

Hybridization and the species problem in conservation

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Abstract Most biologists recognize the “species phenomenon” as a real pattern in nature: Biodiversity is characterized by discontinuities between recognizable groups classified as species. Many conservation laws focus on preventing species extinction. However, species are not fixed. Discontinuities evolve gradually and sometimes disappear. Exactly how to define particular species is not always obvious. Hybridization between taxonomic species reminds us that species classification is not a perfect representation of nature. Classification is a model that is very useful, but not adequate in all cases. Conservationists often confront questions about how to apply species-based laws when hybridization confounds classification. Development of sophisticated techniques and nuanced interpretation of data in the basic study of species and speciation has exposed the need for deeper education in genetics and evolution for applied conservationists and decision makers. Here we offer a brief perspective on hybridization and the species problem in conservation. Our intended audience is conservation practitioners and decision-makers more than geneticists and evolutionary biologists. We wish to emphasize that the goals and premises of legislative classification are not identical to those of scientific classification. Sometimes legal classification is required when the best available science indicates that discrete classification is not an adequate model for the case. Establishing legal status and level of protection for hybrids and hybrid populations means choosing from a range of scientifically valid alternatives. Although we should not abandon species-based approaches to conservation, we must recognize their limitations and work to clarify the roles of science and values in ethical and legal decisions [*Current Zoology* 61 (1): 206–216, 2015].

Keywords Hybridization, Hybrid zone, Conservation, Genetics, Policy, Classification, Delimitation

Conservation of rare or valuable species requires reliable and consistent methods of identifying taxa that have been (or should be) designated for legal protection (Frankham et al., 2002; Allendorf et al., 2013). For the most part, this is straightforward. Most animals, plants, and fungi are clustered in easily recognizable exclusive groups. This is what makes field guides generally useful (Gould, 1992; Sterelny, 1999). Well defined groups are traditionally classified as species (Mayr, 1942). This review is concerned with the cases in which classification is uncertain or unrealistic.

Two key concepts justify species conservation. First, any species might have some utilitarian value to humans, so allowing any extinction might be a lost opportunity to directly improve human well-being. Second, conservationists take the position that each species has “intrinsic value”, and therefore causing extinction is unethical (Soulé, 1985; Callicott, 1989; Sandler, 2012). For exa-

mple, killing the last few individuals of an endangered species would be considered ethically more significant than killing the same number of a common species because the former would result in an extinction whereas the latter might hardly change population density. Both of these positions imply an assumption that species are not arbitrary groupings, but objectively distinct groups whose uniqueness and reality are independent of human perception. Thus, species conservation is founded on the presumption that biodiversity is naturally clustered into distinct, recognizable groups and that preservation of those distinct groups is important for utilitarian and ethical reasons.

Species based conservation is challenged by two major aspects of evolutionary biology. First, evolution has definitively rejected the typological view of species as fixed (unchanging) groups, each with a unique, distinct essence (Darwin, 1859; Mayr, 1982; Futuyma, 2013).

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Instead, species change, new species arise gradually by divergence from common ancestors, and sometimes formerly distinct groups merge via interbreeding to result in a single descendant population of mixed ancestry or a stable hybrid zone. Generally, these processes are slow or characterize such a small fraction of the “lifetime” of an evolutionary lineage that typological species classification is a good description for the majority of biodiversity at any given time (Gould, 1992; Rieseberg and Burke, 2001). But, we should expect to (and do) see a number of cases where evolutionary separation is incomplete. In some of these so-called problematic cases, taxonomists and/or conservationists still wish to recognize the not-quite-distinct groups as having separate and distinct value.

Second, there is no universally accepted definition of “species” or set of criteria for delimiting species taxa. This should not be surprising in light of the dynamic evolutionary view of biodiversity. The debate over species definitions is far too extensive to cover here, but conservationists should be aware of its major features (e.g., Mayr, 1942; O'Brien and Mayr, 1991; Hey, 2009; Frankham, et al., 2012). An emerging consensus seems to be that the species phenomenon is real, but there is no universal rule as to when a particular group should be classified as a single species or multiple species (de Queiroz, 2005; Futuyma, 2013). Whatever else a species is, in conservation biology a species is a group of organisms whose extinction would constitute an ethically meaningful loss of biodiversity (Pasachnik et al., 2010).

Here, we argue that species classification is a model – an idealized representation of nature that does not describe all of the messy details and nuances. It is a model that works very well most of the time, but is not always satisfactory. The problem for conservation is that agencies and organizations cannot always expect to receive a single true answer from scientists on questions about taxonomic status. Sometimes classification must be a policy decision to follow one of many scientifically sound conventions for delimiting taxa or identifying individuals. Greater knowledge and appreciation of genetics and evolution might help managers and decision makers to navigate these challenges.

2 The Species Problem in Evolutionary Biology

What causes the clustered structure of biological diversity – or the “species phenomenon” (Sterelny, 1999) – is a major research theme in basic ecology and evolutionary biology. The species phenomenon is character-

ized by discontinuity, defined as sharp differences with no overlap or connection between separate parts. The major question in the study of speciation is how to explain the evolution of discontinuities (Gould, 1992; Coyne, 1994; Coyne and Orr, 2004). We will not attempt a thorough review (see Coyne and Orr, 2004; Bolnick and Fitzpatrick, 2007; Grant and Grant, 2008; Price, 2008; Fitzpatrick, 2012; Abbott et al., 2013). Instead, we briefly summarize two well-established fundamental principles that are relevant to hybridization and the species problem. These are gradualism and reproductive isolation.

Gradualism is the principle that populations do not instantaneously transform from one state to another, instead large differences arise by the accumulation of smaller changes in the composition of populations (Futuyma, 2013). The distinct groups we come to recognize as species evolve gradually (Fig. 1). Speciation can be very fast or quite slow, but a fundamental prediction of evolutionary biology is that there will almost always be a period of uncertain or incomplete separation (Mayr, 1963; Gould, 1992; Harrison, 1998; Coyne and Orr, 2004). Speciation by polyploidy might be viewed as an exception, but even then complete evolutionary independence is rarely instantaneous, and additional differences in ecology or reproductive biology must accumulate before a formal species classification is justified (e.g., Ramsey and Ramsey, 2014).

Reproductive isolation is related to the principle that maintenance of a given degree of divergence or distinctiveness depends on the tension between processes promoting homogeneity (gene flow and stabilizing selection) and those promoting divergence (mutation, genetic drift, and divergent selection) between populations. In sexually reproducing organisms, discontinuous distributions of phenotypes, and especially genotypes, are unlikely to remain discontinuous if there is regular interbreeding between groups. Therefore, factors that affect the probability of successful reproduction are particularly important (Mayr, 1942; Coyne and Orr, 2004).

Factors reducing successful reproduction are “reproductive barriers” or “reproductive isolation mechanisms”. Evolutionary biologists use the term “reproductive isolation” in two ways. One implies a state of being isolated – a group is either reproductively isolated from another group or not. The other is as a quantitative difference between groups – reproductive isolation between any pair of populations or taxa can range from 0 to 100% and can be measured by estimating probabilities of mating, fertilization, and survival of hybrid off-

spring (Dobzhansky, 1937; Arnold et al., 1999; Ramsey et al., 2003).

Although systematists disagree as to the merits of including reproductive isolation in the technical definition

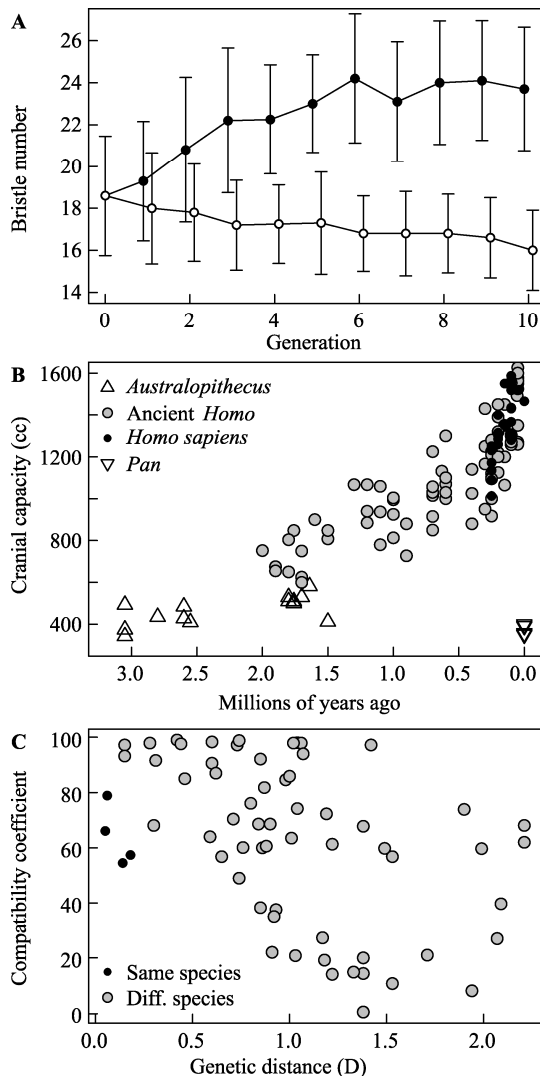


Fig. 1 Gradual divergence

A. Divergent selection on sternopleural bristle number in *Drosophila melanogaster* resulted in discontinuous distributions of bristle numbers in high (filled circles) and low (open circles) selection lines (Barker and Cummins, 1969). Means and approximate 95% interquartile ranges for lines H1 and L1 were derived from Figures 1 and 2 of Barker and Cummins (1969). **B.** Evolution of hominid cranial capacity over the last 3 million years illustrates gradual emergence of a gap between modern humans *H. sapiens*, *Australopithecus*, and chimpanzees (*Pan*). Data compiled from De Miguel and Henneberg (2001) by Matzke (2006). **C.** Negative correlation between reproductive compatibility and genetic divergence in frogs indicates gradual evolution of differences causing hybrid dysfunction (Sasa et al., 1998). We show the full data set to illustrate the entire range of values and compare crosses between populations of the same taxonomic species vs. those classified as different species. Similar patterns have been documented in a variety of plant, animal, and fungal groups (e.g., Coyne and Orr, 1989; Presgraves, 2002; Bolnick and Near, 2005; Widmer et al., 2009; Giraud and Gourbiere, 2012).

of the term “species” or in diagnosing species taxa, there is little or no disagreement on the importance of reproductive isolation for explaining the origin and maintenance of continuous and discontinuous patterns of biodiversity. Distinct forms that freely interbreed will not remain distinct in subsequent generations.

The joint importance of gradualism and reproductive isolation in eukaryotes is seen most clearly in analyses relating the degree of reproductive compatibility between groups and estimates of divergence times between those groups (Fig. 1C). The biological differences most important in maintaining distinctiveness evolve gradually and at widely varying rates. As a consequence, there are in nature many examples where a group of organisms is obviously not a single homogenous population, but, perhaps equally obvious, it cannot be subdivided into distinct and exclusive taxa based on any objective biological discontinuity. These cases may be explained as stable non-homogeneous population structures, previously distinct groups forming hybrid zones, or incipient groups still connected by gene flow (e.g., Endler, 1977; Hewitt, 1988; Barton and Hewitt, 1989; Harrison, 1990; Rundle et al., 2001; Mallet, 2005). How to classify these problematic cases is known as the “species problem”, and it has vexed taxonomists throughout history (e.g., Darwin, 1859; Poulton, 1903; Anderson, 1936; Gould, 1992; Rojas, 1992; Mallet, 1995; de Queiroz, 1998; Hey, 2001; Hudson and Coyne, 2002; Ereshefsky, 2009; Hausdorf, 2011).

3 Problematic Cases: Inadequate Data or Inadequate Model?

Discrete species classification is a model - a simplified representation of nature. Most of the time, patterns of continuity and discontinuity are easily recognizable and well defined groups are classified as separate species by any number of taxonomic criteria. The model works very well as a generalized representation of the non-continuous structure of biodiversity. Models are useful because they simplify complex phenomena and seek generalizations in the idiosyncratic variety of life. The usefulness and generality of species classification is demonstrated by the fact that hybridization and other problematic cases are recognizable as rare and surprising instances where the model does not adequately represent nature. However, because conservation is often concerned with solving specific problems rather than making abstract generalizations, problematic cases must be confronted and understood.

When species classification is difficult to apply, the first question is whether the problem is one of inadequate knowledge of the system, or a true failure of the taxonomic model to represent the system. For example, *Iris setosa* is clearly distinct from its relatives, but plants classified as *I. versicolor* and *I. virginica* have overlapping flower morphology (Fig. 2). This was a classic “problematic case” for taxonomy (Anderson, 1936). Although one can easily derive a rule that classifies most individuals “properly” most of the time (Fisher, 1936), it is not obvious from these data whether the given species names correspond to unambiguously distinct groups.

It turns out that *I. versicolor* arose as an allopolyploid hybrid between *I. virginica* and *I. setosa* (Lim et al., 2007). The three taxon names correspond to three dis-

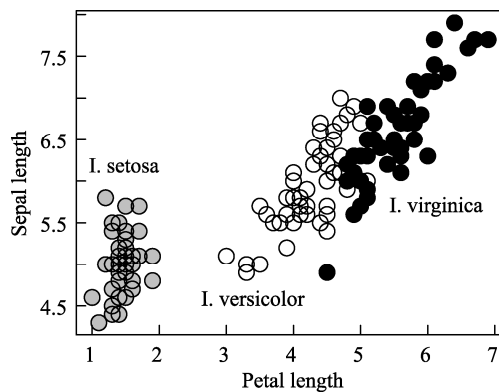


Fig. 2 Inadequate data

Edgar Anderson’s classic *Iris* data illustrate the biological discontinuity characteristic of the species phenomenon, but also a “problematic case” (Anderson, 1936) Did he simply lack the data to properly discriminate *I. versicolor* and *I. virginica* or are they not entirely distinct?

tinct groups differentiated by chromosome numbers and ongoing hybridization appears to be rare. Thus, a three species taxonomy seems to be a good representation. In this case, chromosomal and molecular genetic analyses solved a problem of inadequate data to distinguish real groups in nature.

In other problematic cases, solving the challenge of inadequate data has failed to clarify taxonomy. Instead, the inadequacy of typological species classification was exposed. For example, the gartersnakes classified as *Thamnophis butleri* (Butler’s gartersnake) and *T. radix* (Plains gartersnake) are distinguished by several differences in color pattern, size and shape, behavior, and diet (Rossman et al., 1996). Their geographic ranges are largely separate, meeting only in a narrow band in southern Wisconsin (USA) and possibly Ohio. For several decades, experts lamented that the two species were difficult to tell apart in southern Wisconsin (Rossman et al., 1996; Conant and Collins, 1998), and detailed morphological analysis revealed no clear discontinuity (Casper, 2003). The possibility of hybridization was well recognized by academics (Rossman et al., 1996), but the Wisconsin Department of Natural Resources needed to clarify the taxonomic status of gartersnakes in southern Wisconsin because *T. butleri* was protected under the state’s Endangered and Threatened Species laws, while *T. radix* was not (WDNR, 2006). Analysis of DNA markers (Fitzpatrick et al., 2008) confirmed that snakes in the contact zone cannot be unambiguously identified as belonging to one of the taxa because there is a continuum of genotypes (Fig. 3). The contact zone is a hybrid zone and there is no simple scientific basis for classifying a given hybrid snake as a member

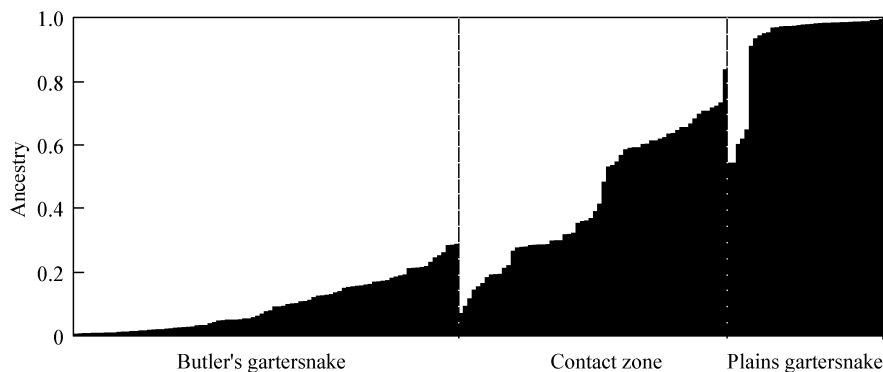


Fig. 3 Molecular genetic analysis reveals a hybrid zone

Classification of gartersnakes as Butler’s or Plains gartersnakes is problematic because there is no morphological or genetic discontinuity. Rather, what appear to be incipient groups are connected by a narrow hybrid zone in southern Wisconsin. This figure was created using AFLP data from Fitzpatrick et al. (2008) analyzed with the clustering program STRUCTURE (Falush et al., 2007), which estimates the proportion of each individual’s genetic ancestry derived from different ancestral groups (in this case, 2). For display purposes, individuals were sorted by ancestry within *a priori* categories based on assumed geographic ranges. These categories were not used in the estimation procedure.

of the legally protected group or not, because the species classification does not adequately represent the pattern in nature (Fitzpatrick et al., 2008; Placyk et al., 2012).

Similar problems cause ongoing controversy over the taxonomic status of North American wolves (NCEAS, 2014), cutthroat trout (Allendorf et al., 2005), dingoes, and wildcats (Daniels and Corbett, 2003), just to name a few. Most of these problematic cases arise because species-based conservation rules have not anticipated hybridization (Haig and Allendorf, 2006).

4 Hybridization

Hybridization is a somewhat paradoxical notion. It is defined as interbreeding between genetically distinct populations (Harrison, 1993), but if hybridization between a given pair of groups occurs with appreciable frequency, it erases that distinctiveness. Often, when we apply terms like “hybrid” and “hybridization” or the less fashionable “intergrade”, we are imposing a discontinuous conceptual model on a continuous pattern of variation. Allendorf et al. (2001) provide a useful categorization of hybridization by initial cause (natural or anthropogenic) and genetic outcome, ranging from zero gene flow when F_1 's are sterile to complete admixture or hybrid speciation (Table 1).

Many species hybridize with closely related species or descend from hybrid lineages (Rieseberg and Wendel, 1993; Barton, 2001; Mallet, 2005). Therefore issues of hybridization are certain to arise with endangered species, especially as conspecific mates become increasingly sparse (Kelly and Forsman, 2004). Biologically, hybridization might affect conservation or recovery of a protected group. Legally, hybridization presents difficulties because it does not fit the typological classification model underlying species-based conservation. Yet legal treatment of hybrids may have direct effects on

species recovery efforts (Haig et al., 2004).

Justifications for different legal treatment of hybrids often depend on whether hybridization occurs due to “natural” range expansions or is directly human-mediated by species introductions (Table 1). When hybridization between formerly isolated groups results from human translocation, greater value is often placed on native genes and genotypes based on appreciation of “naturalness” or authenticity, the potential risk of true extinction, and potential impacts of introduced or hybrid genotypes on third-party community members. In cases of natural hybridization, valuing some genotypes or outcomes over others is less clearly justified from a biological standpoint since genetic divergence and re-mixing is a natural part of ongoing evolutionary processes. However, political considerations such as public attention and investment in recovery of the affected species may come into play.

The genetic and evolutionary consequences of hybridization (natural or anthropogenic) can be complex (Table 1). In rare cases, first generation hybrids (F_1 's) are completely sterile or inviable, so there is no gene exchange between parental species. In these cases, the consequences of concern are ecological rather than genetic (Senanan et al., 2004). Interbreeding might be a substantial waste of reproductive effort and therefore a demographic burden increasing the risk of extinction for parental species. Sterile F_1 hybrids might be effective competitors or predators, negatively impacting the parental species or other community members (Senanan et al., 2004). When F_1 hybrids do survive and interbreed with members of the parental species, the genetic consequence is known as introgression (or introgressive hybridization). Introgression is the evolutionary change wrought by gene flow between hybridizing populations.

Introgressive hybridization is like an isthmus between two islands (Fig. 4). Where does each island end?

Table 1 Heuristic classification of hybridization from Allendorf et al. (2001) with some typical management issues and an additional category (7: extinction via migrational meltdown)

Categories of hybridization (Allendorf et al., 2001)			Typical conservation concerns
Natural	1	Natural hybrid taxon	Same conservation value as taxa of “conventional” origin.
	2	Natural introgression	Taxon of concern might be hard to circumscribe (species delimitation problem).
	3	Natural hybrid zone	Geography might be of some aid in delimiting populations with different management priorities.
Anthropogenic	4	F_1 's sterile (no introgression)	Demographic effects and/or third-party impacts might be important.
	5	Introgression	Taxon of concern is genetically modified and hard to circumscribe.
	6	Complete admixture	Taxon of concern is replaced by hybrid derivative (“genomic extinction”).
	7	Migrational meltdown	True extinction might result from hybrid dysfunction.

Is a given spot on the isthmus part of one or both islands, or neither? Why don't we consider the entire landmass a single island? More to the point, if we choose to declare Island A a National Park, do we expect a professional geographer to use scientific methods to discover the true boundary? No. Although all reasonable people probably have a very similar intuitive understanding of what constitutes "Island A", there is no true boundary to be discovered. A legal boundary has to be *chosen* by an agreement between interest groups. In such cases, the role of science is not to define a boundary, but to inform the interest groups as to any relevant consequences of alternative boundary choices. Likewise, when conservation management demands a taxonomic boundary between hybridizing groups, a legal classification rule must be *chosen* as a policy. Conservation geneticists can help inform the interest groups as to the consequences of alternative choices, but no single true scientific classification should be expected.

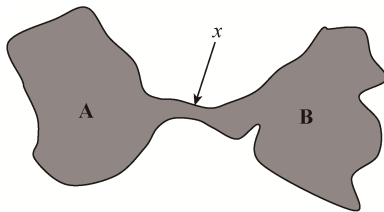


Fig. 4 Taxonomic intuition vs. reality illustrated by analogy to a pair of landmasses connected by an isthmus

"Islands" A and B describe real, clearly recognizable patterns in nature, yet they are not discrete entities and there is no sense in hoping that a single true boundary can be discovered. Whether a location x is to be classified as part of A, part of B, both, or neither is not a scientific question, but a choice with several equally valid alternatives.

Hybridization is most clearly recognizable when two groups were formerly distinct and separate. In such cases, the species classification makes sense as a reference to the historically distinct groups even if it cannot be applied unambiguously to contemporary individuals. In principle, the classification can be applied to genes and traits. Individual organisms are mosaics of genes derived from each ancestral population. Interactions between those genes can be just as consequential as "traditional" ecological interactions between species (mutualism, parasitism, competition, predation). For conservation, it is important to ask whether genetic interactions resulting from hybridization constitute a threat.

5 What is Threatened by Hybridization?

An often cited but philosophically problematic concern is that hybridization with an introduced lineage threatens the "genetic integrity" of a native species or

population (e.g., Latch et al., 2006; Oliveira et al., 2008; Sanz et al., 2008). But what is "genetic integrity" in the context of evolutionary processes, and how would we evaluate whether it has been harmed? As an alternative to this ambiguous phrase, we specify three ways hybridization can be a conservation threat. Hybrid populations might have greater probability of extinction overall, hybrids might be aesthetically or intellectually undesirable (e.g., ecologically inauthentic relative to a non-hybrid native species), and/or hybrids might have deleterious third-party impacts on other native species or ecosystems.

If the primary goal of species conservation is to prevent extinction, we must have a clear definition of extinction. According to the IUCN (2014), a group is extinct when the last individual has died. But there are two very different kinds of extinction meeting this definition. We define "true extinction" or "demographic extinction" as the death of all members of a group *without leaving offspring*. In contrast, "genomic extinction" occurs when all surviving offspring have some degree of hybrid ancestry (Allendorf et al., 2013), that is, there no longer exist any genetically unmodified members of a taxon. This is related to what paleontologists recognize as "phyletic extinction" or "pseudoe extinction". In phyletic extinction, a taxon defined by certain characteristics no longer exists because all of its descendants have evolved to have different characteristics (Simpson, 1953).

Genomic extinction is a near certainty in any case of hybridization between formerly separate taxa. At least from a pedigree standpoint, if all offspring of a hybrid are hybrids, whereas offspring can be "pure" only if both parents derive 100% from the same genetic lineage, then eventually all members of a sexually reproducing population will be hybrids because of the combinatorics of pedigrees in sexual populations (Rohde et al., 2004; Allendorf et al., 2013). Technically, if all descendants of a hybrid are by definition hybrids, genomic extinction could occur even if every introduced gene was expunged and the surviving population was identical to the native species down to the last nucleotide. More likely, at least a small fraction of introduced genes will replace all of their native counterparts, resulting in a population that is irrevocably modified at the genetic level. This might happen rapidly for highly advantageous introduced alleles (Fitzpatrick et al., 2010) or slowly by chance alone (Allendorf et al., 2013). The key question for conservationists is how to determine the value of genetically modified individuals or populations. We provide some ideas in the section on "alternatives to

species-based conservation”, but the issue is far from resolved.

The potential for hybridization to affect the probability of true extinction is not well studied. According to Greig (1979), the Tatra Mountain ibex *Capra ibex ibex* was driven to demographic extinction by a misguided attempt to enhance genetic variation by introducing *C. ibex aegagrus* and *C. ibex nubiana*. The resulting hybrids bred at an inappropriate time of year, leading to failed reproduction. Whether or not this effect played a primary causal role in the extinction of the population is not known, and this example (such as it is) remains exceptional. In most cases, we might expect disadvantageous genes and recombinant genotypes to die out while advantageous variants thrive, resulting in the preservation of locally adapted traits or even enhanced fitness as the evolving hybrid population becomes a combination of the best native and introduced genes (e.g., Anderson and Stebbins, 1954; Arnold and Emms, 1998; Dittich-Reed and Fitzpatrick, 2013). In fact, hybridization can be used as a tool to enhance genetic variation and reduce extinction risk, though such attempts at genetic rescue usually try to encourage interbreeding between groups that are classified as the same species (Hedrick and Fredrickson, 2010).

Finally, hybridization has the potential to impact third-party community members. Ellstrand and Schierenbeck (2000) reviewed evidence that hybridization could contribute to invasiveness in plants. A striking example is the invasion of hybrid *Spartina* in estuaries, where vigorous recombinant genotypes alter patterns of sedimentation and water flow, with many cascading effects on native plants and animals (Ayres et al., 2004; Neira et al., 2005). Hybrids between native and introduced tiger salamanders (*Ambystoma californiense* x *A. mavortium*) also appear to have third-party impacts as some recombinant genotypes grow faster and consume more native prey (Ryan et al., 2009).

6 Alternatives to Species-based Conservation

Conservation policies and actions can be more inclusive (e.g., ecosystem level) or more narrow (e.g., evolutionarily significant units) than the “species level”. The question here is how hybridization impacts these alternative approaches. We argue that hybridization remains important because it can have broad ecological consequences, and because the challenges of classification are not unique to the “species level”. When hybridization is a significant biological factor, conservation strategies

are more likely to be successful if they emphasize ecological authenticity rather than genetic purity, or function more than taxonomy. This assumes that the goal of conservation is to preserve the current function of ecosystems and form of interactions among members of the ecological community.

6.1 Ecosystem-scale approaches

Broader scale alternatives to species-based conservation include approaches that emphasize habitat or community characteristics, ecosystem services, or even cultural or economic values. Many conservationists now prefer these broader-scale strategies, and consider narrower strategies as justifiable only for critically imperiled taxa (Simberloff, 1998; Ruiz-Jaén and Aide, 2005).

Ecosystem-based strategies attempt to span the biological hierarchy (from genes to landscapes) and consider the connections between humans and nature at a location of conservation value (Grumbine 1994). The goal of ecosystem management is to maintain the long-term ability of ecosystems to provide benefits and services (Lester et al., 2010). Basic ecosystem services such as water filtration, waste decomposition, food, and raw materials rely upon the functional roles of the biological components of the ecosystem. Therefore, a major goal of the ecosystem conservation approach is to preserve or restore the functional role(s) of organisms within ecosystems. Given this framework, it might be argued that the genetic authenticity of the organisms is less important than the ecological integrity of the system (Fitzpatrick et al., 2010). Hybridization is important for ecosystem management, not for its taxonomic implications, but because it is a biological interaction that can have broad ecological consequences (Ellstrand and Schierenbeck, 2000).

But “hybrid” is not a uniform biological unit. Two individuals that are both backcrosses (say between F_1 and California tiger salamanders) might be equivalent to the taxonomist, but one might be functionally equivalent to a 100% native salamander while the other has introduced alleles that alter its ecosystem impacts. Thus, the ecosystem manager should be less interested in whether individuals are “hybrids”, and more concerned about what specific genotypes they have, what their likely impacts are, the magnitude of variation and plasticity among hybrid genotypes, and how management or conservation actions might encourage the proliferation of favored genotypes associated with desired ecological functions.

6.2 Finer scale approaches

A great deal of discussion has been devoted to defin-

ing and conserving particular sub-groups within taxonomic species (e.g., Waples 1991; Moritz 1994; Crandall et al., 2000; Frankham et al., 2012; Funk et al., 2012; Allendorf et al., 2013). However, these are generally discrete classification systems, so they can run into the same problem as species classification. Hybridization between Evolutionarily Significant Units or Distinct Population Segments creates the same kind of legal and taxonomic questions as hybridization between species. Finer scale approaches that avoid these problems could be based on functional phenotypic criteria or on geography.

The functional phenotypic approach might be essentially identical to the ecosystem-based approach. Individual hybrid organisms could be selectively protected depending on whether they perform desirable ecosystem functions rather than depending on their ancestry. In principle, other values (e.g., aesthetic, cultural, or economic) could be used delineate desirable vs. undesirable phenotypes. As with the ecosystem approach, the values driving conservation are not intrinsically genetic or taxonomic.

In contrast, geographically defined management units (MU) can be conceptually independent of the individual organisms and their particular genetics. MUs are defined by demographic independence (Palsbøll et al., 2007; Allendorf et al., 2013). That is, rates of dispersal between MUs are sufficiently low that they have separate population regulation, but gene flow (hybridization) is acceptable or even desirable. An individual might be part of a given MU one day, but its status changes as soon as it emigrates to a site outside of that MU. This is in contrast to traditional classification in which an organism is considered to carry its taxonomic identity (therefore its legal status) wherever it goes. The legal status of organisms in a geographically defined MU need not depend on their ancestry or genetics. The obvious downside of this approach, taken by itself, is that immigration might result in undesirable genetic changes if the values defining desirable vs. undesirable are unrelated to the definition of the MU.

7 Practical Concerns Regarding Conservation of Hybrids

The biological complexity of hybrids raises practical questions regarding the implementation of conservation policies. In the US, hybrids do not have described protections under the Endangered Species Act (ESA), leaving their legal status ambiguous. Hybrids are pro-

tected under the Migratory Bird Treaty Act and under the Convention on International Trade in Endangered Species (CITES). In addition to the scientific and legal uncertainties surrounding hybrid classification, public sentiment towards hybrids and towards conservation measures in general are likely to influence how policies are implemented. For example, while hybridization between Barred Owls and federally endangered Northern Spotted Owls is considered relatively inconsequential with respect to spotted owl recovery (Kelly and Forsman, 2004; USFWS, 2011), some biologists have suggested extending protections to hybrids or even to barred owls, arguing that the antipathy towards spotted owls could otherwise lead to purposeful killings under the claim of shooting hybrids (Haig et al., 2004). Likewise in California, hybridization with Barred Tiger Salamanders is listed as a threat to the federally threatened California tiger salamander. However, some managers are concerned that dropping protection for hybrids could serve as an incentive for intentional barred tiger Salamander or hybrid introductions outside of the hybrid zone, by people seeking to order to avoid compliance with ESA regulations that might affect land use or development in the fast-growing Central Valley. Just as scientists must lay out a range of potential outcomes associated with different scenarios of classification, so must managers take into consideration the practical realities of public response to and enforcement of species-based or other ecological protections.

8 Conclusions

A basic premise of conservation biology is that conservation decisions will generally take into account the “best available science” (Soulé, 1985). However, the best science does not always lend itself to simple interpretations or clear cut recommendations. Hybridization raises complex issues of genetics and evolution. In particular, it patently violates the typological model of species classification that underlies many conservation regulations. Therefore, legal questions about the status or value of hybrids might have multiple scientifically valid alternatives. The key question for conservationists is how to determine the value of genetically modified individuals or populations. Most likely, this will always need to be approached on a case-by-case basis.

Decision makers, even those trained in forestry, wildlife and fisheries, are often uncomfortable with genetics and evolutionary biology. Meanwhile, the technical and theoretical tools available to conservation genetics have become more and more sophisticated (Allendorf et al.,

2010). Such advances mean scientists can offer more reliable answers to the questions conservation managers have been asking for decades. But advances also raise new questions and expose flaws in old paradigms. In order to effectively use the best available science, many conservation decision makers and advocates probably need a stronger background in evolutionary biology and genetics than is currently typical of undergraduate programs in environmental studies, political science, forestry, wildlife, and fisheries, along with a capacity to use this knowledge in the context of complex conservation scenarios.

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