Inescapable bottlenecks: Demographic recovery cannot replenish evolutionary potential over conservation timeframes

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Abstract

Maintaining within-species genetic diversity is a central goal of biodiversity conservation, because it determines a species' capacity to adapt to environmental change. Species that have experienced population bottlenecks are expected to suffer from an increased risk of extinction unless their genetic diversity is able to recover. A recent study proposed that rapid demographic expansion in a bottlenecked koala population is restoring evolutionary potential through the recovery of rare genetic variants. Using simulations and population genetic models, we argue that evolutionary potential takes thousands of generations to recover after demographic recovery, well beyond a realistic conservation timeframe. This is because adaptation is more likely to occur from standing genetic variation than from de novo mutations, and evolutionary potential is more closely tied to genome-wide heterozygosity than to the number of rare variants. Reanalysis of koala genomic data further supports this, highlighting that functional genetic diversity remains reduced across all allele frequency classes and providing no evidence that evolutionary potential has been restored. Bottleneck-induced loss of diversity also leads to reduced mutational load, but this should be interpreted with caution because it is the conversion of heterozygous to homozygous load in bottlenecked populations that drives the expected increase in genetic load, not the overall mutational load. Our study shows that some genomic indicators of recovery can be misleading when interpreted in isolation, and that demographic recovery alone is not a viable path to restoring the evolutionary potential of threatened species.

Key words

Evolutionary potential, Genetic load, Koalas, Heterozygosity, Bottleneck, Effective population size, Threatened species

Introduction

Maintaining global biodiversity is essential for the regular and reliable function of the world's agricultural, economic, and health systems (Scheffers et al. 2016). Despite this, anthropogenic influences continue to deteriorate ecosystems, leading to widespread losses in species (Cowie et al. 2022) and genetic diversity (Shaw et al. 2025). Fortunately, the importance of maintaining genetic diversity is becoming increasingly recognised in global conservation policy. The United Nations Convention on Biological Diversity (CBD) Kunming-Montreal Global Biodiversity Framework (GBF) marks a significant improvement in this regard, introducing its support for the preservation of genetic diversity of wild species (CBD 2022). This includes

Target 4 of the agreement which aims to maintain and restore genetic diversity, and as a result, the evolutionary potential of species. Evolutionary potential can be defined as the capacity of a population to adapt in response to novel or changing environmental conditions (Forester et al. 2022). As species face increasingly dynamic environmental conditions, novel diseases and threats, the ability to adapt is vital for long-term persistence. As adaptation requires genetic variation for selection to act upon, maintaining genetic diversity has long been the focus of conservation genetic projects and there is a suite of tools available to management practitioners (Frankham et al. 2019). However, the options for restoring the genetic diversity needed for evolutionary potential in wild populations are much more limited.

One species of great conservation concern is the koala (*Phascolarctos cinerus*), the last remaining representative of the marsupial family Phascolarctidae. The large geographic range of the koala is atypical of a threatened species, as it spans more than 3000 km across the eastern and south-eastern states of Australia (Queensland, New South Wales [NSW], Victoria, and South Australia). Koala populations have faced numerous threats since European arrival, including the fur trade of the late 1800s and early 1900s (Phillips 1990). This hunting, combined with land clearing, wildfires and the spread of disease, caused a large reduction in koala population sizes across Australia by the 1930s, including their extirpation in South Australia and near extinction in Victoria (Phillips 1990; Melzer et al. 2000; Menkhorst 2008). In 1923, a small number of koalas were translocated to two small Victorian islands, where their populations grew and subsequently served as sources for reintroduction across Victoria and South Australia (Menkhorst 2008). The situation for the species changed markedly by the 1980s when koalas had become overabundant in parts of southern Australia, causing the over-browsing of eucalypt trees (Menkhorst 2008; Whisson & Ashman 2020). This led to calls for koala culls to reduce population density, but such measures were avoided by the deployment of contraceptives (Tyndale-Biscoe 1997; Duka & Masters 2005; Hynes et al. 2010).

More recently, koala populations in NSW and Queensland have been increasingly fragmented by habitat loss and expanding urban infrastructure (McLennan et al. 2024). Genomic analyses have identified five genetic populations (Figure 1), which separated from each other following population expansion after the last glacial maximum (Adams-Hosking et al. 2011; McLennan et al. 2024; Kovacs et al. 2026). Contemporary threats to koalas include disease (mainly chlamydia and koala retrovirus), feral dog attacks, vehicle strikes, and bushfires (Menkhorst 2008; Adams-Hosking et al. 2016; Cristescu et al. 2023). The species is thought to have declined by 24% over three generations around 2012 (Adams-Hosking et al. 2016) and was further reduced by the 2019/2020 Black Summer bushfires (Cristescu et al. 2023). In 2022, koalas were listed as Endangered in Queensland, NSW, and the Australian Capital Territory (Department of Agriculture, Water and the Environment 2022).

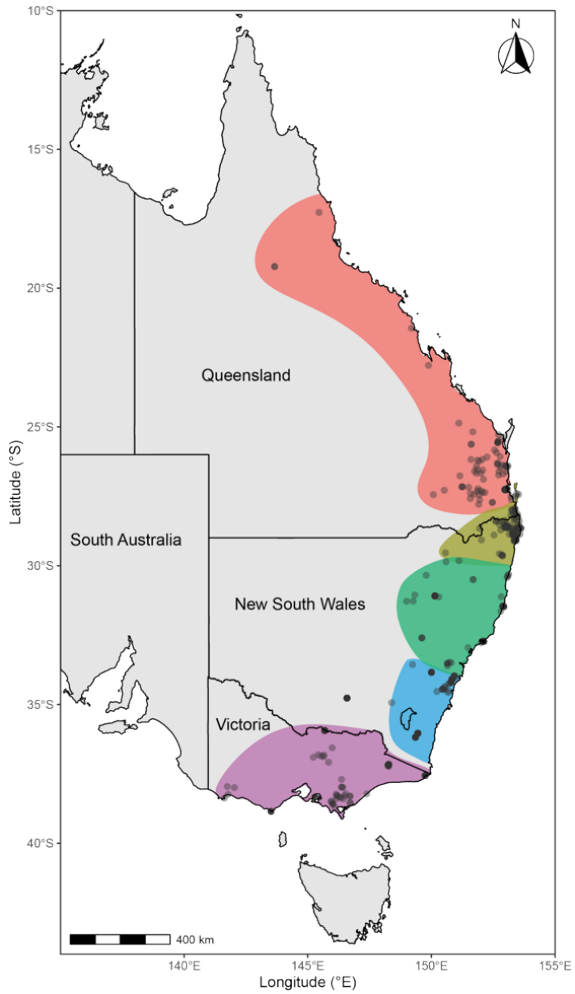

Figure 1. *Map of eastern Australia with dots showing locations of koala samples from Ahrens et al. (2026). Coloured shading indicates the five genetic clusters identified by McLennan et al. (2024).*

The substantial demographic recovery of some Victorian koala populations from the 20th-century population bottleneck is an exciting development for the endangered species, and is in contrast to demographic trends in northern populations. Recently, Ahrens et al. (2026) reported that the demographic recovery has been accompanied by the genetic recovery of Victorian koalas. The study proposed that increased mutation and recombination, driven by an expanding population, has regenerated evolutionary potential. In other words, that rapid growth can allow genetically depleted populations to effectively escape the genetic effects of past bottlenecks and the extinction vortex (Wang 2026). This finding marks an encouraging management outcome for an iconic, endangered marsupial and could provide hope for the practice of conservation genetics more generally. However, the conclusions of Ahrens et al. (2026) apparently contradict conservation genetic theory, which does not predict the recovery of evolutionary potential over such a short timescale.

Here, we discuss the use of genetic diversity measures to infer evolutionary potential and use simulations to estimate the timeframe in which they recover following a population bottleneck. We reinterpret the results of Ahrens et al. (2026) and conclude that the genomic data do not demonstrate the recovery of evolutionary potential in southern koala populations. The increase

in rare alleles is a positive indicator of demographic recovery, but theory predicts that the population remains depleted in evolutionary potential. We argue that genome-wide heterozygosity is a better indicator of evolutionary potential and show that it cannot be restored over conservation management timeframes. These conclusions highlight the importance of preserving pre-existing genetic diversity for maintaining the evolutionary potential of species. We also assess claims of reduced mutational load in Victorian koalas and the use of this as a proxy for genetic load, based on the same dataset (Ahrens et al. 2026), which provide an interesting model for studying the relationship between demographic recovery and deleterious variation. We conclude that further work is needed to determine whether this population has truly escaped inbreeding depression.

Rare allele dynamics do not indicate the recovery of evolutionary potential

Evolutionary potential is lost during population bottlenecks as genetic diversity is eroded by genetic drift (Franklin 1980). This loss can be measured by examining the richness of diversity (quantified by the number of segregating sites or alleles in the population or Waterson's θ) and the evenness of diversity (the allele frequencies of variants, quantified by SNP heterozygosity, H_o and H_e) (Hoban et al. 2022). Richness and evenness can be evaluated together by quantifying the expected genome-wide heterozygosity (also known as gene or nucleotide diversity, π) or the observed genome-wide heterozygosity (also known as autosomal heterozygosity). The site frequency spectrum (SFS) also captures both of these properties by plotting the number of alleles at each frequency to show the balance of rare versus common variants (Figure 2b) (Allendorf et al. 2012). Rare and common alleles contribute equally to richness measures, but rare alleles have a negligible effect on autosomal heterozygosity and reduce SNP heterozygosity (Allendorf 1986). The evolutionary potential of a species depends on both the richness and evenness of genetic diversity (Allendorf et al. 2012), so both are important for describing the genetic composition of a population (Hoban et al. 2022).

At mutation–drift equilibrium, measures of richness and evenness are correlated, but richness is expected to approach its equilibrium value more quickly after a change in population size (Nei et al. 1975, Allendorf 1986). This is because there is an enormous turnover of rare mutations, with each generation carrying a new set of private mutations. When there is a change in population size, the associated change in mutational input and the effects of genetic drift will lead to a rapid change in the number of rare alleles (Figure 2). In contrast, it takes many generations for changes in population size to influence the number of common alleles, except in the cases of extreme bottlenecks.

The population genomic dynamics of koalas can now be studied in detail thanks to the Koala Genome Survey, which sequenced over 400 genomes from across the three eastern states of Australia: Victoria, NSW, and Queensland (Hogg et al. 2023). An initial analysis of these genomes reported lower heterozygosity in Victorian koalas than in those from northern populations (McLennan et al. 2024). Ahrens et al. (2026) further dissected the dataset into 27 populations based on local government areas, showing that each of the eight local populations

in Victoria has reduced autosomal heterozygosity (Fig. 2a in Ahrens et al. (2026)) driven by fewer heterozygotes for common alleles (MAF > 0.05) and low-frequency alleles (0.01 < MAF < 0.05) compared with NSW and Queensland populations. Very rare alleles (MAF < 0.01) are also reduced in five of the eight Victorian populations. A lower number of variants across all three allele frequency bins is consistent with expectations under a severe population bottleneck, where genetic drift reduces variation over sufficient time for the allele frequency distribution to approach equilibrium (Figure 2).

Data reported by Ahrens et al. (2026) revealed that three of the eight Victorian populations have an elevated number of heterozygotes in the rare frequency bin (MAF < 0.01), consistent with recent population expansion. This pattern is supported by demographic reconstructions, whereby two of these populations were estimated to have experienced the largest recent increases in N_e. During population expansion, increased mutational input and reduced genetic drift produce a rapid increase in the emergence and retention of new alleles. Some of these alleles will rise in frequency in the population through drift (and in some cases positive selection), but this process occurs over much longer timeframes (on the order of thousands of generations after demographic recovery). This disproportionate rebound of rare alleles after recovery from a bottleneck is exactly what population genetic theory predicts (Maruyama & Fuerst 1984, 1985; Tajima 1989; Excoffier et al. 2009) and can be observed by simulating the recovery of a population following a bottleneck (as we show in Figure 2) (Haller et al. 2026).

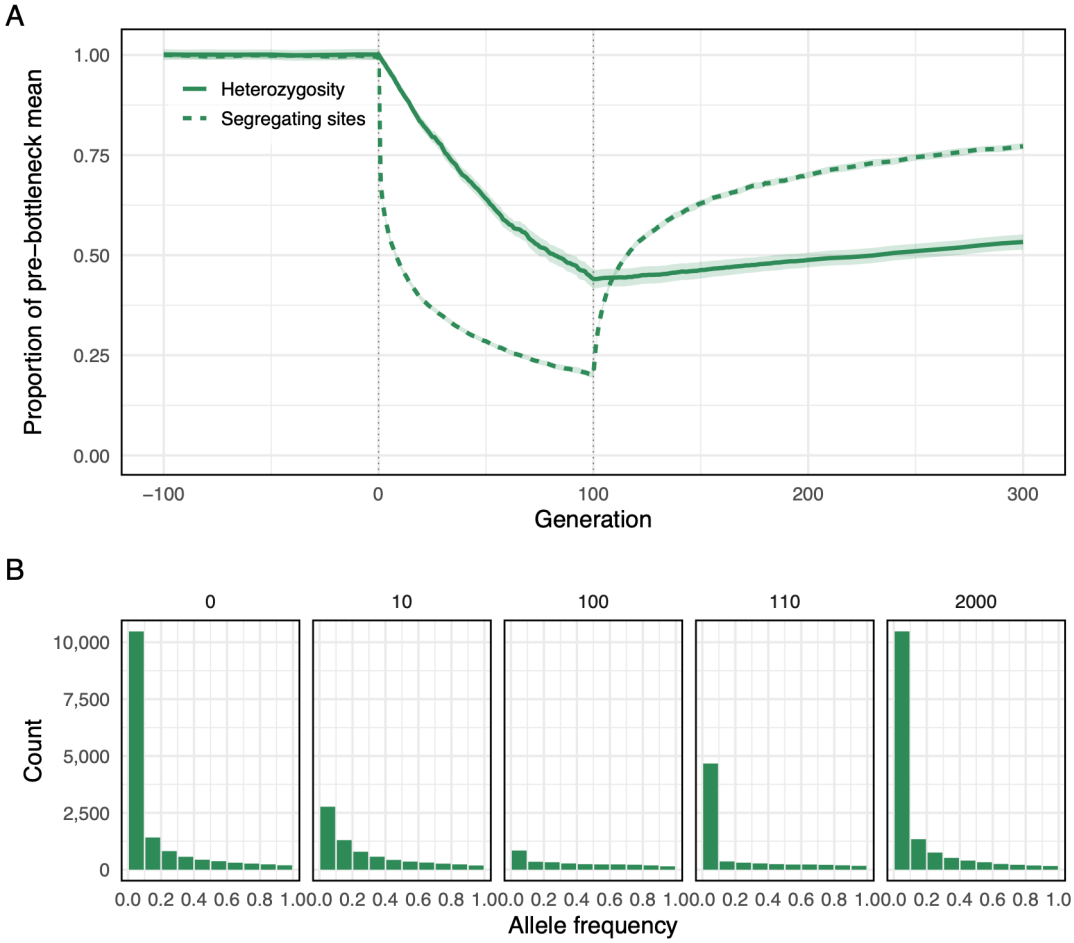

Figure 2. *Simulations of the loss and recovery of diversity during and after a population bottleneck (details available in the Appendix). Simulations were run with an initial population size of Nc = 500 before the population was reduced to Nc = 50 (bottleneck) for 100 generations, followed by a return to Nc = 500. Twenty replicate simulations were run averaging heterozygosity and the number of segregating sites across replicates, with pale ribbons indicating 95% confidence intervals. (a) Comparison of the loss and recovery of the number of segregating sites (dashed line) and heterozygosity (solid line) during and after a bottleneck. (b) Site frequency spectra at five time points through the simulation. Pre-bottleneck, the population is in mutation–drift equilibrium and the site frequency spectrum has an equilibrium distribution. At 10 and 100 generations after the population-size reduction, there has been a large decrease the number of segregating sites which is predominantly driven by the loss of rare alleles. At 110 generations, shortly after the population-size recovery, there has been a large increase in the number of segregating sites which is predominantly driven by the gain of low-frequency alleles. At 2000 generations, there has been enough time for the frequency of rare alleles to increase by drift and the site frequency spectrum returns to its pre-bottleneck equilibrium distribution.*

The recovery of rare alleles has been used widely as an indicator of recent demographic change, but is less commonly used to indicate the recovery of evolutionary potential. Evolutionary potential is determined by the amount of genetic variance in the population, because this variation provides the substrate for natural selection. However, not all forms of genetic diversity are expected to contribute equally to the ability of a population to adapt. According to quantitative genetic theory, the ability of a population to adapt depends on the amount of additive genetic variance. The genetic variance contributed by a bi-allelic locus to a quantitative trait is proportional to $2pq$ (heterozygosity), so rare alleles (when p is very small) contribute minimally to genetic variance (Falconer & Mackay 1996). Hence, genetic diversity metrics that

only measure richness, such as the number of segregating sites, are not expected to correlate as strongly with evolutionary potential as genome-wide heterozygosity, especially in non-equilibrium systems.

Adaptation can occur from *de novo* mutations (e.g. Fulgione et al. 2022; Stone & Wessinger 2024), but standing genetic variation is thought to be more important for adaptation (Barrett & Schluter 2008). This is because *de novo* mutations start at a low frequency while older variants have had time to reach higher frequencies in a population, and are therefore more likely to be exposed to selection. These older variants have lower linkage disequilibrium (they are present on more diverse genetic backgrounds), allowing more effective selection and softening selective sweeps, which would otherwise further reduce genetic diversity (Barrett & Schluter 2008). Standing genetic variation can also increase the likelihood that *de novo* mutations produce new phenotypes, leading to increased evolvability (Tenaillon & Matic 2020). These results suggest that allelic richness is the better indicator of recent demographic processes, and that heterozygosity is the better indicator of the evolutionary potential in a population, at least over the short term.

The number of segregating sites and heterozygosity recover on very different timescales. The recovery of rare alleles can be observed over conservation timeframes (a few generations), whereas the recovery of common alleles and heterozygosity is much slower. Heterozygosity in a population can be estimated using the mutation–drift evolutionary model (Malécot 1948, Kimura and Crow 1964), a well-established relationship that underpins modern conservation genetics (e.g., Frankham et al. 2010; Hedrick 2011; Allendorf et al. 2012). Classic estimates put full recovery after a bottleneck at over 100,000 generations (Nei et al. 1975; Lande & Barrowclough 1987), leading many studies to treat mutation as too slow to be able to restore diversity in threatened species (Lacy 1987; Frankham 2022). However, those estimates were derived for large populations and might not transfer well to small, conservation-relevant populations. Using the same model at conservation-relevant effective population sizes, we estimate that a population with Ne = 500 starting at 50% of equilibrium heterozygosity takes ~1,600 and ~2,500 generations to reach 90% and 95% of the starting heterozygosity, respectively (Figure 3a; details in the Appendix). Since the recovery of heterozygosity occurs over long timescales, genetically depleted populations, like Victorian koalas, will show reduced evolutionary potential over conservation management timeframes.

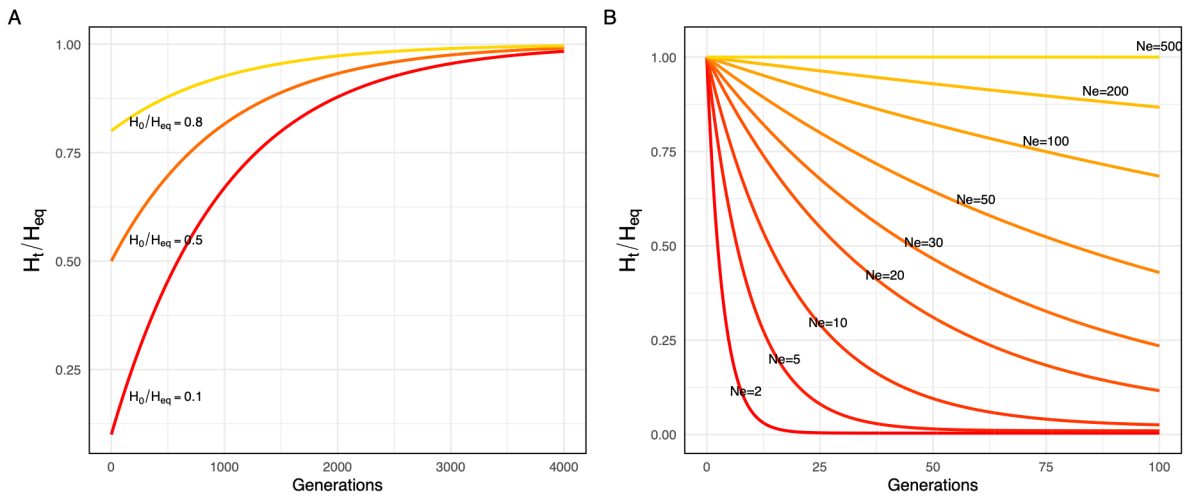

Figure 3. *(a) Recovery of heterozygosity after a population bottleneck. The plot shows the gain of genetic diversity in a population with Ne = 500, starting at 10%, 50%, and 80% of the equilibrium heterozygosity. The y-axis indicates heterozygosity, divided by the equilibrium heterozygosity at Ne = 500. (b) Loss of heterozygosity during a population bottleneck. The plot shows the loss of genetic diversity in a population with various bottleneck sizes, starting at the equilibrium diversity when Ne = 500. The y-axis shows heterozygosity divided by the equilibrium heterozygosity for Ne = 500. Formulas and scripts can be found in the Appendix.*

In contrast to the slow process of recovery, heterozygosity is lost rapidly during a population bottleneck. From equilibrium at Ne = 500, a reduction to Ne = 20 causes 50% of heterozygosity to be lost in just 30 generations (80% in 80 generations); at a bottleneck size of Ne = 5, the same losses occur in 7 and 16 generations, respectively (Figure 3b). This asymmetry, where diversity is lost quickly during a bottleneck but regained slowly afterward, is a direct consequence of how Ne determines the rate at which genetic diversity approaches equilibrium. This also explains why more severe bottlenecks lead to the faster loss of genetic diversity, although they are also approaching a smaller equilibrium value (Figure 3b).

In consideration of these patterns, we assert that it is vital that conservation genetic projects do not equate the quick recovery of rare alleles to the recovery of evolutionary potential following a bottleneck. The recovery of evolutionary potential is more likely to occur on a similar timeframe to the recovery of heterozygosity, meaning that it cannot be expected within the timeframes that are typical of conservation management (Frankham 2022).

Functional variant patterns are consistent with bottleneck-induced reduction

Conservation genetics has historically measured genetic diversity via randomly sampled genetic markers, which are assumed to be evolving neutrally (Kardos et al. 2021). However, there is growing emphasis on analysing functional variants that are more likely to influence phenotypic traits and affect evolutionary potential. A common approach to compare the amount of functional variation between populations is the $R_{X/Y}$ test, which is used to assess whether one population carries a higher proportion of functional to intergenic variants than another (Do et al. 2015). Because most putatively functional variants are expected to be deleterious, an increase in this ratio is typically interpreted as evidence of reduced purifying selection, often

driven by stronger genetic drift (Do et al. 2015). Using this approach, Ahrens et al. (2026) found that koalas in Victoria had a higher ratio of putatively functional to intergenic variants than those in NSW and Queensland. This aligns with $R_{X/Y}$ results from a previous analysis of koala genomes (Gates et al. 2025). Under conventional interpretation, this pattern would suggest reduced efficacy of purifying selection in the Victorian population, consistent with a history of strong bottlenecks and increased genetic drift. In contrast, Ahrens et al. (2026) attributed the elevated proportion of functional variants in Victoria to rapid population growth, relaxed selection, and increased mutational input. However, an increase in mutational input alone is not expected to raise the ratio of functional to intergenic variants, because both classes of variants should increase proportionally. Although a reduction in the efficacy of selection can occur at expansion fronts due to reduced local Ne (Robinson et al. 2022), this too would result in a disproportionate increase in the number of deleterious variants. Therefore, it is most likely that the increase in the proportion of functional variation represents an increase in deleterious variation in the Victorian population, rather than the recovery of beneficial variation.

When analysing the total number of functional alleles, Ahrens et al. (2026) concluded that koalas in Victoria have a higher number of common functional variants compared to those in NSW and Queensland (Figure 4b; Fig. 5 G-J in Ahrens et al.). Rather than counting the number of functional variants in each individual, Ahrens et al. (2026) counted the number of functional variants in each state and divided by the number of samples from that population. This was done to correct for the increased detection of variants in populations with more samples. However, this procedure leads to overcorrection, because variant discovery plateaus, rather than scaling linearly, with increasing sample size. This overcorrection is strongest for common variants (MAF > 0.05): at 50 diploid samples, >99% of true common sites are already recovered (Figure 4a), so standardising by sample size overestimates common-variant counts for the more sparsely sampled populations in Victoria (N = 72) and Queensland (N = 104) relative to the koalas in NSW (N = 242). The impact of uneven sampling on counting rare alleles can be overcome by using rarefaction methods (El Mousadik & Petit 1996; Kalinowski 2004; Hemstrom & Christie 2026) but for higher-frequency alleles, comparing raw counts is minimally impacted by sample size. Comparing the uncorrected number of segregating sites reveals that the Victorian population has the lowest number of common functional variants (Figure 4c), consistent with its already lower counts of low-frequency and rare variants. A further issue is that Ahrens et al. (2026) counted any site with a nonzero alternative-allele frequency in a state, including sites “fixed” for the alternative allele (up to 23% of sites for VIC in some categories; Figure 4b). Fixed sites do not contribute to standing genetic variation and many of these variants are likely ancestral rather than derived, as the reference genome is from a northern population (Johnson et al. 2018). Comparing segregating (non-fixed) functional variants is the more meaningful measure of functional diversity (Figure 4b,c).

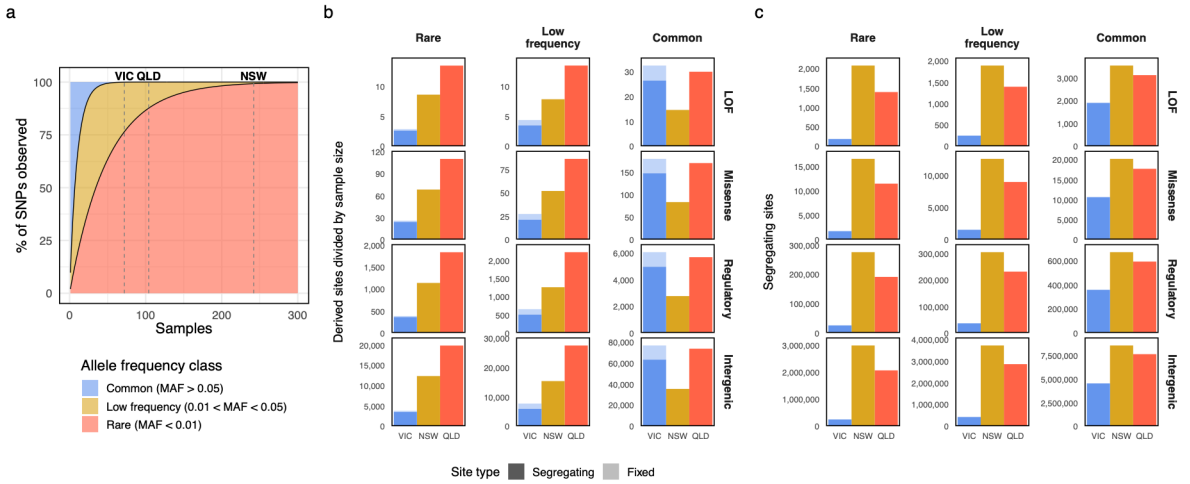

Figure 4. *(a) Expected percentage of SNPs across allele frequency classes that would be observed for different sample sizes of diploid individuals. Vertical dashed lines indicate the sample sizes for Victoria (VIC; N=72), Queensland (QLD; N=104), and NSW (N=242). (b) Numbers of observed functional variants in each state, divided by the number of samples in each population, across three minor allele frequency (MAF) classes, and four functional categories: Loss Of Function (LOF), Missense, Regulatory, and Intergenic as presented in Ahrens et al. 2026. Functional variants separated into those that are segregating or fixed in the state (c) Numbers of segregating functional variants.*

Ahrens et al. (2026) also reported a comparable number of private alleles across states overall, although within the common allele frequency bin, Victorian koalas had the highest number of private alleles and Queensland koalas had a markedly low number. Beyond the same sample-size standardisation issue, this finding is further confounded by sampling design; one of the five known genetic clusters spans the Queensland–NSW border with high gene flow into northern Queensland (Figure 1; McLennan et al. 2024), so splitting this cluster across two states artificially depresses the count of private alleles in the Queensland population.

Taken together, the functional variant data indicate that Victorian koalas have less functional diversity than NSW or Queensland koalas across all three frequency bins, reinforcing the picture of reduced evolutionary potential already evident from heterozygosity and total segregating sites. That the remaining diversity is disproportionately functional is best explained by the greater power of drift during the bottleneck, increasing the proportion of deleterious variants, rather than by any gain in adaptive variation. There is no evidence to support the claim by Ahrens et al. (2026) that "low genetic diversity does not always imply limited evolutionary potential", as the study provides no direct measurement of evolutionary potential, such as heritability or evolvability. A more accurate reading of their findings is that low genetic diversity does not always prevent demographic recovery.

A possible contributor to the successful recovery of Victorian koalas could be higher reproductive fitness driven by reduced genetic load. Genetic load describes the reduction in fitness driven by deleterious variants (Bertorelle et al. 2022). As fitness data is not available

for most non-model species, many studies have instead measured genomic proxies as indicators of genetic load (Dussex et al. 2023). One method for assessing the fitness impact of putatively functional variants is Genomic Evolutionary Rate Profiling (GERP), which allocates a fitness score to a set of conserved loci, based on the number of substitutions observed across a multi-species alignment (Cooper et al. 2005; Davydov et al. 2010). Ahrens et al. (2026) used GERP scores inferred from a 35-species alignment of mostly eutherian mammals to count the number of deleterious alleles among the koalas in each state. GERP has been shown to have lower power for detecting lineage-specific purifying selection (Huber et al. 2020), and with only the tammar wallaby (*Notamacropus eugenii*, family Macropodidae) representing Australian marsupials in the alignment, GERP scores might not capture koala-specific fitness effects particularly well. Ahrens et al. (2026) reported lower segregating mutational load in Victorian than in NSW or Queensland koalas, which they define as the component of genetic load specifically caused by the accumulation of deleterious mutations in the population. However, segregating variation largely contributes to the heterozygous load, where the reduction in fitness for (partially) recessive deleterious alleles is masked (masked load). During a bottleneck, the greater occurrence of deleterious variation in a homozygous state (realised load), due to increased inbreeding and fixation of alleles, is likely to cause a larger reduction in the fitness of individuals (Dussex et al. 2023). As such, measures of homozygous load have been shown to correlate more closely than total load (heterozygous + homozygous) with reproductive fitness (Robledo-Ruiz et al. 2025).

Assessing homozygous load requires variants to be identified as ancestral or derived. This can be challenging in phylogenetically isolated organisms like the koala, which lacks an extant confamilial species for comparison. Gates et al. (2025) used the common wombat (*Vombatus ursinus*; a representative from the closest living family Vombatidae) to polarise koala alleles, and found that the elevated $R_{X/Y}$ ratio in Victorian and South Australian koalas (relative to Queensland koalas) was largely driven by an increase in homozygous functional variants (Subramanian 2026). Increased homozygosity of functional variants suggests a shift from masked (heterozygous) to realised (homozygous) load in these koalas, driven by increased inbreeding in the Victorian and South Australian populations (McLennan et al. 2024; Gates et al. 2025).

It is unclear how these combined factors affect fitness in South Australian and Victorian koalas, with their demographic recovery suggesting they have maintained high reproductive fitness. However, there is evidence for morphological abnormalities in South Australian and Victorian koalas (Seymour et al. 2001; Speight et al. 2020; Tarlinto et al. 2021; Buchanan et al. 2022; Gates et al. 2025; Ramsey et al. 2025). Health assessments of 68 koalas across Victoria in 2024 resulted in 29 individuals (43%) being euthanised based on welfare grounds, with reduced koala health found in high density populations and associated with poor coat condition, dental malocclusion and ‘wet bottom’ (Ramsey et al. 2025). It is not known whether ill-health is the result of increased genetic load or environmental and demographic stressors. The relationship between fitness and genomic predictors of genetic load requires empirical validation before it can be used to inform management decisions (Kardos et al. 2025); estimates of inbreeding, such as runs of homozygosity, have been found to be more informative of reproductive success

than genomic predictors of genetic load (Robledo-Ruiz et al. 2025). Whether demographic recovery is driven by higher reproductive fitness or lower prevalence of threats and diseases (or both) is unclear, but this information is vital for the effective management of declining koala populations in NSW and Queensland.

Implications for koala conservation and the need to preserve genetic diversity

The demographic recovery of Victorian koalas is a genuine conservation success and a clear demonstration of the impact of removing a major threat from a threatened species. Following the criminalisation of koala hunting in Victoria, the release of island populations onto the mainland successfully established expanding populations of koalas across the state, evidently maintaining high reproductive fitness despite elevated inbreeding (Ramsey et al. 2025; McLennan et al. 2024). But this population still has lower heterozygosity than its northern counterparts, and given the timescales established above, heterozygosity will not regenerate within any realistic conservation management timeframe. Victorian koalas also have fewer functional variants than NSW or Queensland koalas across all three frequency bins. Therefore, this population is not an example of escaping the genetic constraints of a bottleneck; bottleneck-induced reduction of evolutionary potential is an ongoing concern, as it is for many threatened species that have experienced demographic recovery (e.g. van Oosterhout et al. 2026).

Unfortunately, for many threatened species that have already lost large portions of their historical genetic diversity, the restoration of genetic diversity in order to recover evolutionary potential, as stated in Target 4 of the CBD GBF (CBD 2022), is not possible through increasing population size within conservation management timeframes. Ultimately, a great deal of effort goes into translating conservation genetic theory into management practice and policy. That effort is best served by recognising the central importance of preserving standing genetic variation, rather than interpreting the rapid recovery of rare alleles after a bottleneck as a sign that evolutionary potential has already been restored.

Human intervention remains necessary to manage extinction risk, and several practices can help to maximise the evolutionary potential within a population's remaining diversity (Bolam et al. 2023). Species that were only recently threatened, or that have longer generations, might not yet have lost substantial diversity even after a demographic decline (Nei et al. 1975; Gargiulo et al. 2025). The results of Ahrens et al. (2026) suggest that this might apply to some NSW and Queensland populations, several of which show depleted rare alleles despite autosomal heterozygosity remaining high. Because rare alleles respond quickly to demographic change, this depletion is an early warning that these populations risk losing higher-frequency alleles too, unless there is demographic recovery (Spielman et al. 2004). Therefore, increasing effective population size in these declining NSW populations is a priority for preventing further loss of heterozygosity and evolutionary potential.

For populations that are already depleted, like the Victorian koalas, restoring diversity requires increasing connectivity to other populations or direct genetic supplementation (Clarke et al. 2024); concerns about outbreeding depression in this context are often overstated (Frankham

2015; Chan et al. 2019). Translocation could help to recover evolutionary potential in Victorian koalas, although further work is needed to evaluate outcomes from previous mixing of genetic clusters (McLennan et al. 2024). Managing connectivity across the species' full range, rather than allowing drift to erode each population independently, is the more realistic route to raising effective population size where it is depleted.

It is also worth being cautious about interpreting the demographic success of Victorian koalas as evidence of escaping the extinction vortex (Wang 2026). Although the impact of infectious diseases in Victorian populations is apparently reduced, they have historically received far less disease surveillance than their endangered northern counterparts, and chlamydiosis has recently been detected in Victorian koalas (Kramer et al. 2025; Ramsey et al. 2025). With reduced evolutionary potential, the ability of these populations to respond to novel and evolving diseases will be limited. Koala densities in parts of Victoria and the Mount Lofty Ranges of South Australia are now high enough to drive substantial over-browsing of eucalypt habitat: modelling suggests continued population growth could lead to widespread food shortages and die-off in South Australia without intervention (Saltré et al. 2026), while in Victoria, higher density has already been associated with reduced koala health (Ramsey et al. 2025). Taken together, high local density, resource stress, and under-monitored disease risk mean that Victorian koalas' demographic recovery should not be read as evidence that the population has a high likelihood of long-term persistence. If density-dependent starvation, disease, or both were to threaten Victorian koala populations again, a population with reduced heterozygosity, reduced functional diversity and potentially elevated realised load would be considerably worse placed to respond than one that had retained its standing variation. The demographic and the genetic stories point in different directions, and it is important that conservation assessments of this population weigh both.

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Declaration of competing interests
None declared.

Data statement
No new data was generated for this study. Simulation and analysis code used to produce the figures in this manuscript is available at https://anonymous.4open.science/r/Inescapable_bottlenecks-3882/.

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