Genomic erosion in the assessment of species extinction risk and recovery potential

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Abstract

Many species are facing unprecedented population size declines and deterioration of their environment. This exposes species to genomic erosion, which we define here as the damage inflicted to a species' genome or gene pool due to a loss of genetic diversity, an increase in expressed genetic load, maladaptation, and/or genetic introgression. The International Union for Conservation of Nature (IUCN) bases its extinction risk assessments on direct threats to population size and habitat. However, it does not assess the long-term impacts of genomic erosion, and hence, it is likely to underestimate the extinction risk of many species. High-quality whole genome sequence data that is currently being generated could help improve extinction risk assessments. Genomic data contains information about a species' past demography, its genome-wide genetic diversity, the incidence of genetic introgression, as well as the genetic load of deleterious mutations. Computer modelling of these data enables forecasting of population trajectories under different management scenarios. In this Perspective, we discuss the threats posed by genomic erosion. Using evolutionary genomic simulations, we argue that whole genome sequence data provides critical information for assessing the extinction risk and recovery potential of species. Genomics-informed assessments of the extinction risk complement the IUCN Red List, and such genomics-informed conservation is invaluable in guiding species recovery programs in the UN's Decade on Ecosystem Restoration and beyond.

Main text

Conservation biology has been aptly called a "mission-oriented crisis discipline"[1]. Management actions must be taken promptly amidst finite resources[2], and decisions are often made based on limited data[3]. Over the past decades, many species have thus been saved from extinction[4,5] but there is still much to accomplish[6]. After the immediate threat to a species survival has been abated, medium- and long-term plans need to be formulated. These plans should be based on the best-available information, and this should include data about the genomic erosion inflicted on the population during its recent decline. Even after a population has recovered demographically, genomic erosion may continue due to a "drift debt"[7,8], changes

to the composition of its genetic load[9] and reduced adaptive potential[10]. In the long-term, genomic erosion reduces population viability, and thus should be also included in species recovery plans[11]. Although genome data contain a wealth of information to assess genomic erosion, the processing and interpretation of these "big-data" require expert knowledge from bioinformaticians and conservation genomicists. We propose that these data should be analysed in a standardised framework. Considerable resources and time are spent on sequencing genomes, and it is our moral and scientific duty to also use these data to support efforts to protect biodiversity. The conservation-relevant conclusions from these analyses should be presented using non-technical jargon in publicly available databases that can be accessed and understood by non-specialists. In this Perspective, we explain how genomic analyses and modelling can be used to assess the impact of genomic erosion on extinction risk and recovery potential. Making insights gained from these analyses available to the entire conservation community will become instrumental in the restoration of biodiversity in the next decades.

Genetics and conservation

Even before the development of molecular genetic markers in the 1960s[12], population geneticists and evolutionary biologists recognised the huge potential of studying the variation at the genetic level[13]. Population genetic data can shed light on the biology of species that would otherwise remain hidden. Molecular markers have been used to inform conservation biology on key population parameters such as migration, parentage, and effective population size (N_e)[14,15,16]. Moreover, genetic data can reveal the impact of the evolutionary and demographic processes that have occurred in the recent and distant past[17,18,19]. Understanding these processes is crucial for the conservation and recovery of threatened species[20,21,22].

The study of genome-wide genetic variation does not only shed light on the evolutionary history of populations, but it can also help assess their adaptive potential and long-term viability[22,23,24,25]. While the importance of genetic insights is increasingly recognised and used to inform conservation action, its integration into policy remains woefully inadequate[26]. Genetic data are not explicitly incorporated in the assessments of species extinction risk[27], and protection of genetic diversity remains an undervalued aspect in biodiversity conservation[28]. Only recently, the Convention on Biological Diversity (CBD) has acknowledged the importance of maintaining genetic diversity in its post-2020 draft framework. However, government policies largely fail to adopt genomics and evolutionary processes in conservation planning[20,21,26].

The management of genetic diversity is critical for the long-term conservation of populations, particularly in a world that faces rapid environmental change. Currently, much progress is being made in conservation genetics by adopting operationally workable measurements, such as the census and effective population size, number of populations, and population connectivity[28]. Unfortunately, the monitoring and preservation of genetic diversity *per se* does not guarantee the long-term viability of populations because there are other threats to genomes and gene pools that can result in species extinction[22,29,30]. Furthermore, many populations continue to decline, and the inflicted damage must also be accounted for. To assess, mitigate and remedy this damage requires a better understanding of genomic erosion.

Genomic erosion

Genomic erosion is a pervasive – but frequently overlooked – consequence of the many threats faced by wild populations, such as overexploitation, invasive species, emerging infectious diseases, hybridisation, and habitat and environmental change. Some of these threats lead to population size decline, whereas others affect the intensity and/or direction of evolutionary forces, or they result in the introgression of the genome by heterospecific DNA[31,32,33,34,35,36]. The damage inflicted by these processes reduce individual fitness and population viability,

even after the immediate threats have been averted. Genomic erosion is manifested as: (1) a loss of genetic diversity, (2) an elevated realised load (that is, the component of genetic load whose fitness effects is expressed[9], and which is caused by an increased number of homozygous loci with recessive deleterious alleles), (3) a mismatch between genetic adaptations and the prevailing environmental conditions (i.e., maladaptation), and (4) genetic introgression due to hybridisation. All four aspects of genomic erosion can reduce individual fitness and undermine viability of populations, both in the short- and long-term[8,29,37,38,39,40]. Although genomic erosion is rarely the primary cause for species extinction, it is tightly coupled to other (external) threats. The reinforcing feedback loops between demography, environmental stress, and genomic erosion can lead to genetic Allee effects[41], mutational meltdown[42], insufficient adaptive evolutionary potential[43], and/or extinction vortex[29]. Accordingly, genomic erosion often plays a critical role during the later stages of population decline, when the fate of a population or species is ultimately decided[44,45]. Furthermore, the impacts of genomic erosion can be felt long after the primary threats have been abated i.e., "drift debt"[7,8,46].

Genomic-informed conservation sciences

Genomic data for many species is being produced at an unprecedented rate. A large portion of this effort has been driven by groups affiliated under the umbrella of the Earth BioGenome Project (EBP)[47,48] (https://www.earthbiogenome.org). As of July 2022, the EBP-affiliated projects have sequenced the genomes of 1,719 eukaryotic species and they aim to sequence one representative species from each of the 9,464 eukaryotic families in its ongoing Phase 1, projected to be finished in 2023[47,49] (Fig. 1). This wealth of data will not only be useful to provide high-quality references genomes, but also to directly inform conservation and species recovery programs (see below). A recent paper set out the standards and recommendations for the EBP with the envisaged applications for advancing conservation only briefly outlined (see point 8 in Lawniczak et al.[50]). Indeed, the full potential of such large-scale genomic datasets within the conservation community has yet to be realised, although important progress is currently being made, for example by the Threatened Species Initiative[51].

Beyond the maintenance of genetic variation

Over the past 50 years, much emphasis has been given to maintaining genetic variation in conservation. We do not challenge the "small population paradigm"[54], nor do we dispute that preserving and restoring genome-wide variation is the most valuable conservation genetics action for many species[22,25,53,54]. Populations with high genetic diversity tend to possess more additive genetic variation and a higher adaptive potential[55]. Furthermore, in populations with high diversity, fewer deleterious mutations are expressed as homozygotes, which has a positive effect on the fitness of individuals. Maintaining a large effective population size (*Ne*) is therefore paramount[28,56,57].

However, the genetic load, maladaptation, and genetic introgression also pose a considerable threat to many species[8,58,59]. Genomics-informed conservation can make a quantitative assessment of the impacts of recent changes in evolutionary forces on individual fitness and population viability. Assessing genomic erosion can guide conservation action and improve the long-term viability of both wild and captive populations. We need to develop a robust predictive approach of population viability and extinction risk that are easy to use and understand. For decades conservation scientists have relied on population viability analyses (PVA) to assess threats and inform conservation actions[60,61]. Unfortunately, these models very rarely take genetic information into account, and they are not designed to incorporate the effects of genomic erosion. A new generation of evolutionary genomics modelling tools[62,63,64,65] now

enables construction of complex, genomic-scale models capable of incorporating demographic, ecological and evolutionary dynamics into a single framework (see below).

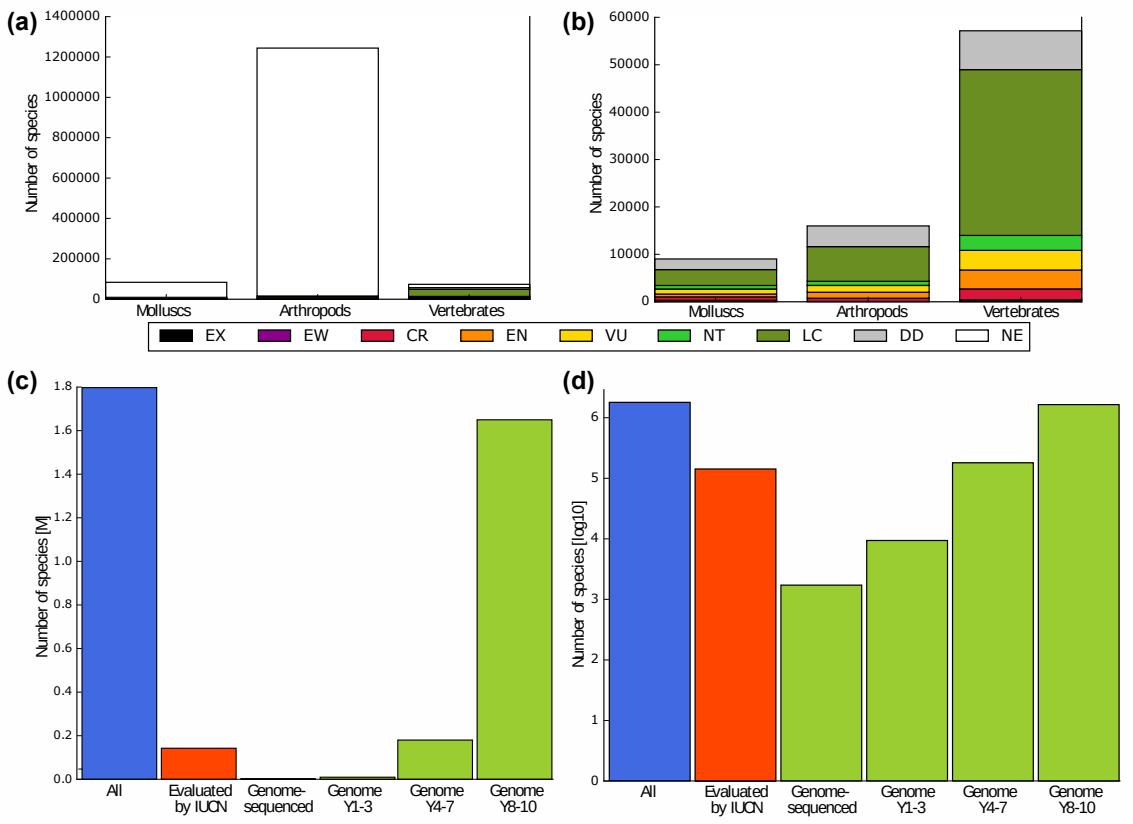

Figure 1. The IUCN Red List assessment and the Earth BioGenome Project (EBP) progress. Taxonomic bias on the IUCN Red List and difference between taxa in extinction rates obscures the true extent of the biodiversity crisis: (a) Species-richness differs markedly between molluscs, arthropods, and vertebrates. (b) Many more vertebrates have been assessed than molluscs and arthropods. The IUCN Red List categories are: EX = extinct; EW = extinct in the wild; CR = critically endangered; EN = endangered; VU = vulnerable; NT = near threatened; LC = least concern; DD = data deficient; NE = not evaluated. The ongoing data generation from EBP projects can help assessing extinction risk and recovery potential for thousands of species: (c) Number of eukaryote species in millions and (d) log10-transformed that has been – and are projected to be – assessed by the EBP (green) and the IUCN (red) in relation to the total number of eukaryote species (blue)). The total number of eukaryote species was obtained from the Catalogue of Life (https://www.catalogueoflife.org); the number of sequenced genomes was obtained from the Supplementary Material of Lewin et al.[47]. The number of genomes that are projected to be sequenced by the EBP in three phases (i.e., approximately three-year (Y) periods) were obtained from Lewin et al.[47], and the number of species evaluated by the IUCN was obtained from the IUCN Red List (https://www.iucnredlist.org).

Enhancing the Red List data

Presently, the IUCN Red List documents 11 well-defined categories of threats (plus one undefined threat category) that can cause population decline and genomic erosion. In addition, for a subset of species, it also reports the trend in population size, the number of mature individuals, the number of subpopulations, the generation time, and implemented conservation actions. These reports on threats and populations decline (cf. the "declining-population paradigm"[52]) can also be used in computer models to predict future extinction risk and inform species recovery plans. The Red List could be further improved by also reporting aspects of species' biology that affects the severity of the impact of threats on genomic erosion. In the following sections we illustrate the importance of knowing the size of the ancestral population, the species lifetime fecundity, and the type of selection affecting fitness. Including these data in the Red List would help integrate the "declining population paradigm" and the "small population paradigm"[52]. The former is the current focus of the Red List, whereas the latter

allows for the use of population genetic and evolutionary theory to predict the impacts of past and present-day threats to population viability (census the "small population paradigm"). This integrated approach would help inform government policies on how to adopt conservation genomics and evolutionary processes in planning[22,66].

Ancestral vs. contemporary population sizes

The IUCN Red List reports that 47.4% of species are currently facing population size declines. This makes these species prone to genetic drift and inbreeding, which increases their extinction risk. However, the impact of drift and inbreeding depends both on the ancestral population size (N_a) and recent change in N_e[67]. Large populations do not only contain more neutral genetic variation, but they also possess more loci with recessive deleterious mutations[9]. This high genetic load makes large ancestral populations more vulnerable to population size declines because it exposes them to more severe inbreeding depression. Furthermore, the effect of population decline on genomic erosion also depends on the type of selection (e.g., negative versus stabilizing selection, and soft versus hard selection), the life-history traits of the species, and the rate of environmental change (see below). Hence, a necessary first step to understand genomic erosion is to characterise the changes in N_e over time[68,69].

Temporal fluctuations in N_e can be inferred from genome sequence data of a single or multiple individuals. Various bioinformatics approaches have been developed to estimate the trend in N_e over time, from tens to millions of generations ago. For a comprehensive review on these methods see Nadachowska-Brzyska et al. (2022)[69], and for considerations of potential biases and result interpretation see Boitard et al. (2022)[70] and Mazet et al. (2016)[71]. Comparing genetic estimates of ancestral population sizes to present-day population size estimates can also identify species that have undergone a recent population size decline. Such comparative approaches can be based on species–area relationship (SAR), citizen science databases[72], and Species Distribution Models[73,74,75]. These analyses can be extended by fitting species abundances to the distribution of their mutation frequencies to predict rates of genetic diversity loss as a function of the species range dynamics (Mutations-Area Relationships, MAR[76]).

Genetic load of unconditionally deleterious mutations

Some mutations reduce fitness regardless of the genetic background in which they occur (i.e., the genetic variants elsewhere in the genome) or the prevailing environmental conditions[9]. Such mutations are unconditionally deleterious, and in large populations, they tend to be kept at low frequencies by negative selection. Due to this low frequency, these recessive deleterious mutations are mostly heterozygous, which means that their harmful fitness effects are not completely expressed. This part of the genetic load is known as the masked load[9], potential load[77], or inbreeding load[78].

However, when a previously large populations experiences a population size decline or fragmentation, inbreeding and genetic drift convert part of this masked load into the realised load[9]. Some of the initially rare mutations increase in frequency and become homozygous (Fig. 2). Mating between related individuals (inbreeding) can also increase the number of homozygous deleterious mutations. When homozygous, these mutations reduce fitness, which results in inbreeding depression. Because species with a large N_a carry many unconditionally deleterious mutations, they are most at risk of extinction after population decline and fragmentation (Fig. 2). On the other hand, ancestrally large populations also possess high levels of neutral genetic diversity. This diversity only decreases slowly during population size decline, but this loss can continue even during population recovery[8]. Hence, neutral genetic variation alone is not always an adequate predictor of the extinction probability[30,79,80]. Rather, the impact of genetic drift and inbreeding need to be evaluated in the context of the past and present demography of the species.

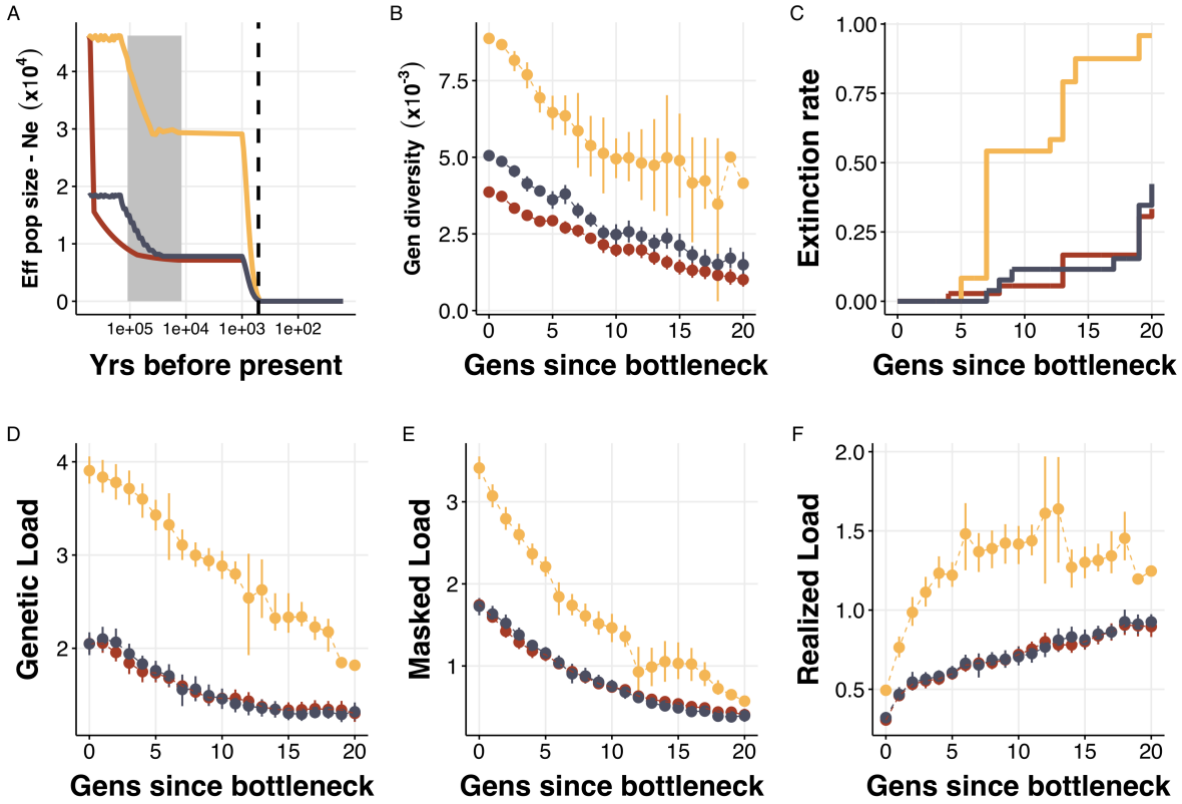

Figure 2. The effects of ancestral population size on unconditional genetic load that is under negative selection. (A) Populations with distinctly different ancestral demographic trajectories experienced a severe population bottleneck (N_e=10). Grey shading represents the Last Glacial Period 110–12 thousand years ago. Dotted line represents the beginning of the Anthropocene in the year 1610[119]. **(B)** The ancestrally large populations (yellow) show the highest nucleotide variation, but panel **(C)** shows that such populations also have the highest extinction rate after a bottleneck. **(D)** This is because the genetic load from unconditional deleterious mutation is highest in the ancestrally large populations (yellow). **(E)** Historically, when the population was still large, the genetic load was not expressed, and this part of the genetic load is known as the masked load[9], or inbreeding load[78]. **(F)** However, population size decline results in inbreeding, during which the masked load is converted into a realised load. This explains why the extinction rate is highest in large ancestral populations. Simulations were performed in SLiM3[62] with a non-Wright-Fisher model adapted to non-overlapping generations and random mating for simplicity. The model simulated an exome of 3000 genes of 3.4Kb each with a recombination rate r=1e^{-4} (no recombination within genes), and a per base mutation rate m=1.4e^{-8}. Deleterious selection coefficients (s) were taken from a gamma distribution (mean=-0.05 and shape=0.5) with a tail of 5% of lethal mutation and negative relationship between s and dominance coefficients (h), following Kardos et al.[25]. We ran 100 replicates per scenario.

Changes in neutral genetic variation can help predict population viability, particularly when combined with data on the genetic load. Inbreeding depression is a function of both the rate of inbreeding and the masked load of mutations. If whole genome sequence data is available, *in-silico* fitness impact predictions of mutations can be estimated using a myriad of approaches (reviewed in Bertorelle et al. 2022)[9]. Sophisticated methods such as CADD (Combined Annotation Dependent Depletion) integrate diverse lines of evidence to score the deleterious effect of mutations in humans and model species[81]. These CADD-scores can be lifted-over to the genomes of (closely) related species (Fig. 3), opening the door for translating valuable insights from model species to threatened (vertebrate) species.

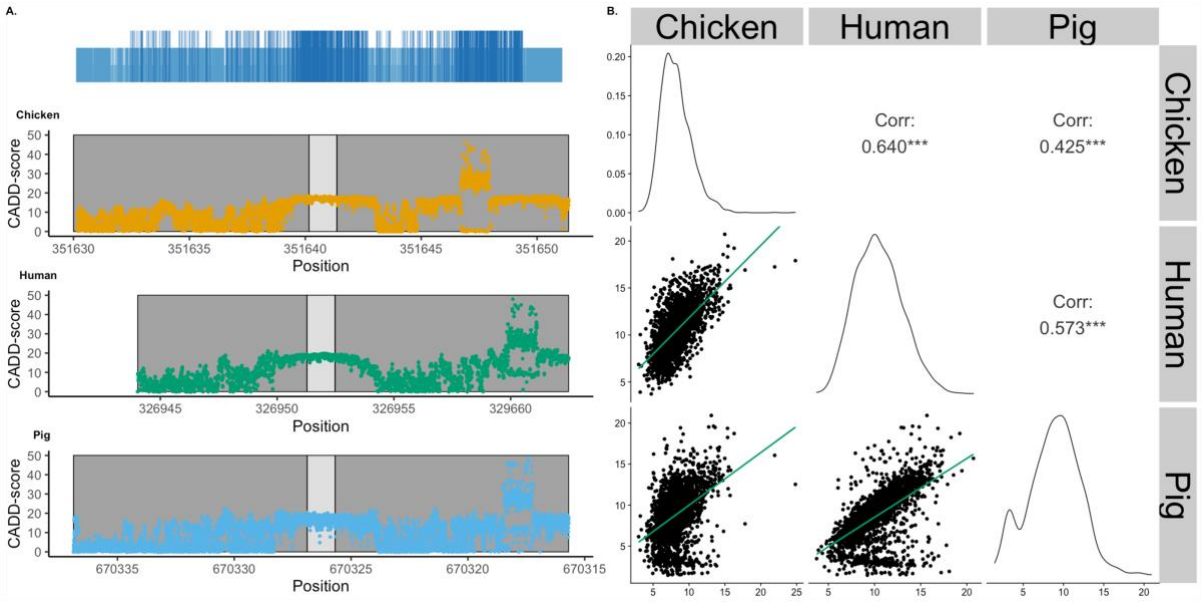

Figure 3. Comparison of Combined Annotation Dependent Depletion (CADD) scores at ultra-conserved elements (UCEs) and their flanking regions in chickens, humans, and pigs. (A) The per nucleotide CADD score for all bases within UCE-1004 and 1000bp of its flanking regions in chicken (orange), human (green), and pig (blue). The level of conservation in the alignment is show on the top (blue bars). The profiles of the CADD scores are broadly similar, with major peaks (15 < CADD-score < 20) in the centre of the UCE. Nucleotides with high CADD scores are evolutionary conserved and mutations at these sites are predicted to have a large negative effect on fitness. Unlike this central region, the highest peaks in the flanking region at the right represent a coding-gene, in which circa one-third of the CADD scores have low values, corresponding to the (silent) 3rd codon position. In the human genome this corresponds to the kinase anchoring protein 6. The chicken and human sequences are in the forward orientation whilst the pig is in the reverse. The values on the X-axis are the nucleotide position divided by 100. (B) Correlation in CADD scores averaged across the 2109 nucleotides (interquartile range 2111 – 2120 nt) per UCE in pairwise comparisons across all 2201 UCEs shared between the three species. The moderately high correlation coefficients and broad similarity of CADD-score profiles suggests it is possible to lift-over CADD scores from a model species to a (closely) related non-model species at the UCEs of vertebrates. The CADD scores were extracted for chickens [120], humans[121] (https://cadd.gs.washington.edu) and pigs[122].

Genetic load of traits under stabilising selection

Besides unconditionally deleterious mutations, an unknown proportion of the genetic load comprises of polymorphisms with context-dependent fitness effects. These polymorphisms can be either deleterious or beneficial depending on their genetic background and environmental conditions[25,82,83]. Such variation is under stabilising selection rather than negative selection. Variation at quantitative trait loci (QTLs) that have an optimum trait value are thought to be under stabilising selection[82,83]. The fitness loss due to variation at QTLs is relatively low because stabilising selection keeps the trait value close to the optimum[83]. Perhaps counterintuitively, the genetic load of traits under stabilising selection increases with populations size (Fig. 4); larger populations possess more genetic variation, and hence, they also possess a slightly higher conditional genetic load[83]. Conversely, the large amount of genetic variation in larger ancestral populations also underpins the adaptive evolutionary response during environmental change. To quote Muller & Kaplan[84]: "*Of course this variation is in evolution a very necessary 'evil', since it allows natural selection a grasp by which in time of changed needs or opportunities the constitution of the population may be altered adaptively.*" In other words, larger populations might be burdened by a slightly elevated (conditional) genetic load, but they are also better able to respond to environmental change compared to small populations (Fig. 4). Species conservation would therefore benefit if the IUCN Red List not only reports the actual threats, but also an estimate of the ancestral and present-day population size of species.

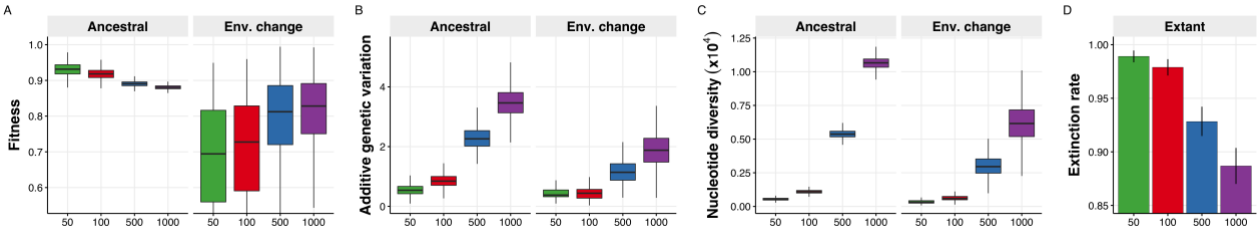

Figure 4. The effects of ancestral population size on a trait under stabilizing selection. Computer simulations in SLiM of populations with different ancestral effective population sizes (*Ne*) with a trait adapted to an environmental optimum. The populations experience a severe population bottleneck (*Ne*=10) that reduces genetic diversity, and five generations after experience an environmental change that shifts the optimum of the trait value. Here we show the distribution of values of across five generations before the population bottleneck (ancestral population) and five generation following the optimum shift. The larger ancestral populations have a slightly lower fitness **(A)** because they possess more additive genetic variance (V_A) **(B)**, mirrored by a higher amount of genome-wide genetic diversity **(C)**. This results in more phenotypic variation around the optimum and it constitutes a genetic load of conditionally deleterious mutations[82]. However, this larger additive variation becomes beneficial when the environmental optimum changes as it underpins the adaptive response to selection. Consequently, larger ancestral populations have a higher fitness after the optimum shift and a lower extinction rate **(D).** V_A is positively correlated to neutral genetic diversity, highlighting the value of high genetic diversity to preserve adaptive potential[25]. For simplicity, we simulated a single additive polygenic trait without environmental variance to illustrate the reduction of V_A[123]. Parameters such as dominance, epistasis and the genetic architecture of the trait might temporarily increase V_A after a bottleneck[124,125,126,127,128]. However, over time, genetic drift is expected to lead to a reduce adaptive response under most conditions[129]. Simulations were performed in SLiM3 as in Figure 4. Genotype values (z) were drawn from a uniform distribution from -0.5 to 0.5 and V_A calculated as $\sum 2p_i q_i z_i^2$ following Falconer and Mackay[123]

Species fecundity and genomic erosion

Understanding the reproductive biology of species is essential to assess the impact of genomic erosion on the extinction risk. How the genetic load affects the extinction risk is dependent on two distinct types of negative selection – hard selection and soft selection. Under hard selection, the mortality or reproductive success of individuals is not dependent on the frequency or density of other phenotypes in the population[85]. In other words, fitness is absolute rather than relative, and it is independent of the fitness of conspecifics. Species with high fecundity (r-strategists) can tolerate a higher genetic load of deleterious mutations because they can tolerate more selective deaths (Fig. 5A-B). The lower extinction risk of r-strategists is thus an indirect consequence of producing large numbers of "expendable" offspring selected for in species with low recruitment rates. Although the extinction risk is affected by the reproductive capacity of species under hard selection, the rate of accumulation of deleterious mutations is not (Fig. 5C).

Under soft selection, the fitness of individuals is relative to that of others in the population. In other words, fitness under soft selection is both frequency and density dependent[85]. The small number of offspring produced by K-strategists offers less substrate for soft selection, which means that even individuals with a high genetic load can still survive and reproduce. This makes K-strategists prone to a rapid accumulation of genetic load compared to r-strategists (Fig. 5D).

In summary, K-strategists may be more prone to extinction due to hard selection, and they are more liable to accumulate a high genetic load of mutations due to soft selection compared to r-strategists (Fig. 5D). The higher genetic load tolerance of r-strategist might also explain why they tend to possess a higher genetic diversity than K-strategists[86,87]. These theoretical considerations illustrate that reporting the lifetime fecundity of species would be a valuable addition to the Red List.

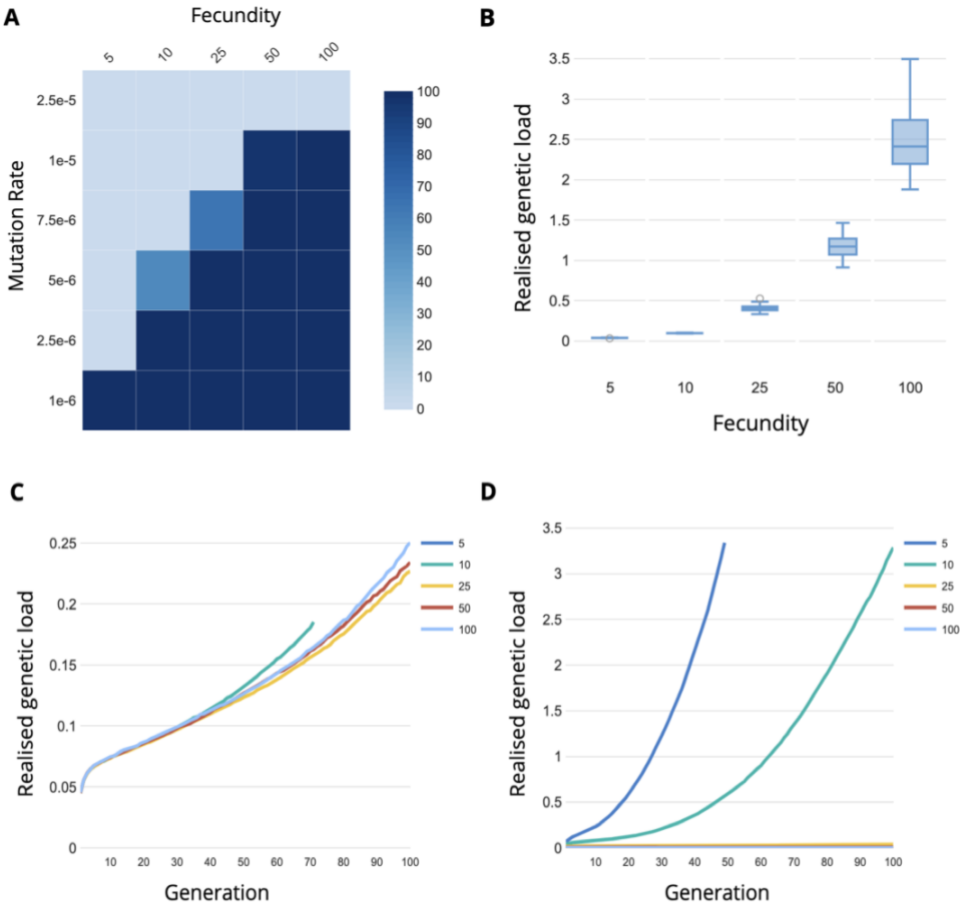

Figure 5. **The effect of hard and soft selection on the extinction probability and genetic load for species across a range of fecundity values and mutation rates. (A)** High-fecund species (r-strategists) can tolerate a higher mutation rate under hard selection, because **(B)** they can tolerate a higher genetic load. **(C)** The rate of accumulation of the genetic load does not depend on species lifetime fecundity under hard selection. **(D)** However, under soft selection, low-fecund species (K-strategists) accumulate load at a faster pace, which could also increase their extinction risk

Genetic introgression and hybridisation

Hybridisation can lead to the exchange of genetic variation between distinct taxa. Such genetic introgression contributes to genomic erosion that can result in a loss in population viability and genetic swamping, which potentially leads to the genetic extinction of species[58,88]. The rate of hybridisation is likely to have increased due to recent range shifts of species caused by global environmental change, as well as the large number of invasive species[88]. In addition, many wild species are threatened with extinction by hybridization with domestic conspecifics[89]. However, this risk is likely to be underestimated in the Red List because it requires genomics techniques to quantify the impact of this threat. Conversely, hybridisation can be beneficial, resulting in heterosis and evolutionary rescue. Currently, we have an incomplete understanding about the role of hybridisation for the continued evolution and long-term viability of species[90,91,92]. In the coming years, analysis of whole genome sequence data will enable us to better quantify the potential benefits and threats of hybridisation in species conservation. Bespoke software has been developed to detect and examine genetic introgression in whole genome sequence data, such as HybridCheck[93], RDP5[94], DensiTree[95] and SplitsTree[96]. Comparative analyses of sequence similarity across large whole-genome datasets can quantify the historic and contemporary incidence of introgression by hybridisation. This would help assess the risk of extinctions due to genetic swamping[88], as well as the potential benefits in terms of evolutionary rescue of taxa in the past.

Species recovery plans and modelling

In the coming decade, there will be increasing emphasis on species recovery plans, including whole ecosystem restoration, reintroductions, demographic– and genetic rescue. The long-term success of such programs hinges critically on our understanding about genomic erosion and the intrinsic links between genetic variation, adaptive evolutionary potential, the genetic load, and the ecological history and present biology of the species. The recent debate about the optimal size of the donor population in genetic rescue is a likely foreshadow of many future discussions[8,97,98,99,100,101,102,103,104].

Individual-based, forward-in-time simulation models will be gaining increasing power and importance in conservation. Simulations of genome-wide variation help us better understand the behaviour of both neutral and non-neutral genetic variation in response to demographic change. Furthermore, when informed by species' ecological histories[105], such simulations will help us assess the present and future impacts of genomic erosion[9,25,99,106,107,108,103,109,110,111]. These methods are advancing rapidly but they need to become more standardised[112]. Furthermore, the correct parametrisation of these models requires a good understanding of the (past and present) biology of the species, as well as access to whole genome sequence data. The latter is crucial to ground-truth the model predictions. Altogether, this requires close collaborations between applied conservation biologists who are working with captive and wild populations, scientists who generate and analyse the whole genome sequence data, and computer modellers. Working together would help us to better forecast the extinction risk of a species and inform species recovery plans (Fig. 6).

Conclusion

To save a species from extinction, conservation biologists need to identify and deal with the immediate threats to the population size, habitat, and environment of species. This has been the focus of species conservation for decades, and understandably, the impacts of these threats on genomic erosion have been largely neglected. However, the long-term successful recovery of species critically depends on our ability to stem and revert genomic erosion. Genomic erosion is not just the loss of genetic diversity, it also manifests itself in an elevated realised load, maladaptation to changing environmental conditions, and genetic introgression. Genomic erosion is a ubiquitous, pervasive threat to the survival of many species, and it continues to pose a risk long after the immediate threats have been abated. To better assess the impact of genomic erosion, we call for two changes.

First, the IUCN Red List would be enhanced by systematically reporting data of species biology that is relevant for genomic erosion and long-term species conservation. We understand that it is currently not feasible to include insights gained from analysis of genome data into the Red List for all species. Fortunately, however, the Red List already reports some data that are directly relevant for assessing genomic erosion for a subset of species. These data include a well-defined list of 11 possible type of threats, estimates of census population size, population size trends, population fragmentation, generation time, and conservation actions. We recommend that these data are recorded for all species on the Red List where possible, and that they are complemented by data of the ancestral population size, details about the most significant selection pressures that result in mortality or failed reproduction, and the lifetime fecundity of species. Those data are invaluable for parameterising models that estimate genomic erosion, the results of which can be presented in a separate database alongside the Red List.

Second, we propose that the large amounts of genomic data currently generated (e.g., by the many EBP related consortiums) should be analysed to improve the assessment of the extinction risk of species. In addition to a single reference genome for each species, population genomic data would further improve the analysis of genomic erosion, and the evaluation of

long-term threats to species survival. Such genomics-informed conservation would help to accelerate the rate of assessment, and it would help reduce the taxonomic bias inherent to the Red List[113] see Fig. 1. In particular, the CBD Aichi Target 12 (preventing extinctions and conserving species), and its likely successor in the Post-2020 Global Biodiversity Framework, calls for a reduction in the extinction rate. The assessment of extinction rate should be based on the best-available data and methods to evaluate all aspects of genomic erosion, and not just genetic diversity. Given their high technical complexity, we believe these analyses should be done in a standardised way[112,114] and with a common set of metrics[115] to help translate this knowledge into conservation management action[116,117,118]. A database that quantifies genomic erosion is likely to become instrumental in underpinning future conservation efforts to help stem the biodiversity crisis in the UN's Decade on Ecosystem Restoration and beyond.

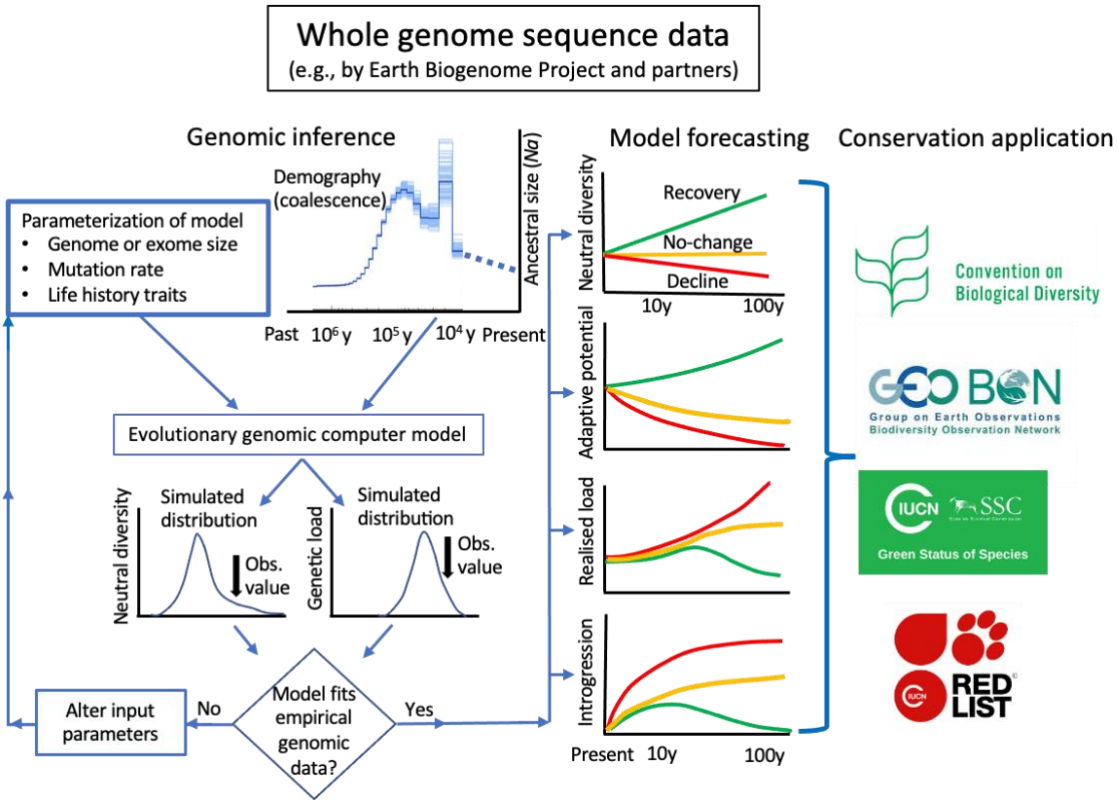

Figure 6. Flowchart of information illustrating the use of genomic data and evolutionary modelling and its application in species conservation. The Earth BioGenome Project (EBP) aims to produce ~1.8 million genome assemblies by 2030. These genomic data can be used to parameterize forward-in-time evolutionary genomics models (e.g., the size of the genome or exome, the mutation rate, etc.). Models can furthermore be parameterized with the ancestral population size (*Na*) inferred by demographic reconstructions from whole-genome data, as well as species-specific life history traits (e.g., fecundity, reproductive mode, longevity, etc.). The output of neutral diversity (e.g., nucleotide diversity, runs of homozygosity (ROH)), and the genetic load components (i.e., masked load and realized load) can be compared to the empirical data from contemporary genomes. If the model fit is poor, input parameters such as the mutation rate can be adjusted. Once the model predicts the empirical data well, the models can be used to forecast genomic erosion and extinction risk in the next 10 or 100 years, simulating different conservation management scenarios. These analyses and computer simulations are relevant for applied conservation, for example by informing the IUCN Red List assessment and in the Green Status assessments of species, and to evaluate progress towards the Goals of the Convention of Biological Diversity (CBD)

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Data availability

The code used to support the arguments in this perspective are openly available in https://github.com/hmoral/genomic_erosion_perspective.

Competing interests

The authors declare no competing interests.

Contributions

CvO and HEM conceived the idea. CvO, HEM, CB, LHU, JJG and GS developed the content and idea. HEM and TB performed simulations. SAS, CB and LHU analysed data. CvO and HEM wrote the manuscript with input from all co-authors.

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