First year paper:

Dynamics of genetic diversity and habitat loss

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Abstract

Existing methods in biodiversity conservation have largely been focussed on preserving geographic areas, habitats, species range limits, ecosystems and species. One, often overlooked, goal of biodiversity conservation is maintaining genetic diversity across species. Recently, there have been calls to begin monitoring genetic diversity levels across species via large-scale genotyping in order to preserve long-term evolutionary potential of species. The hope is that such monitoring will detect species' genetic diversity losses (e.g., due to habitat loss or climate change) to inform conservation actions to protect such species. As genomic datasets grow, they can be combined with population genetics theory to aid conservation policy, but due to the inherent spatial and non-equilibrium states caused by habitat destruction, population bottlenecks and fragmentations, classic population genetic theory cannot be readily applied for predictions. Here, we develop realistic spatial population genetic simulations of species extinction to better understand the dynamics of genetic diversity metrics. In contrast to the mutations-area relationship (MAR), which predicts the loss of genetic diversity as the number of genetic variants with habitat destruction, I find that initially there is almost no impact on π diversity. However, genetic diversity losses are dramatic in the long term even after habitat destruction, which highlights the importance of a theoretical understanding of genetic diversity dynamics and that simple monitoring is not enough.

Introduction

Climate change represents the largest ecological and evolutionary force selecting for warming tolerance and survival. These rapid changes have already driven one thousand species to extinction (IUCN, n.d.; Díaz et al. 2019). What's more alarming is the estimated number – approximately 47% – of plant and animal species projected to have lost part of their geographic range (Wiens 2016; Thuiller et al. 2005). Range contraction events cause reduction in genetic diversity, which could in turn reduce the ability for a species' to adapt to changing climates (Exposito-Alonso et al. 2018; Parmesan 2006; Capblancq et al. 2020). This reduction in genetic diversity could result in a series of dire consequences – such as inbreeding depression that could kick start negative feedback loops of continual genetic diversity loss (Lynch, Conery, and Burger 1995; Spielman, Brook, and Frankham 2004).

Previous studies have emphasised the importance of preserving high genetic variation in both existing wild and domesticated populations to ensure their long-term survival, adaptation and ecosystem resilience (Lacy 1997; Crnokrak and Roff 1999; Hoffmann, Sgrò, and Kristensen 2017; "Correlation between Fitness and Genetic Diversity," n.d.), , COST, G-BiKE 2019,. Population losses and bottlenecks leading to low genetic variation is often associated to reduced adaptive potential (i.e the intrinsic ability for a population to adapt in response to selection) and inbreeding depression (i.e the reduced fitness of offspring within a population of closely-related individuals) (Frankham, Briscoe, and Ballou 2002; Frankham, Ballou, and Briscoe 2004; Lacy 1997). Consequently, conservation geneticists advocate for the maintenance of large, connected natural populations (Frankham, Bradshaw, and Brook 2014). This is particularly important since the recovery of genetic diversity through mutations is extremely slow (Nei, Maruyama, and Chakraborty 1975; Palacio-Mejía et al. 2021; Adams et al. 2022; Exposito-Alonso et al. 2022).

However, due to the limited amount of genetic data available, it is unclear how much genetic diversity should be preserved to ensure that populations can adequately adapt to changing climates, explicit protection for genetic diversity in both wild and domesticated species as well as strategies to measure the effectiveness of these efforts towards the goals (Laikre et al. 2020). Existing metrics such as the IUCN Red List categories of species extinction thread still fail to incorporate genetic diversity in its assessment of species' extinction risk (Schmidt et al. 2023) and rather categorise species based on heuristic demographic factors such as numbers of mature individuals or geographic factors such as geographic polygon area reduction in recent surveys (Garner, Hoban, and Luikart 2020). It has also been previously suggested that IUCN Red List status is not correlated with genetic diversity status (Schmidt et al. 2023), suggesting that Red List categories are not appropriate to capture population genetic processes relevant for population health and conservation policy. Fortunately, conserving high genetic diversity is already recognized under international agreements including the Sustainable Development Goals (SGD), CBD post-2020 goals ((Roe and Others 2010)), Global Strategy for Plant Conservation (GSPC) and many others (Laikre et al. 2020; Hoban et al. 2020; Frankham 2021). Some have suggested that current estimates of retaining 90% of genetic diversity for 100 years (Frankham, Briscoe, and Ballou 2002)) or the previously devised number of 90% genetic diversity for 200 years (Soule and Simberloff 1986) are not appropriate targets for species in the wild, especially in the context of global change and the need for these organisms to have to adapt (Frankham 2021). It was found that even with an ambitious 97% of genetic diversity target over 100 years, this estimate still resulted in harmful losses in the evolutionary potential of wild species (Frankham 2021) and could send many species into an irreversible 'extinction vortex' (Blomqvist et al. 2010). However, it's important to note that these predictions are merely cautionary projections and fail to consider the stochastic demographic processes and spatial structure that exists within populations in the wild.

Under range contraction events, populations are unlikely to be in equilibrium or to reach equilibrium considering that this spans thousands of years. These characteristics violate assumptions that prevent us from making accurate predictions of genetic diversity estimates using population genetics theory. In addition, given our knowledge of extinction debt (Jablonski 2001; Tilman 1994; Diamond 1972), we anticipate that there would be time delays between a bottleneck event affecting a species' and its eventual disappearance making it more important to also track genetic diversity across temporal dimensions. Overall, there seems to be little consensus in the impact of humans on genetic diversity despite the plethora of studies and methodologies used to tackle this issue. The need for both accurate and realistic projections of genetic diversity under range contraction scenarios is pressing, given the urgency in understanding how populations will adapt to climate change.

Currently there are few attempts to quantify how much genetic diversity across species has been already lost due to impacts of humans (DiLeo and Wagner 2016; Monteiro et al. 2019; Carvalho et al. 2019; Millette et al. 2020). Studies meta-analysing tens of thousands mitochondrial cytochrome c oxidase subunit I (COI) sequences, have failed to find any strong or significant effect of human impacts on genetic diversity (Millette et al. 2020). Others using cross-generational genetic comparisons of past and present populations detect weak signals (Leigh et al. 2019). One of the biggest difficulties in assessing current global genetic diversity has also been lack of genetic data globally, such as how much genetic diversity is present within populations, what is a reasonable estimate to conserve despite the challenge in enforcing genetic diversity monitoring and protection and the difficulty in collecting genetic data for all species and their corresponding populations (Hoban et al. 2021; Marks et al. 2021). Studies utilising indirect estimates based on declining population sizes or extinction rates are likely inaccurate (Steffen et al. 2015). For instance, predictions using Living Planet Index of population size decrease, forecasts an estimated 19 to 66% of expected genetic diversity loss assuming panmictic populations under equilibrium (Hoban et al. 2021). The most recent approach attempting to predict global genetic diversity loss utilised a spatial mathematical relationship to estimate the amount of existing genetic diversity given the species' geographic range loss, which suggested that close to 9-13% of genetic diversity have already been lost on average across species (Exposito-Alonso et al. 2022). Such an approach, termed the mutations-area relationship (MAR) does not account for processes such as temporal increase in genetic drift.

Here I aim to leverage continuous spatial population genetics simulation software to shed light on the extent and dynamics of genetic diversity loss in response to population and habitat range losses and fragmentations caused by human impacts. Motivated by MAR, we wish to formulate an easy-to-use equation that could help offer predictions of genetic diversity loss with habitat loss across space and time and non-equilibrium conditions. This work attempts to provide realistic predictions by incorporating complexities in demographic dynamics (age structure, competition, mate choice) and spatial structure. In this paper, we expand the work of (Exposito-Alonso et al. 2022) to include both π and number of segregating sites within and between populations, different fragmentation regimes, and non-equilibrium states across time. In addition, motivated by an urge to incorporate population genetic theory to conservation, I simulate habitat restoration approaches to understand potential paths to genetic diversity recovery.

Materials and Methods

Continuous-space population genomic simulations with SLiM

To study genetic diversity under different scenarios of species ranges and extinctions, we set up forward simulations in continuous 2D space using SLiM v. 4.0.1 (Haller and Messer 2023) (code

available at https://github.com/kmualim/spatial_extinction_sim). We simulated diploid genomes using a single, 10^8 long chromosome, with recombination rate and mutation rate set at 1e8. Utilising the non-Wright-Fisher simulation mode, we allow generations to overlap where single populations of constant census size *N* are simulated with overlapping populations (i.e each SLiM time point can be associated with the opportunity for creation of new offspring and the opportunity for mortality among existing individuals). Spatial structure is established by associating each individual with a continuous 2D coordinate (i.e. latitude and longitude), and by using these coordinates to govern three demographic processes: mate choice, competition, and dispersal. For mate choice, a poisson distribution is used to first generate the approximate number of offspring. If the individual is of fertility age, it chooses a mate randomly based on spatial proximity to generate a set number of offspring. Spatial proximity is just defined as the 10 nearest neighbours. Finally we establish local dispersal, where a newly generated offspring's position is drawn from a normal distribution centred at the location of the maternal individual with a standard deviation of dispersal rate. The effect of spatial competition is based on the local population density felt by each individual. We then scale carrying capacity by a function of habitat size to ensure that a reduction of habitat by 50% also leads to a 50% reduction in carrying capacity. Finally, note that the effective population size in population genetics, N_e , is not a set parameter but an emergent parameter that may differ from census size *Nc* in non-panmictic, spatially-structured populations with complex age structures, reproduction, and overlapping generations (all complexities expected in nature).We then set *Nc* individuals freely moving across the landscape.

To allow time for spatial population structure, we allow this population to evolve forward in time for 2,000 generations. As predicted by the isolation by distance pattern, individuals sampled closely together in 2D space are now more genetically related than individuals sampled far apart. Rather than simulating every mutations, which is a major computational burden, we use tree sequence recording (Haller and Messer 2019; Kelleher et al. 2018) to track the full genealogy of all individuals in the simulation which are either alive at the end of the simulation or sampled through time using the treeSeqRememberIndividuals function of SLiM. While 2000 generations are enough to establish spatial structure, it is insufficient for all sampled individuals to fully coalesce (in which case the value of genetic diversity resulting from these simulations would not be at equilibrium). To be able to start simulations with a large population in space that is at equilibrium without wasting computational resources, we simulated coalescent backwards in time with msprime (Kelleher, Etheridge, and McVean 2016). This process has been referred to as "recapitation" (Haller and Messer 2019), where an incomplete genealogy of a large population with multiple roots (from SLiM) is "recapitated" using coalescent simulation backwards in time. This is made possible by using the tree sequence data structure to record and simulate genealogies in both SLiM and msprime. Since our simulation is only concerned with how processes such as dispersal affect neutral variation across space and through time, we can use the "recapitated" tree sequence to overlay mutations onto the full genealogy of all sampled individuals, also using msprime. The rationale here is that under neutrality, mutations will not affect the structure of the genealogy, so we can simulate the genealogy without mutations first, and overlay neutral mutations second, thereby greatly reducing computational burden. We then extracted the resulting genotypes of all individuals from the tree sequence for downstream analysis. We then partitioned the continuous-space simulations in SLiM into a 6x6 grid for deme or subpopulation sampling. For each grid, we calculated the pairwise π diversity between individuals in all 36 spatial grids. In addition, we tracked each individual's location within spatial grids and tracked the total number of segregating sites at each sampling time point. In further downstream analysis, we approximate that each generation corresponds to 4.5 slim time points as we simulate realistic age-structured populations with overlapping generations.

Genetic diversity metrics

Genetic diversity is measured as π, the average pairwise difference between all possible pairs of individuals, and S, the number of segregating sites. In addition, we proceed to calculate both within-deme (one grid cell) and species-wide metrics of both π and S. Local genetic diversity metrics calculate the average pairwise difference between all possible pairs of individuals (π) within each grid cell across all 36 grid cells. In total, we obtain 36 values of π or S. We then obtain the average of π or S across all 36 grid cells. This ensures that individuals that belong in the same population are compared with each other. Species-wide metrics are calculated by getting the average pairwise difference between all possible pairs of individuals within all grids, so individuals in separate grids are being compared to each other to obtain an average value for all 36 grid cells.

Altering parameters in spatial population dynamics

Given the expectation that key population genetic parameters affect the dynamics of how genetic diversity changes with habitat loss, we wanted to explore how population size and migration rate might affect π diversity estimates under various habitat loss scenarios. We utilised population sizes ranging from 500 to 10,000 and varied dispersal rate respectively to test our variable *Fst* values to mimic low, medium and high population structure. Specifics of combinations of population sizes and dispersal rates can be found listed in the legend of **Figure 3**.

Simulating different scenarios of human impacts on species habitats

Our simulations included two ways of habitat destruction, via local extinction from one leading edge, and random local population extinction that fragments the habitat.

1 Instantaneous range contraction simulations

To assess the dynamics of genetic diversity in populations undergoing range contraction, we simulated range contraction of populations from one leading edge of the landscape. We performed range contraction simulations starting from 10% habitat loss to 90% habitat loss at 10% increments, with 10 replicates at each progression of habitat loss. Each simulation was run for 1,000,000 slim time points before instantaneous habitat extinction of various percentages of habitat loss occurred at 1,000,001 slim time points. After which, we tracked the dynamics of π and *S* diversity in the short-term (at the slim time point right after habitat loss) and in the long-term (at ¾ Ne generations after habitat loss). The long-term approximately corresponded to 62,000 slim time points (approximately 13,800 generations). In these simulations, we utilised a census population size of *N*c=5,000 and a dispersal rate of 0.05.

2 Progressive habitat extinction dynamics

To explore alternative habitat loss scenarios, we also looked at gradual habitat loss dynamics where habitat loss would decrease by 1% every 11 generations. This simulation was run for 2,000 slim time points before gradual habitat extinction of 50% habitat loss which occurred from 2,001 slim timepoints (approximately 450 generations) to 2,250 slim timepoints (500 generations).

3 Instantaneous fragmentation simulations

To assess the dynamics of genetic diversity in populations undergoing habitat fragmentation we used the 6x6 grid and removed grid cells starting from 10% habitat loss to 90% habitat loss at 10% increments, with 10 replicates at each progression of habitat loss. Each simulation was run for

1,000,000 slim time points before instantaneous habitat extinction of various percentages of habitat loss occurred at 1,000,001 slim time points. After which, we tracked the dynamics of π diversity in the short-term (at the slim tick right after instantaneous habitat loss) and in the long-term (at ¾ N_e after instantaneous habitat loss). This approximately corresponded to 62,000 slim ticks (approximately 13,800 generations). In these simulations, we utilised a census population size of *N*c=5,000 and a dispersal rate of 0.05.

4 Habitat restoration simulations

Utilising the 6x6 grid partitioned continuous-space simulations in SLiM, we performed 50% habitat loss simulations (through range contractions or habitat fragmentation scenarios) before fully restoring the habitat back to 100%. This was done by first making grids completely inhabitable (i.e carrying capacity = 0) before restoring the carrying capacity of these grids. Each simulation was run for 1,000,000 slim time points before instantaneous habitat extinction of 50% of habitat loss occurred at 1,000,001 slim time points. To test whether the length of time between habitat destruction and habitat restoration altered genetic diversity metrics, we built two time point scenarios (an early restoration 1 generation after habitat destruction and a late restoration approximately 20,000 generations after habitat destruction). After restoration we tracked the dynamics of π diversity across 62,000 slim ticks (approximately 13,800 generations). In these simulations, we census population size of *N*c=5,000 and a dispersal rate of 0.05.

Results and Discussion

The field of conservation genetics has consistently used genetic diversity (π) and segregating sites (S) as a measure of genetic diversity within populations to plan biodiversity conservation strategies. With the advent of sequencing technology, our ability to sequence more species globally has exponentially increased. However, despite the low cost in DNA sequencing, the task of collecting DNA samples in the field at global scales is still daunting. This is especially true in remote or difficult to assess ecosystems, where collecting DNA samples may simply not be feasible. Theoretical models of population genetics are thus essential to interpret the existing limited genetic datasets to make accurate global extrapolations in complex landscapes. Recently a population genetics-derived model on the relationship between genetic diversity and habitat area, termed the mutations-area relationship (MAR), allowed us to predict the loss of genetic diversity with geographic range reduction (Exposito-Alonso et al. 2022). In this paper, the authors found that a power law MAR was generalizable across 20 diverse animal and plant species, but it presented several shortcomings that I address below, namely (1) MAR's power law method specifically captures changes in segregating sites *S* over area and it's unclear how this generalises to other metrics of genetic diversity such as *π*, (2) MAR only offers predictions in the short term and it's unclear how these predictions generalise over long timescales, and (3) MAR only considers edge contraction scenarios despite existing habitat loss being more closely related to habitat fragmentation. Given our existing knowledge of extinction debt, which demonstrates the time lag between habitat destruction and the eventual disappearance of the species, these instantaneous snapshots of genetic diversity might not be sufficient in providing enough information of how habitat loss affects species survival in the long term.

The simulations I conducted in this paper aims at addressing these shortcomings by offering realistic predictions of how genetic diversity changes with increasing habitat loss over time. Firstly, these simulations present a new way of evaluating how genetic diversity changes under

non-equilibrium scenarios and non-panmictic population scenarios, something that theoretical population genetics theory lacks. These results aim to provide realistic predictions of how genetic diversity changes under habitat contraction scenarios for realistic populations. Second, we track different metrics of genetic diversity, primarily (π and number of segregating sites), to understand how these measurements change under these habitat contraction scenarios. This enables us to understand both the advantages and disadvantages of different quantifications of genetic diversity. Finally, we offer alternative power law scaling relationships that seek to incorporate evolutionary forces like migration rate, genetic drift and population dynamics under longer timescales to understand how genetic diversity metrics (π) might change over time. These long-term trajectories will undoubtedly be useful when considering different conservation strategies and practices, especially in thinking about recovery potential of species.

Loss of genetic diversity continue long after a halted habitat destruction

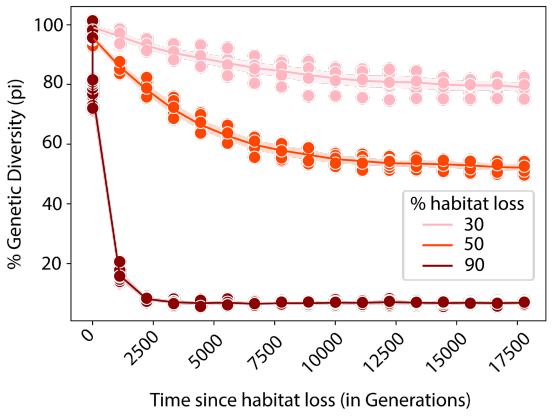

Fig. 1 | Genetic diversity extinction within a species range across 17500 generations
Loss of genetic diversity (π) from geographic range loss driven by climate change leading to carrying capacity loss across 3 different range area losses.

Following the continuous space simulations described in the Methods, we simulated a species with a given population density and dispersal that approximately matches moderate population structure: $z_{MAR} \sim$ 0.2-0.3, or $F_{ST} \sim$ 0.6-0.7. Note that although these values are larger than in humans, they mimic naturally occurring populations of *Arabidopsis thaliana* and other species (Weigel and Mott 2009; Exposito-Alonso et al. 2022). We tracked two common measures of genetic diversity - nucleotide diversity (π) and number of segregating sites (S). First, we explore the dynamics of genetic diversity change across increasing range contraction: 30%, 50% and 90% habitat loss. We then tracked how genetic diversity changed over approximately 20,000 generations. We validated the expectation that genetic diversity continues to decrease long after habitat loss towards a new equilibrium. Genetic diversity metrics at equilibrium seem to be achieved quicker at more drastic levels of range contractions (i.e 90% habitat loss) **(Fig. 1)**. Overall, this suggests that long-term genetic diversity monitoring of wild populations is important for any population that experiences range contractions.

Next, we wanted to understand how genetic diversity metrics differ in both the short and long term time frames across different extents of range contractions (i.e 10-90% habitat loss), where short term is defined as metrics measured immediately after habitat loss while long term is defined as metrics measured approximately 20,000 generations after habitat loss.

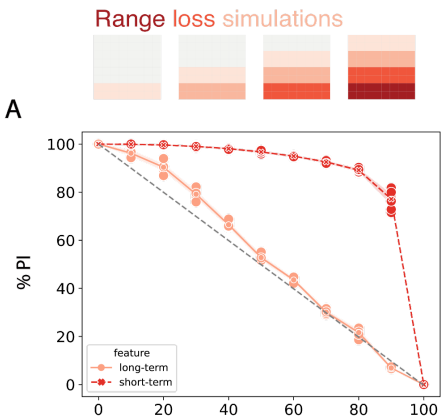

Fig. 2 | Short- and long-term genetic diversity extinction within a species range
(**A**) Loss of genetic diversity (π) or (**B**) Number of segregating sites from geographic range loss driven by climate change leading to carrying capacity loss. Grey line represents the

expected heterozygosity (π) based on $\pi=4Ne\boldsymbol{\mu}$; assuming *Ne decreases exactly as area.*

In the short-term right after habitat destruction, we find that both π and S decreases with increasing habitat loss (π decreases from 100% to 78% (95% CI [74.62, 79.63] across 0, 90% habitat loss **(Fig. 2a)** while S decreases from 100% to 90% (95% CI [92.26, 92.75]) to 43% (95% CI [42.23, 43.61]) across 0, 10, 90% habitat loss respectively) **(Fig. 2b)**. These findings align well with expected values from the approximate power law mutations-area relationship (MAR) (Exposito-Alonso et al. 2022), where genetic diversity loss is expressed as: $1-(1-A_{loss})^z$; where A_{loss} represents the fraction of habitat lost and z represents the scaling coefficient capture the degree of population structure. However, the long-term, termed as 20,000 generations after habitat destruction, we find that π and S decreases more proportionally to reductions in habitat loss (π decreases from 100% to 95% (95% CI [94.95, 97.48]) to 5% (95% CI [5.16, 5.46]) across 0, 10, 90% habitat loss respectively **(Fig. 2a)** while S decreases from 100% to 88% (95% CI [87.99, 89.11]) to 7% (95% CI [6.65, 7.17]) across 0, 10, 90% habitat loss respectively) **(Fig. 2b)**. Because segregating sites *S* are more dependent on sample size than π, , we find greater short and long-term decrease in % segregating sites compared to % π. These results are worrisome, as the long-term power law predictions would approach a scaling coefficient $z \rightarrow 1$.

Within-population genetic diversity may not reflect local genetic diversity loss

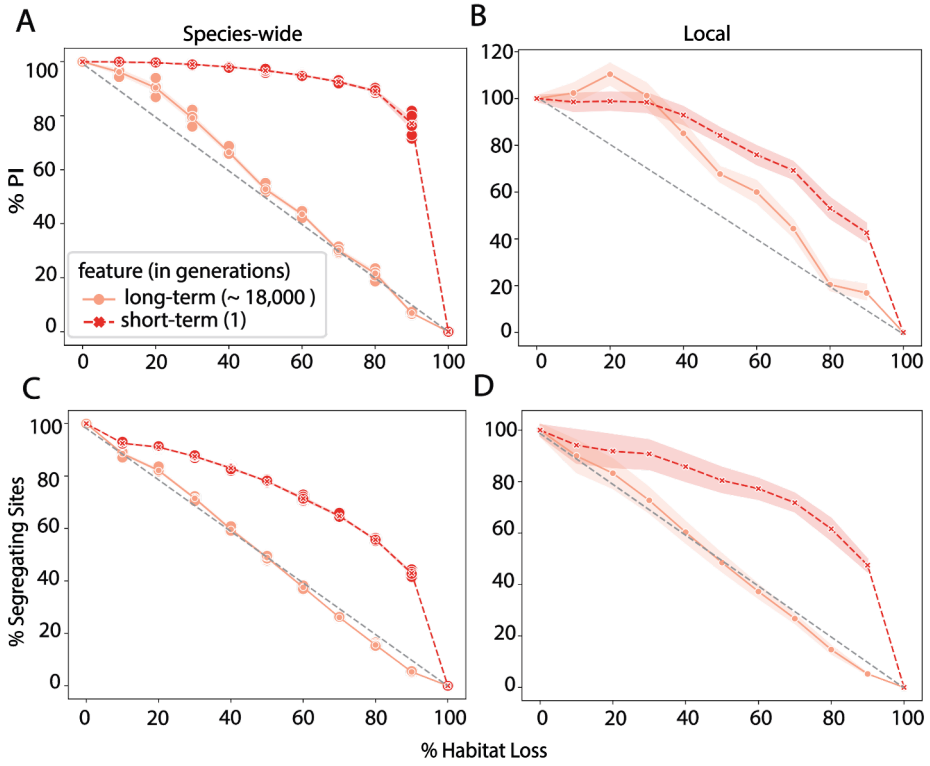

Fig. 3 | Diversity metrics and sampling condition our understanding of species protection under edge contraction scenarios
(**A**) Loss of species-wide genetic diversity (π) with increasing warm-edge destruction (**B**) Loss of local genetic diversity (π) with increasing warm-edge destruction (**C**) Loss of species-wide genetic diversity (number of segregating sites) with increasing warm-edge destruction (**D**) Loss of local genetic diversity (number of segregating sites) with increasing warm-edge destruction

Even in conservation policy guidelines (on Biological Diversity (CBD) 2021; Hoban et al. 2020), it is unclear how genetic diversity should be calculated for a species. For instance, some targets

such as the preliminary proposal of "…genetic diversity of wild and domesticated species is safeguarded, with at least 90% of genetic diversity within all species" apply broadly to species (Díaz et al. 2020), whereas policy articles refer to maintaining genetic diversity within a population (CITE), which may contain only a small fraction of the species-wide genotypes. Given the variability in how genetic diversity can be calculated, we wanted to comprehensively compare trends at different levels. We illustrate that the average within-population genetic diversity might not be reflective of local genetic diversity loss, especially in situations where habitat fragmentation might have occurred **(Fig 6a, b)**. In the case of warm-edge destruction, we find that short-term within-population π is slightly higher than local π across varying levels of habitat destruction while long-term within-population π seems to generally be much lower than local π **(Fig 3a, b)**. On the other hand, both short-term and long-term % segregating sites appear fairly similar for both within-population and local measurements **(Fig 3c, d)**.

Loss of genetic diversity is consistent across different populations sizes (N) as long as population structure remains the same

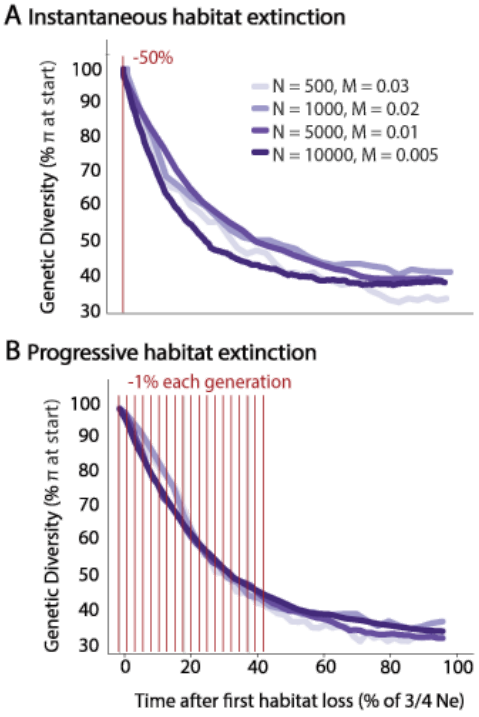

Fig. 4 | Temporal dynamics of genetic diversity loss
(**A**) Long-term trajectories of genetic diversity loss after 50% instantaneous extinction of habitat has halted. Parameters that alter these dynamics include population size (N) and migration rate (M). (**B**) Long-term trajectories of genetic diversity loss with gradual extinction of 50% habitat. Gradual habitat loss was kept at 1% of habitat loss per ~11 generations.

We also wanted to see if these trajectories of genetic diversity vary with the simulation of population size (*N*). Based on the mutation area relationship where genetic diversity equals A^z (Exposito-Alonso et al. 2022), we expect that parameters varying the population structure scaling *z* would alter genetic diversity loss dynamics. We expect that *z* would change proportional to the product of population size and migration, $N \times M$, so adjusting the dispersal rates of populations to obtain a final F_{ST} of approximately ~0.2 (or $10 < N \times M < 100$). We found that despite varying parameters trajectories across time remained consistent **(Fig 4)**. This is true regardless of how fast habitat is lost, i.e. whether it occurs instantaneously or progressively 1% per generation. These results seem contrary to what we expect, that small populations lose genetic variation by genetic drift more rapidly than larger populations. .

Habitat fragmentation leads to unpredictable changes in genetic diversity

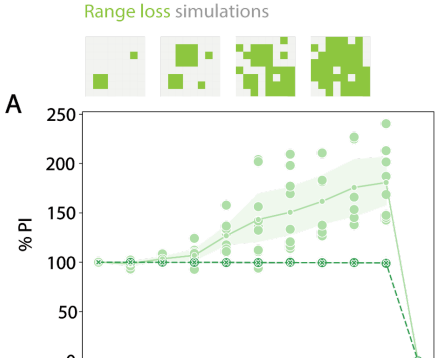

Fig. 5 | Short- and long-term genetic diversity extinction within a species range under habitat fragmentation scenarios
(**A**) Loss of genetic diversity (π) or (**B**) number of segregating sites (S) from geographic range loss driven by habitat destruction with fragmentation. Each point represents a replicate at that specific habitat loss. Simulations were run for 10 replicates.

The mutations-area relationship theory was agnostic to the way habitat area was lost. We then simulated a habitat fragmentation scenario that resembles anthropogenic land use changes (Haddad et al. 2015; Lindenmayer and Fischer 2013; Collinge 2009; Ibáñez et al. 2014). The habitat fragmentation scenarios, where habitat destruction was randomly scattered, led to a short-term genetic diversity (π) that remained constant until almost 100% habitat loss **(Fig. 5a)** while short-term estimates of *S* decrease slightly from 100% to 99% (95% CI [99.96, 100]) to 98% (95% CI [98.97, 99.61]) across 0, 10, 90% habitat loss respectively. These short-term estimates are surprising considering how slight the changes in these values are relative to the edge contraction scenario (**Fig. 1a-b)**.

The most surprising result was that in the long-term, we find that estimates of both π and S are highly unpredictable. Genetic diversity π increases to ~150-210% (95% CI [150.81, 210.85]) at 90% habitat loss with massive variability across 10 replicates (Range of values = 142.7 to 240.5%, Standard deviation = 33.6% , Coefficient of variation = 18.575 , Interquartile range = 60.86%) while *S* increases to ~100-140% at 90% habitat loss, also showing massive variability across 10 replicates (Range of values = 82.34 - 143.16%, Standard deviation = 19.8% , Coefficient of variation = 16.712 , Interquartile range = 31.75). In these simulations, we find that population genetic diversity does not align with demographic losses of the species especially in cases where habitats are fragmented, and may thus fail as early warning of future extinctions.

Upon further analysis, we found that the massive variability across replicates is attributed to the final landscapes connectivity. Replicates with higher within-population genetic diversity have fragmentation maps with largely isolated populations while replicates with lower species-wide genetic diversity have fragmentation maps that still enable gene flow across populations (Fig SX). How fragmented a habitat is can often be captured using connectivity metrics, that could serve as a proxy to understanding gene flows across populations. We postulate that this is largely due to the isolate-breaking effect, where heterozygosity artificially increases due to lack of gene flow between two previously connected populations leading to genetic drift fixing independent alleles.

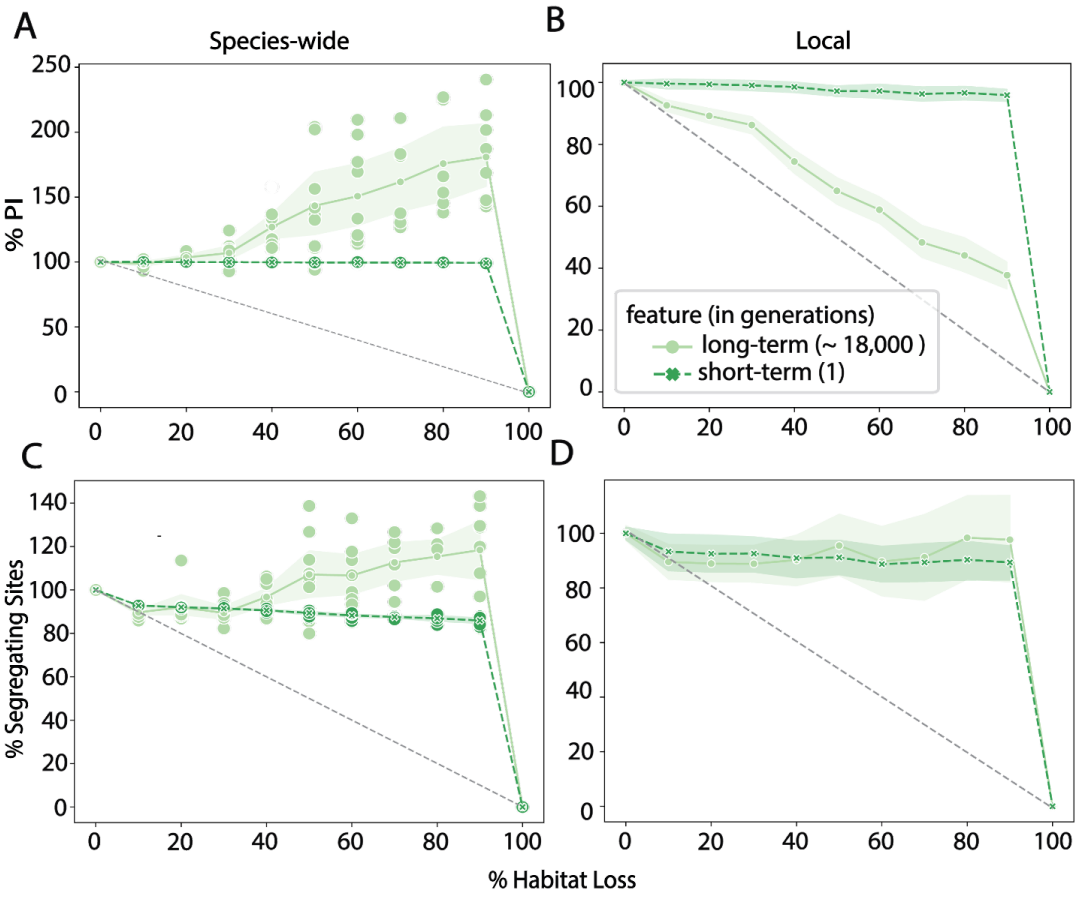

Fig. 6 | Diversity metrics and sampling condition our understanding of species protection under habitat fragmentation scenarios
(**A**) Loss of species-wide genetic diversity (π) with increasing habitat fragmentation (**B**) Loss of local genetic diversity (π) with increasing habitat fragmentation (**C**) Loss of species-wide genetic diversity (number of segregating sites) with increasing habitat fragmentation (**D**) Loss of local genetic diversity (number of segregating sites) with increasing habitat fragmentation

In highly fragmented habitats, where species-wide genetic diversity does not follow habitat loss, we find that only within-species long-term diversity truly reflects the genetic intactness of the species **(Fig 6b, d)**, but unfortunately by definition conservation practitioners would only be able to measure long-term genetic diversity only when it is too late.

With these simulations, we show that habitat connectivity plays an extremely important role in determining the dynamics of genetic diversity loss with habitat loss, suggesting that without a theoretical framework the measure of short-term genetic diversity may not reflect the impacted state of a species, and other metrics like habitat connectivity decrease, or the ratio of local to species-wide genetic diversity might be speculated as most important to report for conservation genetics planning.

Habitat restoration is necessary in the short-term

We finally wonder what may be the dynamics of genetic diversity recovery as habitats are restored. We examined this by simulating habitat restoration at different times: early and late restoration; and tracked species-wide genetic diversity metrics over time. To do this, we utilised simulations to reduce the amount of habitable land and carrying capacity by 50% and varied the amount of generations before fully restoring the habitat to 100% **(Fig 7a, b)**.

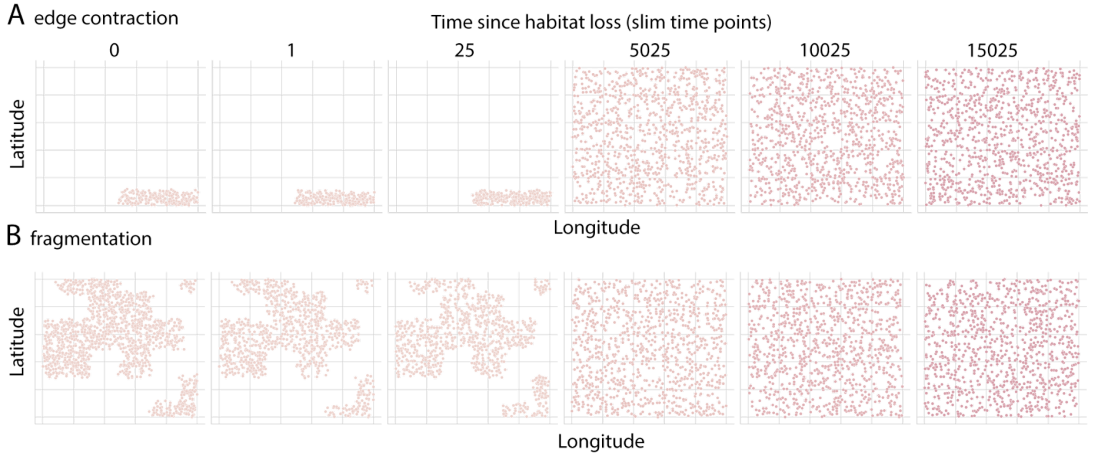

Fig 7 | Locations of individuals in a 6x6 grid during habitat restoration simulations under habitat loss scenarios.
(**A**) Locations of individuals under edge contraction (**B**) Locations of individuals under habitat fragmentation.

Because these simulations are able to capture complex yet neutral evolutionary processes , genetic diversity eventually always bounces back to 100% given sufficient time **(Fig 8)**. This behaviour is more pronounced in the edge habitat loss scenario, where a substantial short-term reduction in genetic diversity is reported at 50% habitat loss before a gradual increase in genetic diversity metrics with time at the point of restoration **(Fig 8a, 8b)**.

Given the complicated genetic diversity trajectories of habitat fragmentation scenarios, we observed less reduction in genetic diversity at 50% habitat loss and a slight increase in genetic diversity metrics at the point of restoration **(Fig 8c, 8d)**.

Overall, these simulations seem to show an overall optimistic conclusion that as long as habitat restoration occurs, genetic diversity will eventually be restored. However, given that these long-term trajectories span tens of thousands of generations, these optimistic conclusions might prove to be unrealistic, and are likely species specific. I argue that fast generation time species will be highly impacted by long-term genetic diversity loss but its genetic diversity loss may be more easily recoverable, for long generation time species it may find impossible to recover their genetic diversity at scales relevant for conservation policy.

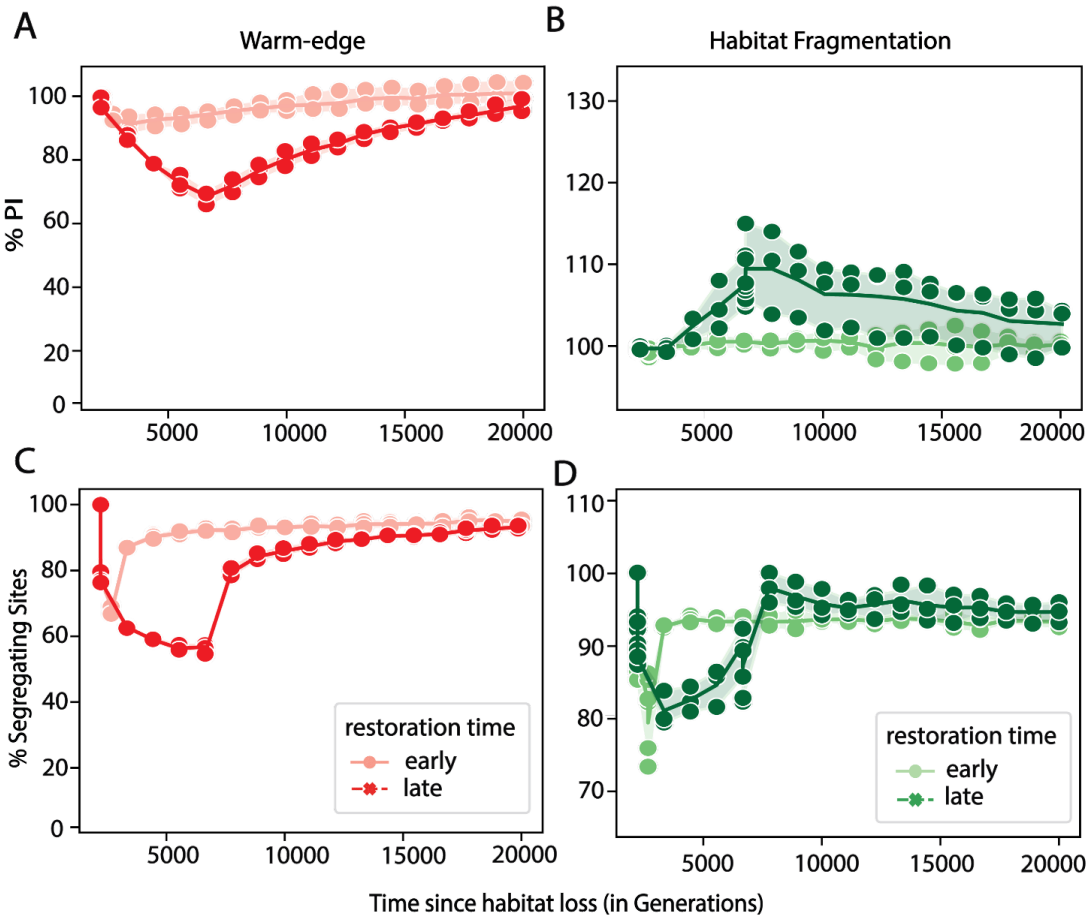

Fig. 8 | Genetic diversity loss and recovery through habitat restoration across edge extinction and habitat fragmentation simulations

(**A**) Long-term trajectories of genetic diversity loss after 50% warm-edge instantaneous extinction of habitat has halted with eventual restoration. Parameters that alter these dynamics include restoration time. (**B**) Long-term trajectories of the number of segregating sites after 50% warm-edge instantaneous extinction of habitat has halted with eventual restoration. Parameters that alter these dynamics include restoration time. (**C**) Long-term trajectories of genetic diversity loss after 50% instantaneous extinction of habitat fragmentation has halted with eventual restoration. The parameter that alter these dynamics include restoration time. (**D**) Long-term trajectories of the number of segregating sites after instantaneous extinction of 50% of habitat with fragmentation has halted with eventual restoration. Parameters that alter these dynamics include restoration time.

Conclusions

This work aims to provide predictions of how genetic diversity metrics, often used to assess population viability and persistance, might change in the long term. The hope is that these findings will help inform and adjust conservation priorities to ensure that existing species that have incurred range contractions are tended to. Long-term genetic diversity predictions are of particular significance since long-term estimates of existing populations are often hard to measure. This is because the predictability of long term effects heavily rely on how habitats are lost, connectivity of the final population and population demographics (such as life history traits and spatial structure) **(Fig 6)**. First, we showcase how genetic diversity trajectories change with habitat loss.

In this work, we find that genetic diversity loss continues long after habitat loss and its rate of genetic diversity decay accelerates in situations where more habitat has been lost **(Fig 1)**. This is likely because smaller populations will experience higher drift-load after a bottleneck event (habitat range contraction) which might cause inbreeding and eventual inbreeding depression (or segregating load) (Kirkpatrick and Jarne 2000; Frankham 2005; Willi, Griffin, and Van Buskirk 2013; LaBar and Adami 2017; Spigler, Theodorou, and Chang 2017). During population declines, genetic drift and inbreeding could lead to the homozygosity of rare and recessive alleles over generations (Pinto et al. 2023). This phenomenon is known as “drift debt”, which is the time-lag of evolutionary genetic change with population size decline (Gilroy et al. 2017). This is particularly concerning given that hundreds of species have already lost close to a third of their original range (Jetz, McPherson, and Guralnick 2012). Using this knowledge, we wanted to understand and compare these predictions to previously estimated projections of existing genetic diversity loss.

We found that short-term predictions of genetic diversity metrics, such as π and S, can be reliably validated using the mutations-area relationship (MAR). However, for long-term projections, especially in the context of extinction debt, relying solely on instantaneous measurements may overestimate genetic diversity within existing populations **(Fig 1)**. To address these challenges, we’ve employed highly realistic continuous space simulations, offering an avenue to dissect situations where traditional population genetics theory and non-spatial methodology might fall short (Kyriazis, Robinson, and Lohmueller 2022). We hope that these simulations offer a way for us to make better informed decisions especially in the context of conservation policy and prioritisation schemes, especially when considering species with shorter generation times, like insects. To fully understand the advantages of the utility of continuous space simulations, we briefly compared these projections to estimated heterozygosity using traditional population genetics theory.

Surprisingly, under edge contraction scenarios, we find that predicted long-term π at equilibrium follows traditional population genetics theory: $\pi = 4N e \mu$ **(Fig 2)**. This is surprising since wild populations violate several assumptions. First, during range contraction, population size is shrinking and populations are not in equilibrium. It is also unlikely that long-term equilibrium would be reached since these time frames span thousands of generations (i.e $10\times Ne$ in continuous spatial simulations) (Kyriazis, Robinson, and Lohmueller 2022). Second, accurate estimations of Ne are difficult to obtain and the methods used to estimate Ne are vast and vary in performance (Harris et al. 2017; Kajtoch et al. 2014; Rieman and Allendorf 2001; Sarno et al. 2015; Wennerström et al. 2017). Wright’s original formulation of Ne assumes a closed panmictic population but in wild populations, individuals are distributed in continuous space across a landscape and mating probabilities are likely to follow a function of Euclidean distance (or isolation by distance; IBD) (Wright 1931, 1943). Thus, while the overall trend for long-term genetic diversity trajectories (slope of the line) might be accurate, the absolute value of genetic diversity predicted may not be reliable (intercept of the line). Finally, omitting crucial information like population demographics, life history traits and population spatial

structure (z_{MAR} , F_{ST}) when estimating genetic diversity under habitat loss regimes could lead to erroneous recommendations for individual species. While utilising expected heterozygosity might be helpful in cases where empirical data and simulations are not readily available, simulations offer a new way to predict genetic diversity loss with habitat loss that takes into consideration population dynamics, demographics and life history traits. We do caution that the reliability of these predictions are incredibly dependent on species-specific genetic and demographic factors. Hence, we proceeded to test out the effect of population structure on genetic diversity trajectories.

We performed tests to understand population size (N) and spatial structure effect on genetic diversity trajectories. Regardless of population size (N), genetic diversity trajectories remain consistent, with spatial structure (z_{MAR} , F_{ST}) emerging as a dominant factor influencing genetic diversity **(Fig 3a)**. Additionally, the rate of range contraction has minimal effect on the rate of genetic diversity decay over time **(Fig 3b)**. Our simulated gradual range contraction of 1% each year to 50% of total habitat loss shows similar genetic diversity trajectories as an instantaneous reduction of 50% habitat loss. The phenomenon of "drift debt" (mentioned above) likely occurs on the order of hundreds to thousands of generations, explaining the lack of observable differences between gradual and instantaneous habitat loss scenarios **(Fig 3)**. Understanding that not all habitat loss is edge contraction, we attempted to understand how genetic diversity trajectories differed under different habitat loss scenarios – specifically habitat fragmentation.

In situations where populations have experienced habitat fragmentation, short-term estimates of genetic diversity (π and S) were harder to predict using methods like MAR, showcasing a potential drawback of relying solely on non-spatial predictions **(Fig 4)**. Despite drastic reductions in habitats, decreases in genetic diversity (π and S) were slight if any at all **(Fig 4)**. What was more puzzling were the projections in the long-term. Across 10 replicates, we found that genetic diversity (π and S) increased with increasing habitat loss **(Fig 4)**. While high genetic diversity (π) is frequently correlated to an increased ability for species' to adapt (Kardos et al. 2021), fragmented populations can also maintain high genetic diversity (π) in the case of fragmented habitat loss (Habel and Schmitt 2018). This is one case where an increase in genetic diversity is not necessarily good since the inflated genetic diversity is likely attributed to neutral (or deleterious) variation that is not likely adaptive (Kardos et al. 2021). Moving forward in the field of conservation genetics would require us to re-establish which genetic diversity metrics are representative of how genetic diversity changes with habitat loss.

We found that global statistics like species-wide genetic diversity might not be particularly informative in cases where habitats are fragmented. Furthermore, our study underscores the significance of measuring local genetic diversity (π or S) over species-wide metrics in fragmented habitats, where random sampling can inflate genetic diversity metrics if individuals are from isolated populations, a phenomenon known as the isolate-breaking effect ((Wahlund 1928)). This finding emphasises the importance of how individuals are sampled in the wild, which genetic diversity metrics are adopted and how to best define populations. Under realistic scenarios, measuring local genetic diversity (π or S) as opposed to species-wide genetic diversity is much more helpful in enabling us to properly assess population viability to changing environments, as well as in informing us about species' conservation priority. These simulations provide a cautionary tale in helping us understand situations where measuring genetic diversity (π) in wild populations could mislead us into thinking that populations are doing okay when they are not. This is because, in the wild, it's often difficult to have a good sense of which individuals are part of which populations. Hence, getting

species-wide statistics especially using traditional population genetics sampling methods should be revisited.

Finally, in light of the United Nation's 30 x 30 goal, our study investigates the restoration of genetic diversity following habitat restoration. Our findings demonstrate that habitat restoration, regardless of timing, leads to the expected recovery of genetic diversity in the long term (Fig 7, 8). As expected, we find that genetic diversity remains stable in fragmented habitats relative to edge range contraction **(Fig 7, 8)**. Hence, making the recovery of genetic diversity more prominent for edge range contraction. However, despite these optimistic trajectories, we strongly emphasise the importance of preventing initial habitat loss through conservation programs since recovery of genetic diversity through natural mutations that are then randomly kept by drift or maintained by natural selection usually takes thousands of generations. Hence, full recovery of genetic diversity within a population will span thousands of generations, as seen in our simulations **(Fig 7)**.

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