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Editorial

Blurred lines: Scientific and legislative issues surrounding hybrids and conservation

Suzanne EDMANDS, Guest Editor

Department of Biological Sciences, University of Southern California, Los Angeles, CA 90089, USA, sedmands@usc.edu

1 Introduction

Hybrids are the result of interbreeding between recognized taxonomic groups such as populations, species or subspecies. This special column focuses particularly on interspecific hybridization. The blurring of lines between neatly defined species causes both academic and practical problems, especially for those still attached to the long-outdated view of species as static, rather than dynamic, entities. Species designations become blurred when previously distinct species come into secondary contact, as well as when incipient species remain connected by gene flow. Botanists are generally credited with understanding the importance of hybridization as an evolutionary process that promotes adaptation and produces novel lineages, while zoologists have been characterized as holding to more eugenic views of hybridization polluting species integrity.

Conservation policy regarding hybrids has been the subject of much debate, but resolution remains elusive. In the United States, the Endangered Species Act (ESA) of 1973 did not mention hybrids, and the U.S. Fish & Wildlife Service (USFWS) developed a *de facto* policy of denying protection to organisms with hybrid ancestry (O'Brien and Mayr, 1991). By 1996 the USFWS, together with the National Marine Fisheries Service, proposed an intercross policy for protecting hybrids under the ESA, though it has yet to be approved (USFWS and NOAA, 1996; Allendorf et al., 2013). Beyond the U.S., endangered species legislation in other countries (with the sole exception of South Africa) also fails to consider hybrids (Haig and Allendorf, 2006). Reluctance to enact explicit policies is probably a result of the complex and idiosyncratic mix of threats and benefits posed by each case of hybridization.

This special column addresses conservation challenges surrounding hybrids, with specific examples from a diversity of animals including stony corals and reef fish (Richards and Hobbs, 2015), salmonid fish (Hand et al., 2015), lizards (Jancuchova-Laskova et al., 2015), birds (Peters and Kleindorfer, 2015) and red wolves (Gese et al., 2015), as well as an overview of current scientific and legislative issues (Fitzpatrick et al., 2015).Together, these papers address a range of important questions: How have human activities altered the dynamics of hybridization, and are these "unnatural" hybrids less valuable than natural hybrids (Peters and Kleindorfer, 2015; Gese et al., 2015)? How can genetic and genomic methods aid in recognizing hybrids and understanding mechanisms of introgression (Hand et al., 2015; Gese et al., 2015)? To what extent can the consequences of hybridization be predicted (Jancuchova-Laskova et al., 2015; Fitzpatrick et al. 2015)? Should any level of hybrid ancestry exclude individuals from protection, even if hybridization is beneficial for the endangered taxon (Richards and Hobbs, 2015; Fitzpatrick et al., 2015)?

2 The Rise of Hybrids in a Human-Dominated World

While hybrids were once thought to be rare, particularly in animals (Mayr, 1963), molecular methods are helping us recognize their ubiquity. Mallet (2005) estimated that at least 10% of animal species and 25% of plant species are involved in hybridization and potential introgression with other species. While much work has focused on terrestrial systems, hybridization is also rampant in marine systems, with rates of interspecific hybridization in reef fishes, for example, reaching as high as 25%–55% (Pyle and Randall, 1994; Kuriiwa et al., 2007; Richards and Hobbs, 2015). It is unclear what fraction of current hybridization can be attributed to human activities (Mallet, 2005), but it is widely agreed that humans are accelerating hybridization rates.

Anthropogenic activities promote hybridization through a variety of intentional and unintentional means. Humans may intentionally introduce populations or species to promote "genetic rescue" (Miller et al., 2012;

Fitzpatrick et al., 2015); support recreational fisheries (Hand et al., 2015); or bolster agriculture, aquaculture or horticulture (Ellstrand et al., 2010). They may also inadvertently introduce organisms as a casualty of global trade (Ellstrand et al., 2010). Anthropogenic activities may further promote hybridization by habitat alteration, ecosystem convergence and climate change (Muhlfeld et al., 2014; Richards and Hobbs, 2015; Gese et al., 2015; Fitzpatrick et al., 2015). Humans may even accelerate hybridization when hunting disrupts breeding dynamics (Gese et al., 2015). To predict the biological consequences of all of these human impacts, it is particularly important to understand how hybrids use resources in changing environments (Peters and Kleindorfer, 2015) and how they themselves change their environments (Ryan et al., 2009; Fitzpatrick et al., 2015).

3 Scientific Issues: Diagnosis, Threats vs. Benefits, Predictability

In the past, hybrids were diagnosed largely based on morphological characteristics, which are often unreliable and do not facilitate distinctions between F1, backcross and later generation hybrids (Allendorf et al., 2013). Molecular methods offer much greater resolution and have been effective in, for example, testing wolf litters in order to remove hybrid individuals (Gese et al., 2015). However, molecular methods cannot always solve the problem of diagnosing hybrids. In cases where lineages are diverging, it can be difficult to differentiate between hybridization and incomplete lineage sorting (e.g. shared ancestral polymorphisms; Richards and Hobbs, 2015). In cases of secondary contact and introgression, there will still be instances when no amount of genomic data can completely resolve the boundary between two parental species and their hybrids (Fitzpatrick et al., 2015). Genomic data can, however, be extremely useful in detecting low levels of introgression, such as super-invasive alleles, and in understanding patterns of introgression in response to environmental change (Hand et al., 2015).

Hybridization is a complex issue because every case involves a different mixture of threats and benefits. One threat is that interbreeding will be unsuccessful and result in no offspring, sterile offspring or inviable offspring, meaning that reproductive effort has been wasted (Dalton et al., 2014; Fitzpatrick et al., 2015). In other cases hybrids may be viable but exhibit reduced fitness, due either to intrinsic incompatibility or loss of local adaptation (Bierne et al., 2011; Brennan et al., 2014). Even if hybridization and introgression enhances fitness, hybrid populations may be viewed as compromised or inauthentic (Price and Muir, 2008; Fitzpatrick et al., 2015). Some of the most problematic cases involve an endangered species interbreeding with a more abundant species, raising the specter of the endangered species experiencing “genomic extinction”, the situation where all surviving offspring have some level of hybrid ancestry (Allendorf et al., 2013). Hybridization can also have deleterious third-party consequences, such as when hybrids eat or outcompete other native species (Ryan et al., 2009; Hovick and Whitney, 2014).

Hybridization also offers a host of potential benefits. In many cases, hybrids are more fit than their parents, exhibiting hybrid vigor in early generations or transgressive segregation in later generations (Bell and Travis, 2005; Fitzpatrick and Shaffer, 2007). By quickly generating new, multi-locus genotypes, hybridization allows adaptive shortcuts (Stebbins, 1959) that can permit colonization of novel or marginal habitats (Richards and Hobbs, 2015), or increase resistance to stressors such as parasites (Bartley et al, 2000; Peters and Kleindorfer, 2015). And conversely to the view of hybridization as “genomic extinction”, hybrid populations can also provide a valuable reservoir of alleles from threatened species (Placyk et al., 2012; Peters and Kleindorfer, 2015). Over the long term, hybridization may play a critical role in promoting new lineages and maintaining biodiversity (Seehausen et al., 2008; Richards and Hobbs, 2015).

The trouble with hybridization is that the potential threats and benefits are so difficult to predict. It can be hard to even predict whether a particular pair of species could successfully produce hybrids, since the relationship between genetic divergence and postzygotic isolation varies widely among taxa (Jancuchova-Laskova et al., 2015; Fitzpatrick et al., 2015). In cases where hybridization and introgression are possible, the long-term consequences remain challenging to forecast. In some taxa, long-term hybridization results in fitness reduction followed by recovery (Erickson and Fenster 2006), while other taxa apparently never recover (Johnson et al., 2010). Results of long-term hybridizations are variable even in experimental crosses between different pairs of conspecific populations: some show increased fitness while others show decreased fitness, and some show extensive introgression while others show nearly complete assimilation by a single population (Hwang et al., 2011; Hwang et al., 2012; Pritchard et al., 2013; Pritchard and Edmands, 2013).

4 Legislative Issues: Values and Future Directions

Legislation decisions regarding hybrids cannot be fully resolved with scientific data and ultimately involve value judgments. When the U.S. first proposed a hybrid policy (USFWS and NOAA, 1996), the term “hybrid” was replaced with “intercross” due to the low value often placed on hybrids (Haig and Allendorf, 2004). Because the intercross policy was never enacted, the U.S. currently treats hybrids on a case-by-case basis, and some self-sustaining species of hybrid origin have been listed under the ESA (Haig and Allendorf, 2004). Cases in which hybridization is driven by anthropogenic forces such as translocation tend to be given lower value than those driven by “natural” forces such as range expansion (Haig and Allendorf, 2004; Fitzpatrick et al., 2015). However it is often difficult to cleanly distinguish between natural and anthropogenic hybridization, and this difficulty will be compounded as climate change continues to induce range shifts (Muhlfeld et al., 2014). With anthropogenically-induced hybridization, native species and native genes are clearly judged as having higher value (Hand et al., 2015; Fitzpatrick et al., 2015).

It is becoming increasingly clear that our current policy (or lack of policy) regarding conservation and hybridization is based on an outmoded view of species as fixed entities and that undervaluing the process of hybridization can, in some cases, lead to irrevocable loss of phylogenetic diversity (Richards and Hobbs, 2015). One alternative is to establish a clear decision-making framework to evaluate each case (Richards and Hobbs, 2015). If this cannot resolve the complexities of hybridization, we may need to progress beyond the species-centered approach and consider a habitat- or ecosystem-based approach (Carroll et al., 1996; Lester et al., 2010; Fitzpatrick et al., 2015). In many cases it will be too expensive or even impossible to eradicate all traces of introgression from introduced species, and we may need to move past conventional restoration and consider a “novel ecosystem” paradigm (Hobbs et al., 2014; Murcia et al., 2014; Fitzpatrick et al., 2015). Whether we consider hybrids as illegitimate offspring or products of an important evolutionary process, their numbers appear to be increasing, and conservation policy must move beyond pretending they do not exist.

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