

How does ecological disturbance influence genetic diversity?

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Abstract

Environmental disturbance underpins the dynamics and diversity of many of the world's ecosystems, yet its influence on the patterns and distribution of genetic diversity is poorly appreciated. We argue here that disturbance history may be the major driver that shapes patterns of genetic diversity in many natural populations. We outline how disturbance influences genetic diversity through changes in both selective processes and demographically-driven, selectively-neutral processes. Our review highlights the opportunities and challenges presented by genetic approaches, such as landscape genomics, for better understanding and predicting the demographic and evolutionary responses of natural populations to disturbance. Developing this understanding is now critical as disturbance regimes are changing rapidly in a human-modified world.

Why should we consider disturbance as a driver of the distribution of genetic diversity?

Environmental disturbance underpins the dynamics and diversity of many of the world's ecosystems [1, 2]. From tsunamis and large wild-land fires to footprints on intertidal mudflats, disturbances drive spatial and temporal variation in the abundance of species and the composition of communities [3-5]. Despite recognition that disturbance plays a key role in shaping biodiversity at the species and community levels [2, 6], its role as a driver of the patterns and distribution of genetic diversity (see Glossary) is relatively poorly understood. This is a major knowledge gap because genetic diversity has important consequences for all levels of biodiversity; it influences the fitness of individuals, the viability of populations, the adaptability of species to environmental change, the evolution of new species, the structure of communities, and the function of ecosystems [7-11]. Therefore, the interactions between disturbance and genetic diversity are likely to have pervasive ecological and evolutionary ramifications [10, 12].

Improving our understanding of how disturbance influences the patterns of genetic diversity is critical for three reasons:

- i. Disturbance patterns are changing rapidly in a human-modified world. Climate change is affecting the intensity and frequency of floods, hurricanes and extreme temperature events [13-16], fire regimes are being modified by human activities such as fire suppression and planned burning [17], and natural disturbances are interacting with novel anthropogenic disturbances [18]. Therefore, disturbance will increase in importance as a driver of the distribution of biodiversity across the genetic, species and community levels.
- ii. The spatial and temporal patterns of genetic diversity can potentially tell us much about the demographic response of populations to disturbance. Genetic analyses have enabled new insights into the ecological consequences of major environmental changes such as habitat fragmentation, but such analyses have been less frequently applied in disturbance ecology. In particular, there has been limited evaluation of the potential for genetic analyses to improve biological inference under dynamic environmental and demographic conditions.
- iii. Disturbance history may be the major driver that shapes the patterns of genetic diversity in many natural populations. This is because disturbance can cause variation in key demographic and biological processes that are known to influence the distribution of genetic diversity [19-22]. Therefore, studies that infer biological processes from genetic patterns, such as landscape genetics [23], must consider disturbance history alongside contemporary landscape patterns.

In this paper, we synthesise knowledge about how disturbance shapes genetic diversity. Our focus is on genetic diversity within species, and how it is distributed within and among individuals and populations in natural landscapes. We first define the key concepts of

disturbance ecology and then identify how disturbance may influence genetic diversity via changes in both selective processes and demographically-driven, selectively-neutral processes. We then discuss the capacity of genetic analyses to inform our understanding of the biotic consequences of disturbance. Finally, we list the key questions that remain to be answered before we can more fully understand the interplay between disturbance and genetic diversity and how these interactions influence species conservation, community composition and evolution.

What is ecological disturbance and why is it important?

Ecological disturbances are commonly defined as *“any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment”* [24]. Disturbances are ubiquitous across the Earth’s ecosystems. They occur from very fine spatial scales, such as trampling and wave-induced boulder turnover [25, 26], to large scales, such as landscape-wide fires and tsunamis [27, 28]. They can also occur over different temporal scales, as short ‘pulse’ disturbances (e.g. vegetation fires), as extended ‘press’ disturbances (e.g. grazing or browsing), or as ‘ramp’ disturbances that increase in intensity and resultant severity over time (e.g. drought effects on streams) [29]. Disturbances can have abiotic sources, such as hurricanes and volcanoes [30, 31], or biotic sources, such as grazing or pest outbreaks [32]. They can also have anthropogenic sources, such as logging [33]. Within the scope of this review, we do not consider disturbance to encompass long-term environmental changes such as climatic fluctuations or habitat clearing and fragmentation, which are also known to have genetic consequences [34, 35].

Large, severe disturbances are often portrayed as natural disasters, because they can threaten human life and have striking short-term effects on plant and animal populations [36].

However, disturbances play crucial roles in the formation and maintenance of ecological

communities [6, 37] and many species are dependent on post-disturbance conditions for survival [38]. Disturbances occur in the context of a disturbance regime, which describes the type, season, frequency and intensity of disturbance at a specific location [39, 40].

Disturbance regimes can have important influences on the evolution of species [41] and the structure and diversity of ecosystems [6]. Changing disturbance regimes pose direct risks for the extinction of species [42], and such changes are occurring worldwide [13-15, 43]. Thus, building an understanding of the biotic consequences of disturbance and changing disturbance regimes is increasingly important if we are to anticipate future biodiversity scenarios [2].

How does disturbance influence genetic diversity through selectively-neutral demographic processes?

To set the context for understanding how disturbance shapes the distribution of genetic diversity, it is important to understand the environmental and demographic changes imposed by disturbance. This is because a large fraction of genetic diversity is selectively neutral, and its distribution is therefore shaped by mutation, migration and genetic drift [44]. Indeed, even functional genetic variation can be strongly influenced by selectively-neutral demographic processes, such as population bottlenecks which can cause a loss of adaptive potential in colonising or remnant populations [45]. Key biological processes underlying neutral genetic patterns that can be affected by disturbance include mortality, reproduction, movement and social behaviour [21, 43, 46, 47]. In this review, we categorise effects of disturbance on demography as the *direct* effects, which relate to how disturbance directly imposes changes on biological processes such as mortality and reproduction, and *indirect* effects, relating to how species respond to the influence of disturbance on habitat suitability and landscape permeability.

Direct effects

One prediction about the effects of disturbance events is that, when severe, they may cause a loss of genetic diversity within populations (in particular, allelic diversity or richness) when population sizes are reduced. Losses of allelic diversity and reduced expected heterozygosity within populations are anticipated where mortality is high and population recovery stems from a few *in situ* survivors or founding colonisers (particularly from a single source), and where ongoing immigration is low relative to the population growth rate (Fig. 1).

To illustrate the interacting influence of mortality and recruitment on the consequences of disturbance for within-population genetic diversity, we present a series of examples. The remarkably low genetic diversity in the Galapagos giant tortoise *Chelonoidis nigra vandenburghi* was attributed to a population bottleneck coinciding with a volcanic eruption causing high mortality in the sole, isolated population of this subspecies 100,000 years ago [28]. In cases such as this, the degree of loss of allelic diversity during population bottlenecks can be influenced by the duration of the bottleneck [48] and the spatial pattern of mortality (because alleles are rarely distributed in a random spatial pattern even within populations) [47]. Populations of the south-east Australian mallee emu-wren (*Stipiturus mallee*) also have low allelic richness because they are extirpated by regular fire and re-established by founder events driven by rare, stochastic colonisation (despite low ongoing migration between established populations) [19]. Other empirical studies have documented no losses of genetic diversity within disturbance-affected populations when survival has been high [49] or recovering populations recruit many individuals from multiple sources [31]. The reproductive strategies of some plants enable them to maintain high genetic diversity within populations even when disturbances like fire cause high mortality, because recruitment comes from seed banks established by pre-disturbance populations, and not from a small number of surviving individuals [50].

Disturbance also directly affects genetic differentiation among populations through its influence on genetic drift and migration. To illustrate, F_{ST} among aquatic snail populations increased due to accelerated genetic drift following drought-induced reductions in local population size [51]. Conversely, F_{ST} among populations of the sailfin molly (*Poecilia latipinna*) decreased when a hurricane storm surge in coastal Florida increased ‘migration’ by directly transporting individual fish between populations [46]. Disturbance can often drive extinction-recolonisation dynamics in natural populations [52] resulting in at least two genetic scenarios. First, F_{ST} can increase with the rate of population turnover where population recovery proceeds via colonisation by a small number of founders, followed by intrinsic population growth (Scenario 1) [53]. Conversely, population turnover may decrease F_{ST} where recolonisation and population growth occurs via high ongoing immigration, particularly from multiple sources (Scenario 2) [53, 54].

Indirect effects

As well as having direct effects on populations, disturbance can affect genetic diversity through its influence on the spatial and temporal patterns of habitat suitability and permeability [55]. Disturbance history at a point in the landscape determines its suitability as habitat for a species by influencing habitat structure, resource availability and community composition. Habitat dynamics that are driven by disturbance can influence how genetic diversity is distributed within and among populations because key biological processes like dispersal and reproduction develop in response to habitat patterns [56]. For instance, many species specialising in ephemeral habitat conditions (influenced by post-disturbance succession) exhibit high dispersal by both sexes consistent with the requirement for regular patch colonisation, and therefore have low genetic differentiation among populations [19, 57, 58], even though fine-scale genetic structure can exist within patches [59].

In Box 1, we present a simulation framework to demonstrate how variation in the regimes and spatial patterns of disturbance in a landscape, coupled with simple ecological requirements of a species, can lead to strikingly different distributional patterns that vary over time and space. These simulations show that changes in fire patterns will affect the distribution of two Australian cool temperate forest species. Increasingly frequent fire (large or small) will reduce the landscape-wide distribution of mountain ash trees (*Eucalyptus regnans*), with flow-on effects for populations of the endangered Leadbeater's possum (*Gymnobelideus leadbeateri*) which depends on old, hollow-bearing mountain ash trees for shelter. This is because, in many places, frequently re-occurring fires will kill regenerating mountain ash trees before they reach reproductive maturity. A similar scenario in fire-sensitive populations of the shrub *Persoonia mollis*, in which frequent fire caused extinction-recolonisation dynamics, was associated with low genetic diversity within populations and weak genetic differentiation between them [60].

In addition to influencing the spatial and temporal dynamics of habitat suitability, disturbance regimes can also influence the permeability of landscapes to dispersal [43, 61]. For instance, fire suppression changed forest structure in a way that reduced dispersal between populations of collared lizards (*Crotaphytus collaris*) inhabiting forest glades in the Missouri Ozarks [20]. Therefore, changes to disturbance regimes can influence the temporal and spatial configuration of suitable habitat. Such changes can cause demographic connectivity of populations to change, with implications for how genetic diversity is partitioned within and between populations. In order to make predictions about the neutral genetic impacts of changing disturbance regimes for particular species, we need to connect the direct and indirect demographic effects of disturbance.

Connecting direct and indirect demographic effects of disturbance for genetic predictions

A key question for future research is whether we can predict the genetic consequences of changes to disturbance regimes for individual species. For Leadbeater's possum, as represented in Box 1, increasing the frequency of large fires may lead to increased F_{ST} with fire-driven population turnover (Scenario 1 as listed in the *Direct effects* section). This is because the number of colonisers to newly-suitable habitat will be low when patches of suitable habitat are large but geographically isolated (Box 1). If the fire frequency (at a point in the landscape) stays the same but fires are smaller, the number of recolonisation sources in the local neighbourhood is much greater because populations are smaller but less isolated (Box 1). Thus, F_{ST} is likely to decrease with population turnover (Scenario 2).

We suggest that species-specific predictive models could be framed around the interacting key processes including spatial and temporal variation in habitat suitability and landscape permeability, and the rates of dispersal, reproduction and mortality [62]. The former indirect processes set the constraints on distribution, abundance and movement across the landscape. The latter direct processes influence the severity and duration of population bottlenecks and the degree to which recovery occurs through survival or immigration, with the source and rate of arrival of immigrants or colonists being critical.

We also need to develop an understanding of how the key biological processes that mediate the genetic effects of disturbance vary through the stages of a disturbance regime [63]. For instance, fire stimulates immigration by some species [64] and reproduction in others [65], while other disturbances can drive shifts between sexual and clonal reproduction [22, 66]. Furthermore, it may be critical to explore how disturbance influences the distribution of genetic variation measured at nuclear versus organellar DNA, because migration operates on these genomes in different ways. For instance, dispersal can differ between the sexes [67], or between seeds and pollen [50].

How does disturbance influence genetic diversity through natural selection?

Natural selection can potentially respond to a number of environmental and biotic processes associated with disturbance [68, 69]. The effects of climatic instability on the morphology of Galapagos finches (*Geospiza* spp.) have provided evidence that disturbance events can cause temporal variation in the strength and direction of selection, leading to unpredictable patterns of evolution [70]. However, on particular timescales, disturbance does not necessarily equate to environmental instability because disturbances can be frequent and predictable occurrences within a long-term ‘stable’ environment [39]. Under such circumstances, local adaptation to disturbance regimes can occur [41]. For instance, topographically-mediated variation in fire regimes can influence spatial patterns of selection for fire response traits in plants, such as resprouting or obligate seeding [71]. Where traits conferring susceptibility or resilience to disturbance are phylogenetically conserved, selection imposed by disturbance regimes can alter the phylogenetic composition of communities [72]. Disturbance regimes can also have ‘flow-on’ evolutionary consequences; an experimental study on bacteria showed that the effects of repeated population bottlenecks on population density and genetic structure influenced the opportunity for kin selection and the evolution of cooperative biofilm-forming behaviour [12].

Although the examples provided above demonstrate that disturbance can influence selection on physiological or behavioural traits, we have less information on how and when genetic diversity itself is likely to be influenced by the selective effects of disturbance events and regimes. Nevertheless, we can make some predictions informed by theoretical and empirical research, and identify promising approaches for studying these questions. We hypothesise that disturbance-mediated variation in selection could cause temporal genetic patterns analogous to ecological succession (i.e. ‘temporal adaptation’ [73]). In such cases, changes in allelic and genetic diversity could vary with disturbance frequency at loci under selection. We

expect selection-driven responses to disturbance to be most apparent when disturbance events are large relative to the scale of dispersal (because migration can decrease local adaptation [74]) and when disturbance is frequent [41]. Lastly, we might expect ongoing feedbacks between the effects of changing disturbance regimes on demography and the functional genetic variation on which selection acts. For instance, experimental studies have shown that seagrass (*Zostera marina*) plots with higher genotypic diversity have greater resistance (survival) and resilience (recovery) to disturbance [11, 75]. Thus, such populations are less likely to suffer losses of adaptive genetic diversity associated with population bottlenecks.

Landscape genomics techniques offer exciting new opportunities to test hypotheses about selection-driven genetic changes in response to disturbance [76]. For instance, analyses of next-generation sequencing datasets of samples taken across landscapes might be used to distinguish the effects of disturbance-driven selection from those of demography on genome-wide polymorphism data [77, 78]. It will be important to determine whether we can detect variation in selection between the different temporal stages of a disturbance regime and between landscapes with different disturbance regimes. Theoretical and simulation research suggests that adaptive loci can respond rapidly to temporal variation in selective pressure, particularly when population differentiation is high [73, 79]. Landscape genomics studies aiming to test for selection-driven genetic responses to disturbance will need to use spatially and temporally replicated contrasts of sites with different disturbance histories to maximise the information provided by such studies. Furthermore, we stress the importance of replication in the design of such studies because false signals of selection can be generated by stochastic processes like accelerated genetic drift ('allele surfing'), at colonisation fronts or in rapidly expanding populations [80], which may be a frequent characteristic of the demography of disturbance-affected populations.

Can genetic analyses inform our understanding of population responses to disturbance?

Our review has highlighted how disturbance influences genetic patterns at the individual and population levels [20, 21], over short and long timescales [81, 82], and by selective and selectively-neutral processes [46, 83]. We have discussed how the genetic effects of disturbance might be predictable using models framed around key ecological and demographic parameters. However, a major challenge for achieving this, and indeed for predicting the conservation implications of altered disturbance regimes, is that we often lack even a basic biological understanding of how species respond to disturbance [84]. Intuitively, genetic analysis itself can contribute to filling this knowledge gap in a number of ways. These include (a) elucidating demographic history associated with disturbance [81, 85], (b) determining the source and rate of recruitment to recovering populations [86], (c) identifying recolonisation routes [31], and (d) determining whether dispersal strategies differ between stable and recovering populations [87]. However, if we are to improve the application of genetic analyses in disturbance ecology, we need to identify the circumstances under which genetic analyses can inform our understanding of species' responses to disturbance, and when they cannot.

Challenges and recommendations for the application of genetic analyses in disturbance ecology

Populations in disturbance-prone ecosystems pose particular challenges for the application of genetic analyses to demographic and ecological research. First, such populations are characterised by temporal variation in abundance, reproduction and dispersal [20-22].

Because genetic diversity is influenced by both current and historical processes [88], it may be difficult to infer population processes from genetic patterns in landscapes with a history of disturbance. Second, multiple biological processes can generate similar genetic patterns [89].

This is because the ways in which we can quantify spatial and temporal patterns of genetic

diversity (e.g. heterozygosity, allelic diversity, linkage disequilibrium, spatial genetic structure between individuals and populations) are far outnumbered by the interacting molecular, behavioural and ecological processes that generate the genetic patterns. This is particularly true in complex dynamic populations [53]. For instance, simulation modelling has shown that variable patterns of genetic structure among Florida sand skink (*Plestiodon reynoldsi*) populations with increasing time since fire might be due to changes in abundance, dispersal, or both [82]. In such circumstances, genetic data alone may be insufficient to resolve different biological hypotheses in disturbance-affected populations.

Below, we offer three recommendations for maximising the utility of genetic analyses for understanding the effects of disturbance on natural populations:

- i. *Where possible, use pre- and post-disturbance samples.*

Genetic patterns are shaped by biological processes over a long temporal window [88]. Therefore, pre- and post-disturbance data will greatly increase the ability to identify the specific genetic changes associated with disturbance events [46] and, therefore, to use genetics to understand species' responses. For instance, residual animals, not immigrants, were identified as the source of recruits to bush rat (*Rattus fuscipes*) populations recovering from experimental disturbance by comparing their genotype likelihoods between pre-disturbance populations and candidate immigrant sources [86].

Where it is not possible to obtain pre- and post-disturbance samples, researchers should be aware of the temporal 'depth of signal' of the markers and analyses used. The sensitivity of a given genetic marker to demographic and evolutionary processes over different timescales will depend on the mode of inheritance and the process and rate of mutation [90]. Measures of genetic structure based on fine-scale spatial patterns of individual multilocus genotypes

can be sensitive to processes occurring over the past few generations [67], whereas F_{ST} can retain genetic signals of processes occurring over hundreds of generations [88].

ii. Take full advantage of non-genetic data.

Where multiple biological scenarios can lead to the same genetic patterns, the use of additional data from other sources (abundance surveys, mark-recapture analyses, etc.) may refine our hypotheses, enabling genetic data to discriminate between competing explanations [91]. For instance, demographic and environmental data were used to establish a small set of plausible models of metapopulation dynamics of tropical freshwater snails [92]. Because these models led to alternative genetic predictions, the authors were then able to refine the understanding of metapopulation processes with genetic data.

iii. Use realistic simulation models to aid biological inference.

Increasing accessibility of spatially-explicit demographic and genetic simulation tools [67, 93] may be particularly valuable in disturbance research. Computer simulations can be used to evaluate the power of genetic analyses to resolve specific biological hypotheses by testing the genetic outcomes of variation in different biological and demographic parameters. They can also be used to evaluate whether cost and effort should be allocated to collecting and genotyping more samples or to generating a greater number of, or more variable, markers to answer specific questions [67, 94]. Furthermore, simulations can contribute directly to the inference of biological processes by comparing the genetic predictions of alternative demographic simulation models with observed data. This can be done with post-hoc simulations to investigate the validity of biological conclusions [82], or within an approximate Bayesian computation framework to estimate biological and demographic parameters [95]. Such approaches, coupled with increasingly sophisticated methods for

simulating disturbances in landscapes [96], will advance our understanding of the dynamics of genetic diversity in disturbance-prone landscapes.

Concluding remarks

Disturbance is an important ecological process but its influence on the distribution of genetic diversity has been largely overlooked. Recent research is beginning to show that disturbance can influence genetic diversity via biological and demographic processes, spatial and temporal variation in habitat suitability, and natural selection and evolution. Key areas for future research (summarised in Box 2) include the evaluation of genetic analyses for understanding demographic and evolutionary responses to disturbance, the impacts of changing disturbance regimes on the distribution of genetic diversity within and between populations, and the conservation and evolutionary relevance of these genetic impacts. Because the regimes of natural disturbances are changing, and the frequency of anthropogenic disturbances is increasing [2], it is imperative that we understand how these changes will impact biodiversity at its most fundamental level, genetic diversity.

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Glossary

Allelic diversity: The number of different alleles per locus in a population. Allelic richness is a measure of allelic diversity standardised for sample size.

Disturbance intensity: Power of disturbing agent at a point (e.g. energy output from fire in W m^{-2} or fireline intensity in kW m^{-1}).

Disturbance regime: Temporal pattern of disturbance events, usually at a point, including frequency, intensity, season and type of disturbance.

Disturbance severity: Magnitude of impact of disturbing agent on above and below ground organic matter (e.g. extent of canopy tree scorch in a fire).

Ecological disturbance: *“any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment”* [24].

F_{ST} : A measure of genetic differentiation describing the proportion of genetic variation among populations relative to that within populations. F_{ST} ranges from zero (no differentiation) to one (complete differentiation).

Genetic differentiation: A measure of how genetic diversity is partitioned among populations within a species (e.g. F_{ST}).

Genetic diversity: Variation in genetic material from an individual, population or species. This can be characterised by multiple statistics, typically calculated at the locus level. These statistics include observed heterozygosity within individuals. At the population level, common measures include allelic diversity, allelic richness, observed and expected heterozygosity. Among-population level genetic diversity is typically represented by measures of genetic differentiation such as F_{ST} and its analogues, often within the framework

of Analysis of Molecular Variance, which allows hierarchical partitioning of genetic variance [97].

Genetic drift: Random changes in allele frequencies between generations due to chance alone. Genetic drift is stronger in small than in large populations because of the increased chance of sampling errors.

Genetic structure: Non-random distribution of genetic diversity that can form over space or time. Spatial patterns of genetic structure can be measured as genetic differentiation between populations (e.g. F_{ST}) or by fine-scale spatial analyses of genotypes within populations [98].

Heterozygosity: Commonly measured as observed or expected heterozygosity. Observed heterozygosity (H_o) is the average observed heterozygosity of individuals at the population level. H_E is the expected heterozygosity of individuals within populations under the assumptions of Hardy-Weinberg equilibrium.

Landscape genetics / landscape genomics: Research fields which combine population genetics (or genomics), landscape ecology and spatial statistics to quantify spatial variation at neutral or selection-driven loci in relation to heterogeneity in physical or biotic environmental conditions.

Mean return interval: Average time between disturbance events

Metapopulation: Part of the spectrum of spatial dynamics where local populations occur in discrete habitat, have asynchronous dynamics, are sustained for at least a few generations, and where some populations become extinct and others are recolonised by dispersing individuals.

Neutral vs selection-driven genetic variation: Neutral genetic variation is not influenced by natural selection, whereas selectively-driven genetic variation has an adaptive advantage or disadvantage and is thus influenced by selection.

Population bottleneck: A rapid and severe reduction in population size that can cause a rapid loss of genetic diversity, which can be accentuated by genetic drift if the population size reduction persists for multiple generations.

Succession: Temporal change in community composition after disturbance.

Box 1. Effects of disturbance regimes on spatial population dynamics

Approach: We use simplified models to demonstrate that variation in the spatial and temporal patterns of disturbance affects the distribution and dynamics of natural populations, with implications for patterns of genetic diversity and differentiation.

Case studies: We illustrate the approach with case studies of a forest plant and animal species affected by fire: mountain ash (*Eucalyptus regnans*), the world's tallest flowering plant, and Leadbeater's possum (*Gymnobelideus leadbeateri*), an endangered arboreal marsupial dependent on hollow-bearing mountain ash trees for shelter.

1 **Habitat suitability:** We established a habitat suitability index for each species. These were
2 defined as simple binary indices (Fig. I) according to two key dimensions of fire occurrence
3 at points in the landscape, time since fire (TSF) and the most recent inter-fire interval (IFI)
4 [39]. We assumed an otherwise uniform landscape. More realistic extensions could include
5 variables related to disturbance type, intensity or season, and other ecological characteristics
6 including topography, climate or vegetation heterogeneity.

7 **Disturbance simulations:** We generated fire patterns on a 150x150 cell landscape, varying
8 frequency (mean inter-fire interval 100 years or 50 years in each cell) and the size of fires
9 (50x50 cells or 5x5 cells). In the Victorian Central Highlands, where our case study species
10 co-exist, the typical regime of large stand-replacing fires involves an inter-fire interval of 75-
11 150 years [99]. We simulated fires over 1000 years and recorded the TSF and most recent IFI
12 for each cell at the end of the simulations.

13 **Predicted habitat suitability maps:** We combined the simulated fire histories with the
14 habitat suitability criteria (Fig. I) to predict the distribution of suitable habitat for each species
15 at year 1000 of each simulation (Fig. II). This combination of simple models reveals that
16 variation in spatial and temporal patterns of disturbance can lead to important differences in

17 the dynamics of species' distributions [100]. Changing the frequency and spatial scale of fires
18 influenced the overall amount of suitable habitat for each species, as well as the size and
19 spatial configuration of suitable habitat patches, which can have important implications for
20 landscape-wide genetic patterns.

21 **Extensions:** Although our case study features fire as a disturbance, the approach is
22 extendable to other disturbance types. It can be extended to more realistic environmental and
23 population scenarios by modelling underlying environmental variation influencing habitat
24 suitability and disturbance [101, 102]. The approach could also include key biological
25 processes such as dispersal and mortality [103], to provide a demographic context for making
26 predictions about the genetic consequences of disturbance.

27

28

29 **Box 2. Key outstanding questions**

30 *What is the power of genetic analysis to elucidate population responses to disturbance?*

31 What can genetic analyses tell us that we cannot learn about disturbance in other ways?

32 Do different combinations of disturbance, demography and species traits lead to
33 distinctive genetic patterns?

34 Can we distinguish the roles of different population processes in driving changes in
35 genetic diversity for particular species and disturbance types?

36 What supporting data (abundance, dispersal, etc.) are most informative for refining our
37 inference from genetic data?

38 How can we take full advantage of next-generation sequencing technology and
39 computational simulation modelling approaches to improve our understanding of the
40 biotic effects of disturbance from genetic data?

41 *What are the genetic impacts of long-term disturbance regimes?*

42 What are the cumulative effects of the long-term sequence of disturbance-driven
43 demographic changes on genetic diversity?

44 How do disturbance regimes influence genetic diversity through their influence on spatial
45 and temporal patterns of habitat suitability?

46 How does natural selection influence the genetic effects of disturbance events and
47 regimes?

48 To what extent does disturbance history account for the contemporary distribution of
49 genetic diversity across landscapes? Can the genetic effects of past disturbances obscure
50 those of contemporary population processes?

51 *What is the conservation relevance of the genetic effects of disturbance?*

52 Do genetic changes resulting from severe or increasingly frequent disturbance reduce the
53 capacity to adapt to other environmental changes?

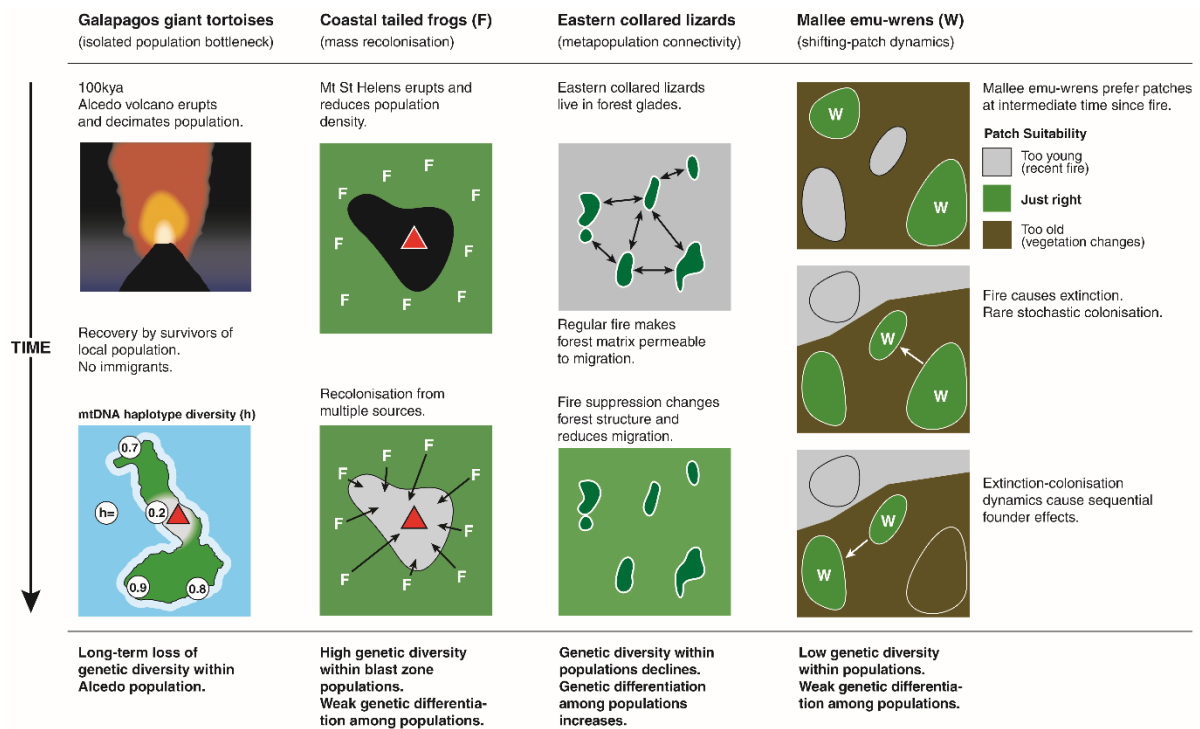
54 What will be the long-term evolutionary consequences of changing disturbance regimes?

55 Does anthropogenic disturbance cause the loss of genetic diversity and thereby reduce the
56 resilience of species to disturbance?

57 Do long-term disturbance regimes cause feedbacks between the demographic and genetic
58 effects of disturbance? For example, do disturbance-induced bottlenecks cause a loss of
59 genetic diversity, thereby increasing the susceptibility of populations to future
60 disturbances?

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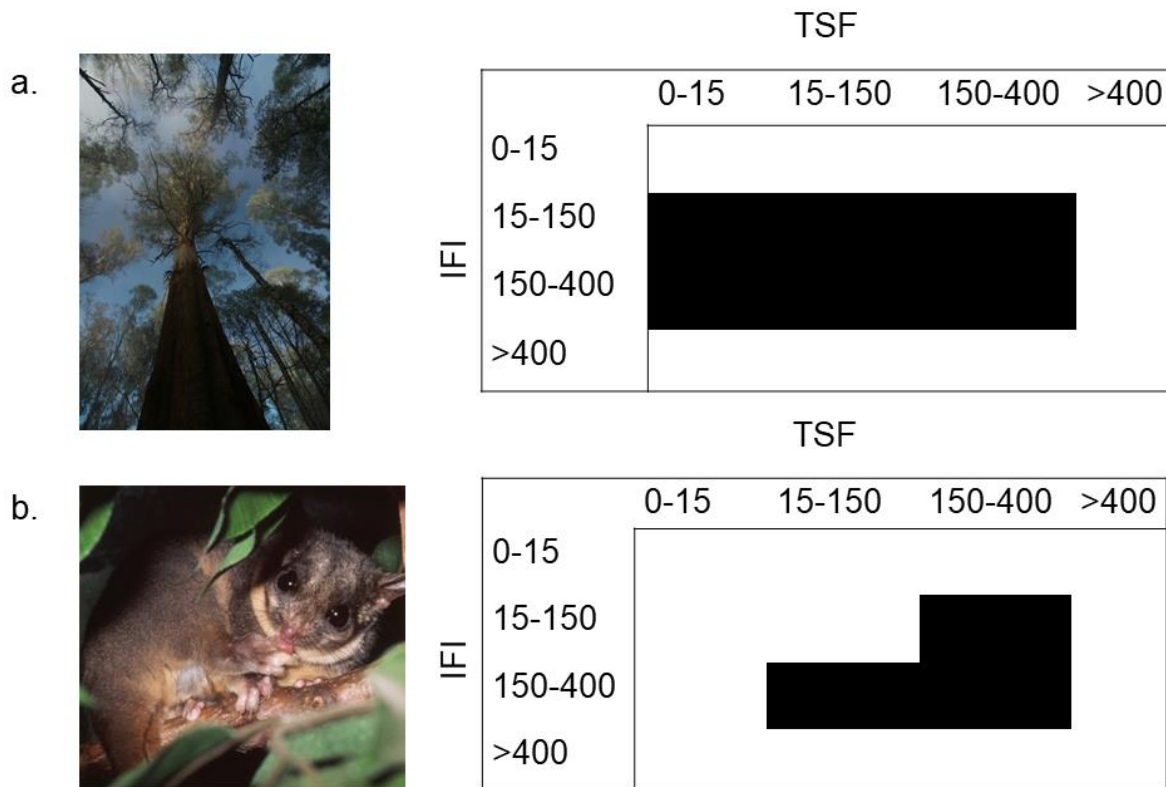
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64 **Figure 1. Contrasting demographic and genetic responses to disturbance.** A set of case
65 studies featuring contrasting genetic outcomes of disturbance events and regimes, and how
66 they affect mortality, migration and habitat suitability. The two case studies on the left
67 (Galapagos giant tortoises [81] and coastal tailed frogs [31]) contrast the neutral genetic
68 consequences of disturbance events causing major mortality in an isolated and connected
69 population, respectively. The case studies on the right (Eastern collared lizards [20, 43] and
70 mallee emu-wrens [19]) show how disturbance regimes affect habitat permeability and
71 habitat suitability, respectively, thereby influencing genetic diversity and differentiation
72 through their effects on spatial population dynamics. Illustration by Clive Hilliker, Fenner
73 School of Environment & Society, ANU.

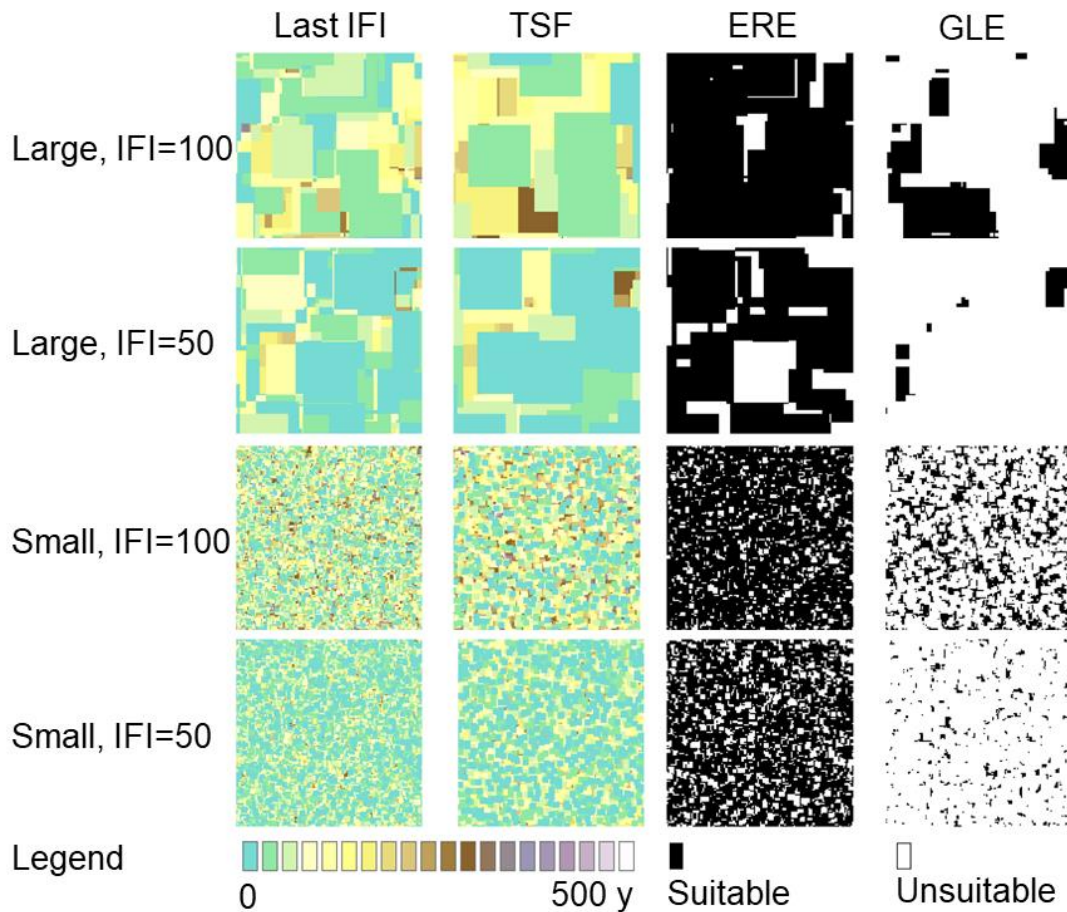
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76 **(Box 1) Figure I. Habitat suitability indices.** Simple binary habitat suitability indices for
 77 mountain ash (top) and Leadbeater's possum (bottom) defined as suitable or unsuitable
 78 depending on the most recent inter-fire interval and the time in years since the last fire.
 79 Mountain ash grows in south-eastern Australia and is killed by severe fires, after which it
 80 regenerates from seed. It becomes reproductively mature after 15-20 years and begins to
 81 senesce from 150-400 years. In the absence of fire, mountain ash stands are commonly
 82 replaced by cool temperate rainforest. Leadbeater's possum is dependent on decayed hollow-
 83 bearing trees for shelter in mountain ash forest. Suitable hollows begin to form in trees that
 84 are at least 150 years old. Leadbeater's possum can persist in young forest stands after fires
 85 that occur in old forest, because hollow-bearing trees killed by fire can remain standing for
 86 decades. Photos: David Blair (mountain ash), David Lindenmayer (Leadbeater's possum).

87



88

89 **(Box 1) Figure II. Fire simulations and predicted distributions.** Simulated fire histories,
 90 including most recent inter-fire interval (IFI) and time since last fire (TSF), and resulting
 91 habitat distributions for mountain ash trees (*Eucalyptus regnans*: ERE) and Leadbeater's
 92 possum (*Gymnobelideus leadbeateri*: GLE) under four different spatial patterns and regimes
 93 of fire. Large (50x50 cells) and small (5x5 cells) were simulated with a mean fire return
 94 interval (per cell) of 100 or 50 years. Species distributions were predicted according to the
 95 habitat suitability criteria from Fig. 1.

96