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Episodic population fragmentation and gene flow reveal a trade-off between heterozygosity and allelic richness

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Abstract

In episodic environments like deserts, populations of some animal species exhibit irregular fluctuations such that populations are alternately large and connected or small and isolated. Such dynamics are typically driven by periodic resource pulses due, for example, to large but infrequent rainfall events. The repeated population bottlenecks resulting from fragmentation should lower genetic diversity over time, yet species undergoing these fluctuations appear to maintain high levels of genetic diversity. To resolve this apparent paradox, we simulated a metapopulation of constant size undergoing repeat episodes of fragmentation and change in gene flow to mimic outcomes experienced by mammals in an Australian desert. We show that episodic fragmentation and gene flow have contrasting effects on two measures of genetic diversity: heterozygosity and allelic richness. Specifically, fragmentation into many, small subpopulations, coupled with periods of infrequent gene flow, preserves allelic richness at the expense of heterozygosity. In contrast, fragmentation into a few, large subpopulations maintains heterozygosity at the expense of allelic richness. The strength of the trade-off between heterozygosity and allelic richness depends on the amount of gene flow and the frequency of gene flow events. Our results imply that the type of genetic diversity maintained among species living in strongly fluctuating environments will depend on the way populations fragment, with our results highlighting different mechanisms for maintaining allelic richness and heterozygosity in small, fragmented populations.

KEYWORDS
boom-bust, bottleneck, desert, genetic diversity, simulations

1 | INTRODUCTION

Animal populations fluctuate in size over time. The causes and consequences of these fluctuations have long been of scientific interest (Elton, 1924). At one extreme are populations that exhibit large episodic fluctuations in size. These dynamics are characterised by periods of low and high abundance where the transition from one state to another can occur rapidly in response to

extrinsic (e.g. climate or predation) or intrinsic (e.g. dispersal or sociality; Boor et al., 2018; Radchuk et al., 2016) factors. For example, in desert environments, episodic population outbreaks can be triggered by infrequent resource pulses driven by large rainfall events followed by population crashes during dry periods of low resources (Dickman et al., 2010; Greenville et al., 2012). Populations that fluctuate in this way are expected to exhibit low levels of genetic diversity because they repeatedly experience bottlenecks (Motro & Thomson, 1982; Nei et al., 1975; Vucetich et al., 1997; Whitlock, 1992; Wright, 1978). Paradoxically, however, field studies often reveal high levels of genetic diversity in populations that undergo large fluctuations (Norén & Angerbjörn, 2014; Row et al., 2016). For example, voles and lemmings (Ehrich & Jorde, 2005; Garcia-Navas et al., 2015; Lagerholm et al., 2017; Oli, 2019) and western tent caterpillars (Franklin et al., 2014) display high levels of genetic diversity and little genetic differentiation between populations despite repeated bottlenecks. This outcome could occur if there were processes operating in populations experiencing high amplitude fluctuations that could offset potential losses in genetic diversity caused by bottlenecks (Ehrich et al., 2009). Specifically, populations undergoing large fluctuations could experience episodes of increased movement and gene flow relative to stable populations and this could maintain genetic diversity over time (Jangjoo et al., 2020).

Our aim in this study is to explore the mechanisms by which genetic diversity could be maintained in populations undergoing large changes in structure. We focus on episodic fragmentation and mixing events, where subpopulations periodically become small, fragmented, and isolated from each other during unfavourable conditions, and hence are likely to lose genetic diversity, but then mix during favourable conditions when gene flow occurs. We use simulations to examine changes in genetic diversity in these populations and compare these to changes that occur in species with relatively stable population size across time. Simulations allow us to estimate population responses to environmental change over longer time intervals than current long-term sampling allows, and simulations can be tailored to fit any system of interest. We base our simulations on the dynamics of small mammal populations in Australian deserts, where species often show contrasting population responses to major rainfall-driven resource pulses (Dickman et al., 2011; Greenville et al., 2012). Boom-bust species like *Pseudomys hermannsburgensis* (the sandy inland mouse) undergo large increases in population size in response to large episodic rainfall events (Dickman et al., 2011; Greenville et al., 2012). Population numbers then decline rapidly in response to declining resources and predation (Greenville et al., 2017), and remain low during extended drought periods, with small populations persisting in spatially fragmented refuges (Cere et al., 2015; Pavey et al., 2017; Wardle et al., 2015). Other species, such as *Sminthopsis youngsoni* (the lesser hairy-footed dunnart) maintain relatively stable population sizes throughout periods of rainfall and drought.

We focus on how these contrasting population dynamics should influence two key measures of genetic diversity, allelic richness and observed heterozygosity (Hoban et al., 2022; Sherwin et al., 2017). Allelic richness is associated with the potential for long-term population responses to environmental change and observed heterozygosity is associated with individual fitness (Caballero & García-Dorado, 2013; Fernández Vilas et al., 2015; Garcia-Dorado & Caballero, 2021). While higher levels of allelic richness and observed heterozygosity are likely to enhance population persistence, we predict these two measures will each respond differently in fluctuating metapopulations relative to stable populations. First, we anticipate that a population undergoing recurrent fragmentation and gene flow will have higher allelic richness than an equivalent large panmictic population because, when fragmented, multiple isolated subpopulations are unlikely to lose the same alleles through drift. If subpopulation connectivity is restored periodically, the allelic richness of the entire metapopulation should be retained relative to a single large population of the same size that could lose alleles due to drift. If the number of subpopulations is high, then the chance of losing an allele due to drift in all subpopulations simultaneously is very small. Second, we anticipate that observed heterozygosity will increase with greater gene flow during periodic mixing events because high gene flow between small, previously isolated subpopulations will mix alleles that have become fixed in one or more subpopulations. The caveat to both of these predictions is that the level of genetic diversity maintained through episodes of isolation and mixing is likely to be dependent on the number of generations spent in each phase; less frequent mixing events mean that subpopulations spend more time isolated, increasing the level of genetic drift to which they are exposed. Alleles are more likely to be lost and their overall frequency in the metapopulation reduced when subpopulation connectivity is infrequent.

Patterns of genetic diversity in species undergoing episodic fragmentation and mixing (gene flow) likely depend on several factors including: (1) the degree of fragmentation (the number of subpopulations in which alleles can shelter); (2) how often subpopulations reconnect to restore gene flow; and (3) the rate of gene flow (the number of individuals that successfully migrate between subpopulations). We used forward simulations based on the population dynamics of *P. hermannsburgensis* and *S. youngsoni* in the Simpson Desert, Australia to examine the importance of variation in the above three factors on patterns of allelic richness and observed heterozygosity. Rates of fixation and allelic loss will depend on starting allele frequency, so we used a starting frequency of 50% in all simulations to isolate the impact of the above three factors on allelic richness and observed heterozygosity. To understand how metapopulation dynamics affect genetic diversity, we compare observed heterozygosity and allelic richness under three scenarios: (1) a panmictic population of fixed size (approximating a species whose numbers do not fluctuate in response to episodic resource pulses, such as *S. youngsoni*), (2) a fragmented metapopulation of the same size with no gene flow and (3) a metapopulation of the same size with periodic fragmentation and mixing events during which gene flow occurs (to approximate species that periodically fragment in response to episodic resource pulses such as

P. hermannsburgensis). We discuss the implications of our findings for species undergoing episodic climate-driven fluctuations under changing climates, and the potential conservation implications given that rapid environmental change is an important consideration in the genetic management of small, fragmented populations and in reintroduction programs.

2 | MATERIALS AND METHODS

To determine how patterns of genetic diversity vary under episodic fragmentation dynamics, we simulated and compared populations under the three scenarios using SLiM version 3.7.1 (Haller & Messer, 2019) run through the slimr package (Dinnage et al., 2022, under review) in R (R Core Team, 2022). SLiM is a genetic simulation framework allowing control over genetic and evolutionary components of populations including mutation rate, mutation type, gene flow, population size and number of generations. The code used to simulate populations is available from a Github repository (https://doi.org/10.5281/zenodo.8361742).

We simulated 5000 neutral SNP loci exhibiting complete independence (recombination rate of 0.5) in 256 individuals that comprised the population or metapopulation for each scenario. We ran all simulations under a Wright–Fisher framework (Fisher, 1922; Wright, 1931) specifying a constant total number of individuals, random mating, equal fitness of all individuals and discreet non-overlapping generations. The single panmictic population (Scenario 1) comprised 256 individuals. For the two metapopulation scenarios (Scenario 2—fragmentation without gene flow and Scenario 3—fragmentation with gene flow), we specified six levels of subpopulation fragmentation, such that the 256 individuals were divided into subpopulations ranging in size from four to 128 individuals when fragmented. These numbers approximate the range in numbers of *P. hermannsburgensis* individuals caught on trapping grids during booms and busts in a long-term study in Australia (Dickman et al., 2010), while allowing for the possibility that in either phase the number of individuals is likely to vary substantially. Gene flow during mixing events was determined by migration rate (Table 1). For Scenario 3, we simulated six levels of gene flow ranging from 1% to 100% of individuals (Table 1). When gene flow occurred, a proportion of individuals were randomly assigned as migrants and mated within a panmictic migrant pool, while the remaining individuals (non-migrants) mated within their respective subpopulations. After a gene flow event, migrant offspring were randomly redistributed among subpopulations. We simulated four levels of mixing event frequency, corresponding to different numbers of generations between gene flow events (Table 1). These intervals include the range typically observed in Australian desert systems (5–10 generations) along with shorter and longer intervals (Dickman et al., 2010, 2011; Greenville et al., 2012). Our simulations therefore include population dynamic scenarios ranging from extreme to mild fragmentation and incorporate realistic rates and frequencies of mixing events with associated gene flow based on observations from Australian deserts but also including a wider range of values to ensure the outcomes are relevant to a broad range of systems.

We used a nucleotide-based simulation in SLiM and allowed mutations at SNP loci to occur by including a mutation matrix that specified the mutation rate between A and C, and G and T nucleotides. We specified a mutation rate of $1e^{-9}$ mutations per base position per genome per generation in the three scenarios (Table 1, Figure 1), a mutation rate that approximates the rate for *Mus musculus* germline and somatic tissues (Lynch, 2010). To assess the sensitivity of our results to this mutation rate, we also ran simulations with mutation rates of $1e^{-7}$ and $1e^{-8}$ (Figures S5 and S6). The allele frequencies for the 5000 loci started at 0.5 (highest possible level of diversity) and were in Hardy–Weinberg equilibrium across the population with genotypes randomly distributed among individuals for each

TABLE 1 Factors used in simulations of three scenarios that explore the effects of fragmentation and rate and frequency of gene flow on allelic richness and observed heterozygosity in metapopulations undergoing episodes of fragmentation and mixing during which gene flow occurs (see also Figure 1).

	Factor	Levels	Results
Scenario 1: Panmictic population	NA	$N=256$ individuals	In text
Scenario 2: "Meta"population with no gene flow between subpopulations	Fragmentation (No. subpopulations)	2 ($N=128$), 4 ($N=64$), 8 ($N=32$), 16 ($N=16$), 32 ($N=8$), 64 ($N=4$)	Figure 2
	Gene flow	Zero	Tables S1–S4
Scenario 3: Metapopulation with gene flow between subpopulations during mixing events	Fragmentation (No. subpopulations)	2 ($N=128$), 4 ($N=64$), 8 ($N=32$), 16 ($N=16$), 32 ($N=8$), 64 ($N=4$)	Figure 3 (Metapopulation)
	Rate of gene flow during mixing	1%, 5%, 10%, 25%, 50%, 100%	Figure 4 (Subpopulation)
	Frequency of gene flow events (Generations between mixing)	2, 5, 10, 20	Tables S1–S4

Note: Parentheses contain the number of individuals within subpopulations (N) at each level of fragmentation.

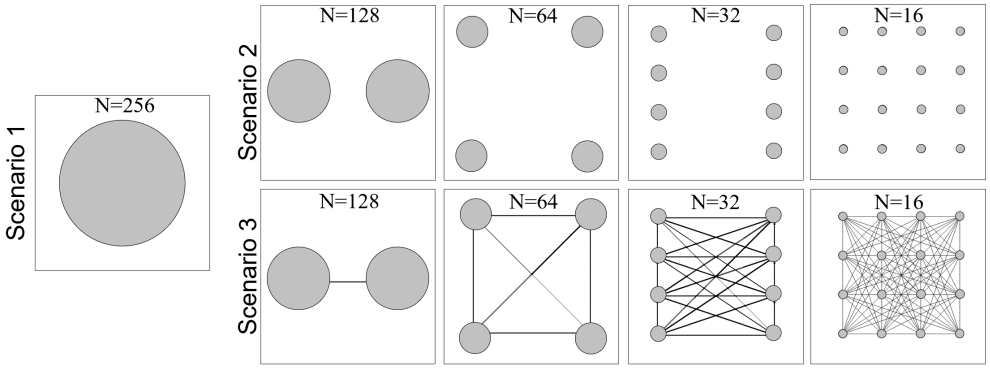

FIGURE 1 Representation of Scenarios 1–3. Scenario 1 is a single panmictic population. In Scenarios 2 and 3, fragmentation increases from left to right. Scenario 2 has zero gene flow between subpopulations (Table 1). Rates and frequency of gene flow in Scenario 3 (grey lines) vary as per Table 1. The total number of individuals in all simulated scenarios is 256 and the number of individuals per subpopulation is shown. For brevity, fragmentation above 16 subpopulations is not shown.

simulation. We ran 50 replicate simulations for each combination of fragmentation, rate of gene flow and frequency of gene flow shown in Table 1.

2.1 | Output

The 50 replicate simulations of Scenarios 1–3 were each run for 500 generations. We extracted allelic richness (the total number of alleles remaining) and calculated observed heterozygosity (the proportion of heterozygous genotypes) from each run for the three scenarios (see Table 1 for numbers of individuals used for subpopulation calculations). We then generated the following output:

(i) To understand genetic diversity in a single panmictic population we collated allelic richness and observed heterozygosity from 50 replicate simulations of Scenario 1 at generation 500.
(ii) To understand the effect of fragmentation without gene flow on allelic richness and observed heterozygosity we collated output from 50 replicate simulations of Scenario 2 at generation 500.
(iii) Because heterozygosity levels are strongly influenced by gene flow, we collated output from 50 replicate simulations of Scenario 3 from multiple generations, beginning with the generation prior to the last gene flow event and ending at generation 500 for each level of gene flow frequency (Table 1).
(iv) To examine a time series of the change in allelic richness and observed heterozygosity, we collated output from a single run of Scenario 3 from every generation for the last 50 generations for all combinations of factors (Table 1).

We report both the allelic richness and observed heterozygosity and the change in allelic richness and observed heterozygosity in the generation after gene flow from 50 replicate simulations of 5000 SNPs in 256 individuals with a mutation rate of $1e^{-9}$. Summary results from simulations involving mutation rates of $1e^{-7}$ and $1e^{-8}$ are reported in the Figures S5 and S6. To further demonstrate the strength and direction of the relationship between our predictors (fragmentation, rate of gene flow and frequency of gene flow; Table 1) and our responses (allelic richness and observed heterozygosity), we calculated Spearman's rank correlations (calculated on the mean effect of each factor) in R using the Stats package (R Core Team, 2022). In simulations, it is possible to achieve significant test results by simply increasing the number of replicates, therefore we do not report associated *p*-values. Output by SLiM was generated as variant call format (vcf) files, which were converted to genlight objects using the vcfR package (Knaus & Grünwald, 2017) in R. The number of alleles retained and the observed heterozygosity were extracted from each genlight object using the dartR package (Gruber et al., 2018) in R.

3 | RESULTS

3.1 | Scenario 1: Single panmictic population

In simulations of a single panmictic population, there were between 7687 and 7861 alleles remaining from the original 10,000 after 500 generations (mean from 50 simulations = 7790). The observed heterozygosity in the single panmictic population after 500 generations was between 0.181 and 0.195 (mean from 50 simulations = 0.188).

3.2 | Scenario 2: *No* gene flow between subpopulations

In simulations at the metapopulation level with no gene flow, allelic richness (measured as the number of alleles retained from the original 10,000) increased in response to the level of fragmentation (number of subpopulations; Table 2, Figure 2, panel a) but observed heterozygosity decreased (Table 2, Figure 2, panel b). At the subpopulation scale, allelic richness and observed

heterozygosity both decreased with increasing fragmentation (Table 2, Figure 2c,d).

3.3 | Scenario 3: *With* gene flow between subpopulations

In simulations with periodic mixing and associated gene flow, the allelic richness of the metapopulation increased with fragmentation (the number of subpopulations) and decreased with rate of gene flow during mixing events. Allelic richness increased as the number of generations between gene flow events increased, although this was less pronounced at lower levels of fragmentation (Table 3, Figure 3, Table S1). The observed heterozygosity of the metapopulation decreased with fragmentation and increased with the rate of gene flow. Observed heterozygosity decreased as the number of generations between gene flow events increased but this was less pronounced at higher rates of gene flow (Table 3, Figure 3, Table S2).

TABLE 2 Spearman's rank correlation of the association between fragmentation and allelic richness and observed heterozygosity in both a *"meta"population* and a single *subpopulation* with zero gene flow (Scenario 2).

	Fragmentation
Allelic richness	
"Meta"population	+0.92
Subpopulation	−0.93
Observed heterozygosity	
"Meta"population	−0.93
Subpopulation	−0.93

The same patterns were apparent with different mutation rates (Figure S5).

In simulations with mixing, the allelic richness and observed heterozygosity of a single subpopulation within the metapopulation decreased with fragmentation. Both measures of genetic diversity increased with the rate of gene flow during mixing events (particularly as fragmentation increased) but decreased as the number of generations between gene flow events increased (Table 4, Figure 4, Tables S3 and S4). The same patterns were apparent with different mutation rates (Figure S6).

3.4 | Comparison of fragmentation with and without mixing (Scenario 2 vs. Scenario 3)

Allelic richness at the metapopulation scale was higher in all simulations of episodic fragmentation and mixing than in a single, panmictic population (Figures 2 and 3, Table S1). However, as fragmentation increased with *no* gene flow and subpopulations became smaller (Scenario 2), allelic richness across the metapopulation increased (Figure 2). Further, allelic richness at the metapopulation scale was greater with fragmentation and *no* gene flow (Scenario 2, Figure 2) than at the same level of fragmentation *with* gene flow (Scenario 3, Figure 3). For each level of fragmentation, allelic richness across the metapopulation was higher when the number of generations between gene flow events increased. When measured within subpopulations, allelic richness decreased as fragmentation increased in both Scenario 2 and 3 even when gene flow rescued allelic richness within subpopulations (Figures 2 and 4). This effect diminished as the number of generations between gene flow events increased.

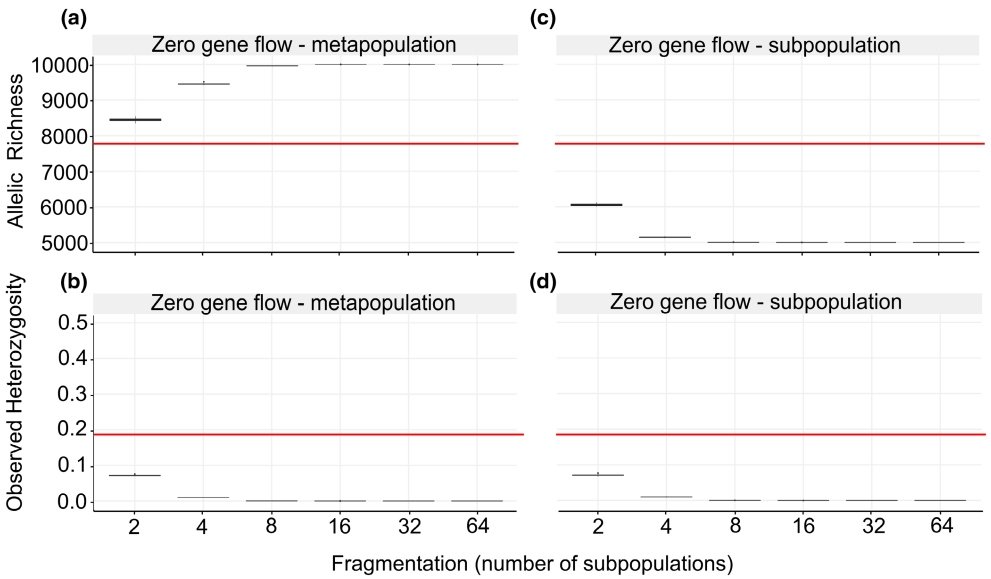

FIGURE 2 Allelic richness (number of alleles retained from original 10,000) and observed heterozygosity from 50 replicate simulations of unlinked neutral loci in a *"meta"population* (a and b) and in a single *subpopulation* (c and d) under various levels of fragmentation and zero gene flow (Scenario 2). Red horizontal line represents the values obtained in Scenario 1.

TABLE 3 Spearman's rank correlation of the association between fragmentation, rate of gene flow and number of generations between gene flow events with allelic richness and observed heterozygosity in a *metapopulation* undergoing episodic fragmentation and mixing (Scenario 3).

Metapopulation	Fragmentation	Rate of gene flow	Generations between gene flow
Allelic richness	0.74	−0.58	0.24
Observed heterozygosity	−0.51	0.70	−0.18

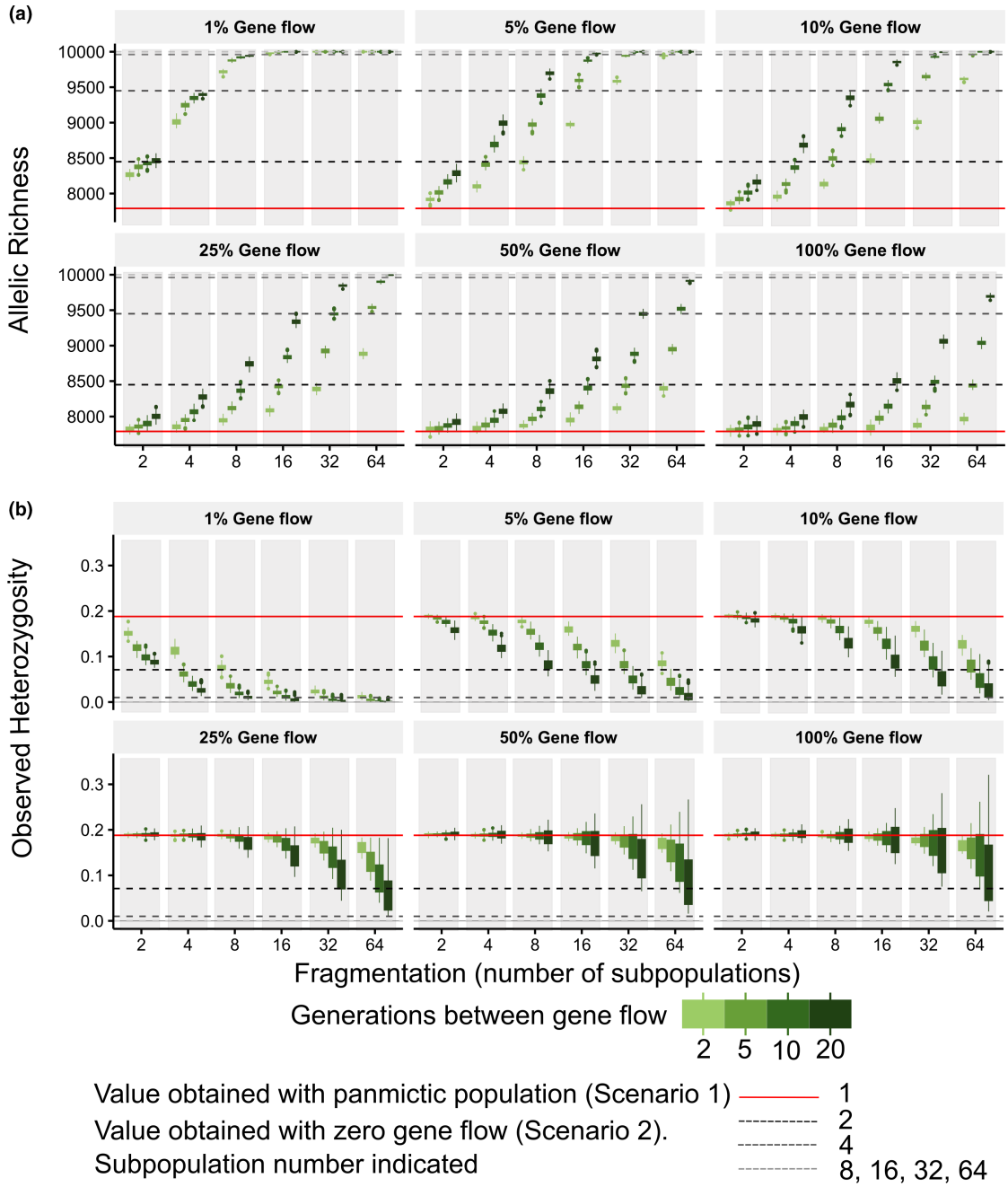

FIGURE 3 Allelic richness (number of alleles retained from original 10,000; a) and observed heterozygosity (b) from simulations of unlinked neutral SNP loci in a *metapopulation* undergoing episodic fragmentation and mixing (Scenario 3). Results are drawn from 50 replicate simulations using output from every generation between the last generation in which gene flow occurred to generation 500. Horizontal lines represent values obtained in Scenario 1 (red) and Scenario 2 with no gene flow (black dashed, two subpopulations; dark grey dashed, four subpopulations; mid-grey dashed, eight, 16, 32 and 64 subpopulations).

TABLE 4 Spearman's rank correlation of the association between fragmentation, rate of gene flow and number of generations between gene flow events and allelic richness and observed heterozygosity in a single *subpopulation* participating in episodes of fragmentation and gene flow within a metapopulation (Scenario 3).

Subpopulation	Fragmentation	Rate of gene flow	Generations between gene flow
Allelic richness	−0.60	0.47	−0.12
Observed heterozygosity	−0.46	0.64	−0.17

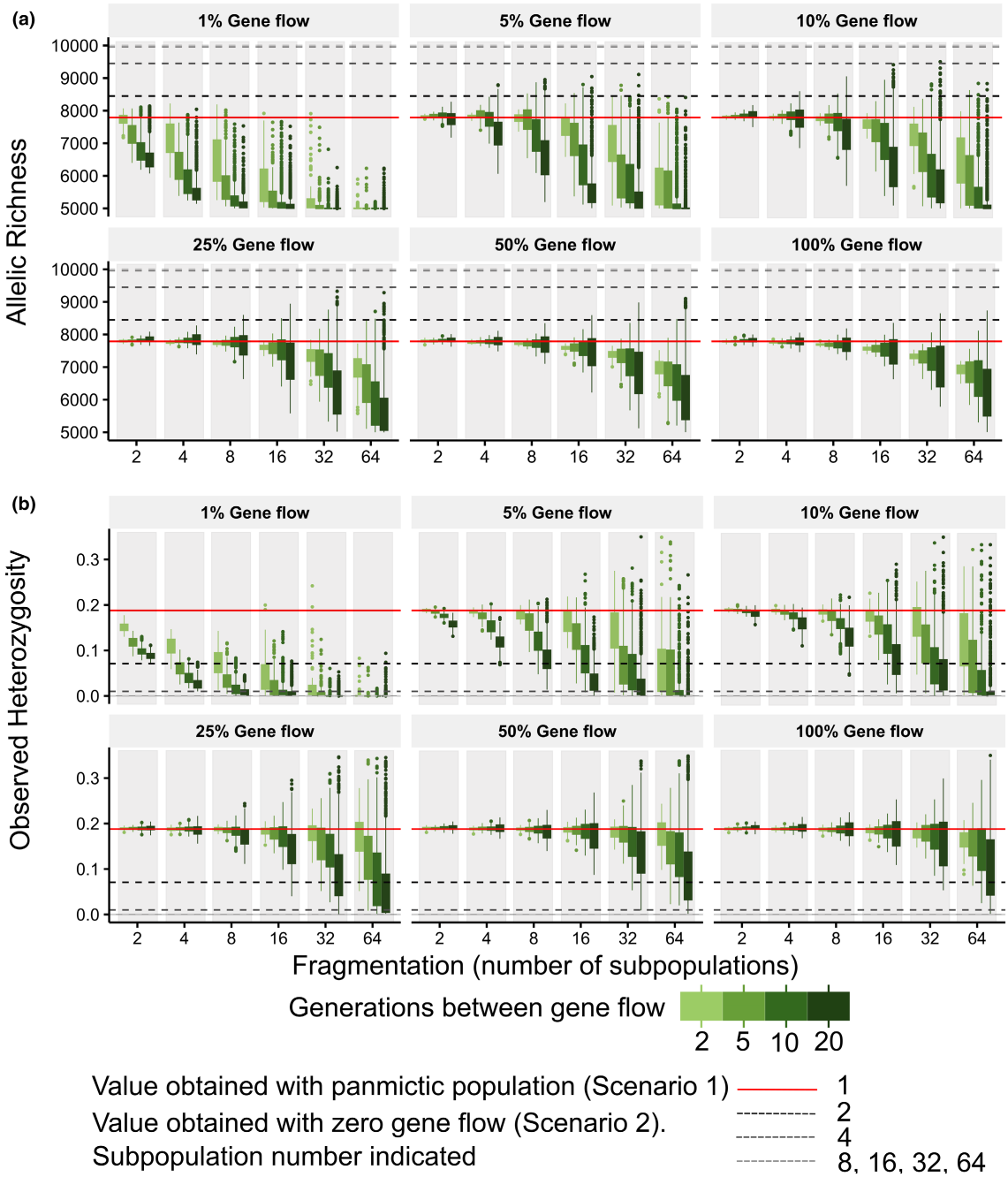

FIGURE 4 Allelic richness (number of alleles retained from original 10,000; a) and observed heterozygosity (b) from simulations of unlinked neutral SNP loci in a single *subpopulation* participating in episodes of fragmentation and mixing within a metapopulation (Scenario 3). Results are drawn from 50 replicate simulations using output from each generation from the last generation in which gene flow occurred to generation 500. Horizontal lines represent values obtained in Scenario 1 (red) and Scenario 2 with no gene flow (black dashed, two subpopulations; dark grey dashed, four subpopulations; mid-grey dashed, eight, 16, 32 and 64 subpopulations).

Observed heterozygosity at the metapopulation scale in episodic fragmentation and mixing simulations (Scenario 3) required gene flow between subpopulations to reach the levels achieved in a single panmictic population (Figures 2 and 3, Table S2). As fragmentation increased without gene flow (Scenario 2), observed heterozygosity decreased rapidly and was always lower than at the equivalent level of fragmentation *with* gene flow (Scenario 3). As the number of generations between gene flow events increased, higher rates of gene flow were required to restore observed heterozygosity in the metapopulation to levels approaching that achieved in a single panmictic population (Figure 3, Table S2). Observed heterozygosity within subpopulations decreased as fragmentation increased in both Scenario 2 and 3. As with allelic richness, gene flow rescued observed heterozygosity within subpopulations, but this effect was dampened as the number of generations between gene flow events increased (Figure 4).

3.5 | Change in allelic richness and observed heterozygosity in the generation after gene flow

In our episodic fragmentation and gene flow simulation (Scenario 3), allelic richness within each level of fragmentation remained constant in the metapopulation after a gene flow event (Figure S1). However, allelic richness within subpopulations increased in the generation after gene flow (Figure S2). The change within subpopulations was positively associated with fragmentation and was generally greater as the number of generations between gene flow events increased (Table 5). However, this response depended on the rate of gene flow. Intermediate rates of gene flow (10%, 25%) resulted in a broader range of allelic richness change in the generation after gene flow than low and high rates of gene flow (Figure S2). When observed across a single simulation run, allelic richness increased sharply in the generation after gene flow within subpopulations but remained stable at the metapopulation scale (Figures S3 and S4).

Observed heterozygosity increased at the metapopulation scale in the generation after gene flow (Figure S1). The change in observed heterozygosity in the metapopulation in the generation after gene flow was positively associated with fragmentation and was greater when gene flow events were infrequent (Table 5). The change in observed heterozygosity of subpopulations in the generation after gene flow was positively associated with fragmentation and the rate of gene flow and was greater when gene flow events were infrequent (Table 5). When observed across a single simulation run, observed heterozygosity increased sharply in the generation after gene flow at both the metapopulation and subpopulation scales (Figures S3 and S4), particularly with an increase in the number of generations between gene flow events.

4 | DISCUSSION

Here we examined the response of genetic diversity to episodic fragmentation and gene flow metapopulation dynamics where, for example, populations become fragmented during low resource periods and then mix during periods of high resource availability. We focussed on two components of genetic diversity—allelic richness and observed heterozygosity (Hoban et al., 2022; Sherwin et al., 2017)—and found differences in the levels of fragmentation and gene flow and the optimum number of generations between gene flow events required to maximise each. Metapopulations undergoing episodic fragmentation and gene flow had higher allelic richness but lower observed heterozygosity than a single panmictic population. Gene flow attenuated this difference however, with both measures approaching that achieved by the panmictic population depending on the rate and frequency of gene flow. When we simulated no gene flow between isolated fragmented subpopulations, both allelic richness and observed heterozygosity of subpopulations reduced with increasing fragmentation as expected (Nei et al., 1975). However, allelic richness of the metapopulation increased with fragmentation, while observed heterozygosity decreased. When we explored this relationship further by allowing gene flow between subpopulations, we found that maximising gene flow between subpopulations restored observed heterozygosity at the expense of allelic richness, particularly as fragmentation increased. Furthermore, allelic richness increased as gene flow events became infrequent while observed heterozygosity decreased. These findings were robust to mutation rate and have important implications for understanding how boom-bust species, isolated during busts and connected during booms through gene flow, maintain genetic diversity in episodic environments.

These findings also imply that metapopulation management of small, fragmented populations and reintroduction programs are likely

	Fragmentation	Rate of gene flow	Generations between gene flow
Δ Allelic richness			
Metapopulation	NA	NA	NA
Subpopulation	0.23	0.10	0.76
Δ Observed heterozygosity			
Metapopulation	0.32	0.24	0.73
Subpopulation	0.29	0.25	0.71

Note: NA indicates no change with any factor.

TABLE 5 Spearman's rank correlation of the association between fragmentation, rate of gene flow and number of generations between gene flow events and the change in allelic richness and observed heterozygosity observed in the generation after gene flow in both a *metapopulation* and a single *subpopulation* participating in episodic fragmentation and mixing (Scenario 3).

to affect the type of genetic diversity conserved. Specifically, maintaining genetic diversity in a metapopulation undergoing episodic fragmentation and mixing is a trade-off between maximising the number of small subpopulations that shelter alleles and minimising the risk of those small subpopulations going extinct. When fragmented, many small subpopulations may collectively provide a source of allelic richness but individually will lose alleles due to drift, and each subpopulation will have higher risk of extinction due to inbreeding depression and demographic stochasticity (Charlesworth & Willis, 2009; Lande, 1988). Fewer large subpopulations will be less likely to suffer inbreeding depression and stochastic extinction, but collectively will have lower long-term potential to maintain allelic richness, and this lowered genetic diversity may reduce the ability of populations to respond to changing environmental conditions. In extreme environments, maintaining high allelic richness could be important in enabling species to respond to episodic fluctuations in resource availability. For example, in the Simpson Desert, small, irruptive mammals like *Pseudomys hermannsburgensis* persist in isolated refuges during bust phases (Cere et al., 2015; Dickman et al., 2011; Pavey et al., 2017). Individuals retract to these refuges during drought when resources are low and irrupt when rainfall triggers a resource pulse. The refuges thus supply the progenitors that recolonise the landscape (Dickman et al., 2010, 2011; Greenville et al., 2012; Wardle et al., 2015). It is reasonable to expect that the spatial and temporal distribution of refuge habitat across deserts results in stochastic patterns of gene flow upon re-emergence during booms and retraction during busts; predictions surrounding the outcomes of the observed patterns of fragmentation and gene flow in desert systems can be tested against our simulated patterns.

Our simulations reveal a trade-off such that when fragmentation is high and gene flow is infrequent, the observed heterozygosity in a metapopulation is reduced, and when fragmentation is low and gene flow is frequent, allelic richness is reduced. Hence, our results suggest that changing climate, which could alter the frequency of gene flow events driven by such phenomena as episodic rainfall, could alter the nature of genetic diversity in systems undergoing episodic fragmentation and gene flow. In Australian deserts, for example, the stochasticity of rainfall and drought events is likely to increase with the El Nino Southern Oscillation (Cai et al., 2021; Holmgren et al., 2001, 2006). Our simulations provide a framework for understanding how these boom-bust populations will respond to changes in the number of generations between booms and busts that will be useful for assessing the implications of climate change on these species and their ecosystems.

Even though fragmentation is considered likely to decrease the probability of species persistence (Brauer & Beheregaray, 2020; Haddad et al., 2015), it may also provide a useful management option in some situations. The amount of genetic variation within a species is a key factor in its long-term response to selection and perturbations (Allendorf et al., 2006; Fernández et al., 2004). Our finding that increasing fragmentation can improve allelic richness across a metapopulation in the absence of frequent and high levels of gene flow among subpopulations suggests that frequent and high levels of gene flow may be unnecessary and even detrimental to maintaining allelic richness. This was also evident in the change in allelic richness in subpopulations after gene flow. Intermediate rates and frequency of gene flow resulted in the most variation in subpopulation allelic richness and appeared optimal for maintaining genetic diversity across the metapopulation. Conservation management of fragmented species may thus be maximised via strategies that manage gene flow based on boom-bust metapopulation dynamics, for example the selected transfer of individuals among isolated subpopulations combined with the maintenance of multiple insurance subpopulations. Even if insurance subpopulations are founded by a few individuals, they will likely harbour allelic richness that can be returned to populations in the wild via introductions at species-specific gene flow rates and frequencies. Our findings add to the early but still unresolved SLOSS debate ("single large or several small" habitat patches for optimal species management; Baz & Garcia-Boyero, 1996; Soule & Simberloff, 1986) by adding a temporal component, which indicates strategies to maximise both observed heterozygosity and allelic richness, and therefore can support the recovery of species affected by fragmentation.

5 | CONCLUSION

Species that exist in landscapes with climate-driven episodic resource availability might be expected to lose genetic diversity because they undergo repeated fragmentation and bottlenecks. However, when components of genetic diversity (allelic richness and observed heterozygosity) are examined separately, each responds quite differently to fragmentation and is maximised under differing regimes of gene flow. The trade-off between maximum observed heterozygosity and allelic richness that we reveal here suggests that, rather than being detrimental, in fluctuating environments fragmentation could maintain high levels of allelic richness without substantial reductions in heterozygosity even with only occasional episodes of connectivity.

AUTHOR CONTRIBUTIONS

PH: Writing original draft preparation (lead), writing review and editing (equal), conceptualisation (supporting), data curation (equal), formal analysis (equal), investigation (lead), methodology (equal), software (equal), validation (lead) and visualisation (lead). CD: Conceptualisation (equal), validation (supporting), writing review and editing (equal) and project administration (equal). RD: Conceptualisation (equal), validation (supporting), writing review and editing (equal), and software (equal). RPD: Conceptualisation (equal), validation (supporting), writing review and editing (equal), project administration (equal), supervision (supporting); SE: conceptualisation (equal), validation (supporting), writing review and editing (supporting), and project administration (equal). AG: conceptualisation (supporting), validation (supporting), and writing review and editing (equal). SS: conceptualisation (equal), validation (supporting), writing review and editing (equal), funding acquisition (lead), project administration (lead) and supervision (lead). ES: conceptualisation

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Code to recreate the simulation and data can be found on Zenodo https://doi.org/10.5281/zenodo.8361742.

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