Mind the lag: understanding delayed genetic erosion

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Abstract

The delay between environmental changes and the corresponding genetic responses within populations is a common but surprisingly overlooked phenomenon in ecology, evolutionary and conservation genetics. This time lag problem can lead to erroneous conservation assessments when solely relying on genetic data. We identify population size, life-history traits, reproductive strategies and the severity of population decline as the main determinants of time lags, evaluate potential confounding factors affecting genetic parameters during time lags, and propose methodological approaches that allow controlling for them. Considering the current unprecedented rate of genetic diversity and species loss, 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.

Keywords

conservation genomics, environmental changes, genetic diversity, genetic extinction debt, life history traits

1. *The time lag between environmental changes and the corresponding genetic responses*

The assumption behind the use of contemporary genetic data in conservation is that datasets mirror the current conservation status of a population [1]. However, genetic parameters often respond to novel environmental conditions and disturbance events with delay, generating time lags [2]. Failure to recognize and account for time lags in genetic responses can lead to erroneous conservation assessments, 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.

Environmental changes generate population genetic changes because individuals respond to novel conditions with differential survival and reproduction, which can lead to a decline in effective population size (N_e) and to reduced fitness over the course of a single or multiple generations (Fig. 1A). If such changes are not reverted, their ultimate effect will be genome-wide genetic erosion. During time lags, moderate to high levels of genetic variation can persist despite deteriorated environmental conditions [2], for example because of persistent individuals surviving adverse conditions. Contemporary levels of population genetic diversity thus bear the legacy of past habitat and landscape characteristics [4,5]. For the same reason, it is also important to account for time lags when designing conservation management actions [6].

Time lags in the genetic response to environmental changes have also been referred to as “genetic extinction debt” or “extinction debt of genetic diversity” [7–10], drawing a parallel with the concept of extinction debt, which describes the delayed loss of species following habitat degradation [11,12]. Extinction debts have received more attention, as they affect entire communities in perturbed ecosystems and environments [6]. However, an extinction debt at the community-level will depend on how environmental changes have acted upon the populations of co-occurring species, and on how quickly changes in the community can be detected. Put simply, extinction debts at the community-level arise from genetic debts at the population level [13], 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 [14], or why threatened species do not necessarily have low genetic diversity [15,16]. Such discrepancies require accounting for delayed genetic responses and do not undermine the importance of exploring genetic variation for conservation practice [17].

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 may lead to setting wrong priorities for the conservation of populations and species, with enormous waste of efforts and resources.

In this article, we explore the biological and ecological factors determining time lags and focus on situations in which time lags may be suspected or exacerbated because of confounding factors. Although in some cases environmental changes improve conditions for survival and have beneficial effects on genetic diversity, we only focus on cases in which deteriorated conditions (e.g. due to habitat loss, fragmentation, climate change, pollution, diseases; [2,11]), have detrimental effects on the survival of individuals or their ability to reproduce, leading to genetic erosion. We finally propose a framework to interpret genetic diversity parameters considering the possible occurrence of time lags.

2. Determinants of time lags: factors delaying the detectability of genetic erosion

Life-history traits and other biological traits (Table 1) play a crucial role in allowing polymorphisms to persist even through deteriorated conditions [18–20], delaying genetic erosion and supporting the build-up of a time lag. Such traits essentially both (1) extend the time available for an individual to reproduce (e.g., long life span [21], vegetative propagation, long generation time) and (2) increase the number of opportunities for reproduction and the number of gene combinations arising from reproduction (e.g., overlapping generations, mating by outcrossing, large numbers of offspring per individual (especially when they reach reproductive maturity; (Table 1)).

The influence of life-history traits on genetic diversity is mainly mediated by effective population size (N_e), which mirrors major, long-term differences in genetic diversity between species of plants and animals [20,22]. At the population-level, N_e affects the rate of loss of genetic diversity by drift: large populations (large N_c, large N_e) preserve genetic diversity whereas populations experiencing strong declines and those with small N_e lose genetic diversity more rapidly [23]. The assumption relevant to conservation genetics is that the contemporary N_e (i.e., referring to recent generations) mirrors the current conservation status of the population and informs on whether this remains large enough to preserve genetic diversity and adaptive potential in the long term [22,24]. The problem is that some populations are slow to respond!

Life-history traits specifically affect how N_e changes in relationship to census size (N_C) [25], with adult life span/adult mortality, age at maturity and lifetime variance in reproductive success having the greatest effects [26]. In particular, life span and age at maturity determine generation time, which is positively correlated with N_e, whereas lifetime

variance in reproductive success is inversely proportional to N_e. Predicting the ultimate influence of the whole suite of life-history traits of a species on N_e is challenging, as many life-history traits will generally affect both generation time and lifetime variance in reproductive success in the same way, generating opposite effects on N_e.

Species with life-history traits favouring time lags include perennial, long-lived plants and other long-lived organisms such as reptiles or sea turtles that produce large numbers of un-nurtured offspring (thereby combining the long life spans characterising *K-strategists* with high offspring numbers characterising *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, other authors previously found that genetic diversity was lost proportionally to the number of generations since fragmentation in a study encompassing different plant life forms [18]. 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. [5]).

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 [19].

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 gene copies, 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].

Table 1. Traits favouring persistence of polymorphisms and delayed genomic erosion despite deteriorated environmental conditions, i.e. time lags, and their relationship with N_e. The difficulty in predicting N_e changes will generally depend on the opposite influence of generation time and lifetime variance in reproductive success, which are in turn affected by other life-history traits.

Life-history traits favouring time lags	**Role in favouring time lags**	**Relationship between life-history traits and N_e or N_e/N_C ratio**	**Key references**
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	-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]

	how fast the progeny representative of progressively eroded genetic diversity will reproduce, all else being equal.		
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 (with mechanisms different from vegetative growth) -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 lifespan 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 environmental changes 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.	[20,22,31].
-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.	[5,30]
Other Biological traits or selective pressure potentially favouring time lags			
Balancing selection on adaptive loci*	Polymorphism can be maintained at adaptive loci that were under past balancing selection.		[36]
Inefficient directional selection* 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.		[37]
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 polyploid populations.	[28]

*The effect of selection only on specific loci might be considered among "confounding factors" (Section 3), as genomic 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.

Selective pressures generated by environmental change may also affect the build-up of time lags, since they affect individuals' likelihood of survival and reproduction. For example, when locally adapted populations become maladapted, the time lag in the genetic response can depend on a delayed response to selection because of lag-favouring life-history traits [37]. 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 [38]. If environmental changes result in strong directional selective pressure on a specific trait, the frequencies of the underlying alleles will show a faster

loss of diversity than the genomic background and may confound the detection of a possible time lag affecting genome-wide diversity [39]. Conversely, loci under balancing selection will show a slower loss of genetic variation than the genomic background [36]. While these processes affect all populations, selection is typically most efficient in large populations, whereas genetic drift hampers its efficiency in small populations [40,41].

Table 1 includes additional ecological 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 contribution.

Box 1 - 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 e.g. herbaceous species [34,42]. Tree species are mostly outcrossing, have a high life-time reproductive output, are subjected to strong selection pressures during early life stages and they are particularly long-lived with overlapping generations [43,44]. In natural undisturbed populations, the genetic diversity of dominant tree species correlates positively with the surrounding species diversity (e.g. [45,46]. 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 [45] possibly due to time lags. The genetic response to disturbance events such as logging, fire or dieback due to invasive pathogens depend (1) on the strength/rate of population size decline, and (2) specific life history traits of the tree species. In the case of extensive clear-cuts, the population size of all tree species declines dramatically causing increased 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 [47,48]. Silvicultural practices, such as avoiding clearcuts, raising minimum logging diameters, and rotation lengths, can attenuate these effects [49,50]. However, detecting recent genetic erosion 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 [51,52].

3. *Factors confounding the interpretation of genetic studies when time lags occur*

When environmental changes 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 individuals simultaneously, depending on reproductive strategies and on the occurrence of genetic structure within a population [53,54], the sampling strategy adopted becomes a major determinant of the analytical outcomes (Fig. 1A). Vranckx and colleagues [8] observed that long-lived species in recently fragmented ecosystems displayed contrasting patterns of genetic diversity (measured as expected heterozygosity and percentage of polymorphic loci) between adults and progenies, with the diversity in the younger cohort being more representative of the recent fragmentation. Sampling juveniles of a long-lived, age-structured orchid after a recent founder event, on the contrary, produced a larger N_e estimate compared with the adult cohort from the same population [55], reflecting the recent population expansion and ongoing gene flow.

The uncertainty associated with sampling design has been extensively discussed in conservation and population genomics, with the consensus being that sampling for analyses based on allele frequency calculations should be representative of the genetic diversity of different individuals in the population, and large sample sizes are generally needed to increase statistical power, especially in large populations (e.g., [56]). Rare allele frequencies, in particular, are not correctly 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 the signatures of genetic erosion will also depend on the choice of molecular markers or genomic regions analysed per se (Fig. 1A; [57]), on whether these genomic regions are under the effect of selection or not, and on the metrics used to assess genetic erosion [58]. 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 of the impact of marker choice on the magnitude of the genetic metrics obtained, some authors warned against the use of thresholds for genetic diversity metrics in conservation [59].

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 [60]. Some authors have observed that genetic diversity may remain high at loci under the past effect of balancing selection, despite an overall loss of genetic diversity due to genetic drift [36,41]. They referred to this

phenomenon as “drift debt”, following the prediction that genetic diversity will eventually be eroded if balancing selection will stop acting upon these loci.

Demographic processes might differentially be detected depending on the genetic diversity metrics considered. Since rare alleles are lost first under population decline, allelic richness, number of polymorphic loci and inbreeding coefficient respond more quickly than heterozygosity to changes in population size. Heterozygosity, in particular, is only affected to a little extent by short bottlenecks [17,61,62].

Complementary information such as sample coordinates 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 [63], recent demographic changes can be captured based on spatial genetic parameters such as *Sp* [64], which is sensitive to differential management and population dynamics [65].

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 genomic erosion may occur with a delay [16].

4. A framework for interpreting genetic parameters despite time lags

Regardless of the time elapsed between the environmental changes and the onset of genetic erosion, the influence of confounding factors on genetic diversity can be mitigated by satisfying some methodological requirements (Fig. 1B). 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 [66], 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.

Provided that the requirements above are satisfied, we summarise three potential approaches (Fig. 1C) that might help detect genomic 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 diversity. Historical samples may provide baseline levels

of variation before the onset of the environmental changes causing genetic erosion [14,62,67]. The main limitation of this approach is the availability of temporal samples. In addition, temporal samples may be not representative, considering past population dynamics and sampling strategies (although see [67]), technical pitfalls such as post-mortem damage patterns, and genotyping errors associated with depth of sequencing coverage [14].

(2) The comparison between historical and contemporary estimates of N_e [68] and N_C may reveal differences in genetic drift over time. 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 may not. The inclusion of temporal sampling of populations, may provide further analytical power to detect population genetic changes, although researchers should be aware of the biases associated with each estimation method [68].

(3) Metrics that focus on processes in contemporary generations potentially mirroring recent environmental change include parameters of the mating system, e.g., outcrossing rates, variance in reproductive success, dispersal kernels and metrics on spatial genetic structure [65,69], as well as metrics summarising rare allele frequencies such as allelic richness or site frequency spectrum [70].

(4) Comparison of genetic or genomic parameters of a population with those of a large and stable reference population may provide a surrogate for baseline levels of genetic variation. Although finding a reference population may be challenging because of the spatial distribution of genetic diversity (e.g., range marginality) and potentially different selective pressures, the intrinsic value of having a reference population may aid the conservation of the most threatened populations.

Concluding remarks and Future Perspectives

Time lags between environmental changes and the corresponding genetic changes is a common but overlooked problem in ecology, evolutionary and conservation genetics. With this opinion article, we offered an organic synthesis of the problem, of the potential factors confounding the interpretations of genetic results, and of the possible methodological approaches and solutions for a correct detection of time lags and interpretations of genetic diversity levels in natural populations, especially those of conservation concern. Our article also identifies **Outstanding questions** that deserve exploration and open new avenues for the correct interpretations of genetic diversity levels in natural populations despite the occurrence of time lags.

Declaration of interests

The authors declare no competing interests.

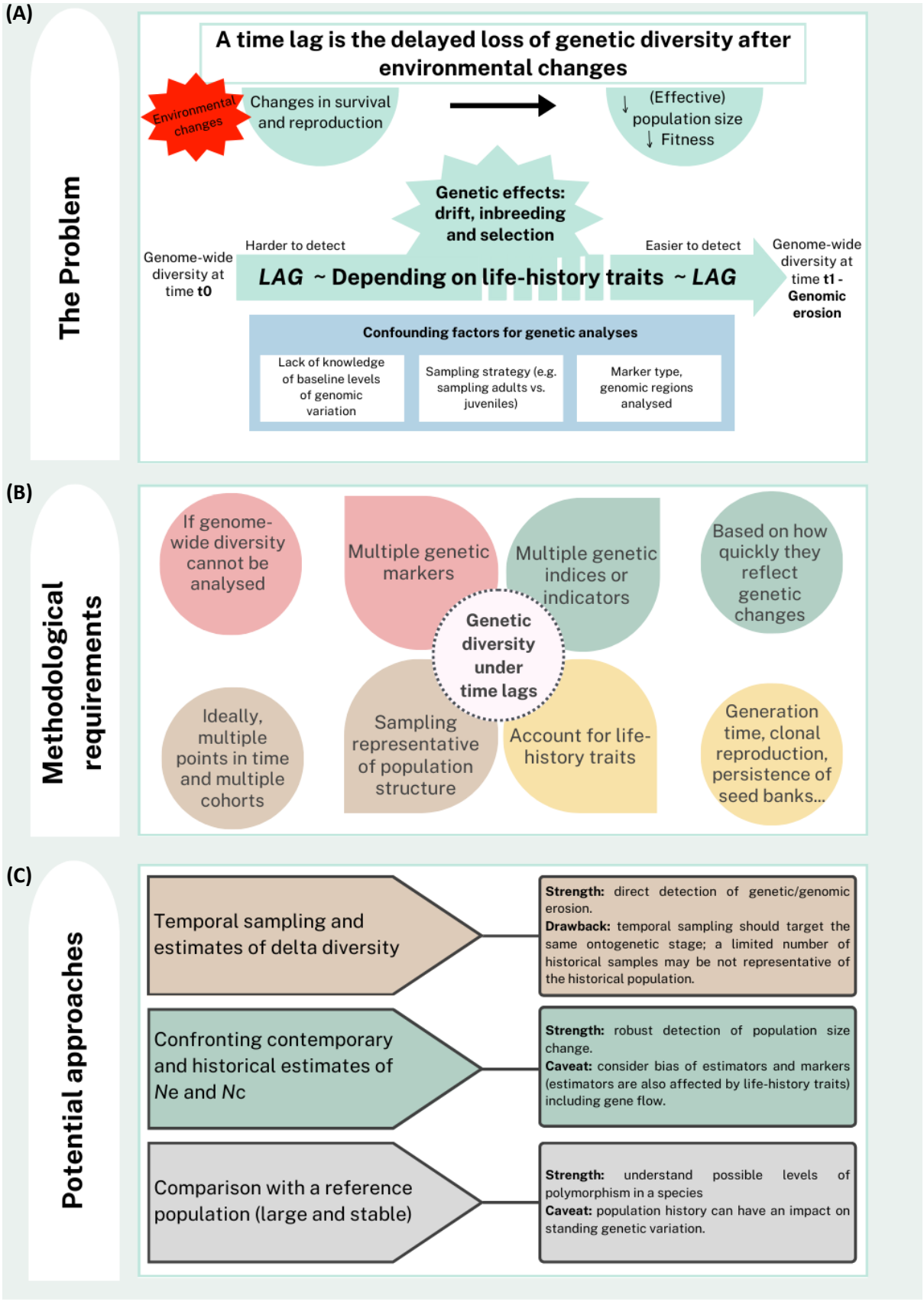

Figure 1. A framework to interpret and analyse delayed loss of genetic diversity after environmental changes and disturbance events. (A) The problem: genetic changes occur as a consequence of environmental changes. The main determinants of time lags include population size and life history traits, while the choice of genetic markers might mask the occurrence of a time lag or confound the

interpretation of genetic diversity. (B) Methodological requirements for the correct interpretation of population genetic diversity under time lags. (C) Potential approaches to detect a time lag and correctly interpret population genetic diversity. (B) and (C) also allow monitoring managed populations to assess whether conservation interventions have been effective, when the life-history traits and reproductive strategies of a species support the build-up of time lags.

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