

Opinion

Ancient and historical DNA in conservation policy

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Although genetic diversity has been recognized as a key component of biodiversity since the first Convention on Biological Diversity (CBD) in 1993, it has rarely been included in conservation policies and regulations. Even less appreciated is the role that ancient and historical DNA (aDNA and hDNA, respectively) could play in unlocking the temporal dimension of genetic diversity, allowing key conservation issues to be resolved, including setting baselines for intraspecies genetic diversity, estimating changes in effective population size ($N_{\rm el}$), and identifying the genealogical continuity of populations. Here, we discuss how genetic information from ancient and historical specimens can play a central role in preserving biodiversity and highlight specific conservation policies that could incorporate such data to help countries meet their CBD obligations.

Genetic biodiversity

Three levels of biodiversity constitute the variation of life on our planet: diversity of ecosystems, species diversity (number and distribution of species), and genetic diversity (amount and distribution of genetic variation within species or populations). The need to monitor biodiversity at all three levels has been globally recognized in international policy since 1993 when the Convention on Biological Diversity (CBD) came into effect. Today, we face dramatic biodiversity loss due to the combined effects of habitat damage, fragmentation and alteration, climate change, and other global change stressors. Most frequently, this loss is calculated in terms of the number of species, but relatively little is known about loss of diversity within species and populations at the genome level (but see [1]). Genetic diversity within species and populations is necessary for long-term survival as it allows resilience and adaptation not only for individuals, but also for populations, species, and entire ecosystems [2]. This diversity is particularly relevant in the Anthropocene, characterized by significant, rapid, and global changes to habitats and environmental conditions. Despite the importance of genetic diversity in biodiversity protection and management, it has rarely been included in policies and regulations [3]. But, with the ongoing development of the CBD post-2020 Global Biodiversity Framework (expected to be concluded in May 2022), there is an opportunity to address this significant blind spot by adopting genetic diversity targets and indicators.

Thanks to the advancing power of DNA sequencing technologies, the generation of population-scale genomic data is becoming increasingly possible. However, simply generating data is not enough – estimates of current genetic diversity are only useful in relative terms or when compared with a baseline. Although one way of achieving comparative context is to compare genomic data from a species of interest against those of other species, ultimately this requires large leaps of faith in deciding which particular species can reliably be compared. An alternative, and potentially

Highlights

Genetic diversity within species and populations is necessary for long-term survival and thus constitutes a key component of preserving biodiversity, but until now, it has rarely been integrated into conservation policies.

Ancient and historical genetic data [ancient/historical DNA (a/hDNA)], such as those from specimens stored in natural history collections, can add a temporal dimension to conservation genetic inferences by providing baseline levels of diversity that contemporary data can be compared with and help guide conservation actions.

To increase the use and impact of a/hDNA research in preserving biodiversity, genetic indicators must be explicitly included in conservation policies, the benefits and limitations of using a/hDNA need to be clearly communicated to all conservation actors, and relationships between academics, museums, conservation practitioners, and policy makers must be strengthened.

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more powerful, approach is to directly make temporal comparisons by drawing on natural history collections and biological archives. Whereas genomic data from historical samples (hDNA; see Glossary) provide a temporal scale that can extend to hundreds of years, aDNA obtained from skeletal remains or sediment cores can expand the temporal scale to thousands of years. While not without its challenges [4], the fact that many of the samples held within these collections and archives date to prior to the onset of extreme anthropogenic biodiversity loss means that baseline data could be generated for many species of conservation interest (provided, of course, sample availability), against which the modern situation can be compared and anthropogenic impact can be assessed.

With an aim to encourage discussion, and ultimately inclusion, of temporal baselines inferred from hDNA and aDNA in guiding conservation policy and actions, we here highlight some of the contributions that such datasets have made so far, as well as the challenges that need to be overcome to fully realize their potential.

Setting baselines with a/hDNA

a/hDNA can guide more nuanced conservation efforts and policies. Here, we describe how these data can be used to assess population genetic patterns and processes that are relevant for endangered species.

The contemporary **population structure** of a species is the consequence of several cooccurring processes, including past connectivity patterns and demographic history. Typically, endangered species have suffered dramatic distribution changes and population size reductions in the past two centuries [5], greatly influencing today's patterns of diversity and population structure. However, these patterns are difficult to interpret using the static snapshot provided by modern genetic data alone. Using information provided by a/hDNA, we can gain critical insight into whether these patterns were driven naturally by the biology of the species or were influenced by human activities. This can help to guide important conservation and management decisions such as whether and how connectivity between populations should be encouraged. This was nicely exemplified in a recent study on the Iberian lynx (Lynx pardinus) [6]. The authors used ancient, historical, and modern genetic data to uncover how the species went from displaying very shallow geographical differentiation thousands of years ago to a structured metapopulation in the past century, and to two differentiated subpopulations by the year 2002, when the lynx populations had been almost driven to extinction by humans. This genetic differentiation was attributed to genetic drift, not adaptation, which allowed the authors to conclude that translocations between the two remaining populations could be an acceptable conservation measure. Another important aspect of the genetic structure of declining populations that can be informed by using a/hDNA is the extent of past diversity that is now lost. For example, in a recent study in eastern gorillas (Gorilla beringei) [7], the authors identified that most of the mitochondrial diversity lost by the species during decades of population declines could be attributed to the extinction of peripheral populations instead of a decrease of genetic diversity within the core range of the species. This can be used to help guide decisions regarding the regions and populations where conservation efforts should be focused.

The levels of genomic diversity within a species are not just a function of the current population size [8–10]. Different combinations of life history traits and past demographic history (e.g., ancient bottlenecks or long-term small population sizes) can lead to the same level of genomic diversity in different species. Therefore, comparing their levels of diversity is not very informative on how threatened one species is compared with another. An alternative strategy is to use a/hDNA from

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specimens that predate the human-driven recent population declines to establish the baseline levels of genomic diversity against which indices of genomic erosion can be compared (i.e., heterozygosity, inbreeding, mutational load) [10]. When scaled with the age of specimens and the species' generation times, these indices should be informative on the rate of change, making them comparable among species. Such inferences are becoming more common in conservation genomic studies and have recently been applied to endangered species such as eastern gorillas [11], the crested ibis (Nipponia nippon) [12], and the white and Sumatran rhinoceroses (Ceratotherium simum and Dicerorhinus sumatrensis, respectively) [13,14]. However, for this to be widely applicable in conservation actions and policy, some conditions need to be verified, especially the genetic continuity between the past and present populations. For example, based on aDNA data from submerged wood remains, the population structure of oaks (Quercus ssp.) in Europe has been shown to be geographically stable since the Neolithic [15]. Additionally, the definition of genomic risk for a population is not well established yet, and the theoretical notion that genetically healthy populations should display high levels of diversity, low levels of inbreeding, and low genetic load is debated in the light of sometimes contradictory empirical data. For example, using a/hDNA data as baseline, species with long-term small population sizes that have low contemporary levels of heterozygosity and high inbreeding have been shown to carry a comparatively reduced level of deleterious mutations, potentially mitigating the effects of inbreeding depression [9,11,16], highlighting the importance of a temporal perspective for assessing genomic risk.

The study of the $N_{\rm e}$ of a species is critical for conservation and can also greatly benefit from the addition of a/hDNA data. N_e governs the rate of change of allele frequencies of a population and therefore affects evolutionary forces such as genetic drift and selection [17]. In fact, N_e is systematically employed as an indicator of population viability, for example, using the 50/500 rule to determine short- and long-term survival [18,19]. As such, $N_{\rm e}$ is considered a key genetic index for animal and agricultural resources for the Food and Agriculture Organization of the United Nations (FAO) [20] and for wild animal populations for the International Union for Conservation of Nature (IUCN) [21], albeit the latter has so far failed to explicitly integrate it into any Red List assessments [22]. There are a plethora of methods to estimate $N_{\rm e}$, both based on contemporary samples or leveraging time series data (reviewed in [17]). The inclusion of a/hDNA data opens the possibility to exploit both types of estimates, helping to provide a more comprehensive picture of the temporal changes in $N_{\rm e}$ of endangered species. For example, estimates of N_e from ancient or historical samples can provide an objective baseline to compare with modern-day estimates, which can be used to better inform conservation strategies.

Increasing the impact of a/hDNA in conservation

While most parties to the CBD recognize the general importance of genetic diversity, in the past, reporting on genetic diversity in wild species has been inconsistent, superficial, or even completely overlooked [23]. However, there is increased emphasis on the importance of genetic variation for species' and ecosystems' resilience to climate change in documents such as the 2030 Biodiversity Strategy of the European Union¹¹, and there is a legal framework for the conservation of genetic diversity in the USA (through the Endangered Species Act) and Canada (through the Species at Risk Act; for additional details, see Table 1). The European strategy is linked to conservation efforts of genetic diversity in forest trees across the continent [24], and there is a proposal for this approach to be extended to other taxa [25]. For a/hDNA to have a meaningful impact on biodiversity conservation policy, we propose that there are several key areas that the community must address.

Glossarv

Ancient DNA (aDNA): DNA extracted from specimens that were collected from a naturally occurring deposit (such as an archaeological site) and typically characterized by small fragment size, very low complexity, and low endogenous content.

Effective population size (Ne): the number of breeding individuals of a population assuming ideal conditions such as random mating and nonoverlapping generations. In most real populations, the census population size is larger than the effective population size.

Environmental DNA

metabarcoding: taxonomic identification of the content of an environmental sample (air, water, soil, sediment, ice core, faeces, etc.) based on the PCR amplification of a short DNA barcode marker, the sequence of which is different in each species.

Genomic erosion: loss of genomic variation and increase of harmful mutations within a population, which may lead to a decrease in fitness. Small and isolated populations, which are especially subject to stronger genetic drift and higher levels of inbreeding, are more prone to suffer from genomic erosion. Historical DNA (hDNA): DNA extracted from specimens that were collected specifically to go into museum collections, frequently when alive, and typically characterized by small fragment size, by low complexity, and with a range of endogenous content values.

Inbreeding depression: reduction in fitness, the ability to survive and pass genetic material, as a consequence of inbreeding caused by mating between close relatives in small and isolated populations.

Population structure: the way that neutral genetic variation is distributed between populations, resulting from past or present departure from panmixia. The combined effects of recombination, mutation, genetic drift, demographic history, and natural selection are the main drivers of population structure.

Sediment DNA: ancient DNA extracted from lakes, caves, permafrost, or other environmental sediments deposited over time, typically used to identify species presence or absence to characterize past ecological communities and identify temporal shifts in species composition.

50/500 rule: a general guideline that to avoid inbreeding depression, a



First, the role that a/hDNA can have in guiding conservation efforts needs to be clearly communicated to all actors, both to promote its application and to set reasonable expectations for the insights that can be offered. Some of the principal situations where a/hDNA can inform conservation efforts include resolving taxonomic issues, determining the historical distributions of species or genetic lineages, detecting changes in population structure, measuring genetic erosion, and guiding the restoration of extinct species and populations, for example, by determining suitable candidates for ex situ breeding programs. In Figure 1, we provide a few examples where a/hDNA has been used to inform conservation actions or policy changes for each of these types of situations and highlight the type of action that was informed.

population must maintain N_e above 50, while $N_{\rm e}$ above 500 is required for the population to maintain evolutionary potential and the ability to evolve in response to environmental changes.

Second, the conservation community must advocate for genetic indicators to be explicitly included in conservation policies. Such action was recently sparked with the publication of the zero draft of the post-2020 CBD. Although the zero draft included genetic diversity as a primary goal, it was perceived as weak, since there was no associated action target [22,26]. The conservation genetic community rapidly responded with multiple critiques and suggestions [22,23,26-28], with the result that the next CBD draft (draft 1) includes a specific milestone for maintaining genetic diversity (Milestone A.3) that will be assessed in 2030. There are many other opportunities where genetic diversity could be included in policies, and more generally, policies where a/hDNA could provide essential data (see Table 1 for some examples), and efforts should be made to keep the advocacy momentum.

Third, relationships within the conservation community must be strengthened, particularly between academics and museums. Museums are fundamental to integrate a/hDNA into conservation since their biological collections typically cover greater temporal and geographic range than field studies. However, museum sampling for genetic analyses is often destructive regardless of the preservation method (i.e., taxidermy/mounted, stored in alcohol, or pinned), and thus, the value of the information gained against the long-term stability of the specimens, their scientific and historical importance, as well as the possible alternatives should be assessed in close collaboration with the museum staff and all work must follow the museum's guidelines (reviewed in [29]). Additionally, researchers need to work more closely with museum personnel to build sincere, productive partnerships that will be of mutual benefit. Instead of a transactional relationship whereby museums simply provide specimens and academics do the rest, a more collaborative approach should be taken. This involves profiting from curators' expertise to assist with study design, interpretation, and feedback and capitalizes on the role that museums have in public education and outreach. These partnerships must also include conservation practitioners, to ensure that results become translated into conservation planning and actions. To achieve this, we need to overcome the educational gaps and establish basic common communication and understanding. At the same time, a/hDNA research must become more accessible to achieve its true potential (Box 1).

Finally, the focus of a/hDNA research must be widened to community-based approaches that can provide a more comprehensive view of the historical conditions of ecosystems. To this end, many relevant works have clearly demonstrated the usefulness of approaches such as sequencing DNA extracted from permafrost and cave sediments (sediment DNA) in providing rich genetic records of paleoenvironments [30,31]. At present, it is becoming feasible to not only focus on a few species but to characterize the multitaxa spectrum at a particular site. In this perspective, it is becoming clear that specific techniques such as environmental DNA metabarcoding hold great promise. Another avenue for generating community-based insights from hDNA would be to focus on suites of samples collected contemporaneously, for example,



Table 1 Examples of specific conservation policies in which a/hDNA data could be useful to integrate

Table 1. Examples of specific cor			
Policy body	Conservation policy	Role that a/hDNA could play	Refs
United Nations Environmental Programme (UNEP)	Convention on Biological Diversity post-2020 targets for biodiversity conservation (negotiations expected to conclude in May 2022). Goal A of the framework: 'The integrity of all ecosystems is enhanced, with an increase of at least 15% in the area, connectivity and integrity of natural ecosystems, supporting healthy and resilient populations of all species, the rate of extinctions has been reduced at least tenfold, and the risk of species extinctions across all taxonomic and functional groups, is halved, and genetic diversity of wild and domesticated species is safeguarded, with at least 90% of genetic diversity within all species maintained.'	Studies of a/hDNA can provide the necessary baseline from which to measure whether the target of 90% of genetic diversity is being maintained. This includes the different components of 'genetic diversity', including the number of distinct populations and allelic diversity and heterozygosity within populations.	[55]
UNEP	Cartagena Protocol on Biosafety 'ensure that the development, handling, transport, use, transfer and release of any living modified organisms are undertaken in a manner that prevents or reduces the risks to biological diversity, taking also into account risks to human health.'	Studies of a/hDNA can provide the necessary baseline to assess introgression of modified organisms or cultivars into wild populations and identify source populations of genetic variants.	[56]
UNEP	Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from their Utilization (ABS) to the Convention on Biological Diversity Legal framework that governs 'the fair and equitable sharing of benefits arising out of the utilization of genetic resources.'	Studies of a/hDNA can provide historical provenance for the origin of genetic variants, clarifying country of origin and entitlement to sharing of benefits.	[57]
United Nations Decade of Ocean Science for Sustainable Development/Intergovernmental Oceanographic Commission (IOC)	The Science we Need for the Ocean We Want: The United Nations Decade of Ocean Science for Sustainable Development (2021-2030), 'to ensure that ocean science can fully support countries to achieve the 2030 Agenda for Sustainable Development.' This includes 'knowledge for implementation of the post-2020 Global Biodiversity	By providing insights into, for example, evolutionary impacts of overharvesting and past connectivity between protected populations, genetic assessments over historical time frames would help reach, for example, the Decade Plan's second desired outcome: 'A healthy and resilient ocean where marine ecosystems are understood and managed.'	[58,59]



Table 1. (continued)

Policy body	Conservation policy	Role that a/hDNA could play	Refs
	Framework' and 'knowledge and solutions for conservation and sustainable use of marine biodiversity [of areas] beyond national jurisdiction.'	Although the Decade Implementation Plan does not specify the need for protection, monitoring, and maintenance of genetic diversity within species, Thomson et al. [59] highlight the important role that improving the 'temporal coverage of genetic assessments and exploring the suitability of archives and museum collections' would have in advancing genetic diversity monitoring in the Decade Plan.	
International Union for Conservation of Nature (IUCN)	Red List of Threatened Species A 'checklist of taxa that have undergone an extinction risk assessment using the IUCN Red List Categories and Criteria.'	A key parameter in status assessments is the proportion reduction in population size over the past 10 years or three generations (whichever is longer). Studies of a/hDNA in could provide data on changes in N _e , which relates to changes in population census size. Additionally, genetic diversity is not well integrated into these assessments [21], and aDNA could play a role in assessing genetic factors should they become a consideration in listing.	[21,60]
European Union	EU Biodiversity Strategy for 2030 Pillar Two: Restoring Nature 'Restore nature and ensure its sustainable management across all sectors and ecosystems.'	This policy includes legally binding targets for ecosystem restoration. Studies of a/hDNA could play a critical role in developing the evidence base for the baseline from which to measure restoration.	[61]
UK Government	Goal: Thriving Plants and Wildlife ' achieve a growing and resilient network of land, water and sea that is richer in plants and wildlife.' Specific indicators: C3: Diverse seas: status of mammals, birds and fish. D1: Quantity, quality and connectivity of habitats. D4: Relative abundance and/or distribution of widespread species. D5: Conservation status of our native species. K3: Status of endemic and globally threatened species in the UK Overseas Territories.	Studies of a/hDNA can help develop baseline data that would contribute to assessment of these indicators by providing data on the number of distinct historical populations and connectivity, providing data on the historical spatial distribution of populations, and assessing population status and genetic diversity relative to historical times.	[62,63]
Canadian Government	Species at Risk Act	Studies of a/hDNA can assist with evaluating the assessment	٧

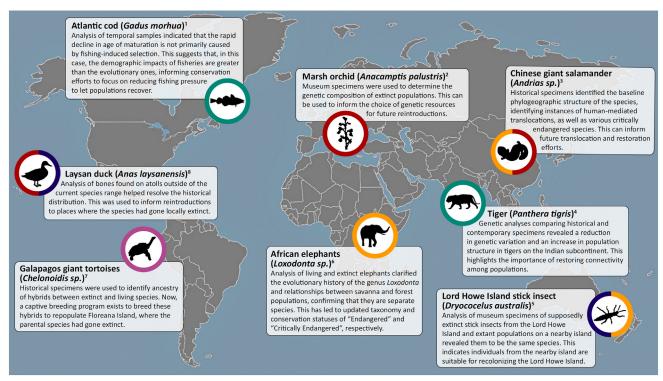
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Table 1. (continued)

Policy body	Conservation policy	Role that a/hDNA could play	Refs
	Purpose is to 'prevent wildlife species from being extirpated or becoming extinct, to provide for the recovery of wildlife species that are extirpated, endangered or threatened as a result of human activity and to manage species of special concern to prevent them from becoming endangered or threatened.' By developing measures for 'monitoring the status of the species' and 'developing and implementing recovery strategies, action plans and management plans.'	of designatable units by providing historical data on the number of subpopulations and their distinctness. Also, a/hDNA can help with developing recovery strategies by understanding current and historical effective population sizes.	

such as those collected during the Challenger expedition (1872-1876) [32] or by P.W. Lund and colleagues in Brazil (1833-1889) [33,34]. Finally, middens of mollusc shells are another potentially rich source of aDNA for reconstructing past coastal communities, with shells up to even 100 000 years old providing successful genetic characterization [35].



Trends in Ecology & Evolution

Figure 1. Examples of studies where ancient and/or historical DNA has provided important conservation insights. Colours around the icons indicate the type of provided conservation insight or informed policy action: blue, determining the historical distribution of species; purple, guiding conservation breeding; red, informing translocations/reintroductions; teal, assessing anthropogenic impacts on genetic diversity; yellow, resolving taxonomic issues. References, for example, 1 [43,44], 2 [45], 3 [46], 4 [47], 5 [48], 6 [49,50], 7 [51,52], and 8 [53,54].



Box 1. Improving access to a/hDNA data

The potential for a/hDNA will only be realized when sufficient datasets exist to provide insights into patterns at the species and/or community scale. Today, thanks to laboratory and data processing pipeline standardization, such studies should be accessible to teams globally. However, advancement is hindered by the limited access to laboratory facilities required to manipulate degraded biomolecules while avoiding contamination. Although to date relatively few countries have such facilities, partially due to the associated costs, basic a/hDNA laboratories are not overly expensive to set up if designed following a few main principles (see, e.g., [38,39]). Other critical infrastructure such as sequencing platforms and powerful computers need not be locally based but can be obtained through commercial services or collaborations. Even when establishing a/hDNA laboratories locally is impossible, data generation could occur in specialist (e.g., Ancient DNA - SciLifeLabilly), or central service hubs (e.g., Darwin Tree of Lifelly), akin to those used to generate other biological datasets of global relevance [40], lowering the costs of data production and enabling distributed researchers to focus on analysis and interpretation.

A second hurdle relates to accessing the samples themselves, and ensuring they can be identified, they can be transferred to the processing laboratories, and data can be released publicly. Publicly available, online collection catalogues are still woefully inadequate when considered on the global scale, with only a small fraction of collected samples listed. Although the value of databasing is obvious, few funders invest in this potential, preferring to fund result-driven research rather than infrastructure projects. Nevertheless, efforts are being made to provide open catalogues of specimens for reuse [41] such as The Open-Specimen Movement [42].

A further challenge is provided by the different legal frameworks at national and international levels related to moving biological samples between countries, and public release of data (such as CITES and the Nagoya Protocol). Although created with the aim of enhancing the sharing of benefits from the use of genetic resources, it is often difficult to obtain permission to export samples from one country to another, or even in some cases between regions of a single country. Further, once data are generated, permission to release them publicly may be withheld, thus limiting their use in providing scientific guidance. Hence, globally agreed protocols for efficient identification and sharing of biological materials for use in noncommercial research are essential to unlock the full potential of historical collections in guiding conservation.

Concluding remarks

We are today on the brink of a crucial step for the next decade's biodiversity policy: the adoption of the post-2020 Global Biodiversity Framework by the CBD. The first draft of the framework has finally acknowledged the importance of measuring and monitoring genetic diversity when defining conservation and management actions. In this perspective, we provide clear information on the realistic contributions that a/hDNA could make to this endeavour.

Box 2. The limits of natural history collections

Although natural history collections are a potential gold mine for conservation genomicists, as with all other potential sources of data, they have limitations that must be considered when planning, analyzing, and interpreting a/hDNA.

First, the specimens within any collection are not a random sample from the species' distributions, but rather reflect, among others, the biological, geographic, or even phenotypic (e.g., deliberate sampling of most impressive individuals) interests of those who built the collections (or their funders) and colonial history and wealth. Collections can only be built and maintained in regions where funds are available to support the endeavour, and the logistics of getting to the field, sampling, preserving, and returning the specimens remains tricky for some regions today and would have been near impossible for large swathes of the planet prior to the 20th century. Thus, when historical samples exist for a given species, complications may arise if their origins differ too greatly from contemporary datasets.

Second, the value of historical samples is considerably reduced if associated metadata such as the date of collection or geographic origin is lacking or incorrect. With regard to the latter, many natural history collections were built not only on samples collected in the field by their staff, but through purchases or trades with third parties, which can introduce considerable uncertainty into the process. And third, just because samples do exist, there is no guarantee that adequately preserved DNA remains inside them. Unless preserved with methods chosen for their DNA stabilizing properties, DNA begins to decay rapidly postmortem in most biological tissues, initially due to the death processes of cells and subsequently due to the effects of, for example, free water, pH, and temperature. While such processes can be slowed through many common measures used to preserve the morphology of museum specimens in the past, such as rapid desiccation or placement in concentrated ethanol, the effect of other preservatives is quite the opposite. In this regard, particularly bad examples include fixation in unbuffered formalin for more than a very short (few hours) time, tanning (in particular with metals), or bone cleansing through maceration in dung or other media.

Outstanding questions

How do we join forces among academic researchers, museum curators, conservation practitioners, and policy makers, to ensure that a/hDNA research realizes its full potential for informing biodiversity conservation?

What are the remaining challenges that prevent the standardization and democratization of genetic diversity indicators so they can be used for conservation?

How do we build and maintain momentum in advocacy for including genetic diversity indicators in conservation policy?

Which taxa are under-represented in museum collections and archival records and therefore are less likely to benefit from including a/hDNA data in conservation policy?

How can access to specialized laboratory facilities and expertise be expanded to reach the global community?



If the current global biodiversity crisis is to be effectively measured, it should incorporate the temporal dimension: has genetic diversity changed through time, particularly in relation to human-related environmental changes? We can answer only by defining a temporal baseline. We here demonstrate that this is the role of a/hDNA, which can be used to estimate the onset, direction, duration, and intensity of processes such as population structure, genomic erosion, and variation in N_e .

We argue that, in order to achieve a greater impact in biodiversity conservation, closer collaboration among a/hDNA researchers, museums, conservation practitioners, and policy makers is required (see Outstanding questions). At the same time, we need to manage the expectations for individual a/hDNA studies; a/hDNA analyses are challenging, samples are limited, not uniformly distributed among taxa, and not all of them will be successful (Box 2). Even though natural history museums and herbaria contain large and diverse collections of samples, nearly representing all known species [36], it is possible that a/hDNA data will not be available for some specific taxa because of their nature or because they inhabit geographical regions with climatic conditions unfavourable for DNA preservation [37]. Moreover, we acknowledge that a/hDNA studies can be expensive and slow, so they need to be prioritized and balanced against other needs and conservation activities.

Despite these limitations, we propose that currently available molecular techniques already make it possible to use a/hDNA to better inform the policy decisions presently being made toward the goal of halting the ongoing global biodiversity crisis.

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Declaration of interests

No interests are declared.

Resources

www.cbd.int/conferences/post2020

https://ec.europa.eu/environment/strategy/biodiversity-strategy-2030_en

iiiwww.scilifelab.se/units/ancient-dna/

ivwww.darwintreeoflife.org/

vhttps://cosewic.ca/index.php/en-ca/reports/preparing-status-reports/guidelines-recognizing-designatable-units.html

References

- 1. Leigh, D.M. et al. (2019) Estimated six per cent loss of genetic variation in wild populations since the industrial revolution. Evol. Appl. 12, 1505-1512
- 2. Frankham, R. (2005) Genetics and extinction. Biol. Conserv. 126, 131–140
- 3. Laikre, L. et al. (2010) Neglect of genetic diversity in implementation of the convention on biological diversity. Conserv. Biol. 24, 86-88
- 4. Card, D.C. et al. (2021) Museum genomics. Annu. Rev. Genet. 55, 633-659
- Dirzo, R. et al. (2014) Defaunation in the Anthropocene. Science 345, 401-406
- Casas-Marce, M. et al. (2017) Spatiotemporal dynamics of genetic variation in the Iberian lynx along its path to extinction reconstructed with ancient DNA. Mol. Biol. Evol. 34, 2893-2907
- 7. van der Valk, T. et al. (2018) Significant loss of mitochondrial diversity within the last century due to extinction of peripheral populations in eastern gorillas. Sci. Rep. 8, 6551
- 8. Liu, S. et al. (2021) Ancient and modern genomes unravel the evolutionary history of the rhinoceros family. Cell 184, 4874-4885.e16
- 9. Morin. P.A. et al. (2021) Reference genome and demographic history of the most endangered marine mammal, the vaquita. Mol. Ecol. Resour. 21, 1008-1020
- 10. Díez-del-Molino, D. et al. (2018) Quantifying temporal genomic erosion in endangered species. Trends Ecol. Evol. 33, 176-185
- 11. van der Valk, T. et al. (2019) Historical genomes reveal the genomic consequences of recent population decline in eastern gorillas. Curr. Biol. 29, 165-170.e6
- 12. Feng, S. et al. (2019) The genomic footprints of the fall and recovery of the crested ibis. Curr. Biol. 29, 340-349.e7



- von Seth, J. et al. (2021) Genomic insights into the conservation status of the world's last remaining Sumatran rhinoceros populations. Nat. Commun. 12, 2393
- Sánchez-Barreiro, F. et al. (2021) Historical population declines prompted significant genomic erosion in the northern and southern white rhinoceros (Ceratotherium simum). Mol. Ecol. 30, 6355–6369
- 15. Wagner, S. et al. (2018) High-throughput DNA sequencing of ancient wood. *Mol. Ecol.* 27, 1138–1154
- Dussex, N. et al. (2021) Population genomics of the critically endangered kākāpō. Cell Genomics 1, 100002
- Wang, J. et al. (2016) Prediction and estimation of effective population size. Heredity 117, 193–206
- Franklin, I.R. (1980) Evolutionary change in small populations. In Conservation Biology: An Evolutionary-Ecological Perspective (Soule, M.E. and Wilcox, B.A., eds), pp. 135–149, Sinauer Associates
- Hoban, S. et al. (2021) Effective population size remains a suitable, pragmatic indicator of genetic diversity for all species, including forest trees. *Biol. Conserv.* 253, 108906
- Food and Agriculture Organization of the United Nations (2019)
 The State of the World's Biodiversity for Food and Agriculture:
 Fao Commission On Genetic Resources For Food And Agriculture
 Assessments 2019. FAO
- Garner, B.A. et al. (2020) IUCN Red List and the value of integrating genetics. Conserv. Genet. 21, 795–801
- Laikre, L. et al. (2020) Post-2020 goals overlook genetic diversity. Science 367, 1083–1085
- Hoban, S. et al. (2021) Genetic diversity is considered important but interpreted narrowly in country reports to the Convention on Biological Diversity: current actions and indicators are insufficient. Biol. Conserv. 261, 109233
- de Vries, S.M.G. et al. (2015) Pan-European Strategy for Genetic Conservation of Forest Trees and Establishment of a Core Network of Dynamic Conservation Units. European Forest Genetic Resources Programme (EUFORGEN), Bioversity International
- Minter, M. et al. (2021) Exploring the potential for 'Gene Conservation Units' to conserve genetic diversity in wild populations. Ecol. Solut. Evidence. 2, e12061
- Hoban, S. et al. (2020) Genetic diversity targets and indicators in the CBD post-2020 Global Biodiversity Framework must be improved. Biol. Conserv. 248, 108654
- Frankham, R. (2021) Suggested improvements to proposed genetic indicator for CBD. Conserv. Genet. 22, 531–532
- Laikre, L. et al. (2021) Authors' reply to letter to the editor: continued improvement to genetic diversity indicator for CBD. Conserv. Genet. 22, 533–536
- Raxworthy, C.J. and Smith, B.T. (2021) Mining museums for historical DNA: advances and challenges in museomics. *Trends Ecol. Evol.* 36, 1049–1060
- Willerslev, E. et al. (2003) Diverse plant and animal genetic records from Holocene and Pleistocene sediments. Science 300, 791–795
- Haile, J. et al. (2007) Ancient DNA chronology within sediment deposits: are paleobiological reconstructions possible and is DNA leaching a factor? Mol. Biol. Evol. 24, 982–989
- Moseley, H.N. (1892) Notes by a Naturalist: An Account of Observations Made During the Voyage of H.M.S. "Challenger" Round the World in the Years 1872-1876, AMS Press
- Calabuig, I. (2019) P.W. Lund collection in the National History Museum of Denmark, Zoological Museum, Natural History Museum of Denmark, Copenhagen https://doi.org/10.15468/ na6tvd
- 34. Seersholm, F.V. et al. (2021) Ancient DNA preserved in small bone fragments from the P.W. Lund collection. *Ecol. Evol.* 11, 2064–2071
- Der Sarkissian, C. et al. (2020) Unveiling the ecological applications of ancient DNA from mollusk shells. Front. Ecol. Evol. 8, 37
- Yeates, D.K. et al. (2016) Museums are biobanks: unlocking the genetic potential of the three billion specimens in the world's biological collections. Curr. Opin. Insect. Sci. 18, 83–88
- 37. Holmes, M.W. et al. (2016) Natural history collections as windows on evolutionary processes. *Mol. Ecol.* 25, 864–881
- Fulton, T.L. (2012) Setting up an ancient DNA laboratory. In Ancient DNA: Methods and Protocols (Shapiro, B. and Hofreiter, M., eds), pp. 1–11, Humana Press

- 39. Knapp, M. et al. (2012) Setting the stage building and working in an ancient DNA laboratory. Ann. Anat. 194, 3–6
- Ratnasingham, S. and Hebert, P.D.N. (2007) bold: The barcode of life data system. *Mol. Ecol. Notes* 7, 355–364
- 41. Brlík, V. et al. (2021) The reuse of avian samples: opportunities, pitfalls, and a solution. *Ibis* 164, 343–349
- 42. Colella, J.P. et al. (2020) The Open-Specimen Movement. Bioscience 71, 405–414
- Pinsky, M.L. et al. (2021) Genomic stability through time despite decades of exploitation in cod on both sides of the Atlantic. Proc. Natl. Acad. Sci. U. S. A. 118, e2025453118
- Hutchings, J.A. and Kuparinen, A. (2021) Throwing down a genomic gauntlet on fisheries-induced evolution. *Proc. Natl. Acad. Sci. U. S. A.* 118, e2105319118
- Cozzolino, S. et al. (2007) Genetic variation in time and space: the use of herbarium specimens to reconstruct patterns of genetic variation in the endangered orchid Anacamptis palustris. Conserv. Genet. 8, 629–639
- Turvey, S.T. et al. (2019) Historical museum collections clarify the evolutionary history of cryptic species radiation in the world's largest amphibians. Ecol. Evol. 9, 10070–10084
- Mondol, S. et al. (2013) Demographic loss, genetic structure and the conservation implications for Indian tigers. Proc. R. Soc. B 280, 20130496
- Mikheyev, A.S. et al. (2017) Museum genomics confirms that the Lord Howe Island stick insect survived extinction. Curr. Biol. 27, 3157–3161
- Palkopoulou, E. et al. (2018) A comprehensive genomic history of extinct and living elephants. Proc. Natl. Acad. Sci. U. S. A. 115, F2566–F2574
- Rohland, N. et al. (2010) Genomic DNA sequences from mastodon and woolly mammoth reveal deep speciation of forest and savanna elephants. PLoS Biol. 8, e1000564
- Poulakakis, N. et al. (2008) Historical DNA analysis reveals living descendants of an extinct species of Galápagos tortoise. Proc. Natl. Acad. Sci. U. S. A. 105, 15464–15469
- Miller, J.M. et al. (2017) Identification of genetically important individuals of the rediscovered Floreana Galápagos Giant Tortoise (Chelonoidis elephantopus) provides founders for species restoration program. Sci. Rep. 7, 11471
- Cooper, A. et al. (1996) Ancient DNA and island endemics. Nature 381, 484
- Reynolds, M. and Klavitter, J. (2006) Translocation of wild Laysan duck Anas laysanensis to establish a population at Midway Atoll National Wildlife Refuge, United States and US Pacific Possession. Conserv. Fuidence 3. 6–8
- Open Ended Working Group on the Post-2020 Global Biodiversity Framework (2021) First Draft Of The Post-2020 Global Biodiversity Framework. UNEP
- Secretariat of the Convention on Biological Diversity (2000)
 Cartagena Protocol On Biosafety To The Convention On Biological Diversity, UNEP
- 57. Secretariat of the Convention on Biological Diversity United Nations (2011) Nagoya Protocol On Access To Genetic Resources And The Fair And Equitable Sharing Of Benefits Arising From Their Utilization To The Convention On Biological Diversity, UNEP
- Intergovernmental Oceanographic Commission of the UNESCO (2021) Implementation Plan for the United Nations Decade of Ocean Science for Sustainable Development, UNESCO
- Thomson, A.I. et al. (2021) Charting a course for genetic diversity in the UN Decade of Ocean Science. Evol. Appl. 14, 1497–1518
- 60. IUCN Species Survival Commission (2012) IUCN Red List Categories and Criteria. Version 3.1 Second edition, IUCN
- 61. European Commission (2020) EU Biodiversity Strategy for 2030: Bringing Nature Back Into Our Lives, European
- Department for Environment, Food and Rural Affairs (2019) Measuring Environmental Change: Outcome Indicator Framework for the 25 Year Environment Plan, Department for Environment, Food and Rural Affairs
- 63. HM Government (2018) A Green Future: Our 25 Year Plan to Improve the Environment, HM Government