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Too simple, too complex, or just right? Advantages, challenges, and guidance for indicators of genetic diversity

Sean Hoban , Jessica M. da Silva , Alice Hughes , Margaret E. Hunter , Belma Kalamujić Stroil , Linda Laikre , Alicia Mastretta-Yanes , Katie Millette , Ivan Paz-Vinas , Lucia Ruiz Bustos, Robyn E. Shaw , Cristiano Vernesi  and the Coalition for Conservation Genetics

Sean Hoban* is affiliated with the Center for Tree Science, at The Morton Arboretum, in Lisle, Illinois, and with Colorado State University, in Fort Collins, Colorado, in the United States. Jessica da Silva* (j.dasilva@sanbi.org.za) is affiliated with the Foundational Biodiversity Sciences Division at the South African National Biodiversity Institute, in Cape Town, South Africa, and with the Centre for Ecological Genomics and Wildlife Conservation, at the University of Johannesburg, in Johannesburg, South Africa. Alice Hughes is affiliated with the School of Biological Sciences at the University of Hong Kong, in Hong Kong, China. Margaret E. Hunter* (mhunter@usgs.gov) is affiliated with the U.S. Geological Survey's Wetland and Aquatic Research Center, in Gainesville, Florida, in the United States. Belma Kalamujić Stroil is affiliated with the University of Sarajevo's Institute for Genetic Engineering and Biotechnology, and with the Society for Genetic Conservation of B&H Endemic and Autochthonous Resources GENOFOND, in Sarajevo, Bosnia and Herzegovina. Linda Laikre* is affiliated with the Department of Zoology's Division of Population Genetics at Stockholm University, in Stockholm, Sweden. Alicia Mastretta-Yanes* is affiliated with the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, and with the Consejo Nacional de Ciencia y Tecnología, in Mexico City, México. Katie Millette is affiliated with The Group on Earth Observations Biodiversity Observation Network, in the Department of Biology at McGill University, in Montreal, Quebec, Canada. Ivan Paz-Vinas is affiliated with the Department of Biology at Colorado State University, in Fort Collins, Colorado, in the United States, and is now affiliated with the Université Claude Bernard Lyon 1 (LEHNA UMR 5023, CNRS, ENTPE) in Villeurbanne, France. Lucia Ruiz Bustos is affiliated with the World Wide Fund for Nature, in Washington, DC, in the United States. Robyn E Shaw* is affiliated with the Department of Biodiversity, Conservation, and Attractions, in the Australian Department of Biodiversity and Conservation Science, in Kensington, Western Australia, and with the Division of Ecology and Evolution, in the Research School of Biology at The Australian National University, in Canberra, Australia. Cristiano Vernesi* is affiliated with the Forest Ecology Unit of the Research and Innovation Centre of the Fondazione Edmund Mach, in San Michele all'Adige, Italy, and with the National Biodiversity Future Center, in Palermo, Italy. The Coalition for Conservation Genetics includes these members not represented above: Chris Funk, Catherine Grueber, Francine Kershaw, Anna MacDonald, Mariah Meek, Cinnamon Mittan, David O'Brien, Rob Ogden, Gernot Segelbacher.

Abstract

Measuring genetic diversity of wild species using DNA-based data remains resource intensive and time consuming for nearly all species. However, genetic assessments are needed for global conservation commitments, including the Convention on Biological Diversity, and for governments and managers to evaluate conservation progress, as well as prioritizing species and populations to preserve and recover genetic diversity (e.g., via genetic rescue). Recently, indicators were developed for tracking and reporting genetic diversity status and trends for hundreds of species. The indicators quantify two simple proxies of within-population and among-population genetic diversity and adaptive potential: small effective population size ($N_e < 500$) and the loss of genetically distinct populations. The indicators must balance scientific credibility, practicality, and simplicity. In the present article, we summarize the advantages of these pragmatic indicators, address critiques by scientists for simplifying assumptions and by policymakers for complexity, and propose potential solutions and next steps. We aim to support practitioners putting indicators into policy, action, legislation, and reporting.

Keywords: conservation genetics, international policy, Convention on Biological Diversity, effective population size, Global Biodiversity Framework

"We see the role of ecology, genetics, and evolution as central to conservation planning."

—Michael Bruford and colleagues (1998)

The Convention on Biological Diversity (CBD), an international treaty on nature conservation, sustainable use, and the fair and equitable sharing of benefits arising from genetic resources among 195 countries and the European Union, has been in force for 30 years. But losses of biodiversity and degradation of ecosystem services continue, including an average 69% decline in monitored vertebrate populations in the last five decades (WWF 2022), alongside alarming losses in genetic diversity (Leigh et al. 2019, Hoban et al. 2021a, Exposito-Alonso et al. 2022).

At a key CBD meeting in December 2022, COP15, countries overcame major disagreements and signed the landmark Kunming–Montreal Global Biodiversity Framework (GBF;

CBD/COP/DEC/15/4, CBD/COP/DEC/15/5) to set a global ambition to reverse biodiversity loss (Díaz et al. 2020). The GBF was developed over four years through negotiations of CBD delegations, scientific deliberations, thousands of stakeholder and peer review comments, and the collection of metadata by the United Nations Environment Program World Conservation Monitoring Centre (Hughes 2023, Obura et al. 2023). This agreement along with others, such as the recently signed High Seas Treaty and the Paris Climate Agreement, could lead to a global turning point for biodiversity conservation. Therefore, the state of nature is at a critical point, necessitating unprecedented attention, capacity, and transformational societal change to ensure a livable planet (Díaz et al. 2020, Obura et al. 2023). Actions must be initiated immediately to achieve the GBF's 23 targets for 2030 and four outcome-oriented goals for 2050. Success or failure will depend

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on political will and action and on accurately monitoring progress toward or away from conservation endpoints.

In the present article, we focus on monitoring using indicators for genetic biodiversity, a neglected but vital element of nature (Hoban et al. 2021a). Genetic diversity is a foundational level of biodiversity, underlying species' ability to adapt to new environments, changing climates, and new diseases. Genetic diversity also supports ecosystem resilience after a disturbance and increases the success of ecological restoration (Des Roches et al. 2021). The CBD mandates countries to monitor, manage, and report on the genetic status of species. This focus extends beyond the CBD to other policies, such as the European Union Biodiversity Strategy, the IUCN Key Biodiversity Areas, and national legislation in numerous countries protecting endangered species through the recognition and protection of genetic diversity (Cook and Sgrò 2017, Hoban et al. 2021b).

To effectively monitor genetic diversity, in an affordable and rapid manner, it was proposed (Hoban et al. 2020, Laikre et al. 2020) to focus on processes that cause genetic erosion, the loss of genetically distinct populations and small effective population sizes (N_e). The loss of distinct populations results in the loss of locally adapted genetic diversity that is distributed across a species' environmental and geographic range, whereas effective population size relates to the number of individuals that contribute genetic diversity to the next generation. N_e is smaller than census size (N_c), because not all individuals of a population reproduce, among other factors. These two indicators can be compiled without DNA-based studies (e.g., using demographic data) and were adopted into the global monitoring framework of the GBF in 2022. During the CBD negotiations, the scientific and policy communities pointed to some challenges of the genetic indicators. In the present article, we respond to those concerns by first defining the indicators and their role in policy. We then elaborate on the advantages, critiques, and feasible near-term solutions for genetic indicators, using real-world examples. We close by reviewing other critical elements for monitoring using genetic diversity indicators and steps for global implementation.

Through this article, we aim to support policymakers in upcoming discussions at national and regional levels regarding putting indicators into policy, practice, legislation, and reporting—for example, through the recently appointed Ad Hoc Technical Expert Group on indicators for the CBD (SCBD/IMS/NP/JC/KM/90718) and other fora established by the CBD executive secretary. We also aim to support national and subnational governments and non-governmental organizations (NGOs) working to conserve genetic diversity for the adaptive potential it provides to populations of species, its intrinsic biodiversity value, and its contributions to ecosystems and people (Des Roches et al. 2018, 2021). Previous papers on the topic of genetic diversity in the CBD presented suggestions for goals and targets, documented the evolution of GBF's language, outlined a plan for trialing the implementation of indicators, and provided updated knowledge on N_e and the $N_e:N_c$ ratio (Hoban et al. 2020, Laikre et al. 2020, Laikre et al. 2021, Hoban et al. 2021a, 2021b, 2021c, 2023a, 2023b). In the present article, we present a concise overview of the headline indicator, the proportion of populations within species with an effective population size over 500 (hereafter referred to as the N_e 500 indicator), and the complementary indicator, the proportion of populations maintained within species (the populations maintained indicator), a list of seven advantages to these indicators, an explanation of nine possible challenges or concerns expressed from a policy and scientific perspective, and a brief road map of the next steps for implementing these indicators.

What are indicators?

Multinational commitments such as the CBD (CBD/SBSTTA/24/INF/31) and the Montreal Process on sustainable forest management (<https://montreal-process.org>) use indicators to assess progress on implementation of conservation measures and guide further conservation actions. Indicators are metrics capable of detecting a change in a system and should be simple (not requiring specialized training or equipment, easy to measure consistently), feasible, relevant, responsive, accurate, scalable, and legitimate (Heink and Kowarik 2010). For example, ecological indicators help to assess the health and function of ecosystems, how humans are perturbing them, necessary actions for improving the system, or the outcome of an intervention (Rapport and Hildén 2013). The GBF targets are designed to be SMART (for *specific, measurable, ambitious, realistic, and timebound*) and to have quantifiable indicators that meet these criteria (CBD/POST2020/WS/2019/6/2), which is an improvement on the previous CBD Strategic Plan for Biodiversity 2011–2020 and the Aichi Targets, whose indicators were largely considered insufficient (UNEP/CBD/COP/DEC/X/2, CBD/COP/DEC/XIII/28, Mcowen et al. 2016, Xu et al. 2021).

The GBF monitoring framework consists of three types of indicators: headline indicators, which capture the scope of a goal or target and are mandatory for parties to report on, and complementary and component indicators, which focus on elements within the goals and targets but are optional (Hughes 2023). Countries are also required to update their national biodiversity strategic action plans in line with the GBF and produce national reports in 2026 and 2029 (CBD/COP/15/L.27). Although 26 headline indicators and several hundred complementary and component indicators were agreed at COP15, much work remains for indicator development and deployment and to build monitoring and reporting capacity within many countries. Several indicators for species and ecosystems are developed, although with recognized significant weaknesses and biases (Fraixedas et al. 2022). Prior to the GBF, indicators for genetic diversity—the most foundational level of biodiversity—were largely restricted to proxies of genetic diversity of domesticated animals and plants, such as the number of threatened local breeds and the number of accessions or strains retained in gene banks (biorepositories that store genetic material, including tissue, seeds, eggs, and sperm). In other words, indicators for consistent and meaningful measurements of genetic diversity of wild species were entirely lacking. Fortunately, genetic indicators are being developed and deployed.

Genetic diversity indicators

Concerns about neglect of genetic diversity in policy had been voiced since 2010 (Laikre et al. 2010). Genetic diversity indicators were proposed at a side event at CBD COP10 but were not adopted in the CBD Strategic Plan for Biodiversity 2011–2020 and the Aichi Targets. A decade later, following a call from the Biodiversity Indicators Partnership that noted a lack of genetic diversity indicators, genetic diversity indicators applicable to all species were proposed, which measured how much of species' geographic ranges (a proxy for among-population genetic diversity) were safeguarded *in situ* by protected areas and *ex situ* by germplasm (e.g., seeds) sampled for long-term storage in gene banks (Khoury et al. 2019). The following year, Scotland introduced a methodology termed the *genetic scorecard*, which documents threats and actions relating to genetic status and gives each species a green, yellow, or red score (Hollingsworth et al. 2020). That same year, Laikre and colleagues (2020) and Hoban and colleagues

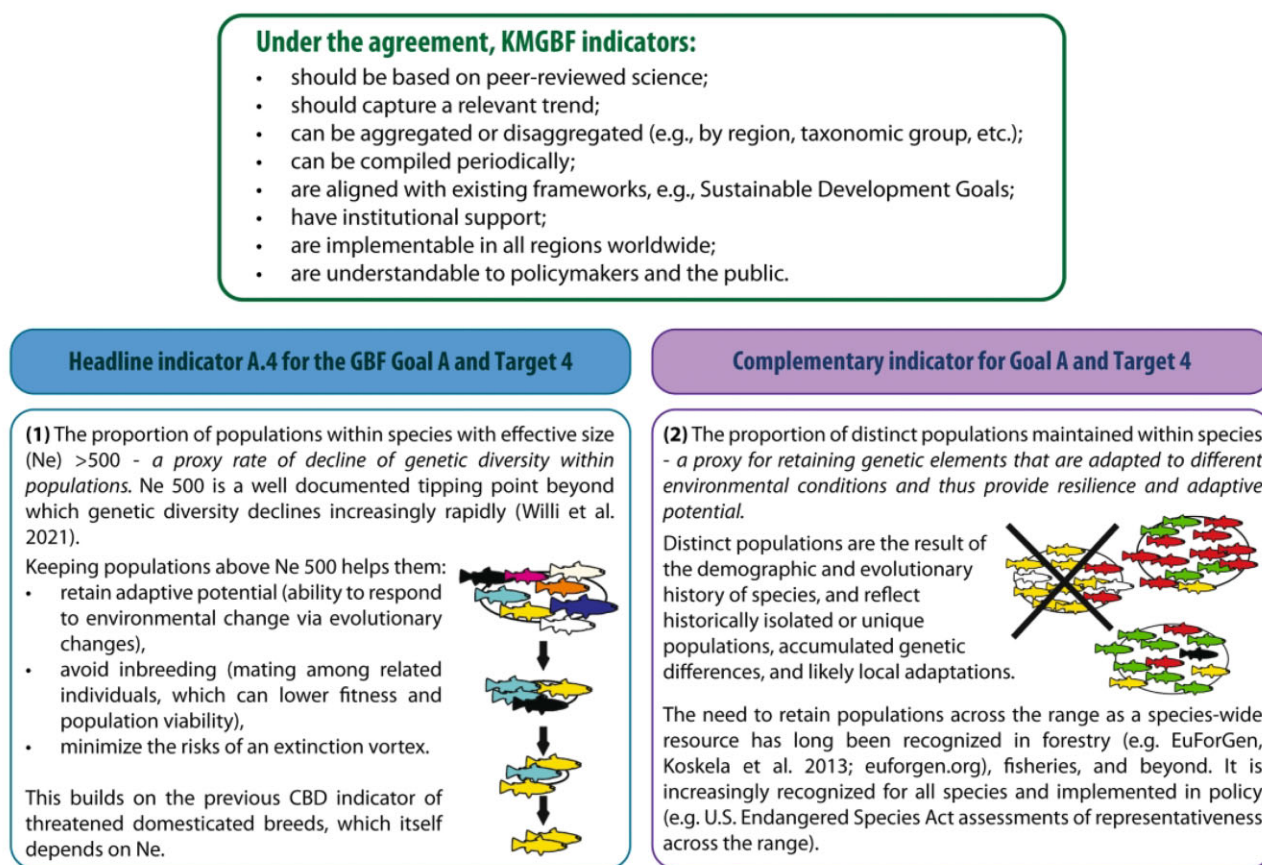


Figure 1. Criteria of indicators in the Monitoring Framework of the Kunming–Montreal Global Biodiversity Framework (GBF). Headline indicator A.4 and complementary indicator for genetic diversity can support monitoring progress on goal A and target 4 on species populations in the GBF. Abbreviation: CBD, Convention on Biological Diversity.

(2020) introduced indicators relating to rapid loss of genetic diversity in small populations, specifically those with an effective size (N_e) less than 500, the loss of genetic diversity when distinct populations are lost, and the development of knowledge of genetic diversity through DNA-based methods focused on conservation and genetic management. The first two indicators, N_e 500 and populations maintained, adopted as headline and complementary indicators in the GBF, respectively (figure 1), are quantitative, proxy based, indicative of a species' overall genetic status or health, deployable in all countries, and connected to conservation genetic theory and practice. Discussion and advances to these indicators were made prior to COP15 (Frankham 2021, Laikre et al. 2021, Hoban et al. 2021b, 2021c, O'Brien et al. 2022, Thurfjell et al. 2022), and following their adoption, work related to their operationalization has accelerated (Hoban et al. 2023a).

These indicators build on concepts such as measuring total species census size relative to a minimum viable threshold of 5000 (the SAFE index, for species' ability to forestall extinction, which recognized exponentially increasing risk as populations become smaller; Clements et al. 2011), measuring the proportion of the species' range lost as representing a loss of adaptive potential (Ceballos et al. 2017), and assessing populations using IUCN Red List criteria. As has been explained previously (Hoban et al. 2020), the two indicators can be calculated for 100 or more species per country (which should be taxonomically and ecologically representative, if possible), can be calculated and reported on starting

now, can be reported every 3–5 years thereafter, and do not use digital sequence information (Scholz et al. 2022). Expert consultation and political discussion will continue throughout 2023 and beyond to further develop and improve these and other indicators for CBD COP16.

Why the N_e 500 and Populations Maintained indicators are appropriate and advantageous

The list of advantages below is summarized in figure 2.

Advantage 1 is that the indicators can be implemented in all countries for many species, because they can be inferred from diverse data sources including quantitative and qualitative nongenetic data. Ideally, indicators provide accurate information for tracking targets, in a standardized methodology, with minimal needs for additional capacity or funds. The N_e 500 and populations maintained indicators aim to leverage all available biodiversity knowledge on local populations, including knowledge that may not be quantitative enough for traditional ecological and evolutionary models. Specifically, their flexible methodology allows many types of data to be employed, including existing national or regional databases or monitoring networks, traditional knowledge from Indigenous peoples (IPs) and local communities (LCs) and other rightsholders, scientific expert consultation, scientific literature, government or NGO reports, citizen science platforms, range maps, and GIS based analysis of habitat and organism density (Hoban et al.

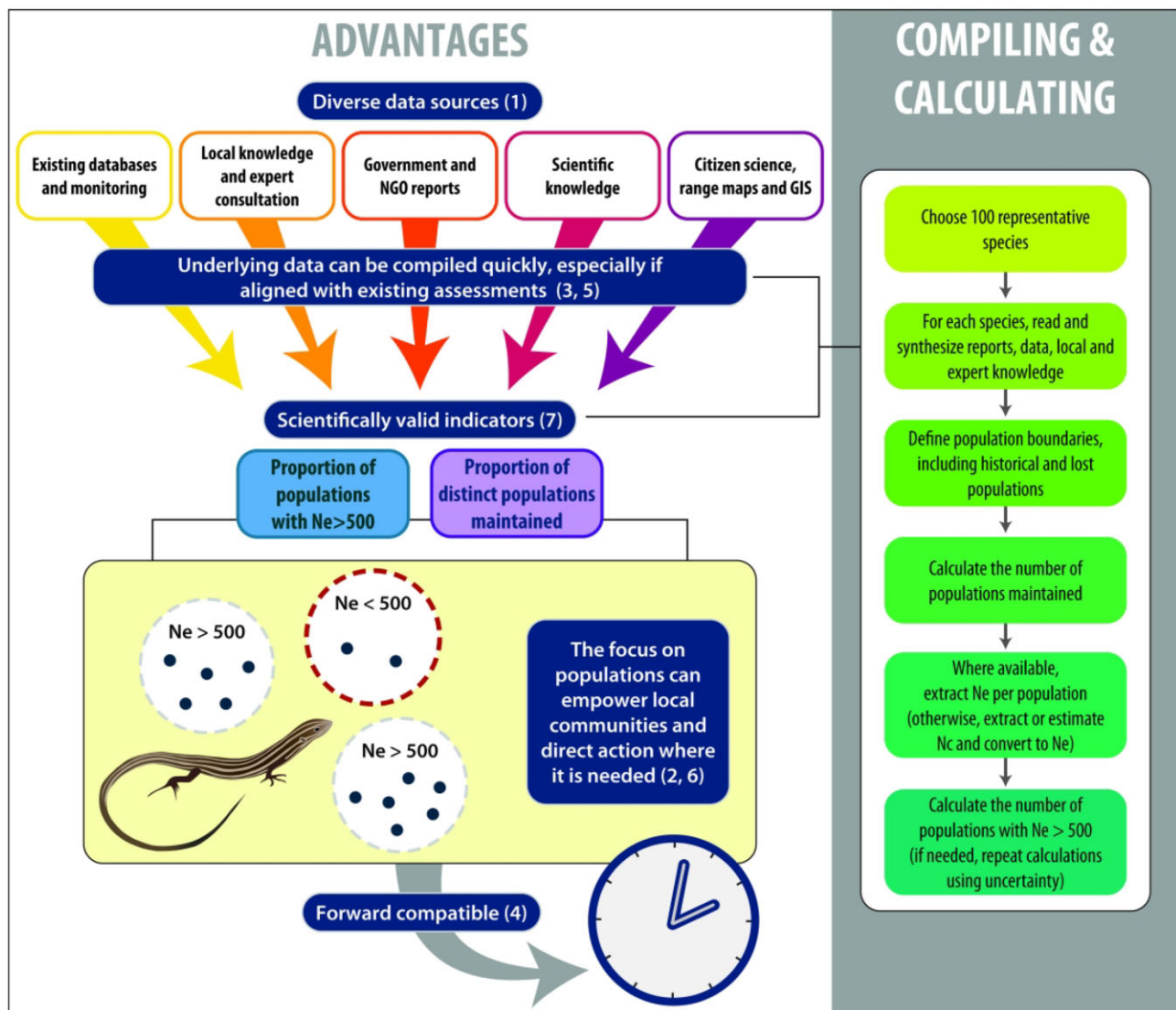


Figure 2. The advantages of diverse data sources to inform the two scientifically validated genetic diversity indicators. The right panel describes the process for each country to select approximately 100 species, gather data, and calculate the values for the two indicators. The numbers in parenthesis refer to the numbered advantages in the “Why these indicators are appropriate and advantageous” section of the text.

2023a). As such, these indicators are accessible, and it is likely that all countries could report on them for at least dozens of representative species.

Advantage 2 is that *emphasizing the local population level may facilitate local empowerment, participation, pride, and action by local communities*. Because they accept a wide variety of data types, including knowledge outside of traditional scientific studies and biodiversity monitoring, the indicators allow local knowledge holders, including IPs and LCs, to lead or contribute to monitoring. Such participation can broaden the base of biodiversity observations, especially in areas where other data are sparse (for an example, see figure 3). This also encourages scientists to collaborate with IPs and LCs and local managers, in compliance with the CARE (for *collective benefit, authority to control, responsibility, ethics*) guiding principles (Carroll et al. 2020, Cook et al. 2021) and to combine and compare data from different ways of knowing. The indicators have the potential for leveraging citizen science data if they are combined with observation models (Van Strien et al. 2013) and for providing a powerful means of tracking change across space

and time at a higher resolution than data collected by scientists alone. The indicators can also provide empowerment and pride; a focus on genetic diversity among and within populations emphasizes the importance of local populations for community-based protection. The active role of IPs and LCs is vital for successful conservation, because they safeguard and often sustainably manage most of the world’s biodiversity (Fa et al. 2020).

Advantage 3 is *speed*. The data supporting these indicators can be gathered for many species relatively quickly—orders of magnitude faster than traditional DNA based genetic assessments.

Although DNA-based studies are preferred to estimate indicators, they remain slow and expensive. A genetic study estimating N_e in five populations might take 1–3 years from planning to DNA analysis and might cost US\$10,000–US\$30,000 for supplies and US\$50,000–US\$200,000 for personnel. The staff members must have technical training in molecular techniques, population genetics, and bioinformatics. Consequently, most countries lack population genetic data for most species. For example, Brazil has approximately 60,000 plants and vertebrate species, but only

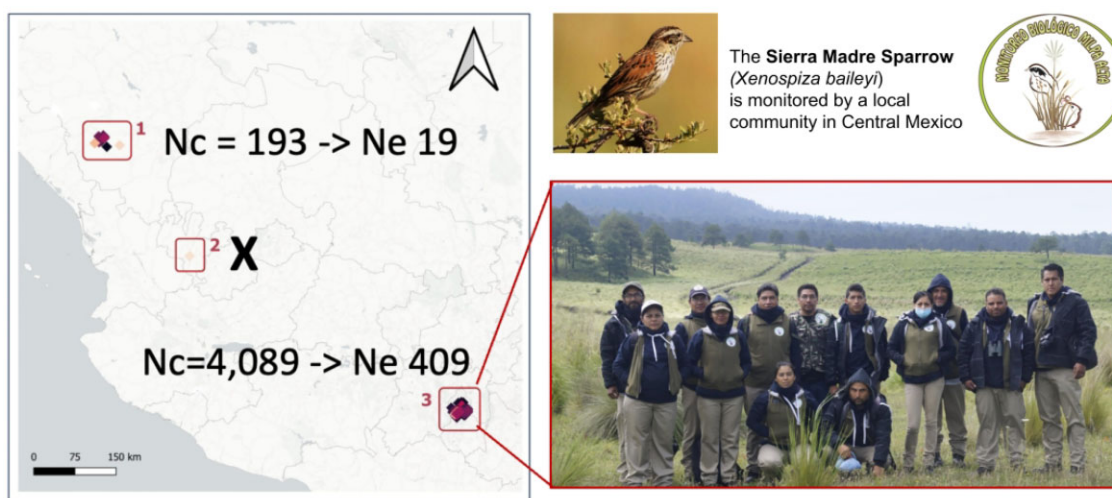


Figure 3. *Xenospiza baileyi* is a sparrow known from three geographically isolated populations in Mexico. The populations maintained indicator is $\frac{1}{3}$ (0.66) because one population is extinct. Census data from local monitoring initiatives can be used to estimate N_e for the remaining populations, showing that neither of them is above N_e 500 (using the conservative $N_e:N_c$ ratio of 0.1), but the southernmost population census is increasing. This population experiences conservation and monitoring actions by a community organization (“Brigada de Monitoreo Biológico Milpa Alta”) run by local inhabitants of San Pablo Oztotepec.

257 have genetic studies (Torres-Florez et al. 2018), less than 0.5%. Across the Americas, only about 350 vertebrate species have genetic data from multiple populations (Lawrence et al. 2019). Documenting genetic diversity lost from populations using historic DNA is often spatially and temporally biased (Jensen and Leigh 2022). Therefore, an indicator based on molecular DNA data is unfeasible. In contrast, data for the N_e 500 and populations maintained indicators can be rapidly gathered using existing reports and scientific and citizen science databases and by consulting experts and IPs and LCs (in our experience, on average, 3 hours per species). For 100 species, this is 300 hours, or about 8 weeks for one full-time person. The individual does not need to be a geneticist, but some help or collaboration from a geneticist is useful, and such collaborations are increasing (Taft et al. 2020, Pärli et al. 2021, Kershaw et al. 2022).

Advantage 4 is that the indicators are forward compatible, meaning they can incorporate new methods that arise because of technological advances; the data collected will now be comparable to data collected using future approaches. Currently, the primary data types used for approximating N_e and populations (Hoban et al. 2023a) is geographic and demographic (maps, N_c , narrative text, natural history texts, texts of national flora; qualitative or quantitative), but as genetic data collection accelerates, information from DNA-based studies can be the basis of the indicators (see Andersson et al. 2022). There are thousands of populations around the world with conservation-relevant DNA data. Temporal DNA monitoring is increasing, which can document indicator-relevant data, such as the occurrence and loss of distinct populations, levels of genetic variation, effective size, inbreeding (Hoban et al. 2023a), and genetic swamping through hybridization (O’Brien et al. 2022). Forward compatibility also encourages future collection of genetic data and capacity building for countries to develop more genetic monitoring infrastructure (including genotypes inferred using remote sensing technology; Meireles et al. 2020).

Advantage 5 is that the indicators can use data from and align with other ongoing biodiversity assessments where they exist. Biodiversity assessments such as Red Listing, work by NGOs monitoring

priority species, and key biodiversity areas typically document species biology, demography, maps, and consult experts—the same knowledge underlying the genetic diversity indicators. Spatial planning and environmental impact assessment, also a part of the GBF, may also incidentally produce the necessary data. For example, Red List workshops or other detailed in-country assessments convene species experts with knowledge of literature and firsthand experience, to assess species threats using demography and data on geographic ranges. With little extra effort—in some cases, a few minutes—experts can translate this to N_c or N_e (again, qualitatively or quantitatively) and populations maintained (Thurfjell et al. 2022), assuming that training, clear guidance, and data storage infrastructure are in place to ensure standardized observation collection. Although we acknowledge that Red List assessments need improvements, including more frequent updates (Fraixedas et al. 2022), we conclude that this synergy can save time and funds.

Advantage 6 is that these indicators are useful for directing action and policy toward those populations and the species that most need it, allowing for prioritization under limited resources, not just for reporting. The N_e 500 indicator highlights which and how many populations within a species need rapid action to elevate them above the N_e 500 threshold (e.g., by reintroducing captive bred individuals, enhancing gene flow or connectivity, genetic rescue). Ranking species by N_e 500 indicator values can prioritize species with many small populations that need intervention now, including wide-ranging species not threatened at the species level but suffering population extinctions. Both indicators, but especially the populations maintained indicator, could highlight species needing greater legal protection. We also suggest that the indicators could be used with a traffic light system of risk, for easy explanation to decision-makers. For example, this could be at the population level: green for N_e much greater than 500, yellow for N_e just above or below 500, red for N_e substantially below 500, with a major alarm for N_e less than 50. Although $N_e < 50$ is not currently part of the indicator, it is a threshold recognized for highly accelerated inbreeding and a loss of genetic diversity and, ultimately, for an increased risk of extinction (Franklin 1980). Similar thresholds

Table 1. Summary of challenges associated with the genetic diversity indicators presented by the scientific or policy communities, as well as suggested solutions to overcome them.

Challenge	Community	Suggested solution
Gathering data is still time consuming (requiring money and capacity)	Policy	Time is required for all indicators. Practical guidelines and new protocols are making it faster
Genetic concepts and terms (including N_e) are hard to understand	Mostly policy	Clear science communication tools can help
Achieving N_e 500 is infeasible for some highly threatened organisms' populations	Policy	Actions to increase N_e as much as possible can still be enacted, to help genetic diversity
N_e 500 may not be needed for some organisms (e.g., island and small habitat endemics)	Policy and scientific	In these cases, a more appropriate minimum N_e may be defined by ongoing research. Also the trend in N_e remains important
A focus on populations may divert funds from species' or ecosystem conservation	Policy	All levels of biodiversity are vital. Extinction starts with population losses
Neutral genetic diversity does not directly support adaptive potential	Scientific	The indicators are proxies of adaptive and neutral genetic diversity
Populations are hard to define	Policy and scientific	In many situations defining populations is feasible (box 1) and, where difficult, tools and guidance can help. In all situations, reporting uncertainty should take place.
The 0.1 assumption for $N_e:N_c$ is too conservative and neglects taxon specific $N_e:N_c$ knowledge	Scientific	Apply specific taxonomic group ratios when possible. Use DNA based N_e estimates if possible. Researchers need to compile $N_e:N_c$ ratios for more species or taxonomic groups
Indicators are too basic because they do not use DNA based metrics	Mostly scientific	Most species do not have DNA data; using non-DNA data allows for assessing exponentially more species. Also, DNA data can be used when available.
N_e 500 is insufficient as a headline indicator	Policy and scientific	Must be reported with the complementary indicator the proportion of populations maintained within species

could apply to proportions of populations lost (Exposito-Alonso et al. 2022).

Advantage 7 is that the indicators are scientifically valid, while meeting all other criteria and being practical. They are connected to core concepts in population and evolutionary genetics: genetic erosion, adaptive potential, and resilience to environmental change. Specifically, they leverage two established concepts: a threshold change at the N_e 500 level and the existence of local adaptation. Other indicators do consider genetic concepts but more tangentially. Khoury and colleagues (2019) used geographic area as a genetic diversity proxy, leveraging the genetic concepts of isolation by environment and isolation by distance. Hollingsworth and colleagues (2020) also considered them, but more qualitatively (good or bad condition). The Living Planet Index is complementary to but insufficient as a genetic diversity indicator, because it calculates the percentage change in N_c rather than the critical N_e 500 threshold. The percentage decline depends on initial N_c (and when it was calculated) and results in variable impacts on genetic diversity (Hoban et al. 2021). We emphasize that a genetic diversity indicator must connect to the core concepts of genetic diversity and must be applicable to most if not all taxonomic groups and species.

Challenges and solutions

We divide the challenges into two rough categories, scientific and policy, although some are common to both. We suggest solutions after each challenge, with a summary in table 1.

Policy challenge: Gathering data on the indicators still requires personnel, time, and funds

When the assessment is first begun, assessing species for these indicators may necessitate training by or collaboration with geneticists. However, support materials exist (e.g., guidance documents, case studies, webinars), critical metadata is being defined, workflows to automate gathering and curating data and metadata are in development, and scripts for automatically calculating indicators from data are being piloted (Hoban et al. 2023b). Moreover, the advantages outlined above, especially regarding flexible data collection and information provided by IPs and LCs, support inclusivity, as well as fairly rapid data collection. As was noted in advantage 5, the indicators can also be assessed as part of other species assessments in progress, such as Red Listing or national priority taxa surveys.

Policy challenge: Genetic concepts and terminology are too technical

We acknowledge that effective population size is a challenging concept. However, the reasoning behind N_e can easily be communicated: Populations lose genetic diversity faster when they are smaller, and that loss accelerates when the populations reach the tipping point captured by the N_e indicator. The concept of thresholds in conservation is common and easily explained (e.g., minimum viable population size). In addition, by engaging stakeholders, we have found that simple graphics can demonstrate how N_e is smaller than census size N_c , and how N_e

influences change in genetic diversity. To overcome this challenge, clear communication is needed—a lesson for future COPs, where indicators perceived as overly complex may be rejected. Improved communication techniques, infographics, and briefs may help overcome hesitancy due to perceived complexity (e.g., Lundmark et al. 2019, Hoban et al. 2023a, 2023b).

Policy and scientific challenge: Achieving N_e 500 may not always be practical

For example, sufficient supplementation or habitat restoration to meet this threshold may be infeasible for some populations of critically endangered species without huge investment of resources. An example is the Sumatran rhino, which has fewer than 100 adult individuals and breeds slowly (Havmøller et al. 2016). Nonetheless, an indicator is still needed to highlight the critical situation for such populations and species, encourage monitoring, and inform strategies for reversing decline and aiming toward N_e 500, even if improving the census size will be slow and laborious (as with many Critically Endangered Red List species).

Scientific challenge: Some species naturally occurring in small population sizes may persist below N_e 500 without negative consequences

For example, microendemic species, or populations on islands or other highly restricted habitats may have evolved to tolerate small populations or persisted at small populations for hundreds of generations (e.g., the Devil's Hole pupfish *Cyprinodon diabolis*; Brown 2021). These species may have experienced purging or other genetic mechanisms (or life strategies such as clonality) to help them persist at a small size for long periods. We suggest that a key knowledge gap to be addressed is enumerating how many and which species fall into these categories and establishing guidance for them. In addition, the N_e 500 indicator is useful because knowledge of baseline N_e or N_c can help identify any change in N_e .

Policy challenge: Focusing on populations might divert resources from other activities needed to halt biodiversity loss at the ecosystem and species levels

A focus on populations is a valid conservation goal, because extinction first starts with the loss of populations; unique genetic diversity can be lost with each population. Moreover, the loss of populations weakens local ecosystems by removing supportive biotic interactions and vital ecosystem services and resilience to environmental change (Ceballos and Ehrlich 2002). Finally, ensuring high values for the genetic diversity indicators can ensure that species stay out of the costly and difficult conservation emergency room (recovery from critical situations; DeWoody et al. 2021). Detecting and targeting interventions is critical to halt losses of populations.

Scientific challenge: A few scientists question the need to monitor and maintain neutral genetic diversity for conservation

Functional genetic diversity (i.e., diversity related to adaptation) may not always be represented by neutral genetic diversity (i.e., diversity assessed by most genetic markers; Kardos et al. 2021, Teixeira and Huber 2021). However, this debate does not affect the genetic diversity indicators, because they are proxies for

both functional and neutral genetic diversity. The populations maintained indicator accounts for functional genetic diversity conserving distinct populations on average conserves functional (or locally adapted) genetic diversity, even if specific alleles or genes are not identified (Meek et al. 2022). The N_e 500 indicator also accounts for functional diversity; below the 500 threshold, adaptive alleles are lost faster because of genetic drift, and the efficacy of natural selection that drives adaptation is reduced (Willi et al. 2021). Therefore, although functional genetic studies are desirable in some cases (e.g., breeding or translocating individuals better adapted to drought), the proposed indicators are a proxy for maintaining functional genetic diversity in sufficiently large distinct populations throughout the species range.

Scientific challenge: Populations are hard to define

We acknowledge that defining populations has generated debate among biologists for decades. However, populations can often be simply defined on the basis of geography or habitat (distinct lakes or patches, mountain tops, discontinuous habitat; see box 1). For numerous other species, defining populations without genetic data is feasible with careful guidance, including using ecoregions, expert-defined adaptive capacity units, or life zones subdivided by biogeography, as proxies of genetic differentiation reflective of local adaptation or long-term evolutionary lineages (Tobón-Niedfeldt et al. 2022). Migratory species can be defined by focusing on breeding populations (e.g., piping plovers, *Charadrius melodus*, winter in a continuous region but breed in geographically distinct locations; Miller et al. 2010). Genetic knowledge from other species (including phylogeographic patterns) can also help. Any uncertainty about the scale of populations or the degree of human-caused fragmentation on genetic distinctions can be incorporated by calculating the indicator under different assumptions of population isolation (e.g., assuming 4, 10, or 20 populations) and taking an average or propagating uncertainty such that the national indicator calculation displays confidence intervals. Showing uncertainty is advantageous; it more accurately reflects knowledge, allows the use of more data, and can highlight gaps and priorities for data collection.

Scientific challenge: The $N_e:N_c$ ratio varies among species, and the previously advised ratio of 0.1 should be refined because it is too broad

Approximating N_e from N_c depends on an $N_e:N_c$ ratio. We acknowledge that this ratio varies on the basis of species' breeding strategy, their sex ratio, and the variance in reproductive success among parents (Frankham 1995, Waples 2002). We note that the methodology focusing on N_e 500 allows the use of different ratios if that information is available (Laikre et al. 2021). The 0.1 ratio (and the rule of thumb N_c 5000) is well supported as a conservative ratio (see Frankham et al. 2017, Frankham 2021, and Hoban et al. 2021c for recent reviews on existing ratios across species). However, it is only a default when no other knowledge exists. For example, many birds and plants have a ratio of 0.3, which would be an N_c of 1500 (see figure 4), although the 0.1 ratio was suitable for about three-quarters of the cases that have been compiled. Other scientists have advocated N_e 1000 instead of N_e 500, which can also be implemented. Work is needed to increase the list of populations, species, and taxonomic groups with estimated $N_e:N_c$ ratios.

Box 1. Defining populations.

Distinct populations can be defined through a combination of genetic data, expert opinion, and spatial data. The information can be averaged across multiple data sources to incorporate uncertainty. Other approaches may be possible, including trait, behavior, and morphology differences and management units.

Box 1. How do we define a population?

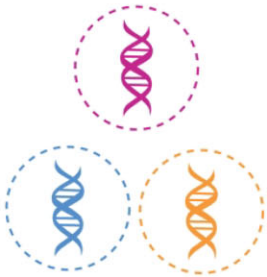
Defining populations can be a challenging task that requires careful consideration. Sometimes populations can be easily defined based on clear boundaries, while in other cases, additional information drawn from the scientific literature, expert knowledge or geospatial data is required. Using a variety of approaches, it is feasible to define distinct populations that are biologically meaningful.

Single approaches

Genetic data

1 Distinct populations

Search existing literature to determine if genetic studies reveal genetically distinct populations.

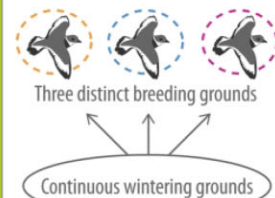


Three genetically distinct populations

Expert knowledge

2 Species biology

Using knowledge of the species' dispersal capacity, define populations based on habitat patches or occurrences separated by the maximum dispersal distance. For migratory species, populations can be defined based on breeding grounds.

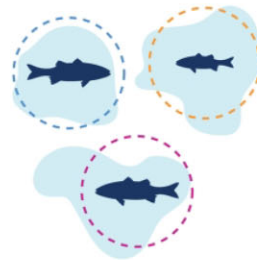


Three distinct breeding grounds

Continuous wintering grounds

3 Biogeography or habitat

Identify locations separated by a major barrier to movement such as a mountain or patches of unsuitable habitat.

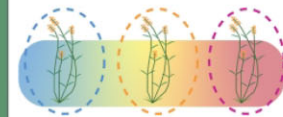


Three distinct locations separated by unsuitable habitat

Spatial data

4 Environmental zones

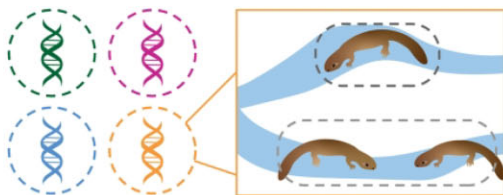
It can be difficult to identify populations in widespread species, especially if some degree of gene flow is present. One approach is to designate populations as individuals or groups of individuals in different ecoregions or life zones, signifying local adaptation.



Three distinct climatic zones

Combined approaches

Combine different approaches to define populations. For example, the eastern hellbender (*Cryptobranchus alleganiensis alleganiensis*) has four known genetically distinct units, which may represent millions of years of evolution. Within these, streams can be used to further subdivide the range into 345 extant and 225 historical populations.



Averaging approaches

Define populations under different assumptions, then take an average or provide a range. This more accurately reflects the level of uncertainty, uses different information and knowledge, and highlights gaps for data collection.



Two genetic lineages
Three locations separated by dispersal
Four distinct life zones
Average = 3
Range = 2 to 4

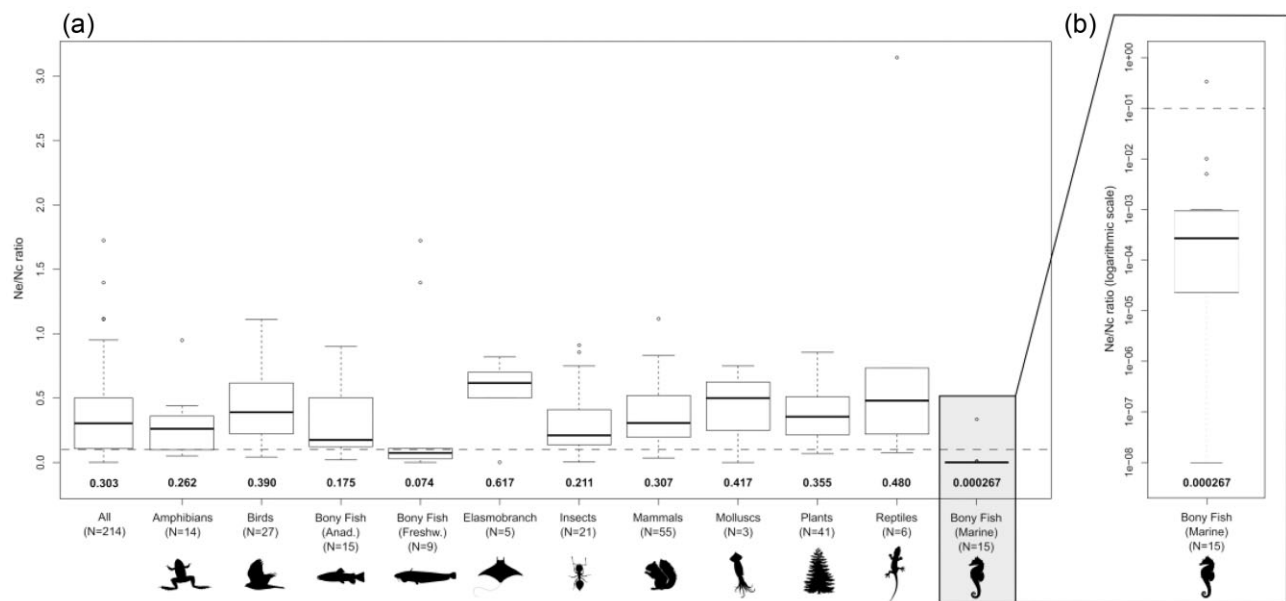


Figure 4. (a) Boxplot of the mean $N_e:N_c$ ratios calculated from values reported in 214 studies reviewed in Hoban et al. 2020 for all taxonomic groups (the “All” box) and per taxonomic group (omitting a few taxonomic groups with low sample size). (b) Boxplot of the mean $N_e:N_c$ ratios (on a logarithmic scale) for bony marine fish species. The thick lines and bold numbers represent the median values. The upper and lower hinges represent first and third quartiles, the whiskers represent the range of data extending up to 1.5 times the interquartile range, and the points represent data outside of this range (outliers). The horizontal dotted line corresponds to the recommended threshold $N_e:N_c$ ratio value of 0.1. Important note: The studies used to estimate $N_e:N_c$ ratios employed various analytical methods to estimate N_e (see Frankham 2021).

Scientific and policymaker challenge: These indicators do not need to use genetic data such as alleles or inbreeding from single or temporal monitoring

We applaud that an increasing number of species have genetic data and that progress is being made in translating genetic data into metrics comparable across species. However, such knowledge is rare in most countries and species (Hogg and Belov 2022), and the gap in sufficient genetic data needs to be addressed. When available, genetic data sets can be used to calculate N_e and help define distinct populations. Collation of genetic data is also vital (Lawrence et al. 2019, Leigh et al. 2021). This could encourage more genetic studies and could remind researchers already conducting genetic studies that clearly reporting N_e and population structure has conservation impact. However, such work is not on the timescale for the GBF for all species, given the scarcity of such data at present.

Final challenge and ways forward

As was noted above, the N_e 500 indicator is a headline indicator under the GBF (it is mandatory for countries to report it), whereas the populations maintained and other genetic diversity indicators are complementary, meaning they are optional and therefore will likely only be implemented by a subset of countries, species, and regions.

It would be problematic if N_e 500 is the only genetic diversity indicator reported, because it was designed to directly complement the populations maintained indicator, to maintain both among- and within-population genetic diversity. The two indicators are equally important. The N_e 500 indicator (currently) does not have a calculation adjustment for when populations are lost. It is currently defined as the proportion of extant populations above 500. If populations are lost, they are no longer in the calculation and

so population loss actually improves the indicator value, an extremely undesirable outcome.

We assert that the ideal situation would be to have both indicators as headline indicators, along with, when feasible, other genetic indicators. Gathering data underlying the two indicators and calculating them can take place simultaneously.

If the N_e 500 indicator is used alone, it must be adjusted to incorporate local population loss. A simple discounting mechanism would assign an N_e value of 0 to recently (after a defined baseline year) extinct populations, keeping them in the calculation as populations with $N_e < 500$. This would ensure the indicator value does not improve following local population extinctions.

An alternative would be to present multiple genetic indicators in a single framework. In this way, the indicators could be complemented with other knowledge on genetic diversity, including genetic statistics and threats to genetic diversity. These elements could all be reported simultaneously as a series of statistics or as a synthetic single measure, such as the Ocean Health Index (Halpern 2020). This builds on the idea of the Scottish scorecard, which compiles information on aspects of species’ genetic health and threats. Ideally, a platform that gathers and compiles all available genetic data, population data, and knowledge-based data, with clear open-source workflows and an output index of health, with statements on data caveats and uncertainty, would be produced and updated in real time (Walters and Scholes 2017).

Elements that may be important to include for reporting genetic diversity status and trends include the proportion of populations with $N_e < 50$ (e.g., populations at severe inbreeding risk, which may be entering an extinction vortex); a count of species in which genetic management is occurring or planned (e.g., translocations); a quantitative assessment of hybridization as a threat (e.g., genetic swamping, genetic “pollution,” extinction

Strengths

- Scientifically sound. Based on core principles.
- Flexible to input data (quantitative, qualitative)
 - No DNA data needed, although beneficial
 - Can incorporate local & traditional knowledge
- Local empowerment of people to take ownership of their populations
- Headline indicator ($N_e > 500$) and Complementary indicator (populations maintained) can be easily updated as new data becomes available
- Genetic indicator assessments can be aligned with existing biodiversity assessments (e.g. Red Listing)
- Useful for directing conservation management action, not just reporting
- Can be disaggregated for subnational reporting and management

Opportunities

- Alignment with existing initiatives (IUCN CGSG, KBA) to define genetically distinct populations
- Genetic and geographic metrics often concur and can be aligned
- Can incorporate a measure of uncertainty to acknowledge assumptions
- As more data is gathered, assumptions (e.g. $N_e:N_c$ ratio) can be refined
- Indicators can be aggregated for global perspectives as more data become available
- Training materials being developed (e.g., Manual, Guidelines, Automated workflows, webinars, workshops)

Weaknesses

- Gathering data may be time consuming
- Populations can be hard to define
- Not all species conform to the 0.1 $N_e:N_c$ ratio
- Does not yet provide a global outlook on genetic diversity
- $N_e > 500$ threshold does not always apply to some species (e.g., islands, small habitat endemics)

Threats

- Limited national capacity may make it hard to gather data
- Only reporting on the headline indicator can have perverse outcomes
 - Neglects loss of populations as only considers extant populations
- Uptake might be limited if management needed to boost populations to $N_e > 500$ is deemed infeasible

Figure 5. SWOT (strengths–weaknesses–opportunities–threats) analysis summarizing the key elements of the adopted indicators. The threats are primarily elements beyond this community’s control. Abbreviations: GI, genetic indicator; IUCN CGSG, International Union for Conservation of Nature Conservation Genetics Specialist Group; KBA, Key Biodiversity Area N_c , census size; N_e , effective population size.

by hybridization); geographic range protected *in situ* and *ex situ*; geographic range likely lost because of land-use change; population trends based on local surveys; *ex situ* conservation efforts, including the number of maternal lines represented *ex situ* (as a proxy for N_e *ex situ*); and information on the genetic knowledge or genetic studies available in a country (Frankham et al. 2017, Laikre et al. 2020). Predictions of the likely genetic diversity loss from simple simulation models could also be reported. Meanwhile, direct assessment of DNA data can complement these proxies, including likely genomic threats (Bertorelle et al. 2022) and observed losses of genetic variants (Andersson et al. 2022).

Conclusions

We summarize the mid- to long-term vision of the genetic diversity indicators using a SWOT (strengths–weakness–opportunities–threats) diagram (figure 5). These two indicators are feasible for all countries, use diverse data, and can empower local monitoring and action (advantages 1–3). We note that the two indicators should be used in combination, because they were designed to complement one another. Assessment can be repeated every 5 years, as required by the CBD, for hundreds if not thousands, of species per country. They can be efficiently completed along with Red Listing or other processes, are comparable across space and time even if new data arise, and can directly inform action (advantages 4–6). They have national and global usefulness to highlight priority species and populations. They are scientifically valid (advantage 7) but are also a communication tool to help policy-makers and the public better visualize and recognize genetic diversity and evolutionary processes. They can systematically mobilize a wealth of currently underused knowledge and data, in a manner similar to the Red List, and would improve the resolution of species trends in species’ assessments.

Work remains to be done, including building capacity, working with species with naturally small ranges, connecting theoretical work (Exposito-Alonso et al. 2022, Tobón-Niedfeldt et al. 2022) to

the indicators, and increasing the list of species with known $N_e:N_c$ ratios. Informatic tools and GIS-based methods are also needed to make the indicators more standardized (e.g., for defining and delineating populations) and useful to more people. We foresee genetic diversity indicators following the trajectory of tools such as the IUCN Red List of Ecosystems and Green Status toward standardized, accessible, widely implemented, and comparable indicators.

In the coming years, CBD parties, national and subnational governments, and NGOs will discuss and begin to implement genetic diversity indicators. We hope the present article helps ameliorate some concerns, provides solutions to challenges presented by these indicators, and provides a blueprint for successful operationalization.

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Author contributions

Sean Hoban (Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Writing – original draft, Writing – review & editing), Jessica M. da Silva (Conceptualization, Formal analysis, Investigation, Methodology, Project administration, Visualization, Writing – review & editing), Alice Hughes (Investigation, Validation, Writing – review & editing), Margaret E. Hunter (Investigation,

Methodology, Project administration, Writing – review & editing), Belma Kalamujić Stroil (Investigation, Validation, Writing – review & editing), Linda Laikre (Conceptualization, Formal analysis, Funding acquisition, Investigation, Resources, Writing – review & editing), Alicia Mastretta-Yanes (Formal analysis, Investigation, Methodology, Project administration, Resources, Visualization, Writing – review & editing), Katie Millette (Investigation, Validation, Writing – review & editing), Ivan Paz-Vinas (Formal analysis, Investigation, Methodology, Project administration, Resources, Writing – review & editing), Lucia Ruiz Bustos (Investigation, Validation, Writing – review & editing), Robyn E. Shaw (Investigation, Methodology, Resources, Visualization, Writing – review & editing), and Cristiano Vernesi (Conceptualization, Formal analysis, Funding acquisition, Investigation, Resources, Writing – review & editing).

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