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Opinion

Mind the lag: understanding genetic extinction debt for conservation

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The delay between disturbance events and genetic responses within populations is a common but surprisingly overlooked phenomenon in ecology and evolutionary and conservation genetics. If not accounted for when interpreting genetic data, this time lag problem can lead to erroneous conservation assessments. We (i) identify life-history traits related to longevity and reproductive strategies as the main determinants of time lags, (ii) evaluate potential confounding factors affecting genetic parameters during time lags, and (iii) propose approaches that allow controlling for time lags. Considering the current unprecedented rate of loss of genetic diversity and adaptive potential, we expect our novel interpretive and methodological framework for time lags to stimulate further research and discussion on the most appropriate approaches to analyse genetic diversity for conservation.

Highlights

Time lag refers to delayed genetic consequences after an environmental shift or population decline.

Life-history traits such as long life span, vegetative propagation, overlapping generations, and mating by outcrossing, support the build-up of a time lag after an environmental shift; confounding factors include sampling strategy and marker choice.

Time lags can be evaluated using temporal sampling, different estimates of effective and census population sizes, and choice of a reference population.

The more widely recognized 'extinction debt' problem in community ecology depends on delayed genetic responses ('genetic extinction debts' = time lags) in the populations composing that community.

Conservation strategies should account for time lags since actions taken today will impact future genetic composition, potentially mitigating negative effects before they become irreversible.

The time lag between disturbance events and genetic responses

Population genetic data are typically believed to inform on the current genetic conservation status of populations (i.e., their likelihood to persist in the long term) [1]. However, genetic parameters often respond to **disturbance events** (see Glossary) with delay, or a **time lag** [2]. Failure to recognize and account for time lags in genetic responses can lead to overrating genetic diversity levels, misguiding the use of resources for biodiversity conservation. At a time of unprecedented biodiversity loss [3], understanding time lags linked to population genetic diversity is therefore not only crucial in ecology and evolutionary genetics, but it is necessary to optimise conservation action.

Disturbance events affect individual survival and reproduction, causing losses of genetic variants or changes in their frequencies, due to **genetic drift**, inbreeding and selection. This can lead to a decline in **effective population size (*N_e*)**, which may or may not lead to a fitness reduction due to decreased **adaptive potential**, and/or increased **genetic load** in subsequent generations (Figure 1). If such changes are not reverted, their ultimate effect will be **genome-wide genetic erosion**, which will affect both neutral and functional/adaptive variation [4]. During time lags, moderate to high levels of genetic variation can persist despite deteriorated conditions [2], for example, because of persistent individuals surviving adverse conditions. Contemporary levels of population genetic diversity thus bear the legacy of past environments [5,6]. For the same reason, today's conservation actions shape the genetic diversity of future populations and their design should thus account for time lags [7].

Time lags in the genetic response to disturbance events have also been referred to as '**genetic extinction debt**' or 'extinction debt of genetic diversity' [8–11], drawing a parallel with the concept of **extinction debt**, which describes the delayed loss of species following habitat degradation [12,13]. Extinction debts have received more attention, as they affect entire communities in perturbed ecosystems and environments [7]. However, as communities are composed of populations from different species, extinction debts at the community-level depend on delayed responses

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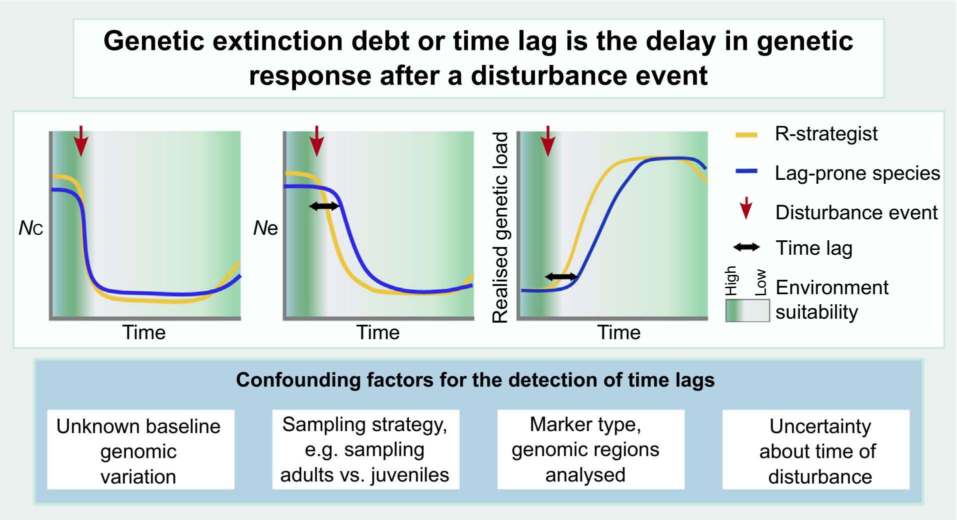

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Figure 1. Conceptual plots showing the time lag or genetic extinction debt problem. A delayed genetic response is expected after a disturbance event, in the example above causing a population bottleneck. While the decline in census size (N_C) can be immediate, changes in effective population size (N_e) and realised genetic load happen with delay, especially in lag prone species. The duration of the time lag mainly depends on the species' life-history traits, but note that the conversion of masked into realised genetic load typically continues after N_e stabilisation in all species [42]. Lag-prone species have traits that extend the time and the opportunities for reproduction (e.g., long generation time and life spans). Short-lived species and those that experience frequent demographic changes (most *r*-strategists) tend to have shorter time lags. Technical factors such as sampling strategy and molecular marker type can confound the detection of time lags and the interpretation of genetic diversity levels.

(genetic debts) at the population level [14] and, therefore, understanding genetic extinction debts or time lags at the population level deserves attention as an independent phenomenon.

Time lags may also contribute to explaining why genetic diversity is a poor predictor of global IUCN threat status [15], or why threatened species do not necessarily exhibit low genetic diversity ([16,17], but see [18]). Such discrepancies require accounting for delayed genetic responses and do not undermine the importance of exploring genetic variation for conservation practice [18,19].

Conservation genetics is still lacking a framework for the interpretation of genetic diversity in light of the possible occurrence of time lags. Without an organic view of the time lag problem, misinterpretations of current levels of genetic variation might lead to setting wrong or no priorities for the conservation of populations and species.

We explore the biological and ecological factors determining time lags and their associated confounding factors. We focus on disturbance events affecting abiotic or biotic conditions (e.g., habitat loss, fragmentation, climate change, pollution, diseases [2,12]) and their detrimental effects on individual survival and/or reproduction, leading to reduced genetic diversity and genetic erosion. We finally propose a framework to interpret genetic diversity parameters considering the possible occurrence of time lags.

Determinants of time lags: factors delaying genetic diversity loss and its detectability

We here generally focus on genetic diversity loss caused by disturbance events; this can be mild or more severe and might lead or not to severe genetic erosion with reduced fitness (in the

Glossary

Adaptational lag: temporal disconnect between a change in the environment and the genetic change required to maintain or recover fitness (see references in [38]).

Adaptive potential: genetic variation needed to respond to selection. This includes functional, as well as neutral and nearly neutral genetic variation that might become adaptive in changing environmental conditions.

Census size (N_c): number of reproductively mature individuals in a population.

Delta values of genetic metrics: comparison of genetic parameter estimates from the population under study between samples collected at different time points (e.g., historical versus contemporary samples).

Disturbance event: any biotic or abiotic change in the population's environment that can negatively affect its survival and reproduction. The impact of the disturbance event on the target population jointly depends on the generation time of the species and the severity and duration of the disturbance event.

Effective population size (N_e): size of an ideal population (assumed to exhibit random-mating and a constant population size with non-overlapping generations) that experiences the same rate of genetic drift and level of inbreeding as the observed population [63].

Extinction debt: delay between a disturbance event that leads to the local extinction of species and the actual moment of extinction.

Genetic drift debt: the time lag in genetic change, including delayed loss of genetic diversity due to (i) past balancing selection (at specific loci) [37]; (ii) lag-favouring life-history traits (genome-wide, this paper); and (iii) the increase in realised genetic load due to inbreeding [64]. A synonym of genetic extinction debt.

Genetic extinction debt: time lag in the genetic response at neutral, nearly neutral, and functional/adaptive loci to a disturbance event (see time lag, disturbance event, extinction debt, genetic drift debt).

Genetic load: genetic variation that reduces the fitness of a population (in comparison with a reference genotype with the maximum fitness). The genetic load is composed of realised load long term). We address determinants that delay genetic diversity loss through favouring the persistence of polymorphisms, i.e., counteracting genetic drift.

Life-history traits and other biological traits (Table 1) play a crucial role in allowing genetic polymorphisms to persist even through deteriorated environmental conditions [20–22]. Such traits essentially both (i) extend the time available for an individual to reproduce (e.g., long life span [23], vegetative propagation, long generation time); and (ii) increase the number of opportunities for reproduction and the number of allele combinations arising from reproduction (e.g., overlapping generations, mating by outcrossing, large numbers of offspring per individual; Table 1).

The influence of life-history traits on genetic diversity is mainly mediated by N_e, which mirrors major, long-term differences in genetic diversity between species of plants and animals [22]. At the population-level, N_e affects the rate of loss of genetic diversity by drift: populations with large **census size N_c** or large N_e preserve genetic diversity, whereas populations experiencing strong declines, historical size fluctuations, or with small N_e lose genetic diversity more rapidly. Contemporary N_e (i.e., referring to recent generations) is used in conservation genetics to assess whether a population remains large enough [24,25], as currently large populations have more chances to preserve genetic diversity and adaptive potential in the long term. However, some populations are slow to respond!

Life-history traits affect how N_e changes in relationship to N_C, with adult life span/adult mortality, age at maturity and lifetime variance in reproductive success having the greatest effects [26]. Life span and age at maturity determine generation time, which scales positively with N_e, whereas lifetime variance in reproductive success is inversely proportional to N_e. Other life-history traits (Table 1) generally affect both generation time and lifetime variance in reproductive success in the same direction, thus having opposite influence on N_e, which will be difficult to predict.

Species with life-history traits favouring time lags include perennial, long-lived plants and other long-lived organisms such as sea turtles that produce large numbers of un-nurtured offspring (thereby combining the long life spans characterising strict *K*-strategists with high offspring numbers characterising strict *r*-strategists). For example, a meta-analysis in plants revealed significant negative effects of recent habitat fragmentation on genetic diversity in herbs or short-lived plants but not in trees [27], suggesting that the longer generation time of trees (Box 1) delays the negative effects of habitat fragmentation. Indeed, a study encompassing different plant life forms [20] found that genetic diversity was lost proportionally to the number of generations since fragmentation. Another notable example of traits favouring time lags is the survival of individuals through seed banks (e.g., in annual plants or fire-adapted species), whose genetic diversity will reflect the population dynamics of previous generations (e.g., [6]).

Species that lack lag-favouring traits, instead, for example, short-lived species and those that frequently experience demographic changes (most *r*-strategists), might more rapidly respond to contingent threats or they might face direct extinction without any warning signals of genetic erosion [21].

Other biological traits such as autopolyploidy can affect the persistence of polymorphism [28] and thus the build-up of time lags. Because of their higher number of orthologous alleles, autopolyploid species lose genetic variation by drift more slowly than diploid species [29] and this reduced loss is also mediated by a larger N_e [28].

(i.e., deleterious alleles that are homozygous and thus expressed) and of masked load (i.e., deleterious mutations in heterozygous genotypes that are not expressed) [65].

Genome-wide genetic erosion: loss of genetic diversity and increase in realised genetic load resulting in maladaptation, decrease in adaptive potential, and reduced fitness [4].

Random genetic drift: change in the frequency of existing alleles from one generation to the next due to chance (random sampling of allelic variants).

Strength of the fine scale spatial genetic structure (*Sp*): synthetic statistic which describes the strength of the spatial family structure within a population. It is estimated from the regression of inter-individual kinship on spatial distance.

Time lag: temporal delay between a disturbance event and the consequent changes in the genetic constitution of the population.

Table 1. Traits favouring the persistence of polymorphisms and delaying genetic erosion after disturbance events and their effects on N_e (effective population size)[a]

Life-history traits and other factors favouring time lags	Mechanisms	Effects on N_e or N_e/N_C ratio	Refs
Long generation time, as a function of age at maturity, survival rate and age-specific fecundity; inverse function of annual mortality rate	-Persistence of individuals and increased opportunity to reproduce: genetic diversity will reflect previous generations -Age at maturity (one of the main determinants of generation time) will dictate how fast the progeny representative of progressively eroded genetic diversity will reproduce, all else being equal	-N_e increases proportionally with generation time. General principle 'lengthening the pre-reproductive period increases N_e'. -Increased age at maturity increases both N_e and N_e/N_C.	[30] [26]
Overlapping generations/iteroparity/age structure	-Increased opportunities for reproduction across age groups: genetic diversity will partially or entirely reflect previous generations	Overlapping generations generate lifetime variance in reproductive success, thus reducing N_e.	[31]
Long life span (longevity)/high survival rate	-Persistence of individuals and increased opportunity to reproduce: genetic diversity will reflect previous generations	The increase in survival rate is associated with a reduction in N_e/N_C (counterbalanced by an opposite effect on N_e associated with a longer generation time).	[26]
Clonal and partially clonal reproduction (in general) Vegetative growth	-Persistence of individuals, increased opportunity to reproduce: genetic diversity will reflect previous generations -As above, plus increase in physical size (with associated increase in organs for sexual reproduction)	-Same as for long life span and long generation time, relative contribution of other life-history traits is generally difficult to disentangle (see Outstanding questions). -As above. If some (larger) individuals will consistently reproduce more (sexually), N_e and N_e/N_C will be significantly reduced because of increased lifetime variance in reproductive success.	[32,33]
Mating system and dispersal strategy	-Outcrossing and long-distance dispersal will promote population connectivity, buffering or delaying genetic erosion -Selfing might initially favour a time lag, as individuals not affected by the disturbance event will continue reproducing as before: genetic diversity in the progeny of selfed individuals will reflect previous generations -Shift from predominant outcrossing to selfing will cause a rapid drop in genetic diversity	The interactive effect of mating system and other life-history traits on N_e is generally difficult to disentangle (see Outstanding questions). -Selfing decreases N_e.	[34] [30]
Large populations/distribution ranges	-Large populations in large distribution ranges have a large reservoir of genetic diversity that can compensate for local genetic diversity losses	Large populations have large N_e.	[35]
Large number of offspring reaching reproductive maturity	-Effective reproduction will tend to buffer or delay genetic erosion, and genetic diversity will reflect previous generations, at least initially- If many offspring are generated by parents whose genetic diversity is representative of the previous generation, it will take longer for genetic parameters to reflect new environmental conditions	Mostly dependent on variance in reproductive success. More reproducing individuals will tend to even out variance in reproductive success, increasing both N_e and N_e/N_C. Few individuals generating large numbers of offspring will increase variance in reproductive success, decreasing both N_e and N_e/N_C.	[22,25,31]
Seed banks (e.g., in annual plants) Diapausing eggs (e.g., in freshwater crustaceans)	-Persistence of individuals, subject to successful germination/survival: genetic diversity will reflect previous generations	Lengthening of the juvenile life-stage increases N_e; analogously, lengthening mean seed dormancy increases N_e.	[6,30,36]
Other biological traits or selective pressure potentially favouring time lags			
Balancing selection on adaptive loci[b]	-Polymorphism can be maintained at adaptive loci that were under past balancing selection		[37]
Inefficient directional selection[b] on putatively adaptive loci under long generation times	-Slow responses to selective pressures generate time lags. In addition, other life-history traits can cause a cumulative effect in the build-up of time lags		[38]

Table 1. (continued)

Life-history traits and other factors favouring time lags	Mechanisms	Effects on N_e or N_e/N_C ratio	Refs
Selection in heterogeneous environments	-Environmental heterogeneity maintains more suitable habitat for individual survival after disturbance	N_e kept high as the environment buffers the loss of genetic diversity	[39]
Autopolyploidy	-Loss of heterozygosity (genetic diversity) is slower in autopolyploids and heterozygosity is higher at mutation-drift equilibrium compared with diploid populations	N_e is larger in autopolyploid populations	[28]

[a] The difficulty in predicting changes in N_e generally arises from opposite effects of generation time and lifetime variance in reproductive success, which are in turn affected by other life-history traits.

[b] The effect of selection only on specific loci might be considered among 'confounding factors' as genetic erosion can be actually detected if analysing other (neutral) regions. However, balancing selection has been included among the determinants of time lags, because it can induce a long-term persistence of polymorphism at the loci it acts upon.

Lag-favouring life-history traits can also lead to delayed responses to selection (i.e., **adaptational lag**), for example, when locally adapted populations become maladapted [38]. Adaptive genetic responses to selection can happen within a few generations and involve, for most traits, small allele frequency shifts at many, partially redundant loci, and are most effective in large populations [40]. Loci under past balancing selection experience delay in the loss of genetic variation compared with the genomic background, a situation named **(genetic) drift debt** [37]. The concept of genetic drift debt was recently expanded to include the delay in the conversion of masked to realised genetic load due to inbreeding [41,42]. We can here further broaden the concept to genome-wide delays in genetic diversity loss due to lag-favouring traits, effectively synonymising it with genetic extinction debt.

Lastly, Table 1 includes additional ecological factors (e.g., heterogeneous environments) and biological traits favouring time lags, but more research is required to understand the entire suite of life-history traits/factors that could affect time lags and to disentangle their relative contributions.

Factors confounding the interpretation of genetic studies when time lags occur

When disturbance events occur, our ability to detect their impact on genetic diversity might be confounded depending on our methodological choices. As we expect that the changes will not affect all

Box 1. Species with lag-favouring traits: trees

Studies on trees have provided a great insight into the persistence of genetic diversity under deteriorated habitat conditions, as these species have many of the life-history traits favouring time lags. Forest tree populations are characterised by high levels of genetic diversity, much higher than, for example, herbaceous species [34]. Tree species are mostly outcrossing, have a high lifetime reproductive output, are subjected to strong selection pressures during early life stages, and they are particularly long-lived with overlapping generations [66]. In natural undisturbed populations, the genetic diversity of dominant tree species positively correlates with the surrounding species diversity (e.g., [67,68]). However, while species diversity is lower in disturbed habitats, this is not necessarily the case for genetic diversity, indicating non-parallel changes after disturbance events [67] possibly due to time lags. The genetic response to disturbance events such as logging, fire, or dieback due to invasive pathogens depend on (i) the strength/rate of population size decline, and (ii) specific life-history traits of the tree species. In the case of deforestation, remnant forest sites can display genetic variation characteristic of formerly continuous stands. The constituent species with already low genetic diversity might thus face higher extinction risks than interpretable based on their genetic variation [60]. Extensive clear-cuts can lead to dramatic declines of population size of tree species causing increased genetic drift which affects allele frequencies in the natural regeneration. Light-demanding and fast-growing pioneer species with efficient seed dispersal emerge first and gain abundance in clear-cut sites while shade-tolerant, slow-growing species emerge with delay and at lower densities, making them more vulnerable to genetic erosion, especially in tropical forest ecosystems [69,70]. Silvicultural practices, such as avoiding clearcuts or avoiding the selective removal of one of the sexes in dioecious species, raising minimum logging diameters, and rotation lengths, can attenuate these effects [71,72]. However, detecting recent loss of genetic diversity in tree populations is difficult, as remnant trees will reflect the genetic diversity of the previous generation, as expected in species with traits favouring time lags. Similar effects are likely in some marine fish, corals, sea grasses, other partially clonal species and in general species with *K-strategy life-history traits* [73,74].

individuals simultaneously, depending on reproductive strategies and on the occurrence of genetic structure within a population [43,44], the sampling strategy adopted becomes a major determinant of the analytical outcomes (Figure 1). For example, recent ecosystem fragmentation was better captured in the genetic diversity (expected heterozygosity, percentage of polymorphic loci) measured in young cohorts versus in adults of long-lived plant species [9]. Similarly, recent population expansion and ongoing gene flow after a founder event were associated with a larger N_e estimated in juveniles of a long-lived, age-structured orchid than in adults from the same population [33].

The uncertainty associated with sampling design has been extensively discussed in conservation and population genomics, with the consensus being that analyses based on allele frequency calculations require sampling that is representative of the allele frequencies in the population and that large sample sizes are generally needed to increase statistical power, especially in large populations (e.g., [45]). Rare alleles are not accurately represented in small sample sizes and this will especially bias the estimation of demographic parameters. Furthermore, sample sizes need to be similar when directly comparing different populations or cohorts.

As changes in allele frequencies may not be simultaneously reflected in the entire genome, our ability to detect early signatures of genetic erosion will also depend on the choice of molecular markers or genomic regions analysed (Figure 1; [46]), on whether these genomic regions are under the effect of selection or not, and on the metrics used [4]. Genomic regions with higher mutation rates (e.g., microsatellites) will exhibit higher indices of genetic diversity than regions usually found in two allelic states (maximum expected heterozygosity equal to 0.5), such as SNPs. Because marker choice impacts the magnitude of the genetic metrics obtained, the interpretation of population genetic metrics requires caution when comparing studies using different marker types.

Genic and adaptive regions under the effect of balancing selection are expected to be more conserved than neutral regions and might remain in the same state even in deteriorated environmental conditions [47]. Genetic diversity might remain high at loci affected by past balancing selection, despite an overall loss of genetic diversity due to genetic drift [37] and therefore a focus on such loci might mask the detection of genome-wide genetic diversity loss.

Demographic processes might differentially be detected depending on the genetic diversity metrics considered. Since rare alleles are lost first under population decline, allelic richness and number of polymorphic loci respond more quickly than heterozygosity and nucleotide diversity to changes in population size. Heterozygosity, in particular, is only affected to a little extent by short bottlenecks [19,48].

Complementary information such as geographic coordinates of samples can improve the interpretation of genetic data. In large populations with effective gene flow and isolation by distance (e.g., in trees), where N_e is difficult to estimate [49], recent demographic changes can be captured based on spatial genetic parameters such as the **strength of the fine scale spatial genetic structure (*Sp*)**, which is sensitive to differential management and population dynamics [50].

Considering the factors confounding genetic interpretations under the occurrence of time lags, it becomes obvious that relatively high levels of genetic diversity may reflect past conditions and that genetic erosion may occur with a delay [17].

A framework for interpreting genetic parameters despite time lags

Regardless of the time elapsed between the disturbance event and the onset of genetic erosion, the influence of confounding factors on genetic diversity can be mitigated by satisfying some methodological requirements (Figure 2A). Researchers should adopt sampling strategies that are representative of the entire target population, accounting for genetic differences between life-stages in species with overlapping generations and barriers to random mating. Most importantly, consideration of population ecology, life-history traits and ploidy level is essential to interpret genetic diversity and the possible occurrence of time lags. When the analysis of genome-wide variation is not possible [51], analyses should target as many markers as possible, covering different genomic regions. Multiple genetic metrics should be used to account for their differential responses to demographic processes. Metrics that focus on processes in contemporary generations potentially mirroring recent disturbance events include parameters of the mating system, (e.g., outcrossing rates), variance in reproductive success, dispersal kernels and metrics on spatial genetic structure [50,52], as well as metrics summarising rare allele frequencies such as allelic richness or the site frequency spectrum [53]. These can be complemented by metrics summarising the proportion of segregating sites such as Watterson's theta, which is a proxy for long-term N_e [18].

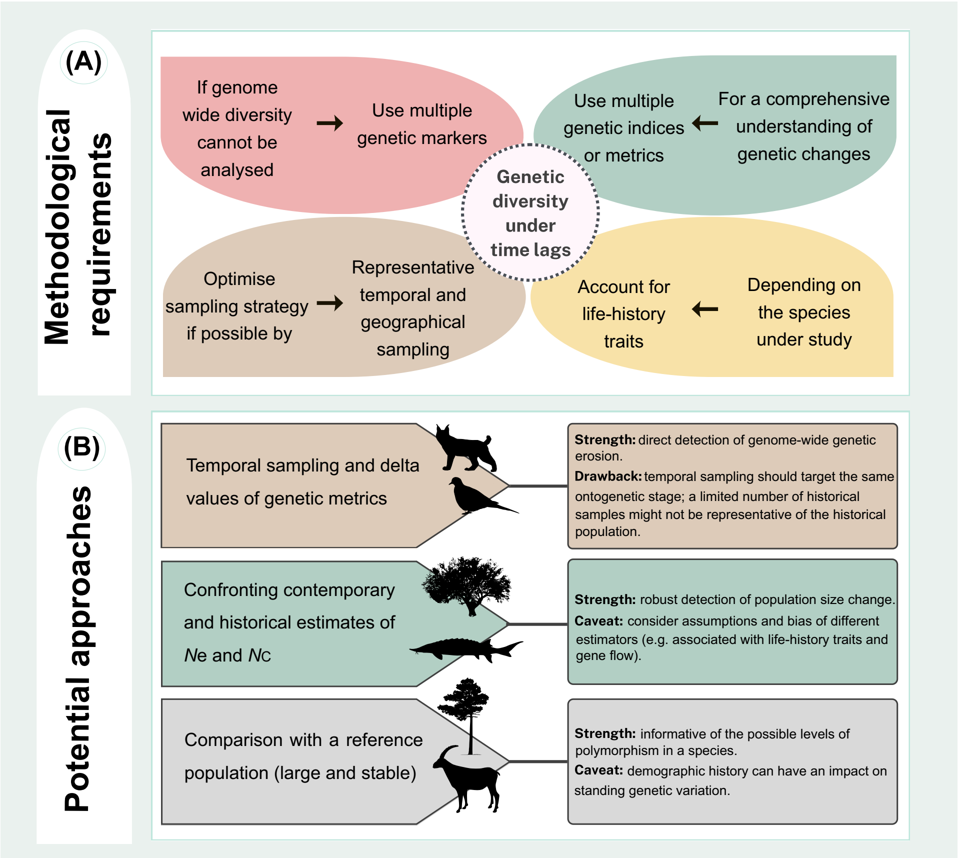

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Figure 2. (A) Methodological requirements for the correct interpretation of population genetic diversity under time lags; (B) potential approaches to detect a time lag and correctly interpret population genetic diversity, and references to studies where similar approaches have been used to analyse genetic diversity, in the Iberian lynx, *Lynx pardinus* [57], the pink pigeon, *Nesoenas mayeri* [58], the Atlantic sturgeon, *Acipenser oxyrinchus oxyrinchus* [59], the legume tree *Dimorphandra exaltata* [60], the alpine ibex, *Capra ibex* [61] and the maritime pine, *Pinus pinaster* [62]. The approaches outlined in (A) and (B) also allow monitoring managed populations of lag-prone species, to assess whether conservation interventions have been effective. Abbreviations: N_C, census size; N_e, effective population size.

Provided that the aforementioned requirements are satisfied, we summarise three potential approaches (Figure 2B) that might help detect early signs of genetic erosion despite the occurrence of time lags.

(1) The joint genetic analysis of samples from contemporary populations and samples collected in the past (e.g., from herbaria, museums, and archaeological sites) is one of the strategies to evaluate loss of genetic variation, through the estimation of **delta values of genetic metrics**. Historical samples provide baseline levels of variation before the onset of the disturbance events causing genetic erosion [15,48,54,55]. The main limitation of this approach is the availability of temporal samples. In addition, temporal samples might be not representative, considering past population dynamics and sampling strategies (although see [54]), technical pitfalls such as post-mortem damage patterns, and genotyping errors associated with depth of sequencing coverage [15].

(2) The comparison between historical and contemporary estimates of N_e [56] and N_C might reveal differences in genetic drift over time (see Figure 1B,C in [54]). Because of the relative simplicity of estimating both historical and contemporary N_e with samples collected in a single point in time, these estimates can disclose loss of genetic variation when other metrics might not. The inclusion of temporal sampling of populations provides further analytical power to detect population genetic changes, although researchers should be aware of the biases associated with each estimation method [56].

(3) Comparison of genetic or genomic parameters of a population with those of one or several large and stable reference populations (ideally from the same gene pool) can provide a surrogate for baseline levels of genetic variation. Although finding reference populations is challenging because of the spatial distribution of genetic diversity (e.g., range marginality) and potentially different selective pressures, the intrinsic value of having reference populations can aid the conservation of the most threatened populations.

Concluding remarks and future perspectives

Time lags between disturbance events and genetic responses is a common but overlooked problem in ecology, evolutionary, and conservation genetics. Here, we unify the concepts of time lag, genetic extinction debt, and genetic drift debt under the definition of 'genetic extinction debt', recognising that they all involve a delayed change in genome-wide genetic diversity, either occurring simultaneously or temporally shifted at neutral and functional loci. We identified questions that deserve exploration (see Outstanding questions) and open new avenues for the correct interpretations of genetic diversity levels despite the occurrence of time lags. These include disentangling the contributions of different life-history traits to genetic extinction debts and distinguishing delayed responses to neutral processes from delays in response to selection. Community ecology and conservation biology can both benefit from a unified framework in which genetic extinction debt is recognised as the basis for extinction debt at the community level. Finally, genetic extinction debt can offer valuable time to implement necessary conservation actions to prevent more severe genetic erosion.

Outstanding questions

How can time lags be quantified robustly across taxa, disentangling the contributions of different life-history traits and the severity and duration of the disturbance event?

What are the relative contributions of demographic processes and selection to the build-up of time lags?

How do genome size and genomic architecture affect the persistence of genetic diversity and thus the build-up of time lags?

Can time lags aid in preserving genetic diversity by granting more time for implementing management actions?

How can we build a framework to unify the concept of extinction debt at the community level with genetic extinction debts (= time lags) at the population level?

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Declaration of interests

The authors declare no competing interests.

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