Hybridization as a conservation management tool

Wing Yan Chan¹,² | Ary A. Hoffmann³ | Madeleine J. H. van Oppen¹,²

¹Australian Institute of Marine Science, Townsville, Queensland, Australia
²School of BioSciences, University of Melbourne, Melbourne, Victoria, Australia
³Bio21 Institute, University of Melbourne, Melbourne, Victoria, Australia

Correspondence
Wing Yan Chan, Room 217, School of BioSciences 2, University of Melbourne, VIC3010, Australia.
Email: w.chan@aims.gov.au

Abstract
The recent extensive loss of biodiversity raises the question of whether organisms will adapt in time to survive the current era of rapid environmental change, and whether today’s conservation practices and policies are appropriate. We review the benefits and risks of inter- and intraspecific hybridization as a conservation management tool aimed at enhancing adaptive potential and survival, with particular reference to coral reefs. We conclude that hybridization is underutilized and that many of its perceived risks are possibly overstated; the few applications of hybridization in conservation to date have already shown positive outcomes. Moreover, perceptions of potential risk change significantly when the focus of conservation is on preserving the adaptive potential of a species/population, instead of preserving the species in its original state. Further, we suggest that the uncertain legal status of hybrids as entities of protection can be costly to society and ecosystems, and that a legislative revision of hybrids and hybridization is overdue. We present a decision tree to help assess when and where hybridization can be a suitable conservation tool, and whether inter- or intraspecific hybridization is the preferred option.

Keywords
adaptive potential, conservation policy, genetic rescue, hybridization, inbreeding depression

1 | AVOIDING EXTINCTION THROUGH GENETIC ADAPTATION

Genetic adaptation is one way by which a population or species may avoid extinction caused by rapid environmental change (Hamilton & Miller 2016; Hoffmann et al., 2015; Hoffmann & Sgrò 2011). Whether a species will adapt in time to escape extinction depends on factors such as the rate of environmental change, the amount of adaptive genetic variation present, and generation time (Hamilton, Royauté, Wright, Hodgskiss, & Ledig, 2017; Hoffmann et al., 2015; Hoffmann & Sgrò 2011). Globally, temperature has increased and continues to increase at a rate not previously experienced by life on Earth for at least 50 (if not hundreds of) million years (Gaffney & Steffen, 2017; Hönisch et al., 2012). Although the 2015 Paris Agreement set the goal to limit warming to less than 1.5°C above pre-industrial temperatures by 2100, this goal is likely unachievable based on current trajectories with global temperatures expected to increase by 2–4.9°C (Raftery, Zimmer, Frierson, Startz, & Liu, 2017). The negative impacts of warming are evident from many examples across the marine and terrestrial environments (Chefaoui, Duarte, & Serrão, 2018; Hughes et al., 2018; Klein, Cahanoovitc, Sprintins, Herr, & Schiller, 2019; Pecl et al., 2017), and perhaps among the most significantly affected ecosystems are coral reefs.
In the last 30 years, half of the world’s corals have been lost (The Ocean Agency 2018) due to anthropogenic stresses including ocean warming. Some level of rapid adaptation and/or acclimatization is possible as demonstrated by a number of cases of increased bleaching tolerance in corals following mass bleaching events (Berkelmans, 2009; Guest et al., 2012; Maynard, Anthony, Marshall, & Masiri, 2008; Penin, Vidal-Dupiol, & Adjeroud, 2013). However, the enormous bleaching-related mortality of corals in recent years suggests that the rate of adaptation and/or acclimatization is unlikely sufficient to keep up with the pace of climate change (van Oppen et al., 2017). In addition, climate models predict that the majority of the world’s coral reefs will experience annual temperature extremes before the end of the century (van Hooidonk et al., 2016). Timely adaptation to avoid extinction may require new genetic variation sourced from elsewhere via human-assisted interventions (Hamilton & Miller 2016; Hoffmann & Sgrò 2011; Kremer et al., 2012; van Oppen, Oliver, Putnam, & Gates, 2015; van Oppen et al., 2017).

Increasingly, management options targeted at enhancing genetic variation and adaptive potential of a species or population are being discussed both within the context of revegetation and coral reef restoration (Breed, Stead, Ottewell, Gardner, & Lowe, 2013; Chan, Peplow, Menéndez, Hoffmann, & Van Oppen, 2018; Hamilton & Miller 2016; Hoffmann et al., 2015; Hoffmann & Sgrò 2011; Jones & Monaco 2009; van Oppen et al., 2017; Vitt, Havens, Kramer, Sollenberger, & Yates, 2010). This represents a shift from a traditional focus on restoring local genetic materials to consideration of using nonlocal genetic variation (Jones & Monaco 2009). Many ecosystems have already been drastically altered by climate change and other anthropogenic disturbances, resulting in not just a mismatch between locally adapted traits and altered environmental conditions (Hamilton & Miller 2016; Jones & Monaco 2009), but also an increase in population fragmentation that reduces genetic diversity and adaptive potential (Edmands, 2007; Hoffmann et al., 2015). Without gene flow from other populations to improve genetic variation and adaptive potential, some populations are unlikely to adapt in time to persist. Furthermore, restoring the genetic make-up of the original population may not achieve long-term conservation targets if populations lack the genetic variants or genes necessary to survive altered conditions now or into the future. For example, American chestnut (Castanea dentata) has been decimated by blight (an introduced fungal disease) because it lacks the genes for blight disease resistance (Clark, Schlarbaum, Saxton, & Hebard, 2016; Newhouse et al., 2014). Restoring the original American chestnut population will therefore not likely result in chestnut forests that persist long term. The large drop in the population size of American chestnut has caused changes in community composition, insect and wildlife dynamics, as well as soil chemical processes in the local forests (Clark et al., 2016). Successful restoration of habitat-forming species like canopy trees and corals is critical, particularly as there is a high probability that flow-on effects to other components of biodiversity will occur.

### 2 IMPROVING CONSERVATION AND RESTORATION SUCCESS VIA HYBRIDIZATION

Hybridization may enhance adaptive potential of a population (Carlson, Cunningham, & Westley, 2014; Chan et al., 2018; Hamilton & Miller 2016; Hoffmann & Sgrò 2011; Jones & Monaco 2009; Meier et al., 2017; van Oppen et al., 2015, 2017; Whiteley, Fitzpatrick, Funk, & Tallmon, 2015; see Table 1 for definitions of terminologies related to hybridization). It increases heterozygosity and creates new genetic combinations, potentially reducing extinction risk by increasing adaptive potential and masking deleterious alleles. Hybridization may lead to new adaptive traits, allowing species to invade new niches and expand their distribution ranges (Becker et al., 2013; Carlson et al., 2014; Hamilton & Miller 2016; Hamilton et al., 2017; Hoffmann & Sgrò 2011; Meier et al., 2017; van Oppen et al., 2015). Genetic rescue or evolutionary rescue can be achieved when a population is successfully restored via hybridization (Table 2).

#### TABLE 1 Glossary of terms

| Term             | Definition                                                                                                                                 |
|------------------|-------------------------------------------------------------------------------------------------------------------------------------------|
| Hybridization    | The successful mating between individuals from two genetically different lineages. It can be either interspecific (i.e., between different species), intraspecific (i.e., between divergent populations of the same species), or involve subspecies. |
| Hybrid vigor     | The condition where hybrid offspring (usually F1s) display higher fitness relative to its parents.                                        |
| Introgression    | The movement of genetic material from one population/species to another via repeated backcrossing.                                      |
| Genetic rescue   | The increase in population fitness and size following the introduction of new alleles by hybridization.                                    |
| Evolutionary rescue | The increase in adaptive genetic variation (rather than just an increase in genetic diversity) that allows populations to survive otherwise extinction-inducing environmental stress. |
### Table 2: Summary of hybridization studies with a focus on population conservation

Studies are selected if their research aim was to examine the usefulness of hybridization in restoration or conservation of a population, and either fitness traits or population size following hybridization was reported.

| Organism               | Latin name                      | Size of receiving population | Size and/or species of introducing population | Type of hybridization | Study environment                  | F* | Traits reported and effect                          | Reference                  |
|------------------------|---------------------------------|------------------------------|-----------------------------------------------|-----------------------|-------------------------------------|-----|----------------------------------------------------|-----------------------------|
| Staghorn coral         | A. tenuis (pair 1), and A. sarmentosa (pair 2) | Five colonies for each species | Five colonies each for A. loriipes (pair 1), and A. florida (pair 2) | Interspecific         | Laboratory (ambient and elevated temperature and pCO2 conditions) | F1  | Survival*, size*, algal endosymbiont uptake†, photochemical efficiency‡ | Chan et al. (2018), Figure 1 |
| Mountain pygmy possum  | *Barramys parvus*               | ~55 individuals              | Five males in 2011, six males in 2014          | Intraspecific         | Nature                              | F1  | Survival*, body size*, reproduction*, longevity*, population size* | Weeks et al. (2017)         |
| Trinidadian guppies    | *Poecilia reticulata*           | <100 individuals             | 75 females, 75 males                          | Intraspecific         | Nature                              | F2, backcross | Survival*, recruitment*, population size* | Fitzpatrick et al. (2016) |
| Scandina-vian wolf     | Canis lupus                     | <10 individuals              | Two males                                     | Intraspecific         | Nature                              | F1  | Reproduction*, population size*                  | Åkesson et al. (2016)       |
| Torrey pine            | *Pinus torreyana* Parry         | 16 island trees              | 10 mainland trees                             | Intraspecific         | Laboratory (common garden)          | F1  | Height†, fecundity*                               | Hamilton et al. (2017)      |
| American chestnut      | *Castanea dentata*              | No. unknown                  | Unknown no. of Chinese chestnut (C. mollissima) | Interspecific         | Laboratory (common garden)          | F3, backcross | Blight resistance*, height† | Clark et al. (2016)        |
| South Island robin     | *Petroica australis*            | Five individuals             | 31 females                                    | Intraspecific         | Nature                              | F1  | Survival*, recruitment*, sperm quality*, immunity* | Heber et al. (2013)         |
| Norfolk Island boobook owl | *Ninox novaseeelandiae undulata* | One individual              | Two male of N. n. novaseeelandiae             | Subspecies hybridization | Nature                              | F2  | Population size*, other traits not measured      | Garnett et al. (2011)       |
| Florida panther        | *Puma concolor cori*            | 22 individuals               | Eight females pumas (P. c. stanleyana)         | Subspecies hybridization | Nature                              | F2  | Survival*, population size* | Johnson et al. (2010)      |
| Mexican wolf           | *Canis lupus baileyi*           | No. unknown                  | Crossing inbred lineages, no. unknown         | Intraspecific         | Nature                              | F1  | Reproduction*, survival* | Fredrickson, Siminski, Woolf, and Hedrick (2007) |

*F refers to the most advanced generation examined in the study (e.g., F1 = first generation)

†Positive effect; #no effect; –negative effect.
Genetic rescue is applicable to small and isolated populations that typically have low genetic diversity and often suffer from inbreeding depression (Carlson et al., 2014; Whiteley et al., 2015). Hybridization may bring evolutionary rescue when a shift toward the optimal phenotype occurs via selection on the newly introduced or recombinant later generation hybrid genotypes (Carlson et al., 2014; Whiteley et al., 2015). In some studies, the term evolutionary rescue strictly applies to adaptation to a changing environment from standing genetic variation (Hamilton & Miller 2016; Hufbauer et al., 2015). We use the broader definition, where evolutionary rescue can involve genetic variation already present within a population, arising from de novo mutations, or being introduced through immigration and hybridization (Carlson et al., 2014; Whiteley et al., 2015).

The value of hybridization in conservation and restoration has been demonstrated in several cases (Table 2). For example, the introduction of a few males from a genetically divergent population to the remnant population of Mount Buller pygmy possum who subsequently mated with the native females (i.e., intraspecific hybridization) increased its fitness and contributed to the prevention of this population from going extinct (Weeks et al., 2015). Other successful examples in vertebrates include hybridization in the Scandinavian wolf, South Island robin, Norfolk Island boobook owl, Florida panther, and Mexican wolf (Table 2). The persistence and ecosystem function of American chestnut may also be successfully restored following hybridization with the Chinese chestnut that harbors genetically encoded resistance to the fungal pathogen causing blight (Clark et al., 2016).

3 | RISKS AND PERCEIVED RISKS OF HYBRIDIZATION AS A BIODIVERSITY CONSERVATION TOOL

Perceptions about risks associated with genetic and evolutionary rescue via hybridization have hindered its application. These concerns include (a) the possibility of outbreeding depression and (b) the loss of parental species via genetic mixing. Outbreeding depression is the reduction in fitness of hybrid offspring crossed from two genetically divergent populations or species (Edmands, 1999). This may occur when hybridization breaks up co-adapted gene complexes or brings together allele combinations with negative effects by segregation and recombination (Edmands, 2007; Hamilton & Miller 2016; Orr, 1996; Turelli, Barton, & Coyne, 2001). For example, hybridization between Calylophus serrulatus (a short-lived perennial plant) from two different environments resulted in reduced body size and fecundity in first generation (F1) hybrids (Heiser & Shaw 2006). Similarly, although hybridization has led to enhanced fitness in certain traits in the first one or two generation(s) of marine copepods and Drosophila spp., later generation hybrids showed relatively lower fitness or no fitness benefit (Edmands, 1999; Parda, 2014).

However, the risk of outbreeding depression has likely been overstated (Frankham, 2015; Hoffmann et al., 2015) and empirical evidence of inbreeding depression is vastly greater than that of outbreeding depression (Edmands, 2007). Simulations and field experiments also show that outbreeding depression is likely temporary and can be overcome by natural selection (Aitken & Whitlock 2013; Erickson & Fenster 2006). For example, although hybrid breakdown occurred in the F2 generation of intraspecific crosses in the legume Chamaecrista fasciculata, there was strong recovery of fitness by the F6 when plants were equally fit or fitter than either parent (Erickson & Fenster 2006). The effects of outbreeding depression versus hybrid vigor are environmentally dependent (Edmands, 2007). A meta-analysis demonstrated that hybridizing an inbred population with another population increased composite fitness (i.e., fecundity and survival) by 148% under stressful environments (more variable natural environments) compared to 45% under benign environments (captive, less variable environments), and the results were similar among invertebrates, vertebrates, and plants (Frankham, 2015). This may be due to a higher buffering capacity of heterozygotes, or because stressful conditions aggravate the deleterious effects of inbreeding depression (Edmands, 2007). The advantage of hybridization is thus likely more common in altered or degraded environments, which are becoming increasingly prominent under climate change.

The loss of parental species identity and genetic uniqueness due to genetic mixing through hybridization is another concern that has been repeatedly raised (Allendorf, Leary, Spruell, & Wenburg, 2001; Muhlfeld et al., 2014; Roberts, Gray, West, & Ayre, 2010). For instance, a change in species distribution ranges has led to hybridization of the obligately estuarine Black bream (Acanthopagrus butcheri) with the migratory marine Yellowfin bream (A. australis), and subsequently only 5% of the populations remained purebred A. australis (Roberts et al., 2010). Similarly, hybridization between African and European honey bees in an attempt to improve honey production of the latter subspecies has led to the disappearance of European characteristics over time (Schneider, Leamy, Lewis, & DeGrandi-Hoffman, 2003).

While the risk of genetic mixing may be applicable in the context of conserving currently defined species, this risk can be perceived very differently if one adopts a gene-centric instead of species-centric view (Crispo, Moore, Lee-Yaw, Gray, & Haller, 2011; Hamilton & Miller 2016; Petit,
A gene-centric view can also reveal conservation opportunities that may have otherwise gone unnoticed under a species-centric view. For example, when a population or species is at risk of extinction, hybridization can preserve part of the parental genome that would otherwise be lost by species extinction (e.g., mountain pygmy possum, Florida panther). The conservation of genetic uniqueness should not be prioritized at the cost of (adaptive) genetic diversity (Coleman, Weeks, & Hoffmann, 2013; Hoffmann et al., 2015). For instance, conservation efforts based on the protection of genetic uniqueness have deliberately isolated \textit{Galanxella pusilla} (freshwater fish) populations and this has likely resulted in a decrease in their genetic diversity and adaptive potential (Coleman et al., 2013).

4 | LEGAL FRAMEWORK THAT IMPEDES THE USE OF HYBRIDIZATION IN CONSERVATION

Other than the perceived biological risks, the uncertain legal status of hybrids has also impeded their use in conservation. A review of 81 conservation policies in Canada and the U.S. showed that only 13 policies (16%) provide guidelines regarding hybrid management (Jackiw, Mandil, & Hager, 2015). For example, the term “hybrid” does not appear in the US Endangered Species Act (ESA; Haig & Allendorf 2006) and there are no official policies for the conservation of hybrids (Wayne & Shaffer 2016). Of the 13 policies, six do not allow hybrid conservation, and consider hybrids as threat to biodiversity or not suitable for conservation (Jackiw et al., 2015). Interspecific hybrids are not protected under the ESA, with the exception of a few plant species that arise as a result of hybridization (vonHoldt, Brzeski, Wilcove, & Rutledge, 2018), and the hybrids of subspecies of the Florida panther (Erwin, 2017; Lind-Riehl, Mayer, Wellstead, & Gailing, 2016). For example, while \textit{Panthera tigris} (tiger) and \textit{Panthera pardus} (leopard) and all their subspecies raised in captivity in the U.S.A. are protected under the ESA, interspecific hybrids of the two are not protected and can be legally killed and traded in the U.S.A. (U.S. v. Kapp 2005). In 1996, an Intercross Policy was proposed to the ESA, outlining possible criteria when a hybrid population or species should receive legal status for protection (Allendorf et al., 2001; Wayne & Shaffer 2016). Over 20 years later, however, the policy remains neither accepted nor rejected by the US Fish and Wildlife Service and the National Marine Fisheries Services, and the legal status of hybrids is assessed on a case-by-case basis upon application (Wayne & Shaffer 2016).

Similarly, the legal status of interspecific hybrids is also unclear under the Environment Protection and Biodiversity Conservation Act in Australia. For example, the Norfolk Island boobook owl population was reduced to a single female in 1986 and two males of New Zealand boobook owl were introduced to rescue the population. Subsequent breeding of the second and third generation hybrids has established a population of 45 individuals (Director of National Parks 2010). In 2010, the Norfolk Island Region Threatened Species Recovery Plan stated that due to the hybrid nature of this population, they are excluded from a recovery plan under the Environment Protection and Biodiversity Conservation Act (Director of National Parks 2010), but the legal status of this population has never been clarified (Garnett, Olsen, Butchart, & Hoffmann, 2011). At an international level, the International Union for Conservation of Nature’s (IUCN) Red List of Threatened Species also excludes consideration of interspecific hybrids for listing, with the exception of apomictic (i.e., asexually reproducing hybrid plants (vonHoldt et al., 2018)). Ignoring hybrids in conservation represents a mismatch between policy, science, and real-world conservation needs (Richards & Hobbs 2015), and a major revision of conservation legislation is overdue.

A revision of conservation legislation should include several considerations. First, the species-centric conservation approach in current legislation (e.g., ESA) is difficult to apply as species are not fixed entities and are always evolving. In addition, the boundaries between species are often not clear-cut, and our understanding of the extent of natural gene flow between species is still limited (Supple & Shapiro 2018). With the advent of genomic technologies, traces of genetic admixture have been found in many “purebred” populations, making many species currently being protected under the ESA no longer compliant to its rigid interpretations (Erwin, 2017; Wayne & Shaffer 2016). For instance, new evidence suggests that red wolves (\textit{Canis rufus}) that are currently protected under ESA are likely hybrids of gray wolves (\textit{C. lupus}) and coyotes (\textit{C. latrans}) (Waples, Kays, Fredrickson, Pacifici, & Mills, 2018; Wayne & Shaffer 2016). Second, incidents of hybridization have increased and will continue to increase in nature as climate change shifts species distributions and brings together previously isolated species and populations (Crispo et al., 2011; Garroway et al., 2010; Hillebrand et al., 2018; Moritz & Agudo 2013; Pauls, Nowak, Bálint, & Pfenninger, 2013; Pecl et al., 2017). Third, the lack of recognition of hybrids can be a lost opportunity to protect entities that can maintain vital ecosystem functions. For instance, the hybrid coral \textit{Acropora prolifera} continues to provide ecosystem functions to Caribbean reefs while its parental lineages, \textit{A. palmata} and \textit{A. cervicornis}, suffer significant declines (Box 1). Given the rate of climate change, environmental degradation, and species loss, rejection of hybrid species and populations can thus be costly to society and ecosystems generally.
5 | MOVING FORWARD IN CONSERVATION STRATEGIES AND LEGAL POLICIES

Enhancing adaptive potential of a population via hybridization is currently an underutilized management choice due to its perceived risks (Fitzpatrick et al., 2016; Frankham et al., 2011; Hufford & Mazer 2003) and limitations in its existing legal framework (Wayne & Shaffer 2016). As explained above, the perceived risks are possibly overstated and applications of hybridization in conservation have resulted in several positive outcomes. We suggest that conservation policies move away from the rigid view of species and focus instead on evolutionary processes that are important to adaptive potential, and on the conservation of ecosystem function. We encourage State and/or Federal agencies to consider a revision on endangered species or biodiversity conservation legislation, and propose a number of recommendations that may assist such a transition:

1. Adopt a dynamic view on “species,” recognizing “species” as continuously evolving lineages and not as fixed entities.
2. Adopt a gene-centric instead of a species-centric view in conservation management practices and legal policies (Crispo et al., 2011; Hamilton & Miller 2016; Petit, 2004), and include the consideration of evolutionary processes that are essential for maximizing adaptive potential (Eizaguirre & Baltazar-Saoores 2014; Hoffmann et al., 2015; Hoffmann & Sgro 2011; Weeks et al., 2011). In this context, hybrid populations (e.g., the coral A. prolifera) that are reservoirs of their parents’ genetic material should receive legal protection status.
3. Prepare to move beyond preserving or restoring local genetic diversity when traditional management has failed...
to maintain the population or ecosystem functions, or failure is imminent. This includes (a) populations that are small, isolated, and suffering from inbreeding depression, (b) populations that lack the genetic variants or genes vital for survival, and (c) populations that are unlikely to adapt in time to keep up with climate change (see decision tree, Figure 2).

4. Assess the risk of alternative management options (e.g., hybridization) against the risk of extinction and ecosystem system function loss if these alternative options are not considered (Hoegh-Guldberg et al., 2008; McLachlan, Hellmann, & Schwartz, 2007; Vitt et al., 2010). Consider what is the likely trajectory of the population at risk if only traditional conservation efforts continue.
6 | ASSESSING THE SUITABILITY OF HYBRIDIZATION AS CONSERVATION TOOL: A DECISION TREE

To assist the transition away from a species-based approach and facilitate decision-making for conservation managers regarding the use of hybridization, a decision tree is presented here as a practical guide (Figure 2). If hybridization is considered appropriate, the next step involves the selection of a suitable population(s) or species to hybridize with the population of concern. Intraspecific hybridization is the first preferred option if it is feasible and beneficial. Since populations of the same species are expected to have higher relatedness than populations of different species, the probability of successful hybridization is expected to be higher and outbreeding depression is less likely to occur. Intraspecific hybridization can be applied if a population of the same species is available and carries characteristics that meet the conservation goal (e.g., has high genetic diversity or can provide specific desired traits; Figure 2). Examples of this include the introduction of conspecific males from healthy and genetically diverse populations to the genetically depleted Mount Buller pygmy possum population (Weeks et al., 2017); and intraspecific crossing of corals from a higher and lower latitude to enhance thermal tolerance of coral populations at the higher latitude (Dixon et al., 2015; van Oppen, Puill-Stephan, Lundgren, De’ath, & Bay, 2014).

If intraspecific hybridization is not feasible or not able to achieve the conservation goal, interspecific hybridization can be considered. Suitable closely related species may bring a greater increase in genetic diversity and adaptive potential, or provide specific adaptations that the species of concern is lacking (e.g., blight resistance of American chestnut). However, a greater genetic distance between species may increase the likelihood of genetic incompatibility and the risk of outbreeding depression, therefore intraspecific hybridization is considered first. After a suitable population/species has been selected and hybridization has been implemented, ongoing monitoring is required to track the success of the program and to carefully monitor its consequences (Figure 2). This can include measurements of population size, population composition (e.g., frequency of hybrid vs. purebred genotypes in different generations), genetic diversity (e.g., level of allelic richness, heterozygosity), fitness, longevity, and ecological functions (e.g., diversity of associated fauna, primary production). It is also important to keep track of which species/populations or individuals acted as maternal and paternal parents of later generation hybrids and backcrossed offspring to help understand genetic factors that have contributed to the observed fitness outcomes.

7 | DIRECTIONS FOR FUTURE RESEARCH EFFORTS AND CONCLUDING REMARKS

When a population is unlikely to adapt in time to survive climate change, results of laboratory and field studies on hybrid fitness become an important piece of information in terms of deciding whether or not to implement hybridization (see decision tree, Figure 2). Since it is not possible to provide experimental data for every species, results of a subset of species or populations may provide proof-of-concept for groups that share similar biological and ecological characteristics. Research to inform decision making should involve multi-generation testing of hybrids in the laboratory and in the wild (Hamilton et al., 2017). Our review shows that long-term studies are rare for hybridization research related to conservation, and most data have been obtained for the F1 and F2 generations (Table 2). To decide if hybridization will likely enhance conservation success, ideally a minimum of two generations should be tested so that the reproductive potential of hybrids, as well as the potential effect of segregation and recombination (e.g., the possibility of outbreeding depression) can be evaluated (Edmands, 2007; Hamilton et al., 2017).

Furthermore, successful restoration of a population at risk is not only measured from an enhancement of individual traits, but also by a significant rebound in population size (Carlson et al., 2014; Whiteley et al., 2015). An increase in hybrid fitness in one or several traits in the laboratory may not reflect results in nature, therefore field studies are essential (Fitzpatrick et al., 2016). When decisions are made and hybridization is implemented, ongoing monitoring should be in place to quantify the fitness advantages associated with hybridization and genetic change (see decision tree, Figure 2; Weeks et al., 2017). In the case where populations are small and isolated, genetic drift and inbreeding can again decrease genetic diversity over time, and multiple or periodic hybridization maybe required (Heber et al., 2013).

Advancements in genomic technologies and climate science call for a review of our current attitude and approach to legal policies for conservation. We are now in a position to make more informed decisions based on better understanding of species delineations and predictions of future climate change. Adopting a gene-centric view and a less rigid position on “species,” as well as recognizing the importance of evolutionary processes and adaptative potential on population survival, will facilitate timely and practical measures to address conservation needs in a changing world.

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AUTHOR CONTRIBUTIONS

All authors contributed to conceptual development and the final edited version of the manuscript. W.Y.C and M.v.O. wrote the manuscript, and W.Y.C. and A.H. designed the decision tree.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

ORCID

Wing Yan Chan https://orcid.org/0000-0001-9875-6903

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