.

[ii] Even if there are cases like the martens of direct translocation, these are unlikely to be the majority of cases.

[iii] I use the term "redundant" here because of its commonality in conservation literature, even if I also include it with the

disjunction of ecologically similar, which may be a better descriptor (Eisenhauer et al., 2023).

[iv] Cases like this are not far-fetched (cf., Fitzpatrick et al., 2020).

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