Redefining the Role of Admixture and Genomics in Species Conservation

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Abstract

The generation of genome-wide sequence data has brought with it both exciting opportunities for conservation and challenges for determining appropriate management practices in the face of complex evolutionary histories. Genomic data can provide deep insight into taxa with complex evolutionary origins, and is a powerful tool for biologists to obtain a more complete view of ancestry. Many policy decisions are encumbered by patterns of gene flow between species that reveal complex evolutionary histories. Here, we review conservation decisions in admixed species and highlight genomics research that demonstrates the commonality of hybridization in wildlife. We encourage a shift toward a web-of-life framework with emphasis on the need to incorporate flexibility in conservation practices by establishing a policy for lineages of admixed ancestry. In particular, we promote a conceptual framework under which hybridization, even extensive hybridization, no longer disqualifies a species from protection; instead, we encourage customized case-by-case management to protect evolutionary potential and maintain processes that sustain ecosystems.

Genomics reveal a web-like evolutionary history

Traditional taxonomic classification is largely based on a tree-of-life (TOL) hierarchy and the biological species concept (BSC), by which descent with modification in a reproductively isolated lineage leads to speciation (Dobzhansky 1935). Modern advances in molecular genetic techniques, however, have revealed limitations to the BSC, challenging the widespread applicability and validity of using reproductive isolation to define species (Mallet 1995). Indeed, recent research has demonstrated that evolutionary relationships more closely resemble a web-of-life (WOL), whereby hybridization is often as important as the TOL evolutionary process of reproductive isolation (Arnold 2016). Neither model on its own provides a blanket explanation for all species, with horizontal gene transfer through hybridization, introgression, and reticulate evolution prevalent in some systems but not others (Arnold & Fogarty 2009).

This revelation of frequent gene flow among taxa necessitates a new outlook for conservation. When applied to conservation, the WOL concept could provide a productive framework for biologists and the public to better understand the role hybridization plays in speciation (Ellstrand et al. 2010; Arnold 2016). If policy favors only the TOL framework, then taxa that experience a high frequency of hybridization with low taxonomic distinctiveness may not receive adequate protection (Rhymer & Simberloff 1996). In many cases, a WOL framework will change the way we prioritize conservation action by focusing on adaptive potential through the protection of genomic and phenotypic diversity, ecological function, and resilience. Consequently, this will require protection of taxa that have experienced gene flow and introgression over the course of their evolutionary histories.

Advances in genomics now provide opportunities to collect magnitudes of more genetic data on wild populations. Until recently, most assessments regarding taxonomic distinctiveness, “genomic purity,” and
hybrid zones were founded on relatively few markers (microsatellites, mitochondrial DNA, Y chromosome, or a few nuclear gene sequences). Important inferences have been elucidated with these traditional markers, but these data have limitations. Evolutionary relationships constructed with markers that are predominantly inherited from one parent as a single non-recombining locus cannot accurately distinguish between species that originate from true bifurcation events and those that arise from hybridization with subsequent introgression (Seehausen 2004). Although these data can elucidate historical evolutionary lineages and divergence events, they are generally ineffective for delineating species where introgressive hybridization and/or incomplete lineage sorting are evident. Genomic sequencing, however, wields more power to differentiate between hybridization and incomplete lineage sorting, improve analytical precision to estimate population parameters, and provide detailed information on adaptive and functional loci, although there are several practical limitations to consider (Harrison et al. 2014). For example, whole genome analysis of polar bears and brown bears identified directional gene flow that was not a threat to polar bear persistence; however, divergence time estimates varied (e.g., 343,000-479,000 vs. 4-5 million years ago, detailed in Cahill et al. 2015), suggesting cautious assessment and validation are required to reach consensus.

Conservation genomics is becoming accessible for a diversity of taxa and promises new opportunities for applied wildlife research (Allendorf et al. 2010; Ellegren & Galtier 2016; Garner et al. 2016). Genomic studies are necessary for providing evidence of the WOL framework, where admixture is recognized as part of the speciation process. Consequently, the WOL framework establishes an inclusive foundation for the conservation of taxa because reproductive isolation is not a prerequisite for taxonomic classification. Though the complexity of the WOL model is a drawback, it provides a more accurate representation of evolutionary processes. This model is, therefore, important for recovery strategies that aim to increase genetic diversity and ecological adaptation of small, imperiled populations (Ellstrand et al. 2010; Jackiw et al. 2015; Arnold 2016).

The evolutionary context of hybridization and admixed genomes

Major shifts in evolutionary space, such as intraspecific adaptations or species radiations, often require novel phenotypes to exploit new niches (Stebbins 1959; Jackiw et al. 2015). Although contemporary, human-mediated hybridization is well established as a conservation concern (Allendorf et al. 2001); under natural conditions, combining genomes via hybridization can rapidly contribute to the generation of novel phenotypic variation to facilitate persistence under new selection pressures, such as rapidly changing climates (Stebbins 1959; Mallet 1995; Becker et al. 2013; Arnold 2016). In an evolutionary context, hybridization was first defined by Stebbins (1959) as the interbreeding between individuals from distinct populations with different adaptive norms, which does not exclude cases of secondary contact. Descendants from a hybridization event carry a mosaic ancestry structure in their genome, and simply labeling the progeny as “hybrids” can be misleading. For example, in a process sometimes referred to as “mitochondrial capture,” animals with introgressed mtDNA are considered hybrids even though backcrossing has effectively eliminated any nuclear signature of the introgressed species (Good et al. 2008; Keller et al. 2010). Similarly, organisms that have ancient or recent hybrid origins but have become genetically distinct are sometimes still considered hybrids (Burrell et al. 2009; Larsen et al. 2010). Again, variability in systems is evidenced in the observation by Stebbins (1959) that the evolutionary role of hybridization is much greater in some lineages than in others.

Many taxa with admixed genomes, particularly mammals, face a challenging stigma that is bound to their history of hybridization. Excluding contemporary cases where anthropogenic-mediated hybridization results in sterile or maladaptive hybrids (Todesco et al. 2016), the view that hybridization “eliminates” species through homogenization (Mayr 1963) is being re-envisioned since hybrids can oftentimes be fertile, genetically isolated from parental forms, and represent viable adaptive evolution (Mallet 1995; Arnold 2016; Hamilton & Miller 2016; Table S1). For example, ancient admixture with subsequent introgression of functional variation in Lake Victoria cichlids allowed multiple adaptive radiation events originating from a hybrid swarm (Meier et al. 2017). As such, hybrid zones can be driven by environmental gradients where hybridization provides a platform on which selection can act by way of stable hybrid forms that contribute to distinct evolutionary change (Stebbins 1959; Becker et al. 2013). The natural emergence of these nascent genomes can be evolutionarily successful because they have a new capacity to respond to changing conditions and new environments. However, admixture can present a problem for conservation when occurring in species at risk of extinction, particularly when anthropogenic events are to blame. Historically, conservation efforts have ignored or even disparaged the protection of hybrids, being particularly appropriate in cases of clear conservation crises such as when hybridization involving an imperiled species can be attributable to
invasive species that were introduced, intentionally or accidentally, by people (e.g., Taiwan Hwamei [Garrulax taewanus] hybridizing with introduced Chinese Hwamei [G. canorum]). Traditionally, these scenarios have warranted the protection of native, nonhybrid individuals and active measures to prevent mixing (Allendorf et al. 2001, Wayne & Shaffer 2016). In other cases, however, hybridization is the result of range expansion by a native species, perhaps facilitated by anthropogenic environmental changes. For example, the Black-eared miner (Manorina melanotis), faced near extinction due to land-use change that simultaneously reduced the amount of suitable habitat and facilitated the spread of the Yellow-throated Miner (M. flavigula) with which it hybridizes (Clarke et al. 2001). We discuss appropriate policy responses to these situations later.

**Regarding the regulation of hybrids and admixed entities**

Established during 1973, the Endangered Species Act (ESA) is used in the United States (US) to list and protect imperiled species and subspecies of plants and animals, as well as discrete populations of vertebrates (Haig & Allendorf 2006; Ellstrand et al. 2010). The US ESA listing process (like most endangered species legislation worldwide) relies on the TOL framework, so extending legal protection to taxa experiencing hybridization has been a contentious issue (Table S1; Jackiw et al. 2015). Currently, hybrids are generally denied protection under the ESA by the U.S. Fish and Wildlife Service (although plant species that arise as a result of hybridization might be covered). In Canada, the Committee of the Status of Endangered Wildlife in Canada, which is a legal entity under Canada’s Species at Risk Act, requires the species to be “taxonomically valid” prior to assessment, but it does define hybrids and provides conservation guidelines for them (Jackiw et al. 2015). The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) has a more accommodating hybrid policy, wherein hybrids with “recent lineage” of at least one species included in Appendices I and II (i.e., species threatened with extinction or species that will become so without controlling trade), are protected as stringently as “pure” listed species (CITES Resolution Conf. 10.17 [Rev. CoP14]). The CITES Resolution also provides loose guidelines for defining “recent lineage,” which is generally interpreted as the previous four generations of a lineage. In contrast, the IUCN Red List guidelines exclude consideration of hybrids, with the exception of “apomictic plant hybrids which are treated as ‘species’” (IUCN 2017).

During 1996, the National Marine Fisheries Service and the US Fish and Wildlife Service (USFWS) proposed an “intercross policy” to protect hybrid populations under the ESA (Haig & Allendorf 2006). This policy was envisioned to assist management of a few problematic taxa, cases in which biologists and legal analysts were at an impasse, and the proposal even stated that “it is not the intent of [the] proposed policy to generally encourage the transfer of genetic material from one species to another” (USFWS & NOAA 1996). Although this policy has not been adopted (Haig & Allendorf 2006), guidance on hybrids is needed now more than ever because significant advances in genetics have shown that admixed genomes, in the absence of human activity, can be an important source of variability from an evolutionary perspective (Table S1).

Indeed, many assessments of endangered species policies have noted the value of extending some protection to hybrids. In their policy review, Jackiw et al. (2015) note that only about one-third (37%) of government conservation policies address hybrids, and even fewer (16%) explicitly provide any management guidelines. Of the 13 documents that contain management guidelines, 6 do not allow hybrid conservation. These patterns suggest that federal agencies view hybrids largely as a threat to taxa deemed worthy of protection and to biodiversity. Consequently, hybridization itself has been considered a threatening process, albeit in most cases where human intervention is culpable. Protection also has been extended to hybrids when they are similar in appearance to one of the presumably “pure” parental types already protected under the ESA (“similarity of appearance,” ESA Section 4(e)). Interestingly, precedent for the affirmative value of hybridization between subspecies was established by the USFWS Florida Panther Recovery Program for genetic rescue when severe inbreeding depression was discovered in the Florida panther (Puma concolor coryi) population (Hostetler et al. 2010). As a remedy, the USFWS approved the translocation of eight females from the Texas subspecies (P. c. stanleyana) and carried out a controlled program of introgression through hybridization. The program was successful; inbreeding depression was alleviated and the panther population increased through strict controlled introgression with admixed offspring federally protected (Table S1).

**Customizing conservation assessments and decisions**

The statutory language of the ESA focuses on protecting “species,” but the law defines “species” to also include “any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature,” as per ESA’s Section (3)(15). This language makes it possible for those
implementing the ESA to accommodate hybridization in the following ways: (1) recognize that a species or sub-species can be the result of hybridization or reflect past or ongoing hybridization and (2) allow natural hybridization to be one of the factors that makes a vertebrate population distinct. Imperiled species that happen to have a hybrid origin should not be denied protection because of their origin: list the entity because the contemporary understanding of speciation recognizes that new species can arise out of hybridization. Controversy usually arises in circumstances where the hybrid species is backcrossing with a parental species. For instance, wolves in the Great Lakes region of United States have admixed ancestry (Rutledge et al. 2015; vonHoldt et al. 2016) and are distinct, in part, because they contain a higher percentage of coyote and/or eastern wolf genes than Rocky Mountain gray wolves. The question in this system, and others, becomes: is it useful or detrimental for conservation to follow a strict ancestry threshold across any system that has experienced gene flow?

Answers to these difficult questions are going to be situation-dependent (Table S1; Lind-Riehl et al. 2016). Where introgression from alien or domesticated species clearly threatens the fitness of native populations, conservation should act to limit hybridization (Table S1). And, in situations where the alien species hybridizing with the imperiled native species can reasonably be eliminated or greatly reduced in numbers, efforts should be made to do so, if only to retain as much of the planet’s biodiversity as possible. Under many circumstances, however, especially those involving hybridization between native species, more flexibility is needed for conservation of imperiled taxa within a WOL model. It is frequently difficult to accurately disentangle evolutionary histories within the WOL framework. This hurdle can be overcome by genome-wide data analysis as described in Roux et al. (2016): they demonstrate that species with genomic divergence between 0.5% and 2% are consistently in the gray zone of speciation where taxonomy becomes contentious. Reliance on this solution, however, presents a further challenge in that genome-wide data are not always available. Yet, genomic data are becoming increasingly more accessible so this limitation should be relatively short-lived. One possible criterion to help policy makers account for hybridization could be to focus on identifying the ecological role or function of species within this gray zone, under the assumption that the “genetic authenticity of the organisms is less important than the ecological integrity of the system” (Fitzpatrick et al. 2015). As such, subsequent effort is needed to determine if the hybrid species’ function is representative of native processes to ensure that the local ecology does not face a loss with the loss of a species, regardless of their genetic “purity” (Jackiw et al. 2015; Wayne & Shaffer 2016). Ideally, there would be follow-up to assess how genetic variation supports that process. For instance, genomic admixture thresholds of 10%-20% may be needed to protect the top-down trophic interaction that mixed ancestry wolves display (Table S1). However, such thresholds may not be beneficial for some admixed taxa, where historic and ongoing hybridization occurs (Przewalski’s horse, see Table S1). This shift in the priority perspective to focus on ecological function and resilience will encourage conservation of a process, rather than “pure” genomes. Allendorf et al. (2004) suggest basing conservation decisions on the evolutionary divergence between the hybridizing taxa and the geographical extent of introgression. We suggest extending these principles further: in addition to focusing on evolutionary divergence, efforts need to evaluate the ecological and behavioral divergence of hybrid taxa and determine at what spatial scale their presence leverages ecosystem effects.

Conclusion

Our goal is to promote and expand the discussion of how to manage taxonomically challenging populations in light of new genomic data and recent insights in evolutionary biology. Faced with climate change, continual loss of habitat, decreased resources, and paucity of mates, many species at risk of extinction will suffer if we cling to an outdated view of hybridization as invariably “bad” and fail to recognize its ecological and evolutionary importance. The perspective of many conservation scientists has already begun to shift away from one focused on the “pure” gestalt of species boundaries to that of a fluid process of dynamic sources of variation (Arnold 2016). We now encourage policymakers to adopt a more flexible strategy that recognizes the new genomic synthesis of species concepts, and to employ such a strategy in case-by-case evaluations. We offer the following general workflow for practical designation within the WOL framework.

In the context of laws like the ESA that focus on species specific protection, hybrid individuals or populations merit protection when: (1) one or both of the parent species is considered to be endangered; (2) the hybridization is not the result of an intentional cross-breeding effort, unless that cross-breeding is part of conservation efforts to introduce needed genetic heterogeneity into a population; (3) the frequency of hybridization is low or has occurred far enough in the past such that the majority of individuals are of hybrid genotypes; and (4) failure to protect the hybrids would likely result in the loss of most or all of the alleles that distinguish the endangered
parental type(s). In situations where one is taking more of an ecosystems perspective or is focusing on ecological interactions, then requirement (3) can be further relaxed if the hybrid population is at risk of extinction and has an impact on the ecosystem comparable to either parental types.

Species management should operate within the integrated framework of the WOL model, and it needs to consider the ecological function of a particular species, not just its genomic uniqueness, when setting policies regarding hybrids. Conveying this new approach to the broader public will be an important part of hybrid conservation, especially given the historical view that hybrids are a threat to biodiversity (which, indeed, is the case for some species, but not all). These challenges are likely to become more frequent as we move further into the Anthropocene era where humans continue to alter evolutionary pathways at unprecedented rates.

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**Supporting Information**

Additional Supporting Information may be found in the online version of this article at the publisher’s web site:

Table S1. Brief review of taxa with detected admixture and gene flow, with consequential management actions and the rationale for those management decisions

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