# Is the sky the limit?
# On the expansion threshold of a species' range.

Jitka Polechová[1,2]
**1** University of Vienna, Department of Mathematics

**2** Institute for Science and Technology (IST Austria), Klosterneuburg, Austria

* jitka@univie.ac.at

## Abstract

More than a hundred years after Grigg's influential analysis of species' borders, research into the causes of limits to species' ranges is more active than ever, fuelled by our need to understand their dynamics in the changing environments. Current predictions are either very specific, requiring measurements of many interrelated parameters, or make restrictive assumptions such as fixing the genetic variance or neglecting the two-dimensional spatial structure of most natural habitats. I show that the range margin can be understood based on just two measurable parameters: i) the fitness cost of dispersal – a measure of environmental heterogeneity – and ii) the strength of genetic drift, which reduces genetic diversity. Together, these two parameters define an *expansion threshold*: adaptation fails when the neighbourhood size is so small that genetic drift reduces diversity below the level required for adaptation to environmental heterogeneity. When the key parameters drop below this *expansion threshold* locally, a sharp range margin forms. When they drop below this threshold throughout the species' range, adaptation collapses everywhere, resulting in either extinction, or formation of a fragmented meta-population. Below the *expansion threshold*, increased dispersal is beneficial, because the reduction of both genetic and demographic stochasticity has a stronger effect than is its cost through increased maladaptation. Because the effects of dispersal differ fundamentally with dimension, the predictions are qualitatively different from those in a linear habitat. The expansion threshold provides a novel, theoretically justified and testable prediction for formation of the range margin and collapse of the species' range in two-dimensional habitats.

## Author summary

Gene flow across environments has conflicting effects: while it increases the genetic variation necessary for adaptation and counters the loss of genetic diversity due to genetic drift, it may also swamp adaptation to local conditions. This interplay is crucial for the dynamics of a species' range expansion. I show that it can be understood based on two dimensionless parameters: i) the fitness cost of dispersal – a measure of environmental heterogeneity – and ii) the strength of genetic drift – a measure of reduction of genetic diversity. Together, these two parameters define an *expansion threshold*: adaptation fails when the the population's neighbourhood size is so small that genetic drift reduces diversity below the level requisite for adaptation to the environmental heterogeneity. This threshold provides a novel, theoretically justified and testable prediction for formation of a range margin and a collapse of a species' range in two-dimensional habitats.


## Introduction

Species' borders are not just determined by the limits of their ecological niche [1, 2]. A species' edge is typically sharper than would be implied by the environment (both biotic and abiotic). Moreover, although species' ranges are inherently dynamic, it is puzzling that they typically expand rather slowly [3]. The usual – but tautological – explanation is that lack of genetic variation at the range margin prevents further expansion [4]. Indeed, a species' range edge is often associated with lower genetic variation [5–10]. Yet, why does selection for new variants near the edge of the range not increase adaptive genetic variance, thereby enabling it to continuously expand [4, 11]? Haldane [12] proposed a general explanation: even if environmental conditions vary smoothly, "swamping" by gene flow from central to marginal habitats will cause more severe maladaptation in marginal habitats, further reducing their population density. This would lead to a sharp edge to a species' range, even if genetic variance at the range margin is large. However, the consequences of dispersal and gene flow for evolution of a species' range continue to be debated [13–15]: a number of studies suggest that intermediate dispersal may be optimal [16–20]. Gene flow across heterogeneous environments can be beneficial, because the increase of genetic variance allows the population to adapt in response to selection [11]. Current theory identifies that local population dynamics, dispersal, and evolution of niche-limiting traits (including their variance), and both genetic and demographic stochasticity are all important for species' range dynamics [11, 16–18, 21–24]. Yet, these core aspects have not been incorporated into a single study that would provide testable predictions for range limits in two-dimensional habitats.

As Haldane [12] previously pointed out, it is important to consider population- and evolutionary dynamics across a species' range jointly, as their effects interact. Due to maladaptation, both the carrying capacity of the habitat and the population growth rate is likely to decrease – such selection is called *hard* [25]. Classic deterministic theory [21] shows that when genetic variance is fixed, there are two stable regimes of adaptation to a spatially varying optimum (see Fig. 1): i) a *limited adaptation*, where a population is only adapted to a single optimum or becomes a patchy conglomerate of discrete phenotypes or ii) continuous or *uniform* adaptation, which is stable when the genetic variance, measured in terms of its cost in fitness (*segregation load*) is large relative to the cost of dispersal across environments (*dispersal load*). Under *uniform adaptation*, a species' range gradually expands – a stable boundary only forms when the genetic variance is too small to allow continuous adaptation to the spatially variable

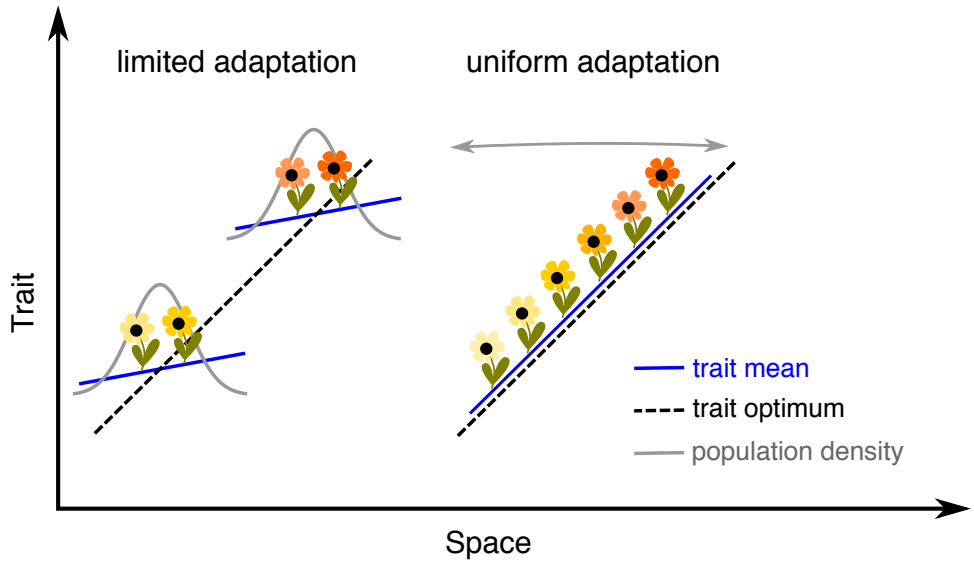


**Figure 1. Two modes of adaptation.** Assuming that genetic variance is fixed, deterministic theory [21] predicts that there are two modes of adaptation to an environmental gradient. When the effective environmental gradient $B$ is steep relative to the standing load due to genetic variance $A$, clinal adaptation fails, and the population only matches the optimum at the very centre of its range (*limited adaptation*). Conversely, when the standing load is large relative to the effective environmental gradient ($A > B^2/2$), a population adapts continuously, gradually expanding its range (*uniform adaptation*). Black dashed lines depict the trait optimum, blue lines depict the trait mean. Population density is shown in gray: it has a sharp margin for *limited adaptation* but is steadily expanding under *uniform adaptation*.

environment and hence the *limited adaptation* is stable. However, when genetic variance can evolve, such a limit no longer exists in infinitely large populations: continuous adaptation is always possible until the combined genetic and dispersal loads are so large that the population density drops to zero [11]. Deterministic theory thus predicts that a sharp and stable boundary to a species' range does not form when the environment changes smoothly. Yet, in finite populations, genetic drift reduces local genetic variance [26], potentially qualitatively changing the dynamics. Indeed, it has been shown that for one-dimensional habitats (such as rivers), a sharp range margin arises when genetic drift relative to selection per locus becomes strong relative to the fitness cost of dispersal across environments [23]. However, most species live in two-dimensional habitats. There, the mixing due to dispersal is more efficient and the effect of genetic drift changes qualitatively, becoming only weakly dependent on selection [27]). Is there still an intrinsic threshold to range expansion in finite populations when dispersal and gene flow occur over two-dimensional space, rather than along a line? If so, what is its biological interpretation?

# Results

I study the problem of intrinsic limits to adaptation in a two dimensional habitat. Throughout, I assume that the species' niche is limited by stabilising selection on a composite phenotypic trait. This optimum varies across one dimension of the two-dimensional habitat – such as temperature and humidity with altitude. Demography and evolution are considered together. Selection is *hard*: both the rate of density-dependent population growth and the attainable equilibrium density decrease with increasing maladaptation. Both trait mean and genetic variance can freely evolve *via* change in allele frequencies. The populations are finite and both genetic and demographic stochasticity are included. The model is first outlined at a population level, in terms of coupled stochastic differential equations. While it is not possible to obtain analytical solutions to this model, this formalisation allows us to identify the effective dimensionless parameters which describe the dynamics. Next, individual based simulations are used to determine the driving relationship between the key parameters, and test its robustness. The details are described in Methods: Model.

The dynamics of the evolution of a species' range, as formalised by this model, are well described by three dimensionless parameters, which give a full description of the system. Details are given in the Methods: Rescaling. The first dimensionless parameter carries over from the phenotypic model of [21]: the effective environmental gradient $B$ measures the fitness cost of maladaptation incurred by dispersal across a heterogenous environment. The second parameter is the neighbourhood size of the population, $\mathcal{N}$, which can be understood as the number of diploid individuals within one generation's dispersal range. Originally, neighbourhood size was defined by [28] as the size of the single panmictic diploid population which would give the same probability of identity by descent in the previous generation. The inverse of neighbourhood size $1/\mathcal{N}$ hence describes the local increase of homozygosity due to genetic drift. The third dimensionless parameter is the ratio $s/r^*$ of the strength of selection $s$ per locus relative to the strength of density dependence, $r^*$. Detailed description of the parameters can be found in Methods: Table 1.

In order to see how the rescaled parameters capture the evolution of a species' range, I simulated evolving populations adapting to a linear gradient in the optimum. Depending on the parameters, the population either expands, gradually extending its

phenotypic range by consecutive sweeps of loci advantageous at the edges or the species' range contracts or disintegrates as adaptation fails. Fig. 2 shows the range dynamics of 750 evolved populations, each based on different parametrizations, in relation to the first two compound dimensionless parameters, i) the effective environmental gradient $B$ and ii) the inverse of neighbourhood size $1/\mathcal{N}$ which describes the effect of genetic drift on the allele frequencies. The individual-based model uses unscaled (naïve) model parameters and includes mutation (see Methods: Individual-based Model and Table 1).

Demographic stochasticity alone is sufficient to drive the species' range to collapse where its local neighbourhood size $\mathcal{N}$ is smaller than about one. For larger neighbourhood sizes, the two parameters $B$ and $\mathcal{N}$ give a clear separation between expanding populations when the neighbourhood size $\mathcal{N}$ is large relative to the effective environmental gradient $B$ (shown in blue, Fig. 2) and the rest, where adaptation is failing. The separation gives an *expansion threshold*, estimated at $\mathcal{N} \approx 6.3\,B + 0.56$ (red line). Above the *expansion threshold*, populations are predicted to expand (see Fig. 3); below it, adaptation fails abruptly. If conditions change uniformly across space (as in these simulation runs, with constant gradient and carrying capacity), this means that adaptation fails everywhere – a species' range then either collapses from the margins (Fig. 2, red hues) and/or disintegrates (Fig. 2, open circles), forming a fragmented metapopulation. The sub-populations forming this metapopulation have only a very narrow phenotypic range and maintain locally only minimal adaptive variance. They correspond to the *limited adaptation* regime identified for a phenotypic model with genetic variance as a parameter [21]. In contrast to one-dimensional habitats [23], these patchy metapopulations are stabilised by dispersal from surrounding subpopulations in the two-dimensional habitat and can thus persist for a long time. An example of such a metapopulation is given in Fig. 4.

Interestingly, the third dimensionless parameter $s/r^*$ has no detectable effect. In other words, whilst the *expansion threshold* reflects the total fitness cost of dispersal in a heterogeneous environment, it appears independent of the strength of selection per locus ($s$). This is both because the effect of genetic drift is nearly independent of selection in two-dimensional habitats [27; see also Fig. S1], and because we are asking whether the species' range expands or adaptation collapses, rather than studying the rate of range expansion quantitively. The dashed lines in Fig. 2 compare the estimated expansion threshold for small and large $s/r^*$.

In nature, conditions are unlikely to change uniformly. Thus, I investigate whether adaptation fails near the *expansion threshold* as conditions change across space. For example, we can imagine that the population starts well adapted in the central part of the available habitat, and as it expands, conditions become progressively poorer (see Fig. S2a); i.e. the effective environmental gradient $B$ gets steeper. As the expanding population approaches the *expansion threshold*, adaptive genetic variance increasingly decreases below the predicted value [11], which would be maintained by gene flow in the absence of genetic drift (Fig. 5a, gray dashed line). This is a result of an increased frequency of demes under *limited adaptation*, leading to higher rates of extinctions and re-colonizations, which reduce both adaptive and neutral diversity (see Fig. 5b). Range expansion then ceases at the *expansion threshold* as the genetic variance drops to the critical value where only *limited adaptation* is stable [21] assuming genetic variance is fixed (Fig. 5a, dotted line). This is because although populations can persist with *limited adaptation* (Fig. 4), the transient amount of genetic variance maintained under *limited adaptation* is almost never consistent with range expansion (see Fig. 2, open circles).

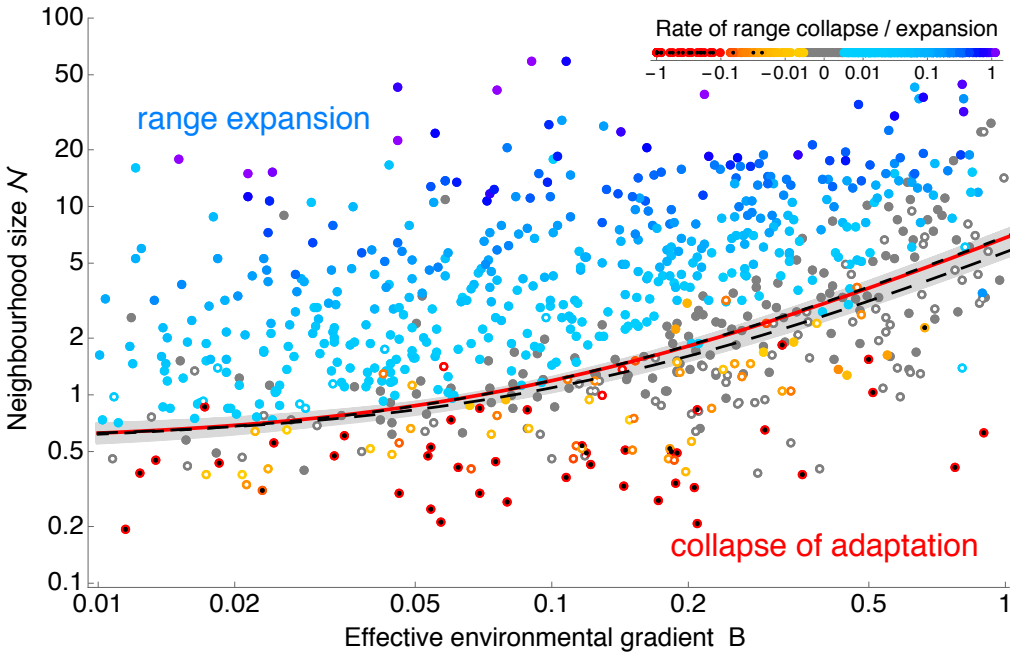


**Figure 2. Two dimensionless parameters, the neighbourhood size $\mathcal{N}$ and the effective environmental gradient B give a clear prediction whether a species' range can expand** (blue hues). The red line shows the fitted boundary between expanding populations (in blue) and collapsing ranges (red hues): populations expand above the *expansion threshold*, when $\mathcal{N} \gtrapprox 6.3\,B + 0.56$. The grey region gives 95% bootstrap confidence intervals, whilst the dashed lines depict the predicted *expansion threshold* for weak selection ($s/r^* < 0.005$, indistinguishable from the whole data set) and for strong selection $s/r^* > 0.005$ (lower dashed line). Stagnant populations, changing by less than five demes per 1000 generations, are shown in grey. Open circles denote populations where continuous adaptation has collapsed and the population consists of many discrete phenotypes adapted to a single optimum each (*limited adaptation*, Fig. 4), whilst local genetic variance is very small (defined as less than 10% of the predicted adaptive variance in the absence of genetic drift). Simulations were run for 5000 generations, starting from a population adapted to a linearly changing optimum in the central part of the available habitat. Populations that went extinct are marked with a black dot. The top corner legend gives the colour coding for the rate of range collapse and expansion in units of demes per generation; rates of collapse are capped at $-1$. The *expansion threshold* is fitted as a step function changing linearly along $B$: all blue dots are assigned a value of 1; all red dots and open circles are assigned a value of 0. The coefficient of determination is $R^2 = 0.964$.

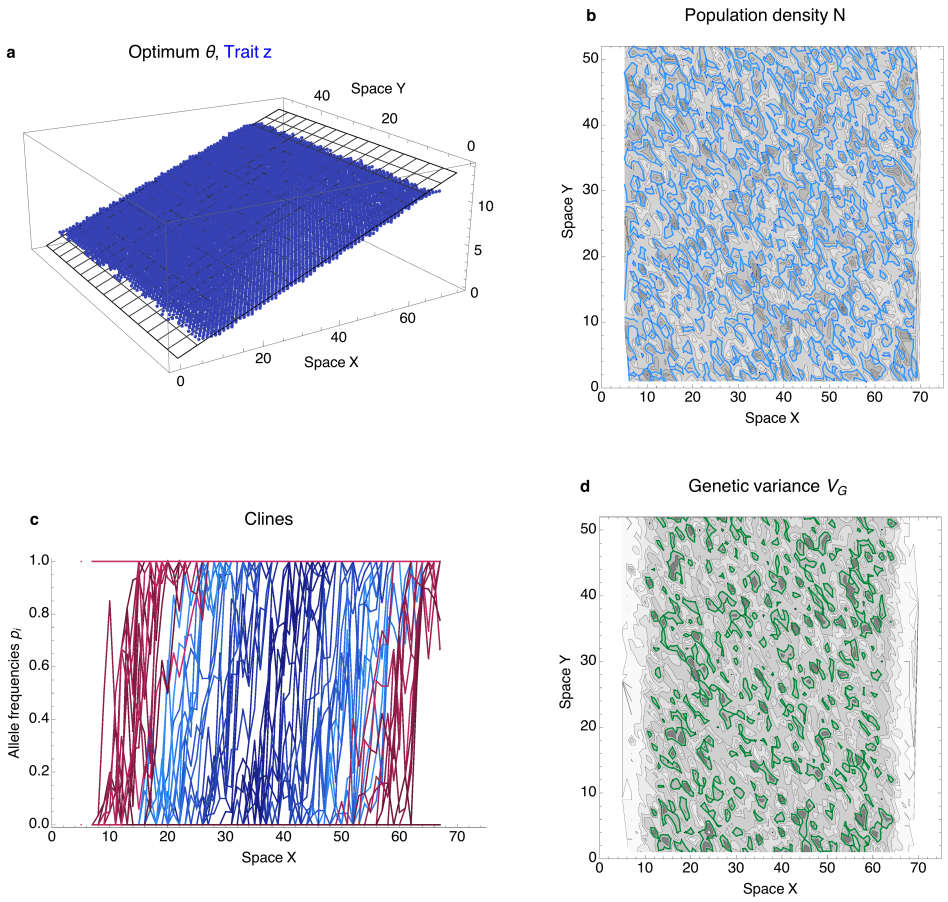


**Figure 3. Uniform adaptation: above the *expansion threshold*, the population expands gradually through the available habitat**. (**a**) Trait (in blue) is closely matching the environmental gradient (grey) along the X axis. (**b**) Population steadily expands, whilst population size varies across space with mean of $N = 19$ (the prediction at ($\hat{N} = 20$) and standard deviation about 5.8. (**c**) Population starts from the centre (blue clines) and as it expands new clines (red hues) contribute to the adaptation – as each allele frequency changes from 0 to 1, the trait value increases by $\alpha$. At each location, multiple clines contribute to the trait (and variance); clines are shown at a middle transect ($Y = 25$). (**d**) Genetic variance changes continuously across space, with median slightly lower than the deterministic prediction (green contour). Deterministic predictions are based on the study by [11], and are explained in Methods, along with the specification of the unscaled parameters. The population was evolving for 2000 generations, starting from a population adapted to the central part of the available habitat.

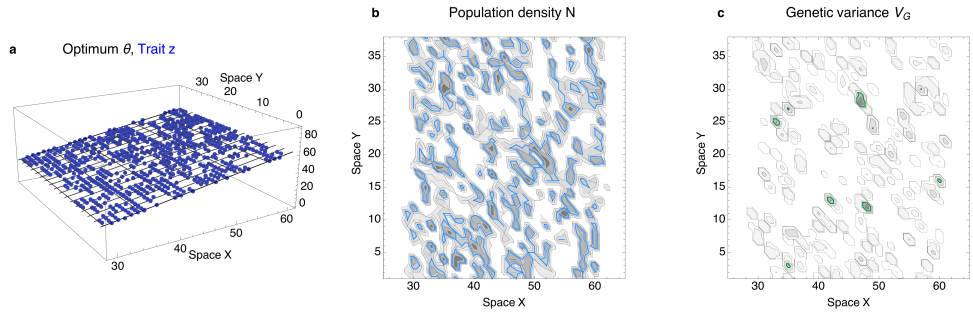


**Figure 4. A metapopulation can form when the population is below the *expansion threshold* throughout its range**. The population fragments rapidly (within tens of generations) to small patches of tens to a few hundred of individuals, whilst losing local adaptive variation. In two-dimensional habitats, such a metapopulation with *limited adaptation* can persist for long times. Nevertheless, the population very slowly contracts, eventually forming a narrow band adapted to a single optimum. (**a**) The distribution of phenotypes across space is fragmented. (**b**) The sub-populations are transient, although they are stabilised by dispersal across space, especially along the neutral direction with no change in the optimum (Y). Locally, the population density may be higher than under *uniform adaptation* (blue contours). (**c**) The adaptive genetic variance stays about an order of magnitude lower than would be maintained by gene flow under *uniform adaptation* (green contours): typically, only a few clines in allele frequencies contribute to the genetic variance within a sub-population. The parameterization is detailed in the Methods: Individual-based model; predicted neighbourhood size is $\hat{\mathcal{N}} = 2.7$, effective environmental gradient is $B = 0.48$. Shown here after 5000 generations – the population collapses to a narrow band (at $X = 45$ and which appears persistent) after a further 20.000 generations.

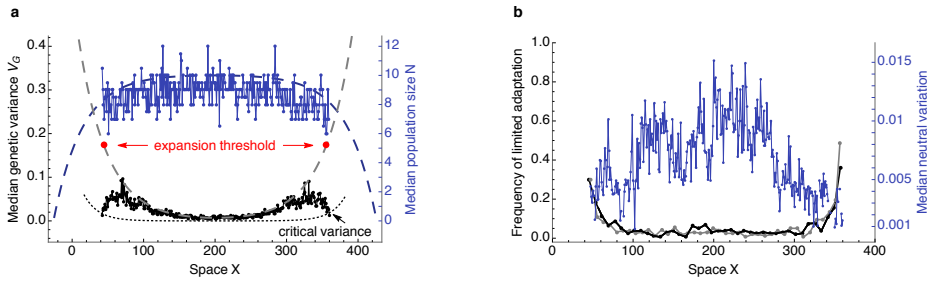


**Figure 5. On a steepening environmental gradient, a sharp range margin forms near the *expansion threshold*.** As the effective environmental gradient steepens away from the central location, adaptive genetic variance must increase correspondingly in order to maintain *uniform adaptation*. (**a**) Median population density stays fairly constant across the range (blue dots), following the deterministic prediction ($\hat{N}$, blue dashed line). Genetic variance (black dots) increases due to gene flow across the phenotypic gradient – the deterministic expectation is given by the gray dashed line. (See Methods: Model for details.) Yet as the environmental gradient steepens, genetic variance fails to increase fast enough and near the *expansion threshold*, adaptation fails. The dotted line gives the corresponding critical genetic variance, below which only *limited adaptation* is expected in a phenotypic model with a fixed genetic variance ($A \approx B^2/2$, where $A$ is the standing genetic load; [21]). (**b**) As the environmental gradient steepens, the frequency of *limited adaptation* within the metapopulation increases (black and gray) and hence neutral variation decreases (blue). The black line gives the proportion of demes with *limited adaptation* after 50.000 generations, when the range margin appears stable; grey gives the proportion after 40.000 generations (depicted is an average over a sliding window of 15 demes). The median is given over the neutral spatial axis Y (with constant optimum); the trait mean, the population trait mean, variance and population density in two-dimensional space is shown in Fig. which also lists all the parameters.

In a large population, the ability to adapt to heterogeneous environments is independent of dispersal: this is because both the local genetic variance (measured by *segregation load*), which enables adaptation to spatially variable environments, and the perceived steepness of the environmental gradient (*dispersal load*), increase quadratically with gene flow [11]. Yet, population density declines gradually due to these combined fitness costs – and this effect gets increasingly detrimental as the population size decreases. In small populations, dispersal has a net beneficial effect because the neighbourhood size $\mathcal{N}$ increases faster with dispersal than the effect of swamping by gene flow ($B$): the drift-reducing effect of dispersal overpowers its maladaptive effect. Hence, near the *expansion threshold*, an increase of dispersal is favourable. This effect is demonstrated in Fig. 6. It gives a general, scale-free prediction of when "intermediate" dispersal is beneficial for adaptation across a species' range.

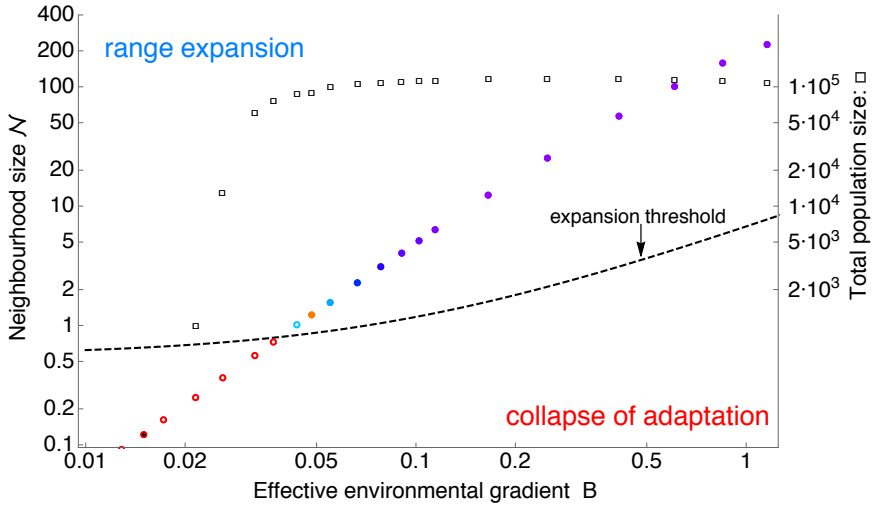


**Figure 6. Increased dispersal can lead to a recovery of a well-adapted population**. This is because neighbourhood size $\mathcal{N}$ increases more with dispersal than does the effective environmental gradient $B$ increase – and hence population gets above the *expansion threshold* (dashed line) as dispersal increases, and recovers *uniform adaptation* throughout its range. In red are collapsing populations (black centre indicates extinction), in blue are well-adapted expanding populations. The hue indicates the rate of expansion or collapse (from light to dark blue) and from orange to red, respectively (the rate of range change is not significantly different from zero for first three simulations above the *expansion threshold*). Open circles indicate *limited adaptation*, where range is fragmented and each subpopulation is only matching a single optimum whilst its genetic variance is very small. Total population size □ changes abruptly as the population recovers continuous adaptation (above the *expansion threshold*). In contrast, local population size stays fairly constant (around $N = 3.5$). Parameters for these simulations are given in the Methods: Individual-based model; the scaling of $\mathcal{N}$ and $B$ with dispersal $\sigma$ is clear from Table 1.

# 1 Discussion

Here I have shown that adaptation fails when positive feedback between genetic drift, maladaptation and population size reduces adaptive genetic variance to levels which are incompatible with continuous adaptation. The revealed *expansion threshold* differs qualitatively from the limit to adaptation identified previously [23] for a population living along a one-dimensional habitat because dispersal in two dimensions weakens the loss of diversity due to genetic drift more effectively, such that it becomes independent of selection. The *expansion threshold* implies that populations with very small neighbourhood sizes ($\mathcal{N} \lessapprox 1$), which suffer a severe reduction in neutral heterozygosity, will be prone to collapse based on demographic stochasticity alone. However, even in the absence of demographic stochasticity, genetic drift reduces the adaptive genetic variance required to sustain adaptation to a heterogeneous environment. The *expansion threshold* describes when this reduction due to genetic drift is incompatible with continuous adaptation, predicting a collapse of a species' range. If the *expansion threshold* is reached at an existing range margin as the species expands through its habitat, a sharp and stable range margin forms. If there is a drop below the *expansion threshold* throughout the species' range, as after a sudden drop in carrying capacity, adaptation abruptly collapses throughout a species' range. The result is either extinction, or a fragmented metapopulation consisting of a conglomerate of sub-populations, each adapted to a single phenotypic optimum. It follows that near a range margin, we expect increased range fragmentation, and a decrease in adaptive genetic variance. The threshold gives a theoretical base to the controversial issue of the importance of evolution (genetics) and ecology (demography) for assessing vulnerability of a species [29, 30]. The predicted sharp species' range edge is in agreement with the reported lack of evidence for *abundant centre* of a species' range, which although commonly assumed in macroecological theory, has little support in data [31, 32].

Importantly, these predictive scale-free parameters can be measured in wild populations: the effective environmental gradient $B$ can be measured as fitness loss associated with transplant experiments across *vs.* along an environmental gradient. The environmental gradient can include the presence of competitors [33]. The neighbourhood size $\mathcal{N}$ can be estimated from neutral allele frequencies [34, 35]. Estimates of neighbourhood size are fairly robust distribution of dispersal distances [36], yet near the *expansion threshold*, both the noisiness of the statistics and the homozygosity will increase due to local extinctions and recolonizations [37]. An alternative estimate of neighbourhood size can be also obtained from mark-recapture studies, by measuring population density and dispersal (as an approximation for gene flow) independently [34]. In general, while the numerical constants may change when natural populations deviate in their biology from our model assumptions, the scale-free parameters identified in this study remain core drivers of the intrinsic dynamics within a species' range. Because the *expansion threshold* is free of any locus- or trait- specific measure, the result it is readily applicable to a species' range- and niche- dynamics which includes adaptation in multiple traits, assuming any pre-existing trade-offs can gradually evolve.

# Methods

## Model

I model evolution of a species' range in two-dimensional habitat, where both population dynamics and evolution (in many additive loci) is considered jointly. The coupling is *via* the mean fitness $\overline{r}(\overline{z}, N)$, which gives the growth rate of the population, and decreases with increasing maladaptation: $\overline{r}(\overline{z}, N) = r_e(N) + \overline{r}_g(\overline{z})$. The ecological component of growth rate, $r_e$, can take various forms: here the regulation is logistic, so that fitness declines linearly with density $N$: $r_e = r_m(1 - N/K)$, where $r_m$ is the maximum per capita growth rate in the limit of the local population density $N \to 0$. The carrying capacity $K$ (for a perfectly adapted phenotype) is assumed uniform across space. The second term, $r_g(\overline{z}) \leq 0$, is the reduction in growth rate due to deviation from the optimum. Selection is stabilising: the optimum $\theta$ changes smoothly with one spatial dimension ($x$): for any individual, the drop in fitness due to maladaptation is $r_g(z) = -(z - \theta)^2/(2V_s)$. A population with mean phenotype $\overline{z}$ has its fitness reduced by $\overline{r}_g(\overline{z}) = -(\overline{z} - \theta)^2/(2V_s) - V_P/(2V_s)$, where $V_P = V_G + V_E$ is the phenotypic variance. The phenotype $z$ is determined by many di-allelic loci with allelic effects $\alpha_i$; the model is haploid, hence $\overline{z} = \sum_i \alpha_i p_i$, where $p_i$ is the allele frequency at locus $i$. Because the loss of fitness due to environmental variance $V_E$ can be included in $r_m^* = r_m - V_E/(2V_s)$; $V_E$ is a redundant parameter. The selection is *hard*: both the mean fitness (growth rate) and the attainable equilibrium density $\hat{N} = Kr^*/r_m = K(1 - V_G/(2r_m V_s))$ decrease with maladaptation. Expected genetic variance maintained by gene flow in the absence of genetic drift is $V_G = b\,\sigma V_s$ [11]; the contribution due to mutation is small, at mutation-section balance $V_{G,\mu/s} = 2\mu V_s n_l$.

## Individual-based simulations

Discrete-time individual based simulations are set to correspond to the model with continuous time and space. The space is a two-dimensional lattice with spacing between demes of $\delta x = 1$. Every generation, each individual mates with a partner drawn from the same deme, with probability proportional to its fitness, to produce a number of offspring drawn from a Poisson distribution with mean of $Exp[r(z, N)]$. The effective diploid population density $N_e$ hence equals half of the haploid population density $N$, and $\mathcal{N} = 4\pi N_e \sigma^2 = 2\pi N \sigma^2$. The life-cycle is selection $\to$ mutation $\to$ recombination $\to$ migration. Generations are non-overlapping and selfing is allowed at no cost. The genome is haploid with unlinked loci (the probability of recombination between any two loci is 1/2). The allelic effects $\alpha_i$ of the loci combine in an additive fashion; the allelic effects are uniform throughout this study, $\alpha_i \equiv \alpha$. Mutation is set to $\mu = 10^{-6}$, independently of the number of loci. Migration is diffusive with a Gaussian dispersal kernel. The tails of the dispersal kernel need to be truncated: truncation is set to two standard deviations of the dispersal kernel throughout, and dispersal probabilities and variance are adjusted so that the discretised dispersal kernel sums to 1 [38, p. 1209]. Simulations were run at the computer cluster of IST Austria using *Mathematica 9 (Wolfram)* ; the code used for simulations is available at request.

**Parameters**: There are in total 10 parameters in the individual-based model but only 7 are used to describe the model dynamics in continuous time. These are listed in the bottom of Table 1. They are the environmental gradient $b = [0.012, 2]$, dispersal distance $\sigma = [0.1, 1.3]$, carrying capacity for a well adapted phenotype $K = [3, 31]$, width of stabilising selection $V_s = [0.005, 6]$, the maximum intrinsic rate of increase $r_m = [0.2, 2]$ and the mutation rate $\mu$, fixed to $\mu \equiv 10^{-6}$. The $[x, y]$ interval gives the

parameter range used in the 750 randomly sampled runs, with their distributions described in Fig. S3. The number of genes and demes are not included in the continuous time description (and hence the rescaling) because it assumes that space is not limiting, and that all loci have equivalent effect with no statistical associations among them. In the individual-based model, the habitat width is set to be wide enough to be effectively two-dimensional under diffusive dispersal for thousands of generations [39] – 100 dispersal distances $\sigma$ along the neutral direction, and at least 10 cline (deterministic) widths wide along the gradient. The number of genes contributing to the adaptation across the species' range is $n_l = [5, 3000]$, with the number of locally polymorphic genes between 1 and 300. Since mutation rate is fixed at $\mu = 10^{=6}$, the genomic mutation rate has a wide range, $U = [5 \cdot 10^{-6}, 3 \cdot 10^{-3}]$, with median of $U = 10^{-4}$.

Parameters for Fig. 3 are: $b = 0.18$, $\sigma = 0.52$, $V_s = 0.23$, $K = 26.7$, $r_{m_0} = 1$ and $\alpha = 0.14$, $s = 0.04$, $\mu = 10^{-6}$, 97 genes. Median genetic variance is at $V_G = 0.031$, deterministic prediction $V_G = b\sigma\sqrt{V_s} = 0.45$ [11]. In Fig. 4, the parameters are: $b = 1$, $\sigma = 0.4$, $V_s = 0.4$, $K = 4$, $r_m = 1.2$ and $\alpha = 0.1$, $s = 0.015$, $\mu = 10^{-6}$, 874 genes. Median genetic variance within patches is around 0.02, whilst the maximum contribution by a single cline $1/4\alpha^2 = 0.0026$; in contrast, variance maintained by gene flow under *uniform adaptation* [11] would be $V_G = b\sigma\sqrt{V_s} \doteq 0.25$. Parameters for Fig. 6 are $b_0 = 0.3$, $\sigma = [0.05, 3]$, $V_s = 1$, $K = 4$, $r_{m_0} = 1$ and $\alpha = 0.05$, $s = 0.1$, $\mu = 10^{-6}$, 1000 genes, 1000 demes along X, 200 demes along Y. These populations were evolving for 500 generations.

**Table 1. Three scale-free parameters: B, $\mathcal{N}$ and s/r$^*$ (top) describe the system**. Middle section gives informative derived parameters. The bottom section gives seven parameters of the model before rescaling; where the seventh parameter, mutation rate $\mu$, can be neglected because variance maintained by mutation-selection balance, $V_{G,\mu/s} = 2\mu V_s n_l$, is typically much smaller than variance generated by gene flow across environments, $V_G = b\,\sigma V_s$.

| param. | dim. | |
|---|---|---|
| $B$ | – | effective environmental gradient $B = b\sigma/(r^*\sqrt{2V_s})$ |
| $\mathcal{N}$ | – | neighbourhood size $\mathcal{N} = 4\pi N_e\sigma^2 = 2\pi N\sigma^2$ |
| $s/r^*$ | – | strength of selection per locus relative to the strength of density-dependence |
| $s$ | $1/T$ | selection per locus: $s \equiv \alpha^2/(2V_s)$ |
| $r^*$ | $1/T$ | rate of return to equilibrium pop. size: $r^* \equiv -N\,\partial\overline{r}/\partial N\|_{N\to\hat{N}} = r_m - V_G/(2V_s)$ |
| $b$ | $Z/D$ | gradient in the environmental optimum |
| $V_s$ | $Z^2T$ | variance of stabilising selection |
| $\sigma$ | $D/\sqrt{T}$ | dispersal per generation |
| $K$ | $T/D^2$ | max. carrying capacity (haploid) K = N when all phenotypes are perfectly adapted |
| $r_m$ | $1/T$ | max. intrinsic rate of increase |
| $\alpha$ | $Z$ | allelic effect |
| $\mu$ | $1/T$ | mutation rate, $\mu \equiv 10^{-6}$ |

**Continuous model**

For any given additive genetic variance $V_G$ (assuming a Gaussian distribution of breeding values), the trait mean $\overline{z}$ satisfies:

$$\frac{\partial \overline{z}}{\partial t} = \frac{\sigma^2}{2}\left(\frac{\partial^2 \overline{z}}{\partial x^2} + \frac{\partial^2 \overline{z}}{\partial y^2}\right) + \sigma^2\left(\frac{\partial^2 \ln(N)}{\partial x}\frac{\partial \overline{z}}{\partial x} + \frac{\partial^2 \ln(N)}{\partial y}\frac{\partial \overline{z}}{\partial y}\right) + V_G\frac{\partial \overline{r}}{\partial \overline{z}} + \zeta \quad (1)$$

The first term gives the change in the trait mean due to migration with mean displacement of $\sigma$, the second term describes the effect of the asymmetric flow from areas of higher density and the third term gives the change due to selection [40, Eq. 2]. The last term $\zeta$ gives the fluctuations in the trait variance due to genetic drift: $\zeta = \sqrt{V_{G,LE}/N}\, dW_\zeta(x, y, t)$, where $dW_*$ represents white noise in space and time [27, 41]. $V_{G,LE} = \sum_i \alpha_i^2 p_i q_i$ denotes genetic variance assuming linkage equilibrium.

The trait mean is $\overline{z} = \sum_i \alpha_i p_i$ for a haploid model,where $p_i$ is the $i$-th allele frequency, $q_i = 1 - p_i$ and $\alpha_i$ is the effect of the allele on the trait – the change of the trait mean $\overline{z}$ as frequency of locus $i$ changes from 0 to 1. For both haploid and diploid models, the allele frequencies $p_i$ change as:

$$\frac{\partial p_i}{\partial t} = \frac{\sigma^2}{2}\left(\frac{\partial^2 p_i}{\partial x^2} + \frac{\partial^2 p_i}{\partial y^2}\right) + \sigma^2\left(\frac{\partial p_i}{\partial x}\frac{\partial \ln(N)}{\partial x} + \frac{\partial p_i}{\partial y}\frac{\partial \ln(N)}{\partial y}\right) + p_i q_i \frac{\partial \overline{r}}{\partial p_i} - \mu(p_i - q_i) + \epsilon \quad (2)$$

The expected change of allele frequency due to a gradient in fitness and local heterozygosity is $p_i q_i \frac{\partial \overline{r}}{\partial p_i} = s_i\, p_i q_i (p_i - q_i - 2\Delta_i)$, where selection at locus $i$ is $s_i \equiv \alpha_i^2/(2V_s)$ and $\Delta_i = (\overline{z} - bx)/\alpha_i$ [11, Appendix 3]. Here, the fourth term describes the change due to (symmetric) mutation at rate $\mu$. The last term $\epsilon$ describes genetic drift [27, Eq. 7]: $\epsilon = \sqrt{\frac{p_i q_i}{N}}\, dW_\epsilon(x, y, t)$; where $N$ is the haploid population density.

Population dynamics reflect diffusive migration in two-dimensional habitat, growth due to the mean Malthusian fitness $\overline{r}$, and stochastic fluctuations. The number of offspring follows a Poisson distribution with mean and variance of $N$, fluctuations in population numbers are given by [42]: $\xi = \sqrt{N}\, dW_\xi(x, y, t)$:

$$\frac{\partial N}{\partial t} = \frac{\sigma^2}{2}\left(\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2}\right) + \overline{r}N + \xi \quad (3)$$

### 1.0.1 Continuous model: Rescaling

The model can be simplified by rescaling [11, 40] time $t$ relative to the strength of density dependence $r^*$, distance $x$ relative to dispersal $\sigma$, trait $z$ relative to strength of stabilising selection $1/(2V_s)$ and local population size $N$ relative to equilibrium population size with perfect adaptation: $\hat{N} = Kr^*/r_m,\ T = r^*t,\ X = x\sqrt{\frac{2r^*}{\sigma^2}},\ Z = \frac{z}{\sqrt{r^* V_s}},\ \tilde{N} = N/\hat{N}$. Note that near the equilibrium of a well-adapted population, $\tilde{N} \approx 1$.

The rescaled equations for evolution of allele frequencies and for demographic dynamics

are:

$$\begin{aligned}
\frac{\partial \tilde{N}}{\partial T} &= \frac{\partial^2 \tilde{N}}{\partial X^2} + \frac{\partial^2 \tilde{N}}{\partial Y^2} + \overline{R}\tilde{N} + \sqrt{\frac{2\tilde{N}}{\hat{N}\sigma^2}}\, dW_{\tilde{\xi}(X,Y,T)} \\
\frac{\partial p_i}{\partial T} &= \frac{\partial^2 p_i}{\partial X^2} + \frac{\partial^2 p_i}{\partial Y^2} + 2(\frac{\partial p_i}{\partial X}\frac{\partial \ln(\tilde{N})}{\partial X} + \frac{\partial p_i}{\partial Y}\frac{\partial \ln(\tilde{N})}{\partial Y}) + \\
&+ \frac{s}{r^*}(p_i q_i - 2\frac{\overline{Z} - BX}{\alpha^*}) - \frac{\mu}{r^*}(p_i - q_i) + \sqrt{\frac{pq}{\tilde{N}\hat{N}\sigma^2}}\, dW_{\tilde{\epsilon}(X,Y,T)} \qquad (4)
\end{aligned}$$

where $\overline{R} \equiv \overline{r}/r^* = 1 - \tilde{N} - (BX - Z)^2/2$.
The rescaled equations 4 and 5 show that four parameters fully describe the system. The first two are i) the effective environmental gradient, $B \equiv b\sigma/(r^*\sqrt{2V_s})$ and ii) the strength of genetic drift $1/\hat{\mathcal{N}} = 1/(2\pi\hat{N}\sigma^2)$. The third parameter is the strength of selection relative to the strength density dependence, $s/r^*$; the scaled effect of a single substitution $\alpha^*$ also scales with $s/r^*$: $\alpha^* \equiv \alpha/\sqrt{r^* V_s} = \sqrt{2s/r^*}$. The effect of this third parameter $s/r^*$ is expected to be small, because typically, $s \lll r^*$. Therefore assuming throughout that $s$ is uniform across loci is a reasonably justified simplification. The fourth parameter, $\mu/r^*$, will typically be very small, and will be neglected throughout. Table 1 (top) summarises the full set that describes the system.

# Supporting information

**S1 Fig. Adaptation to a steepening environmental gradient.** Shows the population trait mean, variance and population density in two-dimensional space.

**S2 Fig. Effect on genetic drift on a cline width in two-dimensional habitats.** The figure shows how the cline width – and hence the local genetic variance – decrease with genetic drift.

**S3 Fig. Distribution of the parameters used in the randomised simulation runs from Fig. 2.**

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