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Forum

Species conservation in the era of genomic science

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Abstract

The exponential increase in the availability of genomic data, derived from sequencing thousands of loci or whole genomes, provides exciting new insights into the diversity of life. However, it can also challenge established species concepts and existing management regimes derived from these concepts. Genomic data can help inform decisions about how to manage genetic diversity, but policies that protect identified taxonomic entities can generate conflicting recommendations that create challenges for practitioners. We outline three dimensions of management concern that arise when facing new and potentially conflicting interpretations of genomic data: defining conservation entities, deciding how to manage diversity, and evaluating the risks and benefits of management actions. We highlight the often-underappreciated role of values in influencing management choices made by individuals, scientists, practitioners, the public, and other stakeholders. Such values influence choices through mechanisms such as the Rashomon effect, whereby management decisions are complicated by conflicting perceptions of the causes and consequences of the conservation problem. To illustrate how this might operate, we offer a hypothetical example of this effect for the interpretation of genomic data and its implications for conservation management. Such value-based decisions can be challenged by the rigidity of existing management regimes, making it difficult to achieve the necessary flexibility to match the changing biological understanding. We finish by recommending that both conservation geneticists and practitioners reflect on their respective values, responsibilities, and roles in building a more robust system of species management. This includes embracing the inclusion of stakeholders in decision-making because, as in many cases, there are not objectively defensible right or wrong decisions.

Keywords: adaptive potential, conservation management, conservation policy, genetics, molecular ecology

The ability to define a species is fundamental to conservation biology and conservation practice. The exponential increase in the availability of genomic data, which we define as the high-resolution information derived from next-generation sequencing methods (Lewin et al. 2022), provides exciting new insights into the diversity of life. However, it can also challenge established species concepts, making it increasingly complex to draw clear boundaries between species (Stanton et al. 2019). New studies are revealing both the degree to which many geographically connected populations are naturally isolated from one another (e.g., cryptic species; Struck et al. 2017) and the extent to which groups that were once presumed to be independent lineages are in fact interbreeding (Coates et al. 2018). Confusion about how to clearly delineate taxonomic groups makes the job of conserving diversity more challenging (Funk et al. 2012, Hohenlohe et al. 2021).

Debate about how to define and label a species existed long before the genomic era, but the resolution of genomic data has exacerbated existing challenges (Stanton et al. 2019). The differing conclusions drawn from the same genetic and morphological data are highlighting the speciation grey zone (Roux et al. 2016), where inferences about how species are categorized are open to interpretation (Coates et al. 2018, Stanton et al. 2019, Bernos et al. 2020). Therefore, although genomic data offer exciting new opportunities to inform biodiversity conservation, they can also reveal hidden complexity and challenges for how to characterize taxonomic entities for conservation (Frankham et al. 2012, Weeks et al. 2016).

Overall, genomic data are demonstrating how challenging it can be to precisely delineate species (Padial and de la Riva 2021), to determine when isolated populations represent important lineages worthy of their own conservation (Stanton et al. 2019), or to identify when isolated populations may require genetic augmentation in order to persist (Bell et al. 2019). Conservation is an inherently value-driven discipline, where practitioners must make decisions about how to use limited resources to achieve the "best" outcomes for biodiversity. The prevailing view found in the genomics literature is that conserving adaptive potential is the top conservation priority for at-risk units of biodiversity (Stanton et al. 2019). But biodiversity policies prioritize the protection of identified distinct taxonomic entities. These are similar but distinct concepts that can conflict. We outline three dimensions of management concern that arise when facing new and potentially conflicting interpretations of genomic data.

Defining conservation entities

The species has long been used as the measure of classifying and managing biodiversity, and it is the unit that underpins many conservation regulatory frameworks (Garnett and Christidis 2007, Coates et al. 2018). Conservation practitioners have always had to contend with a multiplicity of perspectives on what should constitute a species and how one should be identified (Frankham et al. 2012). But the insights gained from genomic data and from the lack of clear, agreed-on boundaries with which to delineate species is problematic for regulatory systems (Garnett and

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Christidis 2017, Stanton et al. 2019), which require evidence-based taxonomic designations (i.e., legally recognized groupings).

Species is not the only legally recognized conservation unit, and regulatory frameworks increasingly recognize subspecific units (Coates et al. 2018). The higher resolution provided by genomic data can be used to assess fine-scale differences in population genetic structure (Funk et al. 2012). The rapid increase in the number of studies using genomic data to estimate differentiation can create a challenge for conservation management, especially when providing conflicting results (Stanton et al. 2019, Bernos et al. 2020). This is particularly true when determining whether differentiation across isolated populations reflects segments of diversity that should be conserved, such as evolutionarily significant units, distinct population segments, and management units (Funk et al. 2012). The number of studies addressing questions of whether populations constitute different conservation units are rapidly increasing (Liddell et al. 2021) and the outcomes of decisions about how to delineate units and the consequences of these decisions for population viability can be controversial (Ralls et al. 2018). Decisions to change taxonomy (e.g., birds; Barrowclough et al. 2016, Simkins et al. 2020) or to alter the number of population units that require separate but intensive management to be viable (e.g., leatherback turtle, *Dermochelys coriacea*; USFWS 2020) can substantially affect conservation policy and the allocation of resources to management (Zachos et al. 2013, Jacobs and Baker 2018).

Deciding how to manage diversity

Genomic data offer important opportunities to better understand the patterns and processes that drive genetic differentiation of populations (e.g., genetic drift versus natural selection; Weeks et al. 2016, Stanton et al. 2019) but also raise a set of management questions (Bernos et al. 2020). Interpreting the conservation implications of observed genetic differentiation ideally also uses knowledge about the population history (e.g., natural versus anthropogenic isolation, time since separation; Mimura et al. 2017) and the consequences for population viability of managing populations in isolation (Weeks et al. 2011, Frankham et al. 2012). Whether seeking to maximize genetic diversity and adaptive potential within populations (Ralls et al. 2018) or preserving unique components of diversity across populations (Funk et al. 2019), there are tools to help practitioners understand the risks and benefits of decisions about whether to mix gene pools or manage populations in isolation (e.g., Frankham et al. 2011, Hoffmann et al. 2021). A choice between preserving as many unique segments of biological diversity as possible versus promoting evolutionary resilience within future environments (i.e., adaptive capacity; Thurman et al. 2020) can yield contrasting management strategies (Ralls et al. 2018) with very different consequences for conservation policies, priorities, and outcomes. Protecting recognized biodiversity units includes protection from introgression with closely related species, subspecies, and populations—the exact opposite strategy one might adopt to increase adaptive potential (Stanton et al. 2019). Although there are strong opinions in the literature (Collar 2018), there are currently no agreed-on guidelines for deciding between such options.

Evaluating the risks and benefits of management actions

There is a growing movement within conservation decision-making to explicitly balance the risks and benefits of alternative management actions (Hemming et al. 2022). Furthermore, there have been important moves to increase the collaborative partnerships among scientists and conservation practitioners (Bernos et al. 2020). Through groups such as the International Union for Conservation of Nature's Conservation Genetics Specialist Group and the Society for Conservation Biology Conservation Genetics Working Group, researchers are fully participating in this ongoing shift toward partnering scientific discovery with management action. Recently, the Coalition for Conservation Genetics has brought together multiple groups with the goal of raising awareness of the importance of genetic diversity, developing tools and analyses for the use of genetic data in conservation, and fostering partnerships between scientists and practitioners to achieve change in policy and practice (Kershaw et al. 2022). These are laudable goals, and the coalition recognizes that practitioners are often faced with competing scientific recommendations that all purport to be essential for conservation (Kershaw et al. 2022). Collaborations between geneticists and practitioners, ideally bringing together diverse perspectives, offer great potential to advance the role of genetics in conservation policy and practice, an area of global biodiversity action that required additional attention (e.g., Jacobs and Baker 2018). But an important omission from the current discussion is how practitioners should reconcile the results from the developing science of conservation genomics with the values underlying the selection of management objectives and associated priorities for conserving diversity.

We argue that in the excitement over the potential for genomic data to inform conservation efforts, these scientific–management partnerships may overlook the important issue that it is vital to explicitly acknowledge and discuss the values that underlie preferences for one option over another. We recognize that management decisions must flow from clear objectives (Schwartz et al. 2018). Once they are identified, the science can be an integral part of planning effective actions to achieve the stated objectives. However, although scientists often have a valuable perspective on what those objectives should be, we find that there are often two shortcomings that inhibit robust and transparent decision-making.

First and foremost, it is not the role of scientists by themselves to set management objectives for species conservation. Setting management objectives requires answering the question *What does success looks like?* (see Redford et al. 2011), and its antithesis, *What does failure look like?* These questions must be answered by practitioners, in consultation with a wide range of stakeholders, of which scientists are one group. Only then can scientists and practitioners make plans to support the achievement of those objectives.

The second concern is fully integrating uncertainty into these decisions. Genomic data carry the potential to greatly increase the resolution and reduce our uncertainty in assessing the genetic distinctiveness of populations, the risks associated with low genetic variation, and even the importance of critical functional genes (Stanton et al. 2019). However, uncertainty in how to interpret genomic data to inform conservation decisions persist, even among scientists (Shafer et al. 2015, Bernos et al. 2020). With this in mind, we consider the role of scientists in the process of setting objectives and designing management actions that best fulfil societal values for biodiversity protection.

The role of values in setting management objectives

The selection of objectives for conserving biodiversity is directly informed by values (goals and principles that guide human behavior; Manifredo et al. 2017), which underpin how individuals define what constitutes success and failure. The different objectives that arise from divergent values can lead to different priorities for conservation action (Angermeier 2000). Often, questions about conservation priorities are framed within the context of striving to maintain distinct, genetically depauperate entities versus maintaining more viable but less distinct entities (see Fitzpatrick et al. 2015). However, underpinning these priorities can be ethical and philosophical perspectives on whether or not conservation should be interventionist (e.g., mixing gene pools). Questions of whether a population warrants separate protection may be an expression of the view that all biodiversity has intrinsic value and should be conserved (Sandler 2012) or of the importance of a taxonomic group to local indigenous communities.

Hybridization offers another issue where underlying values can shape divergent priorities for conservation action. Some stakeholder groups argue that individuals resulting from hybridization between closely related species represent a threat to the "pure" forms and should therefore be removed (e.g., Grevy's zebra, *Equus grevyi*, and the plains zebra, *Equus burchelli*; Cordingley et al. 2009), displaying their underlying values. An alternative perspective is that hybridization is a natural process and could even be a conservation tool to promote rapid adaptation to environmental change (e.g., evolutionary rescue; Chan et al. 2019).

As clear as the genomic science may be on any particular case, stakeholder preferences may vary from polarized arguments about the need to or the need not to intervene, through to a nuanced preference determined by the best available estimates of the likelihoods of success or failure of alternative management actions. In our experience, it can be difficult for scientists to acknowledge that their own values influence the management objectives and actions they espouse. For example, promoting translocations to reverse inbreeding depression in small, isolated populations with individuals from a long-separated population (e.g., *Burrymus parvis*; Weeks et al. 2017) is valuing the long-term population persistence over maintaining the genetic composition of the population. Even though recommendations can be based on weighing the risks of inbreeding depression versus outbreeding depression (Frankham et al. 2011), the risk tolerance of scientists may not match the risk tolerance of other stakeholders. Scientists can advocate for a position, but ultimately, they are just one of many stakeholder groups that practitioners must consult in setting management objectives, and some recommendations may be unacceptable to society.

Diversity of scientists' values can lead to divergent perspectives

Levin and colleagues (2021) introduced the Rashomon effect in conservation, whereby management decisions are complicated by conflicting perceptions of the causes and consequences of the conservation problem. The Rashomon effect works well to describe the challenges practitioners face in decisions about the genetic management of entities. To illustrate how this might operate, we offer a hypothetical example of this effect for the interpretation of genomic data and its implications for conservation management.

Imagine the case of a once broadly distributed passerine species. The existing taxonomy defines five closely related groups classified as different subspecies under the relevant legislation. The different subspecies can be distinguished by variations in the shade of yellow of the nape. Significant habitat loss and fragmentation over the past 200 years have meant that the populations of different groups have become increasingly isolated from one another. Several subspecies have large, healthy populations, whereas others are declining, with one restricted to only three reserves.

In order to identify possible conservation actions to support the management of the species as a whole, practitioners seek genomic data to help inform their decisions. The data show genetic differentiation across the species, with fine scale differentiation at both the subspecies and the population level (figure 1). The small populations have low levels of genetic diversity, low effective population sizes, and populations of at least one subspecies show high levels of inbreeding. The subspecies with larger populations have higher levels of genetic diversity.

One conclusion that could be drawn from these data is that the measurable genetic differentiation between populations suggests that each of the currently recognized subspecies warrants their own conservation status. The presence of phenotypic variation across the groups reinforces the argument in support for their status as separate species, requiring separate management. The measurable differences between these groupings are interpreted as unique diversity that must be preserved (figure 1). To preserve genetic integrity, scientists could recommend intensive management for each of the groups, including that a captive breeding program be established with individuals from the smallest group at highest risk of extinction in order to bolster their populations (figure 1).

An alternative conclusion could be that much of the measurable genetic differentiation across the grouping is the result of the declines that occurred as habitat loss caused populations to become smaller and more isolated over time. There is a signature of historic gene flow across the species complex as a whole, suggesting that the previous subspecies classifications may have been strongly influenced by phenotypic variation. The genomic data are more consistent with the levels of differentiation expected on the basis of the effects of genetic drift in small allopatric populations. The low levels of genetic diversity and high levels of inbreeding suggest an elevated extinction risk for the whole species complex (figure 1). At least two subspecies only occur in small populations that are suffering from inbreeding depression. Augmenting gene flow could improve the genetic health of these populations. From this conclusion, scientists could recommend genetic management by moving individuals between populations of genetical differentiated groups to prevent the extinction of the inbred populations and promote the adaptive potential of the whole species cluster to future change (figure 1).

But another group might not seek detailed evidence about genetic differentiation, demographic history, and historical distribution but might simply assert that the pollination services offered by the species are a vital ecosystem service. The smaller populations are at a significant risk of extinction, and the level of fragmentation is such that the species will be permanently lost from those areas. Their position is that ensuring the ecological niche of pollinator is filled takes precedence over resolving the taxonomic status of each group (figure 1). Individuals should be translocated from the large, healthy populations to bolster the smaller, at-risk populations and prevent local extinction that would lead to the loss of pollination services.

In the cases illustrated above, the Rashomon effect occurs because there are plausible, alternative perspectives. Different conclusions may arise for at least two reasons. First, the scientific assessment involves uncertainty, such that the science can only provide some probability statement about likely outcomes. Second, scientists, practitioners, and stakeholders each inform their

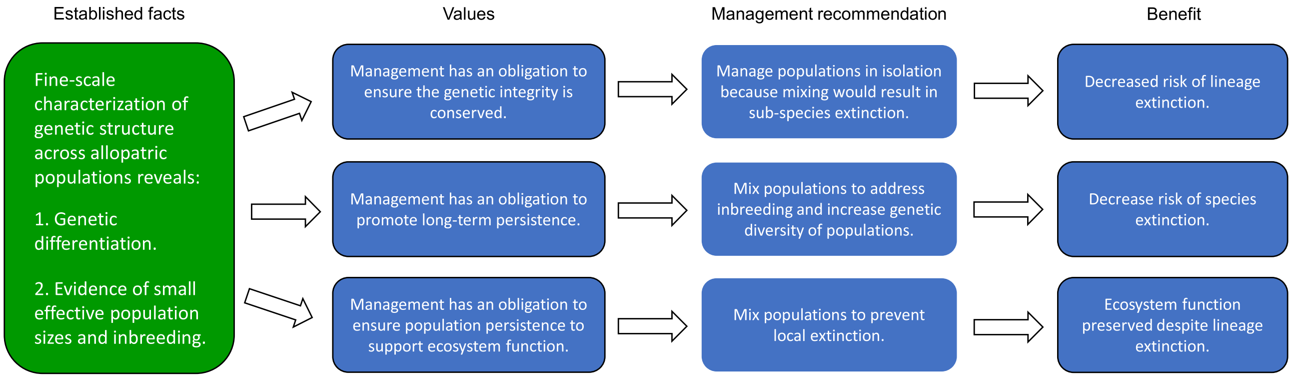

Figure 1. An example of the Rashomon effect when interpreting genomic data in relation to three different sets of values. The established facts (far left box), when filtered through different value sets can lead to different management recommendations prioritizing different potential benefits.

interpretation of the science against a backdrop of perspectives on the long-term need for a species to adapt to evolving environmental conditions, the risks associated with low standing genetic variation, the importance of the species to ecosystem functions, and the importance of independently evolving lineages (figure 1). The important point in our present discussion is that more science, reducing the uncertainty about either biogeographic history or population viability, will not resolve contrasting recommendations based on values. For some, the persistence of a lineage within an ecosystem is of utmost importance. For others, it is the genetic integrity of a phenotypically distinct grouping. Whether the smallest grouping is worth preserving as a unique entity is a question of values and not science, even though estimating how best to preserve it is valuably informed by science. Practitioners, with consultation from a broad array of stakeholders including scientists, must decide, contingent on the best available data and cognizant of the chance of success and risk of failure, whether the management objective is to preserve a unique segment of diversity through intensive management interventions (e.g., captive breeding), to preserve the adaptive potential of the broader species complex by intervening to maximize genetic diversity (e.g., gene pool mixing), or to preserve ecosystem function by preventing local extinction (e.g., translocations; figure 1).

The implications of rigid regulatory systems versus management flexibility

Regardless of the perspectives of practitioners, scientists or stakeholders, the management objectives for small, isolated populations must recognize that management actions are constrained by existing regulatory frameworks. Although they offer some degree of flexibility for managing discrete populations, these frameworks also restrict management flexibility by setting rules that must be followed once taxonomic grouping are formally defined. Such rigidity has stimulated proposals for revision of taxonomic grouping (e.g., raising subspecies to species; Zachos et al. 2013). The time and evidence required to change the taxonomy that warrants separate management interventions (i.e., taxonomic inertia; Stanton et al. 2019) may prevent practitioners from being caught in a churn of taxonomic revision (Garnett and Christidis 2017, Collar 2018) but may, nevertheless, require limited resources be allocated to consider the proposals (e.g., leatherback turtle; USFWS 2020). However, this can also inhibit the flexibility to undertake small-scale experiments to trial proposed management actions.

The way forward

Genomic scientists are increasingly engaged with resource managers, who use decision-support frameworks to address critical management issues (Bernos et al. 2020). The importance of this trend cannot be underestimated both to support decision-makers to interpret the science and to ensure scientists understand the implications of their recommendations (e.g., Jacobs and Baker 2018, Stanton et al. 2019). Furthermore, we do not consider the challenge of scientists limiting their purview to informing issues, rather than deciding them, to be confined to managing at-risk populations. However, the rapid evolution of genomic technologies marks this area of science as one where practitioners are seeking sophisticated technical information that stakeholders are challenged to interpret. This is compounded by scientific uncertainty, opposing underlying conservation values, and a constraining policy realm that makes decision-making particularly difficult. The often decades-long debates about how to appropriately manage iconic species, such as the red wolf (www.fws.gov/project/red-wolf-recovery-program), the Florida panther (www.fws.gov/story/2022-04/florida-panther), the California gnatcatcher (www.fws.gov/story/coastal-california-gnatcatcher), among others, highlight the depth of these challenges.

Understanding that values shape scientific interpretation and that scientists are only one of the stakeholders with decision leverage is an important step toward constructive engagement with challenging, contested conservation decisions. By recognizing the Rashomon effect, it should be expected that others may look at the same data and validly come to a different conclusion about conservation objectives and management direction. The rapidity of biodiversity loss is driving a sense of urgency and concern that a lack of decisive action is leading to increased rates of extinction (Barnard et al. 2021). Engaging scientists, practitioners, and stakeholders in deliberative decision processes are likely to slow—not speed up—the decision-making process (Beier et al. 2017). The challenge facing the community of conservation geneticists is being responsive to the real sense of urgency while also remaining true to the mandate as engaged scientists: to inform but not dictate management decisions.

Toward this goal, we recommend that conservation geneticists reflect on the potential to set guiding principles on issues common to most of these decision processes. For example, common challenges include what factors to consider when managing a species complex. To what extent should low standing genetic variation, the role of anthropogenic disturbance as an isolating force, the role played by individuals from a lineage in ecosystem functioning, and supporting adaptive potential be taken into account, and when should different elements be prioritized? It would also be important to set guidelines to help practitioners understand when recommendations about taxonomy are likely to be a matter of scientific uncertainty (e.g., sample size, the number and type of markers, statistical frameworks) or which species concept is being applied (e.g., phylogenetic versus biological) and their consequences (i.e., taxonomic inflation versus taxonomic inertia; Stanton et al. 2019). These are not simple matters, and understanding how to factor specific contexts into generalized risk assessments is an ongoing challenge where there are few good rules of thumb (Thompson et al. 2023).

From a practitioner's perspective, we recommend that explicit recognition of the roles and responsibilities of scientists in the collaborative decision-making partnership is a must. We recognize that reaching scientists for a truly collaborative assessment has historically been difficult. Clear collaborative guidelines and boundaries are necessary in order to find a collaboration that is productive and rewarding to all. A clear distinction regarding how endangered species policies do or do not constrain decision-making is also essential, along with considering potentially unintended consequences of decisions that interface with international agreements (e.g., CITES; Jacobs and Baker 2018). If current legal structures tip the balance toward retaining the genetic isolation of formally described taxonomic units, then researchers and stakeholders need to understand the conditions these policies impose and what is required to overturn them. We recognize the difficulties that practitioners face when engaging scientists in challenging conservation problems where genomic data will inform decisions. Working with a wide range of stakeholders, at the outset, to establish decision criteria—how much evidence, of what nature, and with what outcome certainty will lead to a change in management—is critical to efficient and socially accepted decisions. Framing these decision criteria should include a careful explication of the type of genomic data that constitutes valid evidence. These will not be one-off conversations but will need to continue to evolve, just as the technology and inferences that can be drawn from genomic data evolve. Although scientists are often eager to get on with the science, establishing decision criteria beforehand can make for more efficient science to inform a decision. Overall, collaborative approaches that include awareness of the different values of stakeholders and that set out clear criteria in advance will facilitate evidence-based decision-making that enhances conservation outcomes.

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Author contributions

Carly N. Cook (Conceptualization, Writing – original draft, Writing – review & editing), Kent H. Redford (Conceptualization, Writing – review & editing), and Mark W. Schwartz (Conceptualization, Writing – original draft, Writing – review & editing).

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