Evolution of Species' Range and Niche in Changing Environments

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Abstract

In times of accelerating climate change, there is an urgent need for a predictive theory of species' range shifts, adaptation, and species' resilience under changing environments. Current predictions are limited, as they rely on theory that neglects important interactions between ecological and evolutionary forces. Here, I show that the feedback between selection, genetic drift, and population dynamics fundamentally changes these predictions. This eco-evolutionary feedback creates a tipping point where genetic drift overwhelms selection, and species' range contracts from the margins or fragments abruptly – even under gradual environmental change. This tipping point is determined by three parameters: two quantifying the effects of spatial and temporal variability on fitness, and one capturing the impact of genetic drift. Importantly, I show that by increasing the "neighbourhood size", dispersal can counteract the loss of genetic variation, which would otherwise limit evolvability and increase extinction risk. This suggests that increasing local dispersal, possibly via assisted migration, can facilitate evolutionary rescue when local population size is small. While standard ecological niche models assume that species' ranges shift with environmental change, this study shows that eco-evolutionary feedback can lead to a sudden range fragmentation into disjunct subpopulations with depleted genetic variance, increasing the probability of extinction.

Keywords: eco-evolutionary dynamics, gene flow, adaptation, range margin

Introduction

As environments change over time, species' ranges may shift, expand, or contract, while their ecological niches change through adaptation. These evolutionary and ecological processes are interconnected: population growth is determined by the mean fitness of the population, while the rate of adaptation depends on the genetic variance, the strength of natural selection, and the genetic drift [1–3]. Even considering a single focal species, the interaction between demographic and evolutionary dynamics in spatially and temporally varying environments is complex and difficult to predict. Theoretical progress has often relied on simplifying assumptions such as treating genetic variance as fixed [4–7] or neglecting two-dimensional spatial structure and modelling a small number of loci, particularly in evolutionary rescue models [8–10]. In contrast, the ecological niche modelling (ENM) framework typically considers multidimensional niche space that includes both biotic and abiotic components but does not account for adaptive potential [11], with only recent advances incorporating adaptive genetic diversity [12, 13].

Adaptive genetic variance drives the rate of evolution while also evolving under eco-evolutionary feedback. Importantly, the effects of spatial and temporal variability interact, influencing adaptation rates and the probability of evolutionary rescue [14–21]. In spatially structured populations, gene flow across heterogeneous environments maintains a substantial proportion of genetic variance: the relative contribution of mutation-selection balance diminishes with increasing environmental heterogeneity and dispersal. While the increase in genetic variance due to temporal variation is inherently transient, driven by recurrent sweeps of beneficial mutations [22], this variability can persist over longer time scales in spatially structured populations. Therefore, it is important to consider spatial and temporal variation jointly and to include the feedback between population and evolutionary dynamics, while accounting for genetic and demographic stochasticity in two-dimensional habitats. However, to date, we still lack analyses integrating all these components and their interactions. This study demonstrates that this complexity is essential for capturing the essence of the eco-evolutionary dynamics of a species' range and niche, and provides novel predictions.

One of the key factors influencing species' range dynamics and the resilience of populations facing rapid environmental change is dispersal [23, 24]. A central concept in Wright's [25] shifting balance theory, population subdivision and dispersal play a complex role even on smooth fitness landscapes [26]. Haldane [27] introduced the idea of a feedback between asymmetric gene flow and the reduction of local population size as a key driver of stable species' range margins – an example of migration meltdown [28] due to "swamping" gene flow. However, increased gene flow does not necessarily hinder adaptation to environmental gradients. As genetic variance increases due to gene flow across heterogenous environments [29, 30], it not only elevates the standing load (fitness cost of genetic variance) but also accelerates the rate of adaptation and reduces lag load – the fitness cost of the distance between a trait mean and its

optimum [31]).

Dispersal also influences stochasticity as it enlarges neighbourhood size, thereby decreasing the power of genetic drift relative to selection. Defined by Wright [32, 33], neighbourhood size quantifies the strength of genetic drift in populations distributed across continuous space and corresponds to the population within one standard deviation of the dispersal distance σ. In two dimensions with diffusive dispersal, neighbourhood size is given by $\mathcal{N} = 2\pi\,\sigma^2\,N$, representing the population within a circular area of diameter σ and local density N – effectively a local mating pool. Interestingly, although a sufficiently large neighbourhood size is critical for the maintenance of adaptive diversity across space [34–36], it is – unlike effective population size or census size – currently almost never explicitly considered in conservation guidelines [though see [37–39]]. Despite a growing understanding that higher dispersal and gene flow may enhance population resilience, especially under changing environments [40], the importance of population structure, and neighbourhood size in particular, remains neglected.

Model and methodology summary

The core features of the model are eco-evolutionary feedback through the coupling between fitness and population growth, the inclusion of both genetic and demographic stochasticity, and a quantitative genetic model in which both the trait mean and its variance evolve. The effect of environment (biotic and abiotic) is represented by a gradient in the optimum value of a trait of the focal species. The optimum changes through time along one spatial coordinate: an example could be a spatial gradient in optimal flowering time, changing with altitude (but not along the contours of a hill) and time. Both range and niche shifts are possible, as suitable habitats can be accessed through dispersal, while the selected trait – including its variance – evolves in response to environmental change.

Individual fitness depends on both the local density and distance of the trait from the environmental optimum. The population growth is given by the mean fitness, which reflects the local density and phenotypic distance from the optimum. Selection is hard (*sensu* [41]): i.e., the locally attainable density ("carrying capacity") declines with maladaptation. An additive quantitative trait that influences adaptation to the environment is determined by a large number of loci with exponentially distributed effects α_i. There is free recombination but there are no differences between sexes; for simplicity, individuals are assumed to be hermaphroditic and haploid. Thus, there are no dominance effects; yet there is epistasis as the fitness effect of each allele depends on other allele frequencies via the trait mean. The dispersal distances are normally distributed, independent of fitness and do not evolve through time. The model is written as both an individual-based discrete-time simulation and as an analytical continuous-time model of joint evolutionary and population dynamics.

The dynamics of this complex model is elucidated with the help of the following steps. First, the continuous-time model is rescaled in terms of dimensionless parameters. This reduces dimensions of the system, simplifies the analysis and facilitates the future testing of predictions. Second, the outcomes of the individual-based model are compared to known analytical expectations of simpler systems: namely to the deterministic equilibria and the predictions of a phenotypic model with fixed genetic variance. An illustrative example of the individual-based model is given at Figure S1.

Results

Scale-free parameters of the model

This model of species' range and niche dynamics has over ten parameters, which arise from coupling the classic formalizations of evolutionary and ecological dynamics. Fortunately, there is a rescaling which both reduces the apparent dimensionality of the problem and facilitates interpretation. Upon nondimensionalization, we obtain five dimensionless parameters that describe the core system (extending from [5, 42, 43]). The first parameter measures the effective rate of change of the optimum through time: $k^* = k\,/\sqrt{V_s\, r^{*3}}$ relative to the strength of stabilising selection V_s and the rate r^* at which the population returns to its demographic equilibrium, where k is the rate of temporal change. The second parameter $B = b\,\sigma/(\sqrt{2V_s}\, r^*)$ describes the effective steepness of the environmental gradient b across space x in terms of the expected reduction in fitness due to dispersal σ. The third parameter is the neighbourhood size $\mathcal{N} = 2\pi\,\sigma^2\,N$, which describes the population attainable within a generation's dispersal and measures the weakness of genetic drift on local scales; N is the local population density. (There is a 2 rather than 4 as the model is haploid – for a diploid organism, neighbourhood size doubles.) The fourth parameter is the strength of selection $s \equiv \alpha^2/V_s$ relative to the rate of return of population to a demographic equilibrium s/r^* and finally the fifth is the scaled mutation rate μ/r^*. Further details on the model and its scaling are provided in the Methods.

Known predictions: fixed variance or no temporal change

The rate of adaptation increases with the product of selection gradient and additive genetic variance [2, 44]. The genetic variance itself increases with the effective environmental gradient B such that in the absence of stochastic and demographic effects, the scaled genetic variance is $A = V_G/(r^*\,V_s) = \sqrt{2}B$ [45]. We might thus expect that with increasing heterogeneity of the environment, measured by the effective environmental gradient B, the genetic variance will steadily rise and thus support adaptation to ever-increasing temporal change k^*: yet, this would only be true in infinitely large populations. Increasing spatial heterogeneity aids adaptation until the load due to genetic variance becomes too large: eventually, the coupling between evolution and demography incurs a load high enough to drive the population to extinction. Furthermore, long before the deterministic extinction, genetic and demographic stochasticity reshape the dynamics.

The influence of the effective environmental gradient B and the effective rate of temporal change k^* on the rate of species' range and niche expansion is demonstrated in Figure 1. It shows that there is a fundamental bound to species' range expansion at $k^* = \sqrt{2}A = 2B$ (red dashed line), which extends from the threshold derived by [31] for a given genetic variance in the absence of spatial structure. The depicted line uses the predicted deterministic genetic variance maintained by gene flow across heterogeneous environments. Yet, adaptation to temporal change fails considerably before this upper bound is reached. This is because genetic drift depletes genetic variance when neighbourhood size $\mathcal{N}$ is small, which hinders adaptation. In the absence of temporal change, the limit where continuous adaptation to environmental gradients is possible is given by $\mathcal{N} \gtrapprox 6.3\,B + 0.56$ [43]. Below this limit, genetic drift is too strong relative to selection for stable clines to form. This threshold is depicted by a green diamond ⧫ in Figure 1.

Expansion threshold

When the optimum changes through time, the above limit to adaptation changes. A moving optimum induces a lag load. This demographic cost further lowers the neighbourhood size and thus depletes genetic variance as genetic drift becomes stronger. The expansion threshold in changing environments is determined jointly by the effective environmental gradient B, the neighbourhood size $\mathcal{N}$ and the effective rate of temporal change k^*. Its approximate form, expressed for the critical effective rate of temporal change k_e^*, is given by $k_e^* = 2B\,(1 - 8/\mathcal{N})\sqrt{1 - (6.3B + 0.56)(\sqrt{2}B + 2h^2)/(2h^2\mathcal{N})}$, is shown by a green curve in Figure 1; $h^2 \equiv V_G/V_P$ gives the narrow-sense heritability for the additive trait. Note that this approximate threshold, which marks the transition between expanding well-adapted populations with variance maintained by staggered clines in allele frequencies *vs.* collapsing populations where genetic drift overwhelms selection and the variance is depleted, only depends on the balance of k^*, B and $\mathcal{N}$. In contrast, rates of adaptation and range expansion also depend on the mutational input μ/r^* and the selection strength per locus, s/r^*. The robustness of the threshold to selection per locus $s \equiv \alpha^2/V_s$ is demonstrated in Figure S3.

The estimate of the generalised expansion threshold utilises the expected increase of demographic loads due to k^* and B as well as the reduction of genetic variance due to genetic drift. In two-dimensional habitats, the decrease of genetic variance with drift can be described as $V_G \approx V_{G,det}(1 - 8/\mathcal{N})$ for $\mathcal{N} > 8$, where $V_{G,det} = b\,\sigma\sqrt{V_s} + V_m$ gives the deterministic variance [45] – see Figure 2. This estimate assumes that the reduction in genetic variance in two dimensions takes the same form as in one dimension [35], with the dimension-appropriate neighbourhood size, and the constant of 8 is numerically fitted. When the optimum changes both in time and space, the selection arising from the distance between the trait mean will favour clines in additional allele frequencies, which then shift through space. The resulting increase in variance is thus stable over longer time scales; quantitative analysis of the evolution of variance in both spatially and temporally variable environments will be the subject of a forthcoming paper.

Fragmentation

A notable phenomenon that arises beyond the expansion threshold as the environment changes through time is range fragmentation (see Figure 1 D). Fragmentation is rapid and occurs in both physical space and trait (niche) space (Figure S2). It stems from the inability to sustain continuous adaptation when genetic drift is strong: clines in allele frequencies, which steepen due to genetic drift, become unstable. As fewer (and steeper) clines are maintained, local genetic variance declines. With variance falling below the threshold consistent with continuous adaptation, population fragments as genetic variances plummets. With very low adaptive variance, fragmented populations can persist only by tracking old habitat through space. Even if this habitat remains available, these populations tend to slowly decline in size; their resilience is low owing to a combination of limited adaptability and high demographic stochasticity. Fragmentation can also occur in the absence of temporal change, facilitated by higher demographic stochasticity [43]. When environments change in time faster than the k_e^* threshold, fragmentation, associated with fast depletion of variance is observed even for larger neighbourhood sizes (see Figure 1).

Dispersal and neighbourhood size

Larger neighbourhood size (the population accessible by dispersal) promotes adaptation by mitigating genetic drift and supporting adaptation to steeper environmental gradients B and faster temporal change k^*. Supplementary Figures S4 and S5 show that the expansion threshold k_e^* decreases with neighbourhood size $\mathcal{N}$. Even when the total population size is kept approximately constant (by scaling the neutral width of the habitat inversely with local carrying capacity), adaptation fails sooner as neighbourhood size decreases (Figure S4, $\overline{\mathcal{N}} = 8$ *vs.* Figure S5, $\overline{\mathcal{N}} = 14$).

Neighbourhood size also increases with dispersal, but so does the effective environmental gradient B. However, in two dimensions, neighbourhood size $\mathcal{N} = 2\pi\sigma^2 N$ increases with the square of dispersal distance σ^2, while the effective gradient $B = b\,\sigma/(\sqrt{2V_s}\,r^*)$ increases only linearly. Figure S6 demonstrates that when genetic drift is strong, the benefits of reducing genetic drift *via* increased dispersal outweigh the costs associated with increasing dispersal load.

Adaptive phenotypic plasticity

Last, I briefly explore the effects of adaptive phenotypic plasticity. Figure S7 demonstrates that adaptive phenotypic plasticity does not extend the range of survivable rates of temporal change in the same manner as it does for spatial variability. Adaptive phenotypic plasticity implies that the expressed trait z is closer to the optimum θ than expected based on its genetic basis alone, $(z-\theta) \to (1-\mathfrak{p})\,(z-\theta)$, where $\mathfrak{p}$ denotes adaptive plasticity. This means that the spatial gradient B appears shallower by $1-\mathfrak{p}$. While this reduces the demographic load and lowers the impact of genetic drift, it also diminishes the increase in genetic variance due to spatial variability. Thus, when genetic variance evolves in response to the effective environmental gradient, the effects of plasticity on adaptation to a steady temporal change largely cancel

out. This finding contrasts with predictions assuming fixed genetic variance in the selected trait, where the benefits of plasticity in response to variation in time and space are equivalent [6, 46].

Discussion

There is an urgent need for predictive theory to forecast adaptive responses and population resilience in changing environments [14, 47, 48]. While phenotypic models provide a useful reference [6, 7], the absence of evolutionary genetics not only precludes any inference based on genetic data but also weakens the reliability of predictions. Both the effects of gene flow and the possible benefits of adaptive plasticity change fundamentally when population genetics is included [43, 49]. Adaptation typically involves changes across many loci, and predicting the trajectory of each of them is not feasible [50]. In contrast, predictions based on higher-order parameters derived from fundamental population genetics (such as additive variance in the selected trait) tend to be robust [51, 52].

This theory provides quantitative predictions concerning species' range limits, adaptation, and resilience. It explains that a gradual increase in the rate of temporal change, as well as a decrease in neighbourhood size $\mathcal{N}$, can lead to a tipping point where adaptation collapses. Neighbourhood size, the population accessible by dispersal within a generation, can decline due to limited dispersal (e.g. reduced connectivity) or a decrease in local population density. Beyond this eco-evolutionary tipping point, genetic drift becomes too strong relative to the strength of environmental change, leading to the collapse of clinal adaptation. The population may decline gradually, with the species' range contracting from the margins, or fragment abruptly. While fragmentation due to spatial variation alone is limited to low neighbourhood sizes [43], a sharp increase in range and niche fragmentation is predicted when the loss of fitness due to temporal change exceeds the expansion threshold at the tipping point. Since fragmentation is associated with a loss of genetic variance in the selected traits as well as increased demographic stochasticity, recovery is likely to be hindered even if conditions later improve.

Importantly, the predictive parameters are measurable: thus, the theory can be tested and offers applications in conservation genetics. Neighbourhood size $\mathcal{N}$ can be estimated from ecological parameters of local density and dispersal as well as from population-genetic parameters – specifically, the rate of increase in neutral F_{ST} with distance [53, Eq. 11]. However, F_{ST} will be affected by population dynamics: see [38, 54] for estimates and discussion of assumptions. Demographic load parameters B and k^* quantify fitness loss due to spatial and temporal environmental variability. The dispersal load can be estimated from transplant experiments: moving a well-adapted population by a distance σ reduces fitness by $B^2 r^{*2}$. The fitness cost of temporal change $k^{*2} r^*/2$, over a characteristic time $1/r^*$, is more challenging to infer: in some cases, past generations' fitness can be assessed using seeds or diapausing animals, or

more commonly, by substituting space for time [55, 56] in spatial transplant experiments – see [5, Discussion].

There are three major limitations to this theory. First, it considers a single trait under stabilising selection assuming no rigid genetic trade-off, which could further limit adaptation [57]. Second, it considers gradual change in continuous environments. In reality, the environment may be patchy and selection fluctuates through time, with extremes potentially incurring higher fitness costs than the steady change. Each of these complications are likely to hinder adaptation [58, 59]. Third, the theory considers a single focal species. Although the environmental optimum can include both abiotic and biotic components [60], the theory neglects the evolution of species' interactions over similar time scales [61]. While none of these concerns invalidate the scale-free parameters, they imply that the numerical value of the expansion threshold should be considered an approximate baseline, rather than a definitive value.

The theory shows that when dispersal is predominantly local (diffusive), eco-evolutionary dynamics is determined over local scales. A minor proportion of long-distance dispersers does not substantially change the predictions [see [62] in the absence of temporal change]. Therefore, the theory does not require spatial gradients to be linear; it also applies to other forms of gradual change, such as steepening gradients [43, 63–65]. Because the dynamics is local and the predicted range margin is abrupt, the theory makes no claims about the abundant center of a species' range [66, 67].

Conservation genetics has been increasingly incorporated into conservation practice, and a decline in heterozygosity or effective population size N_e would be a clear cause for concern [68]. Yet, the utility of any cut-off value for effective population size N_e remains contested [69–72]. At the same time, assisted migration [40, 73] is increasingly advocated as a strategy to facilitate adaptation under climate change. Until now, no comprehensive predictive theory has incorporated the effects of gene flow across variable environments on local polygenic adaptation and species' range dynamics under temporal change. This theory provides a foundation for predicting when an increase in local dispersal is likely to be beneficial and identifies a critical threshold beyond which the population may be at risk of collapse or abrupt fragmentation.

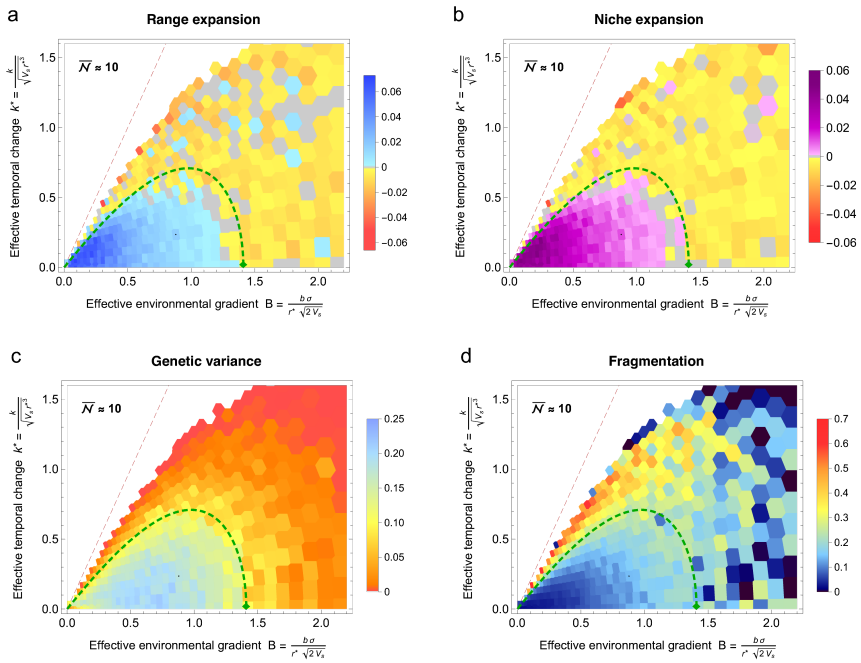

Fig. 1 Coevolution of species' range, niche and local genetic variance. Each rectangle represents an independent simulation from an array of changing environmental gradients b and rates of temporal change k. The expansion threshold is shown in a green dashed curve, approximated by $k_e^* = 2B\,(1-8/\mathcal{N})\sqrt{1-(6.3B+0.56)(\sqrt{2}B+2h^2)/(2h^2\mathcal{N})}$. Species' range (**a**) and niche (**b**) expand when sufficient variance (**c**) is maintained by the gene flow across the environmental gradient and contract otherwise. **a**, The rate of range expansion relative to the initial range size is shown in blue, while the rate of niche expansion (**b**) is shown in purple. The rates of range and niche contraction are shown in orange and red hues, while grey indicates no significant change (95% CI) and white space represents extinctions within 500 generations. **c**, Genetic variance initially increases with both spatial and temporal variability but collapses abruptly at the expansion threshold as the effect of genetic drift overwhelms selection. **d**, Species' range fragments abruptly as temporal change increases. Fragmentation is measured as the proportion of unoccupied space within the species' range. Note that fragmentation correlates with an increased probability of local extinction, resulting in high stochasticity in fragmentation on very steep gradients, as fragmentation of the last subpopulation is zero. Median neighbourhood size $\overline{\mathcal{N}} = 2\pi\sigma^2 N \approx 10$ ranges between 8 and 17 (and is higher for lower B and k^*, where the overall demographic load is lower); median total population size is about $3.2 \cdot 10^3$ for all surviving populations, ranging from 450 for expanding populations to $3 \cdot 10^5$ at $T = 500$ generations. See Methods (supplementary text) for parameters.

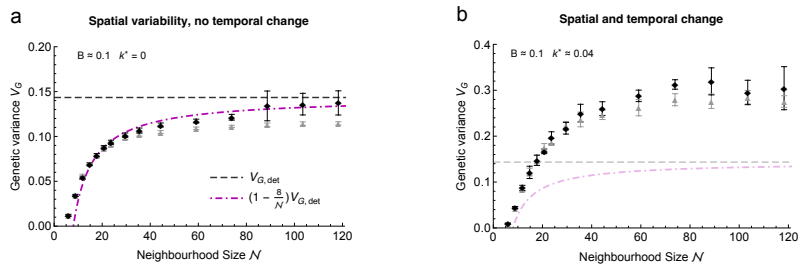

Fig. 2 Genetic variance is significantly reduced when neighbourhood size $\mathcal{N}$ is low. a, In stable environments, the decrease in genetic variance due to drift in two-dimensional habitats follows $V_G \approx V_{G,det}(1 - 8/\mathcal{N})$, shown as a dash-dotted magenta curve. Deterministic variance (dashed line) is given by $V_{G,det} = b\,\sigma\sqrt{V_s} + V_m$ [45], where the mutational variance is $V_m = 2\mu\, n_l V_s$ and n_l denotes the number of loci. **b**, When the environment changes through time (at $k^* \ll k_e^*$), genetic variance can increase substantially as newly selected alleles spread through the population. Black diamonds: neutral habitat width is fixed at $y_d = 100$, which ensures a two-dimensional population structure – but it also means that total population increases with $\mathcal{N}$. Gray diamonds represent simulations where neutral habitat width is scaled inversely with carrying capacity ($y_d = 600/K$), maintaining similar population size $N_{tot} \approx 1.5 \cdot 10^5$ as $\mathcal{N}$ increases. This demonstrates that neighbourhood size, rather than total (effective) population size, drives the increase of genetic variance. Only when the neutral habitat width y_d becomes too narrow due to scaling (gray, $y_d \lessapprox 40$ for $\mathcal{N} \gtrapprox 50$), genetic variance increases less than expected. This is because in the limit of a one-dimensional habitat ($y_d = 1$), the strength of genetic drift scales with $1/(\sqrt{s}\,\mathcal{N}_{1D})$ [35, 74, 75], where the one-dimensional neighbourhood size is $\mathcal{N}_{1D} = 2\sqrt{\pi}N\sigma$ [32]. Error bars show standard deviations (10 replicates). Parameters as in Figure 1, $b = 0.2$, $k = 0$ (**a**) and $k = 0.05$ (**b**) with run time $T = 300$ generations and neighbourhood size $\mathcal{N} = 2\pi\sigma^2 N \approx 2\pi\sigma^2 K(1 - B/\sqrt{2})$, where local carrying capacity K ranges from $K = 2$ to $K = 50$.

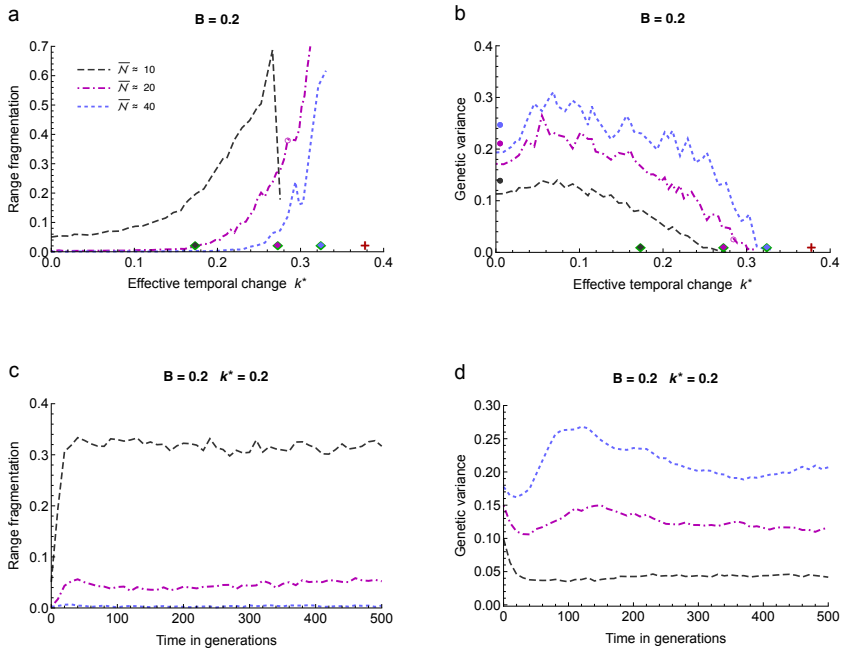

Fig. 3 Species' range can fragment abruptly when environments change through time and the neighbourhood size is small. a, Range fragmentation increases with the effective rate of temporal change k^* and decreasing neighbourhood size $\mathcal{N}$. **b**, Genetic variance decreases with genetic drift (decreasing neighbourhood size $\mathcal{N}$) and is highest for intermediate rates of temporal change before declining again. Small dots at $k^* = 0$ represent the predicted genetic variance in stable environments, accounting for genetic drift. The expansion threshold $k_e^*(B, \mathcal{N})$ is shown in green-outlined diamonds in (**a, b**), with colour centres matching the respective neighbourhood sizes. Beyond the expansion threshold, fragmentation occurs rapidly (**a, c**) and is accompanied by a loss of local genetic variance (**b, d**). The bottom row (**c, d**) shows the temporal dynamics: for $\overline{\mathcal{N}} \approx 10$ (black, dashed), $k^* = 0.2$ is above the expansion threshold and thus the population is highly fragmented; while for $\overline{\mathcal{N}} \approx 20$ (magenta, dot-dashed) and $\overline{\mathcal{N}} \approx 40$ (blue, dashed), $k^* = 0.2$ is below the expansion threshold, resulting in little to no fragmentation. The neighbourhood sizes correspond to local carrying capacities $K = 5, 10, 20$, and are only slightly below the maximum attainable neighbourhood size $\mathcal{N} = 2\pi\sigma^2 K$. Parameters as in Figure 1; the small magenta circle in (**b**) marks an illustration shown in Figure 4.

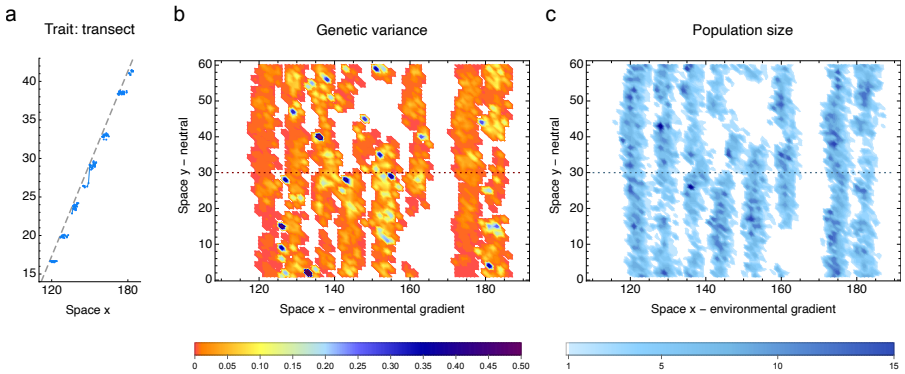

Fig. 4 Example of species' range fragmentation due to a fast temporal change. a, In fragmented populations, trait mean (blue line) no longer tracks the optimum (grey dashed line) but instead, disjunct subpopulations are each adapted to a single optimum and move through space tracking their niche. Blue dots show individual trait values. The subfigure (**a**) shows a transect at the central neutral habitat ($y = 30$), marked by the dotted line in (**b, c**). **b**, Genetic variance is depleted considerably below the expected value of $V_G \approx (b\,\sigma\sqrt{V_s} + V_m)(1 - 8/\mathcal{N}) = 0.21$, although local spikes of high variance (blue hues) persist. **c**, Local population size is close to the carrying capacity $K = 10$, yet 40% of the space is unoccupied, and the population gradually contracts over time. Subpopulations are connected *via* gene flow along the neutral habitat (y) but largely isolated along the environmental gradient (x). Parameters are the same as in Figure 3 (K = 10, magenta), with $k^* = 0.285$, indicated by a small circle there. This example is chosen just beyond the expansion threshold $k_e^*(B, \mathcal{N}) \approx 0.273$, where some clines in allele frequencies still persist and therefore variance is not uniformly low. The dynamics of fragmentation are illustrated in Supplementary Movie S1, demonstrating that fragmentation occurs abruptly and follows a marked increase in lag (and thus lag load) behind the moving optimum.

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Supplementary Materials

Methods
Supplementary Text with Table S1 and Figures S1 to S7
Movie S1