Concern over hybridization risks should not preclude conservation interventions

Claire Hirashiki\(^1\) | Peter Kareiva\(^2\) | Michelle Marvier\(^3\)

\(^1\)Institute of the Environment and Sustainability, University of California, Los Angeles, Los Angeles, California
\(^2\)Aquarium of the Pacific, Long Beach, California
\(^3\)Department of Environmental Studies and Sciences, Santa Clara University, Santa Clara, California

Abstract

Conservation interventions such as assisted migration and genetic alterations are controversial in part because, through unintended hybridization events, they may imperil native species. Threats could stem from hybrid offspring having altered fitness or from genetic swamping due to extensive introgression of non-native genes. Over the last 40 years, papers discussing hybridization increasingly use value-laden terminology (e.g., “genetic contamination”). Such terms presume that any amount of hybridization equates to harm, but this perspective is at odds with modern evolutionary theory’s recognition of hybridization as a creative force that can accelerate evolution or spur adaptive breakthroughs. To assess the evidence undergirding perceptions of hybridization threats, we examined the IUCN’s Global Invasive Species Database (GISD). Of 870 invasive species, the GISD identified 35 as potentially threatening endemic taxa via hybridization. For each of these 35 species, we assessed the quality of data that the GISD cited pertaining to hybridization. Direct evidence for hybridization was cited for only 16 species, and there was neither direct nor indirect evidence demonstrating reduced fitness of hybrid offspring for 18 species. In our era of rapid environmental change, it is time to examine hybridization case-by-case and not to presume that hybridization always presents a threat to biodiversity, but rather, to consider it as a potential pathway to species survival.

Keywords

adaptation, biodiversity, conservation, conservation interventions, evolution, hybridization, invasive species

1 INTRODUCTION

Given the pace and severity of climate change, conservationists are increasingly considering interventions such as assisted colonization and assisted evolution to improve species’ resilience to climate disruption (Hoegh-Guldberg et al., 2008; Smith, Kinnison, Strauss, Fuller, & Carroll, 2014). Similarly, in light of ongoing extinctions, there are advocates for introducing non-native species to replace lost ecological functions (Donlan et al., 2006). However, concerns surrounding “unintended consequences” may stymy action on these fronts (Hewitt et al., 2011). One concern is the possibility of hybridization between introduced species and resident native species, which

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consequently may cause “genetic contamination” or other negative outcomes due to altered fitness of hybrid offspring (Bucharova, 2017; Ricciardi & Simberloff, 2009). The concern expressed by conservationists stems largely from the observation that anthropogenic movement of species and habitat alteration has increased the occurrence of hybridization far beyond that of a baseline background level (Rhymer & Simberloff, 1996). On the other hand, evolutionary theory and field studies have established pathways by which hybridization increases biodiversity and facilitates rapid adaptation to a changing environment (Chan, Hoffmann, & van Oppen, 2019; Marques, Meier, & Seehausen, 2019)—a reality that contrasts with the characterization of hybridization predominantly as a threat to native biodiversity.

Two notable reviews have extracted percentages or frequencies from the literature as a way of estimating the relative importance of hybridization as an extinction risk. First, Rhymer and Simberloff (1996) noted that of 24 species listed under the U.S. Endangered Species Act that had become extinct, hybridization was implicated in three of the extinction events (or 12.5%). They conjectured that those instances are only the “tip of the iceberg” but also recognized that hybridization can be a constructive evolutionary process. Todesco et al. (2016) used a Web of Science search with the keywords “extinction” and “hybridization” as a means of assessing the extinction risk associated with hybridization. They found 143 case studies with both keywords, of which 48% considered hybridization to be an extinction threat. However, Todesco et al. did not assess the type, nor the quality, of evidence underlying the claims that hybridization was an extinction threat.

We acknowledge that threat differs from risk: threat implies a certain negative outcome is plausible, whereas risk refers to the likelihood of that negative outcome. However, the literature can be confusing, because conservationists often use risk and threat interchangeably. For example, it is common practice to rank conservation threats (as in, “habitat loss is the single greatest threat to biodiversity, followed by the spread of alien invasive species”; Wilcove, Rothstein, Dubow, Phillips, & Losos, 1998), when in truth, they are implicitly assessing risks. Further, some conservationists use “risk” as an all-encompassing term that refers to both chance of occurrence and magnitude of consequences.

While treating hybridization as a potential threat is warranted, conclusions about relative risk require a deeper examination of data. Endangered species face so many threats, that assessing the level of risk associated with each threat is crucial. For instance, when discussing the controversy surrounding the introduction of eight Texas cougars into Florida to hybridize with Florida panthers, Rhymer and Simberloff (1996) remark that concern regarding this intervention was a “tempest in a teapot,” because other threats to the Florida panthers were far more significant risk factors. In this paper, we explore the evidence that the extinction risk posed by hybridization is substantial. To assess the strength of evidence, we use the Global Invasive Species Database (GISD). The GISD is a curated and respected repository of expert opinion and published literature that the IUCN supports and draws on when producing documents such as “100 of the world’s worst invasive species” (Lowe, Browne, Boudjelas, & de Poorter, 2000). By restricting our search to the GISD, we ensured a coherent and well-defined sampling universe that has been used for several lines of research (e.g., Padayachee et al., 2017; Turbelin, Malamud, & Francis, 2017; Westphal, Browne, MacKinnon, & Noble, 2008). Our goal is to assess the type and amount of evidence cited in the GISD to ascertain a balanced view of the extent to which hybridization is a risk to biodiversity. It is important to ask whether narratives surrounding hybridization as a risk are well-founded, because presumptions about hybridization may impede interventions designed to reverse the declines of wild populations and facilitate adaptation to rapid climate change.

2 HOW FREQUENTLY DOES HYBRIDIZATION IMPERIL SPECIES?

To evaluate the risk posed by hybridization, we turned to the GISD, which is publicly accessible online (via http://www.iucngisd.org/). As of September 2020, the GISD included information on 870 plants, animals, fungi, bacteria, protists, and viruses from around the world that are designated as invasive species by IUCN Invasive Species Specialist Group members and invasive species specialists. Previous attempts to evaluate threats and risks to biodiversity similarly restricted themselves to limited sampling universes (Lawler et al., 2002; Rhymer & Simberloff, 1996; Todesco et al., 2016; Wilcove et al., 1998). Our investigation makes use of the documentation associated with the GISD to take a deeper look at the quality of evidence associated with calling out hybridization as an extinction risk. In lieu of labeling hybridization a risk or a threat, the GISD uses the seemingly more neutral term “mechanism of impact,” but the interpretation of impact is without exception, unambiguously negative (Blackburn et al., 2014).

At the time of our query, the GISD encompassed 870 invasive species, 35 of which were identified in the database as exerting an impact via hybridization. Table 1
compares the taxonomic composition of these 35 species relative to that of the other 835 invasive species in the GISD. Vertebrate animals are substantially overrepresented as hybridizers, which is noteworthy given that hybridization is more common among plant species (Mallet, 2005; Yakimowski & Rieseberg, 2014). This may reflect a bias in the kinds of species for which IUCN experts are most concerned about genetic purity. Indeed, heightened concern regarding hybridization in vertebrates may be a broader phenomenon. For example, extraordinary measures are taken to assure genetic purity in North American bison (Hedrick, 2009).

Next, for each of the 35 species, we looked into the quality of the data suggesting that a particular species represents a risk to biodiversity due to hybridization. To address this question, we examined the references cited in the GISD’s full account for each species. A total of 1,249 cited sources were obtained (some cited sources were unobtainable online or the referenced websites had become permanently unavailable). We did a preliminary screening of the references by searching each one for root words related to hybridization, including “hybrid-,” “inter-,” “cross-,” “breed-,” “reproduc-,” and “mat-.” The result is a library of 226 studies potentially providing evidence that one or more of the 35 focal species poses a hybridization risk (range = 0–25 hybridization-related sources cited per species account, average = 6.5, median = 6). We then closely examined these 226 sources to ascertain the evidence they provided in support of listing hybridization as a mechanism of impact. Note that our conclusions about “absence of evidence” pertain to the references associated with the GISD database and not the entire scientific literature.

In examining each of the 226 references identified above, we asked whether the source documented (a) the occurrence of a hybridization event, and (b) changes that would affect (either positively or negatively) the fitness of hybrid generations relative to their parent species. In determining whether there was direct evidence of fitness impacts, we accepted data on proxies for fitness such as growth or reproduction. It is clear that squandering reproductive effort on hybrids of low fitness is a threat. However, hybrids of high fitness can also be a threat if invasiveness is further increased or because hybrid success enhances the possibility of backcrossing, and if that backcrossing is common, then it could produce a genetic swamping. We further categorized the evidence as direct (the cited source presented original data regarding hybridization or fitness change in the hybrid generations) or indirect (the cited source referred to other publications as well as reviews or summaries that mentioned hybridization or fitness changes in hybrids). The results are tallied in Table 2, with details of the evidence for each species provided in the supplemental materials (Table S1).

One key conclusion to be taken from Table 2 is that in a majority of cases (54%, or 19 out of 35), species were singled out as a hybridization risk without providing any direct evidence of hybridization occurring. A second result that stands out in Table 2 is the scarcity of direct
evidence of hybridization altering fitness (26% of the species, or only 9 out of 35). The challenge of assessing fitness changes may be partly due to the difficulty of distinguishing differences between the parent species with F1, F2, and subsequent hybrid generations. Large-scale commercial releases of artificially propagated species (e.g., hatchery fish) could provide an opportunity to better understand hybridization risks, if the genetic impacts of these releases were better monitored (Laikre et al., 2010).

It is worth noting that the 226 references varied enormously in the quality of data (if any) brought to bear on assessments of hybridization as a risk or a threat. In some cases, hybridization was mentioned as a threat on the basis of as little as observing specimens that appeared morphologically intermediate between presumed parental types, as demonstrated in the case of the red fox below (Thornton, Creel, & Trimble, 1971). In contrast, some articles established the danger an invasive species (mallard ducks, *Anas platyrhynchos*) posed because of hybridization with a native population (New Zealand native grey duck, *Anas superciliosa*), using genetic proof of extensive introgression (Gillespie, 1985; Rhymer, Williams, & Braun, 1994).

Overall, among the 226 studies cited in the GISD profiles for the 35 hybridizing species, we found very little data that substantiated the assumption that hybridization was a significant risk. Nonetheless, one of the cited articles claimed that hybridization is the “second most important threat to biodiversity after habitat degradation” (Barbanera et al., 2009).

We recognize that the IUCN assessments are conducted by invasive species experts, and therefore the paucity of evidence reported in Table 2 may simply reflect that experts considered it unnecessary to look further back in the chain of evidence. To explore this possibility, we dove one layer deeper in that chain of evidence to see whether cited sources that did not themselves provide direct evidence of hybridization at least cited other works that did provide that direct evidence. We performed this exercise for both of the species with no evidence and a sample of 5 of the 17 species with only indirect evidence (see Table S1 for number and categorization of GISD sources related to hybridization and species selected for further literature analysis). Our investigation uncovered that the cited sources typically did not yield direct evidence.

For example, of the total 15 sources listed in the GISD’s bibliography for the European fan worm (*Sabella spallanzanii*), only two mention hybridization but without specific reference to *S. spallanzanii*. The first (Thresher & Kuris, 2004) broadly discusses stakeholder opinions of invasive marine species management. The other (Currie, McArthur, & Cohen, 2000) speculates, “Further ecological impacts may include alterations to trophic pathways (Parry et al., 1996) and hybridization (Kohler & Courtenay, 1986).” However, Kohler and Courtenay (1986) do not provide any discussion specific to *S. spallanzanii*. Thus, none of the cited sources, nor the works cited in those sources, provided any direct evidence that *S. spallanzanii* hybridizes, let alone has an impact as a result.

A second example is the red fox (*Vulpes vulpes*). For this species, the GISD cited Lewis, Sallee, and Golightly Jr (1999) as evidence of hybridization impacts. Lewis et al. (1999) do not provide direct evidence on this point, but they did cite Thornton et al. (1971). However, Thornton and colleagues merely mention “probable interspecific hybrid[s]” based on three fox specimens with unusual pelage coloration and a single fox skull that appeared intermediate between the non-native red fox (*Vulpes vulpes*) and the native Sierra Nevada red fox (*Vulpes vulpes necator*). These examples are illustrative of our larger effort to trace the chain of citations. The conclusion is that claims of hybridization occurrences are often not well documented and can be rooted in outdated evidence, from a period when it was common to determine hybrid status based solely on intermediate morphology or appearance.

3 NEITHER “GOOD” NOR “BAD”—A NUANCED VIEW OF HYBRIDIZATION AND CONSERVATION

Hybridization can increase or decrease biodiversity, or cause no change at all. It may push native species to genetic oblivion or it could present a means of preservation, if the influx of additional genetic variation can rescue a dwindling population or provide the raw material for adaptation to changing environmental conditions. From a conservation perspective, it is useful to delineate the following possible outcomes of hybridization between a threatened species and another species:

1. negligible impact and minimal introgression of genes into the species of concern;
2. introgression of some genes into species of concern, but no discernible fitness or functional consequences;
3. introgression of some genes into species of concern, and significant positive impacts, such as increased fitness under warmer temperatures or hybrid vigor;
4. introgression of some genes into species of concern, and significant negative impacts, such as reduced
survival of hybrid offspring or reduced attractiveness to potential mates;
5. major introgression of genes into species of concern or genetic swamping, such that the result is effectively a fundamentally altered species.

Outcomes 1, 2, and 3 above would not increase the risk of extinction. Outcome 4 is unambiguously an extinction risk. The interesting case is Outcome 5: if the hybrid population replaces a native lineage, many conservationists would consider that a bad outcome (because a native genome has been extensively mixed with that of a non-native species). However, an alternative view is that hybridization has created a more resilient and successful population than previously existed. Moreover, if elsewhere on the planet the original native species persisted without having experienced hybridization, then Outcome 5 would actually represent an increase in global biodiversity.

Knowing a priori which outcomes of hybridization to expect is likely impossible at this time. Even after hybridization is well underway, it can be extraordinarily challenging to determine whether hybridization will create adverse consequences in any particular case. California tiger salamanders (*Ambystoma californiense*; CTS), a federally and state-endangered species restricted to central California, provide an interesting case study with which to examine the complexity of thinking regarding hybrids and biodiversity conservation. In the 1950s, barred tiger salamanders (*Ambystoma mavortium*; BTS) from Texas were used as bait for sport-fishing in California (and throughout the United States), from whence they escaped and established wild populations. BTS readily hybridize with CTS individuals, and subsequent research has demonstrated that hybrid offspring often have a fitness advantage over “pure” CTS (Fitzpatrick & Shaffer, 2007; Johnson, Johnson, & Shaffer, 2010; Ryan, Johnson, & Fitzpatrick, 2009). Over time, genes from the introduced BTS will likely continue to spread through the CTS population, potentially resulting in “extinction-through-hybridization” of the CTS population.

While hybridization is officially recognized as a threat to the long-term existence of CTS, we can ask—from an ecological perspective—what effect would the replacement of CTS with CTS/BTS hybrids actually have? If one population of salamander were replaced with another that is more fit, is that really a net loss? The answer could depend on whether there are ecological consequences associated with the elevated fitness. Native *Ambystoma* larvae have proven to affect community-scale interactions indirectly via trophic cascades and directly as top predators of their habitats (Holomuzki, Collins, & Brunkow, 1994). To address the issue of ecological consequences, Searcy, Rollins, and Shaffer (2016) used replicated mesocosms to compare the community-level effects of hybrid salamanders compared to those of the native parent species. They compared the aquatic community under three pertinent salamander conditions: genetically “pure” CTS (the original baseline condition in California), full hybrids as often now occur on the California landscape (with ~70% introduced BTS genes), and a salamander-free baseline treatment that would result from a concerted program of hybrid eradication. For two of the nine response variables, the full hybrids did affect the ecological community in a way that was statistically distinguishable, due to the lower *Notonecta* counts and higher chlorophyll density in their mesocosms compared to those of the native salamanders. The authors hypothesize that the full hybrids were more voracious predators than the native salamanders, as *Notonecta* typically are unfavorable prey. The authors could not explain the change in chlorophyll density, but did note it could have an effect on turbidity. Ultimately, the community-level effects of the hybrids were far more similar to those of the native salamanders than to the salamander-free treatment. This result leaves us with a somewhat muddled answer. The hybrids are not ecologically equivalent to the natives, but they result in an ecological community that is substantially more “intact” in the sense that community composition is more similar to the CTS condition than would result if there were no salamanders at all. Searcy et al. ultimately recommend managing against the hybrids, but if hybrid presence is inevitable, it would be better to allow their population to remain and avoid the potential of having no salamanders.

Further complicating the answer, Cooper and Shaffer (2019) found that CTS/BTS hybrids are more flexible in their abilities to tolerate thermal extremes than pure CTS, suggesting that hybrids may be better suited to a warming climate. While hybridization is, by definition, a threat to the “genetic integrity” of CTS, it may also be a path to the long-term survival of many of its genes on the California landscape.

As this case study illustrates, even with a rich understanding of the ecology, it can be exceptionally difficult to determine whether hybrids constitute a conservation problem or potentially a conservation solution. Blanket assumptions that hybridization is always a negative or a net loss are unwarranted.

4 | VIEWS OF HYBRIDIZATION FROM ARISTOTLE TO 2020

Historically, humans have regarded hybrids through a dual lens of utilitarianism yet aversion (Li Causi, 2009). As far back as the early first millennium B.C.E.,
civilizations in the ancient Near East crossbred camels to create hybrids with desirable traits, such as greater load-bearing capacity and amiable disposition (Potts, 2004). Aristotle (2008) wrote about interbreeding partridges with hens, as well as dogs with wolves or foxes. Despite intentionally creating hybrids, the ancient Greeks and Romans conflated hybridization with adultery as an act in violation of nature (Li Causi, 2009). This belief in hybrids’ artifice and unworthiness was reiterated in Comte de Buffon's *Histoire Naturelle, générale et particulière, avec la description du Cabinet du Roi*, which suggested that all hybrids are sterile and thus could not be considered species (Li Causi, 2009; Lovejoy, 1911; Mayr, 1982). Early perceptions of hybrids consistently considered hybridization to be unnatural—a human device.

It was only with the emergence of modern evolutionary biology that hybridization came to be recognized as a natural, and often evolutionarily creative, process. Stebbins (1959) identified hybridization as the instigator of major evolutionary leaps for plants because of its ability to introduce genetic novelty. Barton (2001) explored a variety of population genetic models that revealed in theory how hybridization could dramatically enhance the rate of evolution.

In parallel, the relatively young academic discipline of conservation biology developed its own views on hybridization—views that are somewhat contrary to perspectives of hybridization in the evolutionary biology literature. Conservation biologists predominantly characterize hybridization as a force that threatens biodiversity and therefore should be prevented (Ricciardi & Simberloff, 2009). Hybridization is thought to contribute to extinction of distinct species through either of two possible mechanisms: (a) outbreeding depression and its associated reduction in local adaption and hence fitness, or (b) extensive genetic mixing such that the original unique evolutionary lineage is genetically swamped and replaced by a different lineage (Rhymer & Simberloff, 1996).

Conservationists are predominantly concerned about hybridization that occurs as an indirect result of human activities (Allendorf, Leary, Spruell, & Wenburg, 2001; Genovart, 2009). Anthropogenic disturbances undoubtedly have caused a massive reshuffling of species distributions. Beyond the introduction of species due to human-mediated transport and land-use change, humans have exacerbated climate change, which has also proven to increase interactions between otherwise isolated species (Garroway et al., 2010; Muhlfeld et al., 2014). The consensus within the conservation discourse is that anthropogenic hybridization is to be prevented, as opposed to natural hybridization, which is tolerated as an uncommon natural phenomenon (Allendorf et al., 2001; Genovart, 2009; Piett, Hager, & Gerrard, 2015; Vilà, Weber, & Antonio, 2000). However, recent genomic data have revealed that natural hybridization events (not caused by humans moving species around the globe) are far more common than previously believed (Taylor & Larson, 2019). Indeed, genomic data reveal a web-like tree of life with lineages frequently exchanging genetic material. These genomic studies have also uncovered examples of hybrid speciation (Taylor & Larson, 2019). Detailed genetic analyses of *Heliconius* butterflies suggest that introgression of genetic material in these butterflies led to a burst of speciation (Edelman et al., 2019). Hybridization has also enhanced population variability in Galapagos finches, thereby accelerating adaptive evolution and potentially enhancing species survival in the face of climate change (Grant & Grant, 2019). Taken together, these new data reinforce a concept introduced by Anderson and Stebbins Jr (1954) that views “hybridization as an evolutionary stimulus.” Recently, Thomas (2013) argued that speciation by hybridization is likely to be a major feature of biodiversity’s future; he noted that in the last 150 years, five new plant species have originated in Great Britain as a result of hybridization with non-native species.

Hybridization as a potential promoter of biodiversity is not an idea that has gained much traction in the conservation community. To the contrary, conservationists have, over the last four decades, increasingly vilified genetic mixing as a form of pollution (Figure 1; see caption for explanation of Google Scholar query).

### 5 | DOES CONSERVATION NEED TO RECONSIDER ITS STANCE ON HYBRIDS?

As noted, conservationists have increasingly adopted value-laden descriptions such as “genetic pollution” to describe hybridization with introduced species. We argue that “genetic purity,” “genetic contamination,” “genetic pollution,” and “genetic integrity” should be dropped from the conservation lexicon. These words reflect bias, not objective science.

Even more problematic, terms such as “genetic purity” trace back to racist values that permeated the founding of conservation. As other authors have discussed (Brechin, 1996; Mann, 2018), key founders of the United States environmental movement, including John Muir, Aldo Leopold, Theodore Roosevelt, and Gifford Pinchot, openly supported eugenics and voiced beliefs of xenophobia and white supremacy. Madison Grant, a founder of conservation and proponent of national parks,
was known for co-establishing the Bronx Zoo, preserving the California redwoods, and saving Bison from extinction. However, what is not often discussed is Grant’s authorship of a book entitled The Passing of the Great Race. Concerned about the fate of the “pure Nordic strain” and the “utter swamping of the white man,” Grant (1916) openly lamented “the transfer of power from the higher to the lower races.” Indeed, Nazi Germany’s “racial hygiene” was directly influenced by the American conceptualization of natural law (Spiro, 2009). Even within the last decade, white supremacists have attempted to destigmatize racist concepts through the pseudoscience of “race realism” (Rushton & Jensen, 2005). Their claim of “fighting for nothing less than the biological survival of our race” (Johnson, 2011) bears an unsettling resemblance to Grant’s and other early environmentalists’ belief in Social Darwinism. Given this history, it is especially important that rhetoric celebrating “genetic purity” is removed from the lexicon of conservation once and for all—such language has no scientific value and only serves to normalize racist tracts. Probyn-Rapsey (2015) identifies these loaded terms as the mobilization of race panic, by which authors knowingly or unknowingly lend scientific authority to anti-miscegenation. Instead, phrases such as “genetic mixing” or “genetic admixture” could offer objective terminology for discussing hybridization (Rhymer & Simberloff, 1996).

Biases regarding hybridization may also arise from how one views ecological change. Conservation has been criticized for being nostalgic and overly conservative, clinging to a romantic definition of biodiversity from the pre-Anthropocene and overlooking unconventional methods that allow for human involvement (Marris, 2013; Rohwer & Marris, 2015; Rohwer & Marris, 2021). If change were more acceptable, the replacement of a native species with an altered hybrid species might not be resisted, especially if the new hybrid species filled the role of an already extirpated parent taxa or enhanced a desired ecological function. Biermann and Mansfield (2014) raise the fundamental question: “who or what is worthy of living—what kinds of biological diversity are promoted ... and what kinds are not?” Moreover, decisions to accept or eliminate hybrids require thought beyond basic population biology, as they involve ethical considerations and sometimes reflect cultural bias (Stronen & Paquet, 2013).

In addition to being more thoughtful about loaded phrases (e.g., genetic purity) when writing articles and reports, conservation biologists should re-examine national and international policy regarding hybridization. A review of 81 Canadian, American, and international conservation policies revealed that only 6 (7%) allowed for hybrid protection, whereas the others failed to mention hybrids or even deliberately excluded them (Jackiw, Mandil, & Hager, 2015). Currently, the IUCN (2019) does not allow for the inclusion of hybrids on the Red List. Hybrids also do not merit protection under the U.S. Endangered Species Act. Interviews conducted from 2014 to 2015 of 20 U.S. Fish and Wildlife Service biologists revealed that negative perceptions of hybridization dominate in the agency, although those with direct experience with hybridization tended to take a more nuanced view. Overall, the interviewed biologists expressed a desire for a more “flexible” policy, as long as it entailed procedural guidance on how to approach hybridization issues (Lind-Riehl, Mayer, Wellstead, & Gailing, 2016).

Our examination of the GISD database uncovered scant evidence that hybridization poses a pervasive risk to species survival. Because conservation interventions require funding and other resources, it is essential to prioritize actions that are likely to be cost-effective (di Fonzo et al., 2017). Directing limited resources to the eradication of hybrid individuals could foreclose opportunities for more effective conservation efforts. Especially problematic are the instances in which unsubstantiated concerns regarding hybridization’s unintended consequences have been used to argue against translocation.
and assisted colonization strategies that may be urgently needed to prevent species loss (Miller et al., 2012; Thomas, 2009). It is essential that claims about hybridization risk are examined carefully. For example, Ralls, Sunnucks, Lacy, and Frankham (2020) argue that there is more empirical data supporting the value of genetic rescue using hybridization than there is evidence demonstrating the putative harm of actively introducing genetic variation. In their examination of the conservation management literature on island foxes and Isle Royale wolves, Ralls and colleagues reveal a methodological bias against genetic rescue among conservationists, due to assumptions and parameter limitations inherent to simulation modeling, as well as the uncertainty of using genomic variants as fitness indicators.

Synthesizing the several observations made in this article, the key point is that conservationists should be wary of presenting hybridization in black-and-white terms. Even in cases, such as that of the California tiger salamander, where a great deal is known regarding genetics and ecology, it is challenging to determine whether hybridization represents an existential risk or a potential survival mechanism for native species. As a major source of genetic novelty, hybridization could provide genetic raw material and introduce valuable genetic variation for rapid adaptive evolution or genetic rescue in times of severe environmental change (Chunco, 2014; Hamilton & Miller, 2015; Ralls et al., 2020; Scriber, 2014). This does not negate the very real threat hybridization can sometimes represent, especially if introgression swamps out local evolutionary uniqueness. However, given the right conditions, hybrids could become a major asset in shaping that future. Minimally, we should not presume that any potential for hybridization is a reason to abandon assisted migration or other much-needed conservation interventions. Instead, conservationists should look to the evidence and keep an open mind about potential effects, either positive or negative, resulting from hybridization.

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CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS
Claire Hirashiki, Peter Kareiva, and Michelle Marvier contributed to the conceptualization of the ideas. Claire Hirashiki conducted the literature review and data analysis. Claire Hirashiki, Peter Kareiva, and Michelle Marvier wrote the manuscript.

ETHICS STATEMENT
This research did not require ethics approval.

DATA AVAILABILITY STATEMENT
The data supporting the study’s findings can be accessed by contacting the corresponding author.

ORCID
Claire Hirashiki © https://orcid.org/0000-0003-3824-5321

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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