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Increasing temporal variance leads to stable species range limits

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Abstract

What prevents populations of a species from adapting to the novel environments outside the species' geographic distribution? Previous models highlighted how gene flow across spatial environmental gradients determines species expansion vs. extinction and the location of species range limits. However, space is only one of two axes of environmental variation — environments also vary in time, and we know temporal environmental variation has important consequences for population demography and evolution. We used an individual based evolutionary model to explore how temporal stochasticity in environmental conditions influences the spread of populations across a spatial environmental gradient. We find that temporal stochasticity greatly alters our predictions for range dynamics compared to temporally static environments. When temporal variance is equal across the landscape, the fate of species (expansion vs. extinction) is determined by the interaction between the degree of temporal autocorrelation in environmental fluctuations and the steepness of the spatial environmental gradient. When the magnitude of temporal variance changes across the landscape, stable range limits form where this variance becomes large enough to prevent local population adaptation and persistence. These results illustrate the pivotal influence of temporal stochasticity on the likelihood of populations colonizing novel habitats and the location of species range limits.

Key words: species range limits; temporal stochasticity; adaptation; geographic distributions; invasion; fluctuating selection

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Introduction

Species' distributional limits are ubiquitous biogeographic phenomena that have provided a longstanding puzzle for biologists [1,2]. The proximate causes of distributional range limits are relatively simple and can be classified into two broad categories — either populations have not colonized suitable areas outside their current range margin (a distribution limited by dispersal) or the environment outside that margin is sufficiently unsuitable to keep population growth below replacement (a distribution limited by adaptation). However, the *ultimate* causes of a range limited by adaptation are the subject of much deliberation — why do populations not simply adapt to the novel environmental conditions beyond their range edge? This question is especially perplexing as this exact process — adaptation to novel environments — presumably gave rise to the species' *current* distribution.

The fact that spatial environmental gradients play a major role in determining organisms' distributional limits is a longstanding and often eminently obvious observation — as the environment changes across space, so do the observed flora and fauna. Climbing a mountain slope, one can readily observe how communities change across this gradient in temperature as individual species reach their elevational limits. But *within* species, there is ample evidence for populations successfully adapting across all sorts of abiotic and biotic environmental gradients [3–8]. What causes this adaptive process to cease and a range limit to form? Theory has only relatively recently begun to shed light on the demographic and evolutionary mechanisms underlying the relationship between spatial environmental gradients, local adaptation, and species distributions. For a species occupying a landscape with a spatial environmental gradient (e.g., in soil pH, precipitation, etc.), theory tells us that several mechanisms may constrain adaptation, and subsequently, expansion at the edge of a range. Kirkpatrick and Barton's foundational models showed that steep environmental gradients and high gene flow can swamp adaptation at the range edge to create stable range limits [9,but see 10]. More recent models utilizing simulation approaches have highlighted how demography, genetic drift, expansion load, and not only the slope, but the shape (e.g., linear vs. non-linear) of the spatial environmental gradient influence adaptation, range expansion, and the formation of stable range limits [11–14]. In all of these theoretical treatments, the spatial environmental gradient (manifesting as a spatial gradient in phenotypic optima) is key to understanding when populations can expand and when stable range limits form on a landscape.

However, habitats vary not only in space, but also in time. Indeed, in nature, temporal stochasticity in the environment is the rule rather than the exception [15–17]. Variation in weather within and between years provides the most obvious illustration of abiotic temporal stochasticity. Biotic environments also fluctuate through time as populations of predators, mutualists, pathogens, and competitors wax and wane. Both theoretical and empirical work demonstrate that temporal environmental stochasticity has important consequences for population demography [18,19,reviewed in 20] and evolution [17,21–24]. For example, Ripa and Lundberg's classic work [25] illustrated how a population's extinction risk is greatly influenced

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by the degree of temporal environmental autocorrelation, and recent experimental work has confirmed these theoretical predictions [26]. Temporal environmental stochasticity is also often supposed to generate fluctuating selection due to phenotypic optima changing through time. Though our understanding of the prevalence of fluctuating selection in natural populations is still incomplete and plagued by sampling error [27,28], several recent rigorous studies indeed show strong temporal fluctuations in selection [e.g., 29,30], implying fluctuating phenotypic optima through time. In microcosm experiments, temporally fluctuating environments have been shown to both facilitate [via increased population sizes during benign periods and thus more effective selection [31]] and impede [via relaxed selection during benign periods [32]] adaptation to directional environmental changes.

Because of the evidence that temporal environmental stochasticity can influence key aspects of population demography and evolution, there is reason to suspect it could influence species range dynamics. However, all evolutionary range limit models to date assume temporally constant environments. Yet in nature, the environment will always vary in both space and time, and it is easy to imagine myriad ways that temporal stochasticity might affect the fate of populations spreading across a spatial environmental gradient. Temporal stochasticity in the environment could slow adaptation along a spatial gradient via fluctuating selection. Alternatively, positive demographic effects of temporal stochasticity, such as high fecundity in a relatively favorable year, could boost population sizes and increase range expansion and the efficacy of natural selection. Temporal environmental stochasticity will directly affect extinction probabilities via demography [25], and could further influence adaptation by influencing levels of genetic variation [33]. Importantly, just as spatial environmental variation can manifest with different patterns (e.g., linear / non-linear gradients), environments can vary through time in different ways. First, environmental stochasticity can exhibit temporal autocorrelation patterns that are negative (e.g. dry years tend to be followed by wet years and vice versa) or positive (e.g. dry years tend to be followed by another dry year), or reflect uncorrelated random noise [34]. Second, temporal variance may not be equal across space — i.e., some parts of a geographic landscape may experience more temporal variance than others. For instance, positive relationships between demographic variability and distance from a species' range center suggests that some range edge habitats may be more temporally variable than range core habitats [35,36].

We explored the influence of temporal environmental stochasticity on species range dynamics using an individual-based, forward genetic simulation model, building from the work of Polechová and Barton [11] and Bridle et al. [13]. We use this model to ask how temporal environmental stochasticity influences the colonization, spread, and range limits of populations across a spatial environmental gradient. In the model, a single population initially colonizes the center of a spatial environmental gradient, and we track the demography, evolution, and spread of populations across the landscape with the environment varying in space and time. As assumed in previous models, spatial environmental variation manifests as a spatial gradient in the optimum phenotype for a polygenic quantitative trait under stabilizing selection (Fig. 1). The new addition of *temporal* environmental variation manifests as temporal stochasticity in patch

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phenotypic optima, with optima fluctuating generation to generation around the patch's long-term mean optimum.

We vary both the steepness of the underlying spatial environmental gradient and two different aspects of temporal stochasticity in tandem. First, we vary the temporal correlation pattern of the environment — ranging from positive temporal autocorrelation (consecutive generations experience similar environments), to no autocorrelation (environments fluctuate randomly generation to generation), to negative autocorrelation (consecutive generations experience strongly dissimilar environments). We also vary the geography of temporal stochasticity (Fig. 1); the two geographic modes of temporal variation are:

1. **Varying intercept**: all points along the spatial gradient experience temporal environmental stochasticity equally. This would be the case if, say, temperatures or precipitation changed across a landscape by a similar magnitude and direction year to year (e.g., a landscape-wide drought). It manifests as stochasticity in the intercept of the spatial gradient in phenotypic optima, fluctuating around the long-term mean spatial gradient (Fig. 1b)
2. **Varying slope**: the magnitude of temporal environmental variance increases away from the landscape center (which is the point of initial colonization in the simulation). This would be the case if, say, there was increased temporal variance in inundation at the edge of a wetland compared to the center, or increased temporal variance in rainfall as one goes from mesic to arid habitat. It manifests as stochasticity in the slope of the spatial gradient in phenotypic optima, with a constant intercept at the range center. Thus, the phenotypic optimum displays larger fluctuations around the long-term average with increasing distance from the range center (Fig. 1c).

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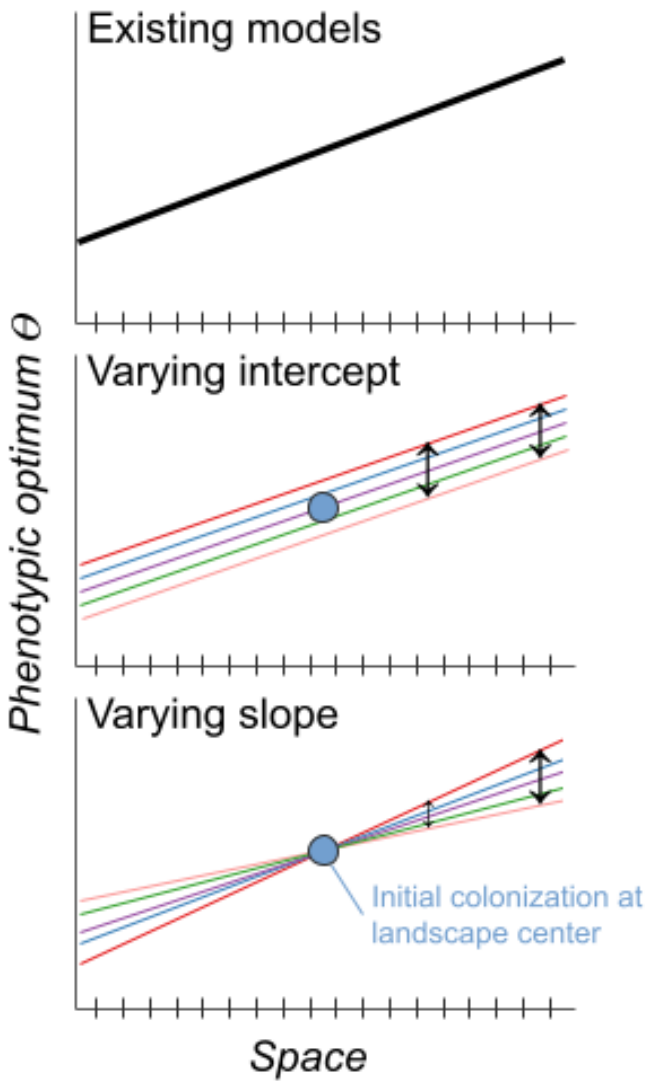

Figure 1. Conceptual diagram illustrating how temporal stochasticity is incorporated in the model. (A) illustrates how spatial environmental variation is modeled in existing range limit models, with a temporally constant spatial gradient in phenotypic optima. In our model, there is intergenerational stochasticity in phenotypic optima around the mean optimum at each point in space, according to two "geographic modes" of temporal stochasticity. In the "varying intercept" scenario (B), the intercept of the spatial phenotypic optimum gradient fluctuates such that all patches experience the same magnitude and direction of deviation from the mean optimum each generation. In the "varying slope" scenario (C), the slope of the spatial gradient fluctuates stochastically around the mean slope. The gradient is "anchored" at the center of the landscape, thus, the magnitude of temporal variance increases with distance from the landscape center. The blue dot in panels (B) and (C) represent the initial founding population in the simulation, which then spreads (or does not spread) across the landscape. Black arrows indicate the magnitude of temporal variance at that point on the landscape [equal at all points in (B) and increasing with distance from the landscape center in (C)].

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Materials and Methods

We used SLiM [37] forward genetic evolutionary modeling software to simulate range dynamics. SLiM has recently come to the fore as a flexible, fast, and powerful tool to model individual genomes under a wide variety of spatially and temporally explicit evolutionary scenarios. Our model extends the work of Polechová & Barton [11], as well as Bridle et al. [13], by incorporating temporal stochasticity into individual-based evolutionary range limit models of adaptation across spatial environmental gradients.

Data Availability Statement

All SLiM and R code, simulation parameters, and the simulation results needed to reproduce the figures in this manuscript, are available on Figshare: https://doi.org/10.6084/m9.figshare.c.5552028.v1

Model Details

Genetics and mutation

Individuals were diploid and either male or female, with obligate sexual reproduction, and a single chromosome 100,000 bp long. There were two mutation types: 1) neutral mutations, and 2) mutations that contributed additively to a quantitative trait [i.e., biallelic quantitative trait loci (QTL) with no dominance]. The overall mutation rate was set to 1e-7 (SLiM default; Table S1), and mutations were 10 times more likely to be neutral than QTLs. QTL effect size was drawn from Normal(0, 1). Recombination rate was set to 1e-8 (SLiM default).

Mating and population dynamics

The simulated landscape comprised a one dimensional array of 201 patches. This is most analogous to a natural landscape that approximates one dimension, like a river, river corridor, mountain ridge, or valley. Each patch hosted a local population subject to density-dependent regulation, with carrying capacity constant across the landscape (here, K = 50). Following Bridle et al. [13], individual fitness (W_i) was calculated as

$$W_i = 2 + 2r\ (1 - N_x/K) - s(b\,x - z_i)^2/2 \qquad (1)$$

Where r is the population maximum rate of increase, N_x is the number of individuals in population x, K is the carrying capacity of each patch, s defines the strength of stabilizing selection for the fitness optimum, b is the slope of the gradient in phenotypic optima, and z_i is the phenotypic value of the individual. Thus, the first part of equation (1) describes standard logistic growth and the second part introduces the fitness cost scaled by the deviation of an individual's phenotypic value (z_i) from the local optimum (bx). For females, W_i defined the mean of a Poisson

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distribution for the number of offspring that female produced (female fecundity); for males, W_i defined the likelihood of a male mating (W_i corresponded to a male's weight in a weighted draw from the pool of available males in a population). Males could mate multiple times. After mating occurred within a population, offspring dispersed according to a Poisson dispersal kernel with mean (m) = 0.8. The direction of dispersal (left or right along the gradient) was unbiased and random.

Environmental variation

Environmental variation manifested as changes in the optimum phenotype of the quantitative trait across space and time. The slope of the spatial environmental gradient (b) represents the change in phenotypic optima across the landscape (Fig. 1a). To illustrate how b manifests as a fitness cost of dispersal, let us assume populations are at carrying capacity ($N = K$). Then the fitness cost of dispersal to patch $x+1$ for an individual perfectly adapted to patch x is,

$$\Delta_W = -\ 0.125b^{\ 2}/2 \tag{2}$$

Thus if $b = 1$, a female perfectly adapted to patch x will experience a fitness cost of $\Delta_{W_F} = 0.0625$upon migration to patch $x+1$, or a fitness decrease of ~3.125%.

Temporal environmental stochasticity was implemented as intergenerational stochasticity in patch phenotypic optima. Temporal stochasticity in optima was modeled as:

$$\sigma_t = a\sigma_{t-1} + d\Phi_t \tag{3}$$

where $\sigma_0 = 0$, d scales the magnitude of noise $\Phi_t \sim$ Normal(0, $\boldsymbol{\tau}$), and a represents the degree of temporal autocorrelation. Temporal autocorrelation could be positive ($0 < a \leq 1$), negative ($-0.99 \leq a < 0$), or uncorrelated ($a = 0$) temporal stochasticity. (We prevented a from going all the way to -1 because, due to $\sigma_0 = 0$, this would be identical to $a = 1$.) We set $d = (1 - a^2)^{0.5}$so that$Var(\sigma)$is equal for all values of a. $\boldsymbol{\tau}$ differed between the two geographic modes of temporal variation (see below).

We modeled two geographic modes of temporal variation (Fig. 1). First, we modeled changes in the spatial gradient **intercept** between generations (Fig. 1b). In this scenario, each generation σ_t was calculated and the phenotypic optimum in every patch on the landscape was adjusted by this amount. Thus, the slope of the spatial gradient ($\boldsymbol{b}$) remained constant while its intercept varied. Second, we modeled changes in the spatial gradient **slope** between generations (Fig. 1c). In this scenario, each generation σ_t was calculated and the spatial slope in optima was adjusted by this value, making it either shallower or steeper, "pivoting" around the center of the landscape (the founding patch). This had the effect of phenotypic optima varying more the further a patch was from the landscape center — ie, temporal variation was greater with distance from the range center.

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For the "varying intercept" scenario we set $\boldsymbol{\tau}_{intercept} = 2$ for Φ_t. In this scenario, if $a = 0$ (no temporal autocorrelation), $\Phi_t \sim$ Normal(0, 2) results in the absolute value of the standardized linear selection gradient, $|\beta|$, averaging ~0.09 across generations, and $\sigma_\beta \approx 0.06$. This selection gradient is estimated as the slope coefficient of the linear regression of relative fitness on the phenotypic trait values of two hypothetical phenotypes: a phenotype perfectly adapted to its patch's current trait optimum, and a phenotype adapted to the patch long-term mean optimum. We standardize this gradient by multiplying it by the phenotypic standard deviation, σ_P, which we estimate at 1.7 (the mean σ_P in the central patch in our "varying intercept" simulations after 20,000 generations). These selection gradients are well within the range of selection gradients and their variance in nature, [median $|\beta| = 0.16$ in Kingsolver et al. [38]; $\sigma_\beta = 0.099$ in de Villemeruil et al. [39], averaging across birds and mammals].

In the varying slope scenario, $|\beta|$ and σ_β increased with distance from the landscape center as temporal variance increased. We set $\boldsymbol{\tau}_{slope} = 0.05$ for a relatively conservative value that still produced range limits on our 201-patch landscape; this resulted in patch conditions mimicking the "varying intercept" scenario (mean $|\beta| \approx 0.09$ and $\sigma_\beta \approx 0.06$) at 40 patches away from the landscape center. For the "varying intercept and slope" scenario, respective $\boldsymbol{\tau}$ values remained the same ($\boldsymbol{\tau}_{intercept} = 2$ and $\boldsymbol{\tau}_{slope} = 0.05$).

Simulation process

Burn-in

Each simulation began with a burn-in period of 20,000 generations. At the start of the burn-in, 100 genetically homogenous, perfectly adapted individuals were founded in the central patch of the landscape. Mating and dispersal happened as described above, but the landscape was limited to 21 patches wide (10 patches on either side of the founding patch). Carrying capacity in each patch was 100 individuals (thus, landscape-wide K = 2,100). There was a modest spatial environmental gradient in optima across these 21 patches (b = 0.5), and modest temporal fluctuations in the intercept of the spatial gradient in optima [deviations drawn from Normal(0,1)]. The goal of this burn-in period was to minimize the impact of initial conditions and allow the different simulations to converge on similar levels of genetic diversity [during the burn-in, mean heterozygosity of neutral mutations (π) in the central population usually reached an equilibrium before 18,000 generations]. At generation 20,000, a random subset of 50 individuals was selected from the 21-patch landscape and migrated to the central patch for the "founding event". All other individuals were then removed from the simulation.

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Main simulation

After the burn-in period, the main simulation began with the prescribed parameters and no dispersal limits, with 50 individuals in the founding patch. Simulations ended after 20,000 generations, or if all populations went extinct, or if at least one of the most peripheral landscape patches reached a population size at least half the carrying capacity (i.e., the species had filled the entire landscape). We ran 1000 simulations for each of the three temporal stochasticity scenarios (varying intercept, varying slope, varying intercept and slope) with parameter values pulled randomly from uniform distributions: b[0-3], $a_{intercept}$[-0.99-1], a_{slope}[-0.99-1].

Results

Varying intercept

When temporal environmental stochasticity was equal in all patches on the landscape ("varying intercept" scenario; Fig. 1b), a clear relationship emerged between the degree of temporal autocorrelation (a) and the slope of the underlying spatial gradient (b) in determining whether populations spread across the landscape or went extinct (Fig. 2). Range expansion was favored when temporal stochasticity was more positively autocorrelated and spatial gradients were shallow. Shallow spatial gradients favored rapid range expansion, and the rate of range expansion slowed as spatial gradients steepened and environments became less positively autocorrelated. The ultimate fate of the species in each simulation was either eventual extinction or continual expansion; stable range limits did not form, though expansion could be extremely slow across steep spatial gradients (light blue points in Fig. 2). (Here and below we use "species" to describe the group of populations on the landscape.)

As in previous models, steep spatial gradients introduced strongly maladaptive gene flow that incurred a demographic cost, allowing drift to overpower selection and stymie adaptation. Temporal stochasticity in phenotypic optima exacerbated the negative effects of spatial gene flow by introducing a fitness cost even for stationary individuals well-adapted to their patch's long-term mean optimum; i.e., temporal fluctuations in optima meant that no genotype could completely escape maladaptation across generations. In environments with temporal stochasticity, populations were often able to adapt to the underlying mean spatial gradient in optima if the spatial gradient was not too steep. However, a large deviation from the mean optimum in a generation had large negative demographic consequences due to individuals being strongly maladapted in most patches. If then the following generation experienced a strongly different optimum, which is more likely the less positively correlated the temporal environment is, extinction risk was high (Fig. 2b,c). Thus, temporal stochasticity introduced an extinction risk due to fluctuating phenotypic optima that had strong effects on mean fitness.

With a temporally constant environment (i.e., $a = 1$) expansion was prevented where the spatial gradient slope (b) was $\gtrapprox 2.5$, similar to that predicted from the model of Polechová & Barton [11], $b \gtrapprox 2.1$.

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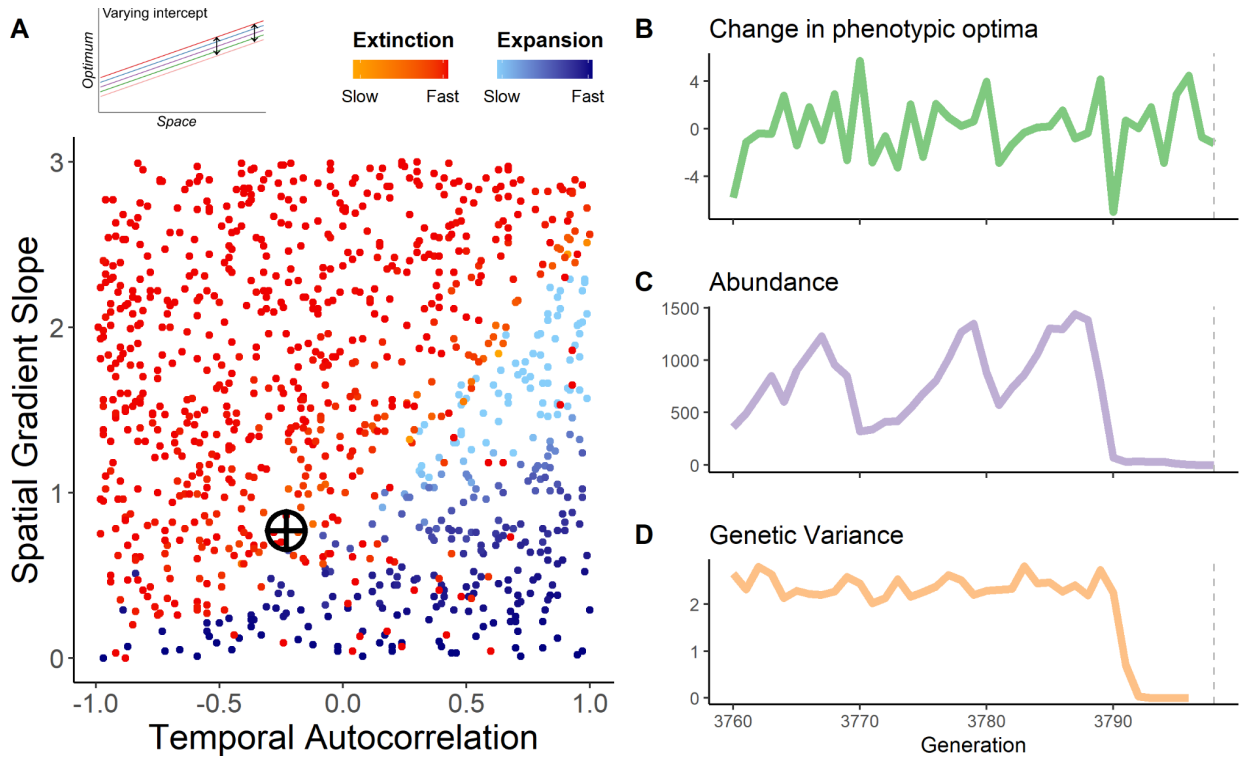

Figure 2. Range dynamics under the "varying intercept" scenario. (A) When temporal stochasticity manifests identically across the landscape, range expansion is favored when temporal stochasticity (*a*, X-axis) is more positively autocorrelated and spatial gradients (*b,* Y-axis) are shallow. (A temporal autocorrelation of 1 is a temporally static environment, as modeled in previous range limit models.) Each point represents a simulation (N = 1000). No stable range limits formed in this scenario; species either continually expanded or went extinct. All blue points are simulations where species were able to spread, and red/orange points are simulations where species went extinct; points are colored by how quickly they expanded or went extinct. (B-D) Details of one simulation (marked with crosshairs in panel A) prior to extinction. Panels track (B) temporal changes in patch phenotypic optima, (C) landscape-wide population abundance, and (D) mean population genetic variance across generations prior to extinction (grey dashed line).

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Varying slope

When the magnitude of temporal variance increased away from the landscape center ("varying slope" scenario), stable range limits formed (Fig. 3). The exact location of the range limit fluctuated over time as extinction/colonization dynamics played out at the range edge; thus, we define stable range limits as the most distal patches on either side of the founding patch that did not go extinct for at least 950 of the 1000 generations before the end of the simulation (which lasted 20,000 generations). Range limits formed where increasing temporal variance caused populations to fail to adapt to the optimum of edge patches because temporal fluctuations in optima caused populations in those patches to often go extinct (or close enough to extinction to strongly undermine genetic variance and adaptive potential).

Range width (distance between range limits) remained relatively constant across a wide range of spatial gradient slopes, but then began to decrease with steeper spatial gradients (Fig. 3A). The high fitness costs of dispersal across steep gradients (due to maladaptation) combined with the negative fitness effects of temporally fluctuating optima to increase extinction risk more quickly as populations moved away from the center. This led to narrower range widths than for species spreading across shallower gradients. Positive temporal autocorrelation tended to increase range width, and strongly positive temporal autocorrelation ($a \approx 1$), especially across shallow spatial gradients, sometimes resulted in complete filling of the landscape (open points in Fig. 3). Because environmental conditions at the landscape core were stable, species usually only went extinct with very steep spatial gradients.

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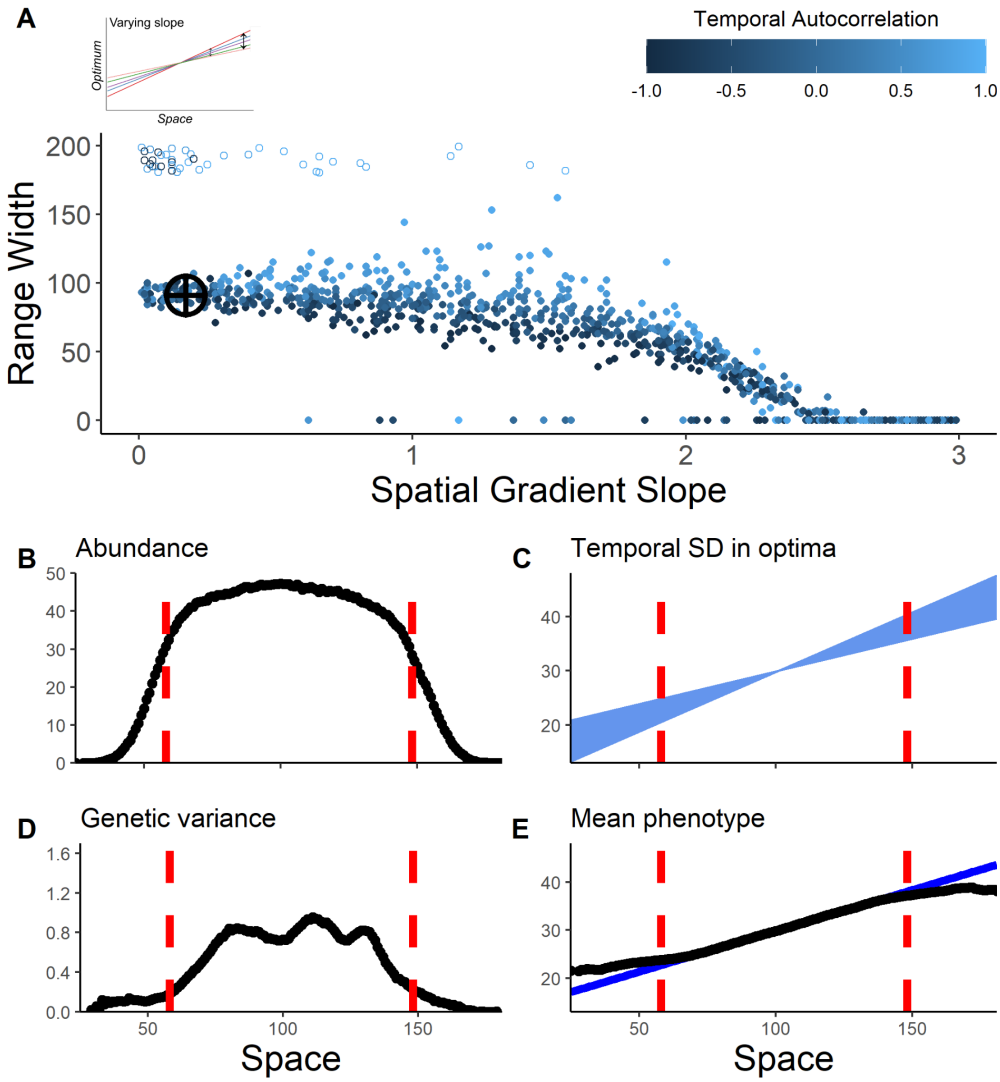

Figure 3. Range dynamics under the "varying slope" scenario. When temporal variance increases away from the landscape center, stable range limits form where temporal variance is too high to allow further adaptation and persistence. (A) Effects of the spatial gradient slope (X-axis) and degree of temporal autocorrelation (point color) on a species' ultimate range width (Y-axis). (Range width is the number of patches between the species' two stable range limits.) Each point represents a simulation (N = 1000) at the end of 20,000 generations. Open points near the top of the Y-axis are simulations where the species reached at least one edge of the landscape. (B) abundance, (C) temporal variation in optima, (D) genetic variance, and (E) mean phenotype of populations in a single simulation (b = 0.17, a = 0.48) after formation of stable range limits (dashed red lines), averaging over the final 1000 generations of the simulation. We define stable range limits as the most distal patches that did not go extinct for at least 950 of the 1000 generations prior to the end of the simulation. (C) shows the standard deviation of the temporal changes in phenotypic optima, to illustrate how temporal variance increases away from the

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landscape center. In (E), black points show the mean phenotype and the solid blue line indicates the underlying mean spatial gradient in phenotypic optima.

Varying intercept and slope

When both the spatial gradient slope and intercept varied stochastically through time, there was a contraction in the parameter space where range expansion was possible (Fig. S1). In general, species persistence and range expansion required positive temporal autocorrelation in the gradient intercept (i.e., $a_{intercept} > 0$). The degree of autocorrelation in slope of the gradient had only a modest influence on extinction and range width (Figs. S2, S3), and so here we focus on scenarios with no autocorrelation in gradient slope (i.e., $a_{slope} = 0$) for simplicity. However, the presence of this additional source of temporal stochasticity in trait optima increased extinction probabilities compared to scenarios with only a varying intercept (compare Figures 2A and S1A). Interestingly, in the parameter space where temporal autocorrelation in gradient intercept was positive and thus expansion was possible, simulations in which the slope of the spatial gradient was very shallow were more likely to go extinct than those with steeper spatial gradients (Fig. S1A, lower right corner). This is because steeper spatial gradients increased genetic variance across the landscape via gene flow, which better equipped populations to withstand temporal fluctuations in optima. Due to varying gradient slopes (and thus an increase in temporal variance with distance from the landscape center), stable range limits formed for all species that avoided extinction (no extant species expanded to fill the landscape). Range width was overall smaller and more variable when the spatial gradient intercept varied along with the slope (compare Figures 3A and S1B).

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Discussion

Our simulations show that temporal stochasticity in the environment substantially alters our predictions for range dynamics across spatially variable landscapes. When environmental conditions change from generation to generation similarly across the landscape ("varying intercept" scenario), the ultimate fate of species is determined by the interaction between the degree of temporal autocorrelation in environmental fluctuations and the slope of the spatial environmental gradient. As found in previous results [11], species extinction becomes more likely as the slope of the environmental gradient increases. However, positive autocorrelation of temporal stochasticity can allow populations to expand along even very steep gradients. Negative autocorrelation, though, increases demographic fluctuations and increases extinction risk due to fluctuating phenotypic optima resulting in frequent maladaptation. When temporal environmental variance increases toward the periphery of a landscape ("varying slope" scenario), stable range limits form where temporal environmental variance becomes too large for population persistence and adaptation. The ultimate width of the species' range is primarily a function of the underlying spatial environmental gradient. When spatial gradients vary in both intercept and slope through time, range expansion overall becomes less likely. Together these results illustrate how temporal stochasticity in the environment has a pivotal influence on the likelihood of a species colonizing a new landscape, the speed of range expansion, and the location of a taxon's range limit.

When temporal variance has no spatial structure ("varying intercept"), we can clearly delineate the parameter space where colonizing populations go extinct, versus where they expand across the landscape. When the underlying spatial gradient is shallow, expansion can occur across a wide range of temporal correlation patterns, but increasingly positive autocorrelation is required for expansion as the spatial gradient steepens. Environmental noise in nature seems to largely range from random to positively autocorrelated [34]. Indeed, these simulations indicate that if environmental conditions were strongly negatively autocorrelated through time, colonization and expansion would be very rare. Increasing temporal variability is one predicted (and observed) consequence of contemporary climate change, and our simulations suggest this increased variability could influence the probability that populations will be able to successfully track climatic changes via shifting spatial distributions. For example, the upslope colonization process of an alpine plant due to warming could be stymied if temporal stochasticity is augmented by climate change. Our model suggests increased temporal environmental stochasticity due to climate change could further reduce fitness of edge populations, potentially hampering their ability to track or adapt to changing mean conditions. Furthermore, if a species' current range limit is due in part to increased temporal environmental variance, then models forecasting future distributions built solely using the mean, and not variance, of predicted climate will likely be inadequate.

The biogeographic fact that all species have limited distributions is often at odds with the ability of evolutionary range limit models to produce *stable* range limits. For instance, when

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Barton [10] adjusted Kirkpatrick and Barton's foundational work [9] to allow genetic variance to evolve, range expansion was continuous and limits failed to form. Polechová & Barton [11] provided a solution to this conundrum by incorporating genetic drift and demographic stochasticity in their models, but still found that stable limits only formed with nonlinear spatial gradients [see also [12,13]]. Similarly, in our model there are no stable range limits when there is no spatial trend in temporal variance (i.e., varying intercept scenario). However, we do see stable range limits form when there is a spatial gradient in the magnitude of temporal variance — i.e., temporal variance increases with distance from the center of the landscape (varying slope scenario) — even across linear spatial gradients. This result suggests that there is a critical threshold of temporal environmental variance that can stop range expansion and enforce a stable range limit. Do we find evidence for such a pattern in nature? The idea that environments at the edge of species' ranges tend to be more temporally variable has been assumed more often than empirically shown, but some demographic studies do suggest range edge habitats to be more temporally variable than range core habitats [35,36,40–43]. Beyond indirect inference of temporal environmental stochasticity via demographic data, there are surprisingly few direct measurements of temporal environmental variability across species ranges. One exception is Eckhart et al. [44], who showed that for the California annual plant *Clarkia xantiana* ssp. *xantiana*, interannual variability in precipitation increased toward the subspecies' eastern range margin. Our model supports the notion that increased variability in precipitation could contribute to the stable range limit observed in this species.

These results lead to several testable predictions. First, do we see temporal environmental variance increase toward species range edges? For climatic variables this would be fairly straightforward to test, as we have excellent databases for both species distributions and long-term weather. From this same data set we could ask whether, looking across species distributions, we see a positive relationship between the steepness of putatively important spatial gradients across a species range and the temporal autocorrelation in that environmental variable. Figure 2 would suggest this relationship — colonization across steep spatial gradients should only be possible in fairly stable environments (i.e., environments with positive temporal correlation). For example, we might expect to observe that species with populations spread across steep altitudinal gradients experience more positively correlated temporal stochasticity than species spread across more shallow spatial gradients (e.g., a primarily latitudinal rather than altitudinal gradient).

Here we have focused on spatio-temporal environmental variation and its influence on trait adaptation in populations of a single species. Our understanding of species range dynamics could be further improved by extending this model to include other genetic, life history, and ecological factors that can potentially have large influences on population dynamics and spread in nature. As Antonovics [45] pointed out, evolution of *multiple* traits may often be required for populations to expand into novel habitats. Genetic correlations between traits whose evolution is required to colonize novel habitat may greatly influence the probability of colonization [46,47]. Incorporating phenotypic plasticity and its evolution would also be a valuable extension of the

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current model [48]. In terms of life history, the effects of overlapping generations may be very important in temporally variable environments [33], especially if an organism's life cycle includes dormant stages (e.g., seed banks). The addition of species interactions such as competition would further illuminate how ecological phenomena interact with evolutionary processes to modulate range dynamics [49–51]. Simulating spread across a patchy landscape, as opposed to the smooth gradients in trait optima modeled here, could also substantially change our predictions for population colonization and spread.

Species range limits are as ubiquitous as they are puzzling. What prevents adaptation from allowing species distributions to continually grow by "accretion like the rings of a tree" [52]? Recent theoretical advancements have highlighted the importance of genetic drift and nonlinear spatial environmental gradients in controlling range dynamics and the location of stable range limits [11–13]. Here we showed how temporal environmental stochasticity, an ever-present feature of natural systems, strongly contributes to determining whether a colonizing population will expand into novel habitat or go extinct, and can readily enforce stable range limits. By expanding range dynamics models to the temporal dimension, we gain more realistic, comprehensive insight into the mechanisms and processes underlying biogeographic patterns, insights of great relevance to invasion biology, the limits to adaptation, and the fate of populations with environmental change.

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Supplementary Material

Table S1. Parameter values for the SLiM simulation model.

Parameter	Definition	Value
	Varying parameters	
b	Slope of spatial gradient in phenotypic optima	[0-3]
a	Degree of temporal autocorrelation	[-0.99-1]
	Static parameters	
K	Patch carrying capacity (individuals)	50
r	Maximum rate of increase	0.8
s	Strength of stabilizing selection	0.125
m	Expected dispersal per generation (mean of Poisson dispersal kernel)	0.8
μ	Mutation rate per base position per generation	10^{-7}
r	Recombination rate (crossover events per base position per generation)	10^{-8}
$\boldsymbol{\tau}_{intercept}$	SD of the Gaussian distribution used to implement temporal stochasticity in the "varying intercept" scenario	2
$\boldsymbol{\tau}_{slope}$	SD of the Gaussian distribution used to implement temporal stochasticity in the "varying slope" scenario	0.05

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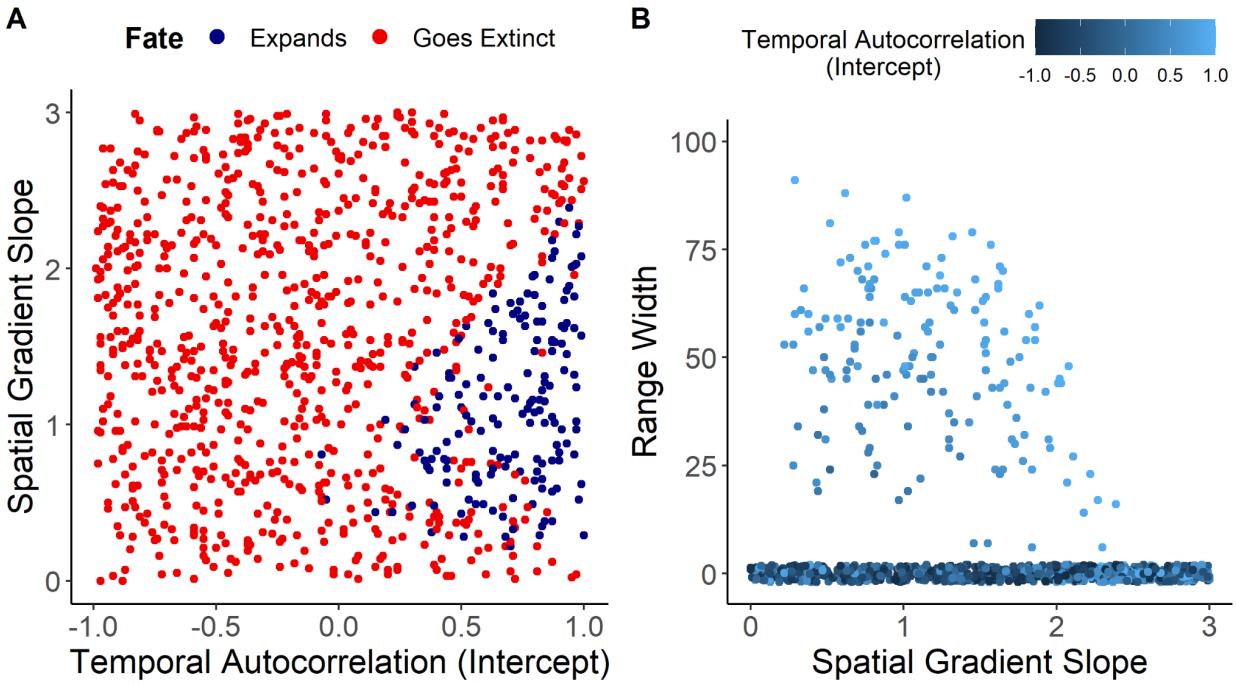

Figure S1. Range dynamics when both the slope and intercept of the spatial gradient vary through time. Each point represents a simulation (N = 1000). (A) shows the fate of species (expansion vs. extinction); compare to Fig. 2. All blue points are simulations where species were able to spread, and red points are simulations where species that went extinct. (B) shows effects of the spatial gradient slope and degree of temporal autocorrelation in gradient intercept (point color) on a species' range width after the formation of stable range limits; compare to Fig. 3 (but note different Y-axis limits). Species with range width = 0 (jittered points at bottom of plot) went extinct; stable range limits formed for species that avoided extinction. In both (A) and (B), the degree of temporal autocorrelation in gradient slope is fixed at $a = 0$ (i.e., random fluctuations in slope). Three dimensional plots including a range of a values for the varying slope parameter are found in Figures S2 and S3.

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Figure S2. (View file **figS2.html**.) Fate of populations when both the slope and intercept of the spatial gradient vary through time. Each point is a simulation (N = 1000). This plot includes a range of autocorrelation values (a) for slopes, as opposed to Fig. S1A where a_{slope} was fixed at zero. All blue points are simulations where populations were able to spread, and red points are simulations that went extinct.

Figure S3. (View file **figS3.html**.) Range width when both the slope and intercept of the spatial gradient vary through time. Each point is a simulation (N = 1000). This plot includes a range of autocorrelation values (a) for slopes, as opposed to Fig. S1B where a_{slope} was fixed at zero. Plot shows effects of the spatial gradient slope, degree of temporal autocorrelation in gradient intercept, and degree of temporal autocorrelation in gradient slope (point color) on a species' range width after the formation of stable range limits. Simulations with range width = 0 went extinct and are marked with hollow points.