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LETTER

Climate change fluctuations can increase population abundance and range size

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Abstract

Climate change threatens many species by a poleward/upward movement of their thermal niche. While we know that faster movement has stronger impacts, little is known on how fluctuations of niche movement affect population outcomes. Environmental fluctuations often affect populations negatively, but theory and experiments have revealed some positive effects. We study how fluctuations around the average speed of the niche impact a species' persistence, abundance and realized niche width under climate change. We find that the outcome depends on how fluctuations manifest and what the relative time scale of population growth and climate fluctuations are. When populations are close to extinction with the average speed, fluctuations around this average accelerate population decline. However, populations not yet close to extinction can increase in abundance and/or realized niche width from such fluctuations. Long-lived species increase more when their niche size remains constant, short-lived species increase more when their niche size varies.

KEYWORDS

climate change, moving-habitat model, population persistence, temporal variability, thermal niche shift

INTRODUCTION

Many species face unprecedented pressure since the rapid warming of the earth causes temperature isoclines to move, so that the spatial location and shape of a species' optimal thermal conditions (suitable habitat) changes. For short, we say that their fundamental thermal niche shifts (Hurford et al., 2019). On average, shifts occur towards higher latitudes and/or altitudes (Houghton et al., 2001). Individuals have to move with their niche or adapt locally to avoid extinction (Aitken et al., 2008; Chen et al., 2011; Davis et al., 2005). Such climate-induced range shifts have been observed in most major taxa (Parmesan & Yohe, 2003). In general, the faster the climate changes, the harder it is for a species to keep up with its niche (Bedford et al., 2012; Loarie et al., 2009; Schloss et al., 2012), and several species are at risk of climate change-induced extinction (Leroux et al., 2013; Williams et al., 2003). Behind the fundamental thermal niche, deaths exceed births, known as 'extinction debt' (Tilman et al., 1994). Ahead of the niche, due to dispersal limitation, the lag between the location of the niche and the density of the population increases (Hurford et al., 2019), as does the 'colonization credit', the future potential range of the species (Talluto et al., 2017) (Figure 1a). For example, extinction debt and colonization credit are widespread and affect bird species in about half of the area of the entire US (Haddou et al., 2022).

While we have some understanding of how changes of climate averages (e.g. temperature, precipitation) affect populations, the effects of fluctuations around these average changes are much less understood (Thornton et al., 2014). Future expected locations of a fundamental thermal niche are available and utilized, for example in species distribution models (Leroux et al., 2013), but

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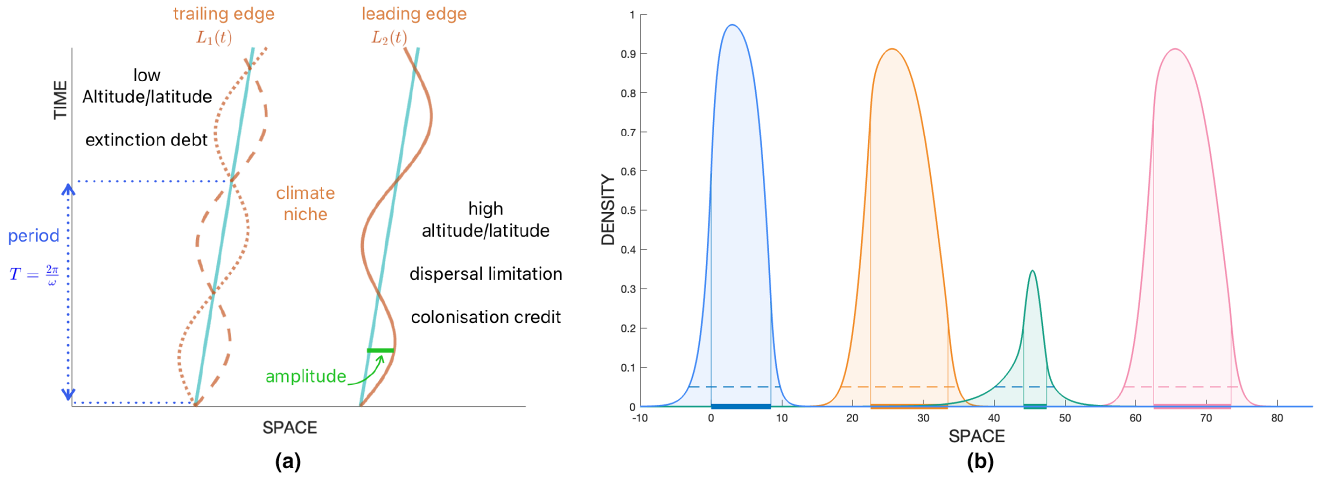

FIGURE 1 (a) Illustration of how the climatic niche shifts in space and time. The straight cyan lines represent the location of the niche at the average speed without fluctuations. The solid orange curve on the right indicates the leading edge with fluctuations around the average speed. The dashed (dotted) orange curves on the left indicate the trailing edge in the constant (variable) niche-size scenario. (b) The profiles of the population densities under different scenarios and at different times. Under a constant shift speed, the population develops into a fixed-shape travelling pulse (blue). Under a variable shift speed, the shape of the pulse changes periodically in time: the population is maximal in the orange and pink pulses (which are 10 periods apart) and minimal in the green pulse in between. The vertical lines and thick coloured line segments on the horizontal axis correspond to the fundamental thermal niche at that time. The dashed horizontal lines indicate the range of the population, that is the spatial extent over which the population density exceeds a certain threshold. Higher altitudes/latitudes (cooler average temperatures) are to the right; lower altitudes/latitudes (warmer average temperatures) are to the left.

fluctuations are rarely considered (Benning et al., 2022; Holt et al., 2022; Rafajlović et al., 2022; Shen et al., 2022). Populations experience extinction debt and colonization credit as fluctuating in space and time. Such complex feedbacks hamper our ability to determine which species are most vulnerable to climate-induced fluctuating niche shifts.

In general, environmental fluctuations can have positive or negative effects on populations, such as a decreased or increased ability of a population to persist (Schreiber, 2010), a decreased or increased population abundance (Stevic, 2006), or positive and negative effects on multi-species coexistence (Chesson, 2000). In spatially structured environments, the interplay between environmental fluctuation and spatial dispersal can produce counter-intuitive outcomes such as a population persisting in a landscape of sink patches (Schreiber, 2010) or a sink-population reaching 'inflationary' high densities (Gonzalez & Holt, 2002), in particular when fluctuations are temporally autocorrelated. Fluctuations in the shift speed of the fundamental thermal niche could lessen the negative impacts of the extinction debt by temporarily placing individuals behind the niche back into the niche and allowing them to reproduce, in particular if individuals are long lived, for example trees.

To explore how fluctuations around the mean speed of niche shifts affect the persistence and abundance of a species in a changing climate, we employ a 'moving-habitat model' (MHM) (Harsch et al., 2014). Such models describe how the density of a population changes in space and time due to the simultaneous impact of dispersal and demography; see Harsch et al. (2017) for an overview. MHMs represent the fundamental thermal niche as a region where the net growth rate is positive and track the location of this region in space. Outside this region, net growth is negative. Individuals disperse throughout the landscape with movement behaviour that may differ between the niche and outside and may be biased towards the niche (Haynes & Cronin, 2006; Schultz & Crone, 2001). Most MHMs to date have considered simplified scenarios where the niche shifts at a constant speed and retains a constant size (Berestycki et al., 2009; MacDonald & Lutscher, 2018; Potapov & Lewis, 2004). In that case, a population will die out if the shift speed is too high compared to reproduction and dispersal, although populations with too high dispersal will also die out due to a minimal patch-size effect (Cobbold & Stana, 2020). If the shift speed is low enough, the models produce a 'travelling pulse' solution that describes how the population manages to track its niche across space and time. Few individuals are located ahead of the niche, while the proportion of individuals behind the niche, the 'zombie population' (Decker et al., 2021), might surpass that within the niche and thereby considerably increase the spatial range (the realized niche) of the population (MacDonald et al., 2021). One prediction of these models is that even though an increased shift speed decreases the likelihood of the population to persist, it can increase the overall abundance before extinction (Berestycki et al., 2009; MacDonald et al., 2021). This increase occurs because the niche shift decreases population density in the niche and, therefore, reduces competitive pressure, which leads to higher production in the niche. If mortality is low enough outside the niche, increased production in the niche can overcompensate for loss from mortality outside the niche. What then is the effect of fluctuation in the niche shift over time?

In our MHM, the leading and trailing edge of the niche can shift at different and non-constant speeds to include fluctuations in location and size of the niche. Such fluctuations arise from random climatic conditions and large-scale weather patterns such as El Niño, but also from topography and landscape features, for example when larger plateaus are located along mountain slopes so that the area of the niche increases when the plateau is included (see Supporting Information). We are only aware of one theoretical study on this issue: Shen et al. (2022) demonstrate that when the niche size is constant and the location fluctuates periodically around the mean shift speed, then population persistence decreases with the amplitude of fluctuations. Our simulations here confirm this result and, in addition, show that population abundance may be highest at intermediate fluctuations. In fact, we find that the positive effect can be so strong that the minimal population abundance over an entire period can exceed population abundance in the absence of fluctuations. We also consider a novel scenario where niche size varies periodically. Again, we find that population abundance may be highest at intermediate amplitude of the fluctuations, but the positive effect on the population is generally smaller in this case. Overall, we find that intermediate fluctuations in climate change can have positive effects on species abundance, in particular, if mortality outside the fundamental thermal niche is low.

METHODS

Our MHM is based on reaction–diffusion equations that describe how a population density evolves in continuous space and time according to simultaneous random dispersal and net growth. The rate of change of the population density $n(t,x)$ at time t and location x is

$$\frac{\partial n}{\partial t} = \underbrace{d\frac{\partial^2 n}{\partial x^2}}_{\text{dispersal}} + \underbrace{g(n,x,t)n}_{\text{net growth}}, \tag{1}$$

with diffusion coefficient d (mean squared displacement per unit time) and net per-capita growth rate $g(n,x,t)$ (births minus deaths) at time t and location x. When and where g is positive (negative), the population grows (declines).

The fundamental thermal niche of the species at time t is the interval from $L_1(t)$ (trailing edge, warm end of the niche) to $L_2(t)$ (leading edge, cold end of the niche); see Figure 1a. On average, both edges move at speed c upwards in altitude or latitude. For simplicity, we model variation around this average by a sinusoidal function with amplitude A and period T. In the *scenario of constant niche size* (L), we choose

$$L_2(t) = ct + A\sin(2\pi t/T) \quad \text{and} \quad L_1(t) = L_2(t) - L, \tag{2}$$

which corresponds to the solid (leading edge) and dashed (trailing edge) orange curves in Figure 1a. In the *scenario of variable niche size*, we choose

$$L_2(t) = ct + A\sin(2\pi t/T) \quad \text{and} \quad L_1(t) = ct - A\sin(2\pi t/T) - L, \tag{3}$$

so that the average niche size over one period is L as in the previous scenario. This corresponds to the solid (leading edge) and dotted (trailing edge) orange curves in Figure 1a. To ensure that the niche size remains positive in this second scenario, we limit the amplitude to half the average niche size ($|A| < L/2$).

Ahead of the leading and behind the trailing edge, population growth is negative, which we model by a constant rate of mortality (m). This helps us limit the number of parameters. We believe that our results remain qualitatively the same when mortality increases with distance from the niche. Inside the niche, the population grows logistically; see Supporting Information for details. In principle, mortality, dispersal behaviour and habitat preference can vary in space (MacDonald et al., 2021). Here, we focus on the effects of fluctuations in niche shift, as given by amplitude (A) and period (T) and keep the other parameters constant (Table S1).

Using simulations, we find two possible long-term outcomes: either the population goes extinct or it persists in a 'periodic pulse', where the density after one period equals the density of the previous period, shifted by the average distance that the niche moved (average speed c multiplied by T). We calculate the *total population density* as the integral under the pulse and the *range* as the spatial extent over which the population density exceeds a certain threshold (Hurford et al., 2019; see Figure 1b). Hence, the range corresponds to the realized spatial niche of the species.

To determine whether a population can persist, we check whether it can grow when rare. Since we use logistic growth, there is no Allee effect. Hence, we linearize the model at low density and calculate the (asymptotic) population growth rate (the dominant eigenvalue λ) from one period to the next. When $\lambda > 1$ the population can persist, when $\lambda < 1$, it will go extinct.

We compare the outcomes with temporal fluctuations ($A > 0$) to those without ($A = 0$) for longer and shorter periods (T). As emphasized by Hastings (2012), we focus on the relative scales. For fixed population dynamics parameters (see above), a short period indicates that the population life cycle is slow relative to environmental fluctuations, for example trees or larger mammals. By contrast, a long period indicates that the life cycle is fast relative to the fluctuations, for example smaller mammals, insects or annual plants. Similarly, for a fixed dispersal parameter, a short (long) period indicates that dispersal is slow (fast) relative to environmental fluctuations. For simplicity, we focus on the time scale of the life cycle only.

Our simulations are based on a recently developed and validated, highly efficient numerical scheme. We use a linear coordinate transformation to turn the moving habitat into a stationary one and then employ a semi-implicit method to solve that stationary problem. We choose a spatial grid whose points are concentrated near the boundaries of the niche and become progressively sparse away from the niche. This allows us to obtain high accuracy at these boundaries where solutions have the steepest gradients. At the same time, it limits the number of grid points, which, in turn, ensures fast computations; see MacDonald et al. (2021). To calculate the dominant eigenvalue, we combine this numerical method with the power method (see e.g. Zhou & Kot, 2013). Our MATLAB code is available on GitHub.

RESULTS

Population persistence

To evaluate the effect of climate fluctuations on population persistence, we choose parameters such that the population persisted in the absence of fluctuations (zero amplitude), then increase the amplitude and calculated the population growth rate (λ) to determine whether the population could grow from low density and persist. For any given average speed of climate change (c), we choose a niche at 1.5 times the minimal niche length for persistence, $L^*(c)$ (Supporting Information), so that the dominant eigenvalue satisfied $\lambda > 1$. As we increase the amplitude (A), the dominant eigenvalue decreases until, at some critical amplitude, A^*, the dominant eigenvalue equalled one, and the population cannot persist for any values $A > A^*$ (Figure 2). Hence, in both scenarios and independent of the period, increasing fluctuations decrease population persistence, which is consistent with the result for constant niche size by Shen et al. (2022).

When the average speed of climate change (c) is larger, a population can persist under stronger fluctuations (larger A^*) (left plot, Figure 2). However, the minimal size of the niche (L^*) also increases with c (middle plot). In fact, while the minimal niche size grows by a factor of almost three for the range of shift speeds that we used in the simulations, the critical amplitudes in all four scenarios increase less than twofold (compare the left and middle columns of Figure 2). Hence, as the average speed increases, a population can withstand only smaller climate fluctuations, *relative* to the minimal size of its fundamental thermal niche (right column of Figure 2).

We see that species can persist under larger fluctuations in the scenario of a constant niche size than in the scenario of variable size (curves without circles are above those with in Figure 2). Similarly, species whose life cycle is fast compared to environmental fluctuations can withstand larger fluctuations (green curves are above blue curves in Figure 2). Hence, according to our model and within the parameter ranges that we explored, long-lived species in an environment with strong fluctuations in the size of their niche are the most vulnerable to extinction from fluctuations around the average speed of climate change.

Population abundance and range

To evaluate the effect of climate fluctuations on total population abundance and range size, we simulate the

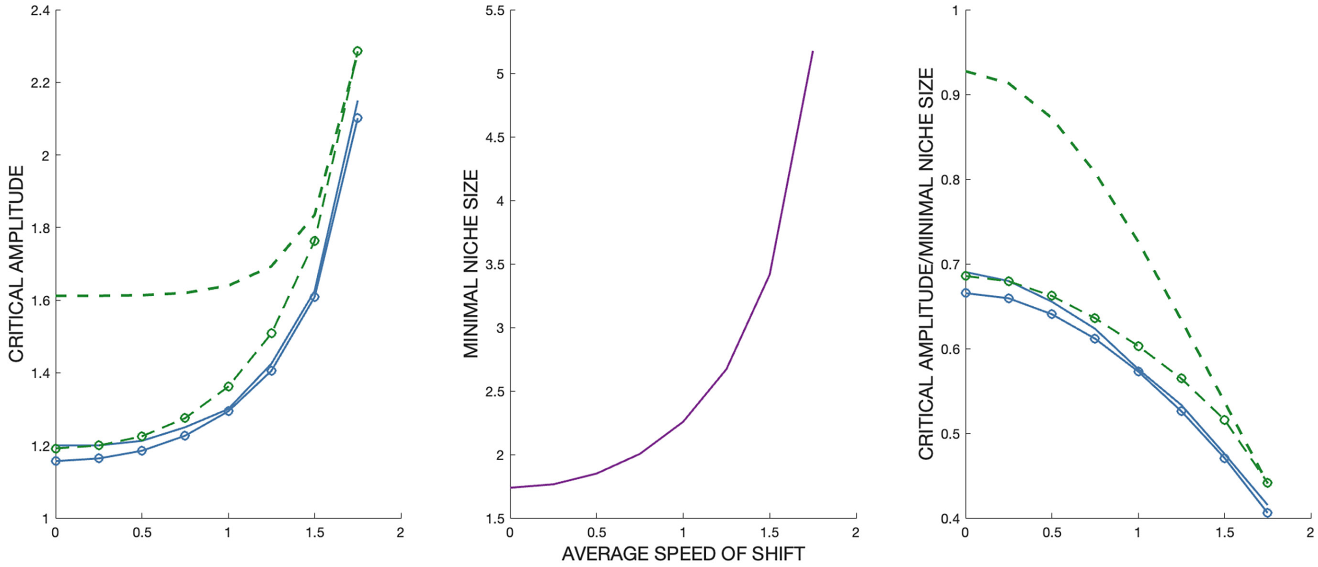

FIGURE 2 Critical amplitudes (left plot), minimal niche size (middle plot) and their ratios (right plot). Blue solid curves correspond to short periods/long-lived species whereas green dashed curves stand for long periods/short-lived species. Open circles indicate variable niche width, no circles indicate constant niche width. Parameter values are as in Table S1 with $m = 1.4$, $T = 4$ (green) and $T = 1$ (blue).

nonlinear model with a large (average) fundamental thermal niche (five times the minimal niche size), so that persistence is guaranteed for relatively large fluctuations. As an initial condition (at $t=0$), we choose the travelling pulse that arises when the niche moves at constant speed without any fluctuations ($A=0$). We then simulate the dynamics with fluctuations ($A>0$) and compare with the initial condition.

In all simulations, we observe a pulse that oscillates in time: total population abundance and population range are periodic (Figure 3). When the fundamental thermal niche has constant size (left column), the maximum *and* minimum values of total abundance and range can increase compared to the scenario without fluctuations (which is given at $t=0$ and indicated by the horizontal line). The effect is particularly strong when climatic fluctuations are fast compared to the species' life cycle (blue curves), but also occurs when they are slow (green curves). Hence, long-lived species are predicted to increase their abundance and range the most in the constant niche-size scenario, but even for short-lived species, minimum abundance and range with fluctuations may exceed the values without. The increase in maximum and minimum total abundance can be larger at slow shifting speeds (18% in upper panel versus 3% in lower panel, see also Figure 4). While several authors estimate actual speeds of isocline shifts (Ordonez et al., 2014), our speeds are relative to the species' dispersal ability (d) and growth rate (r), which we scaled to unity. Leroux et al. (2013) estimated all three quantities for several butterfly species and identified those most likely to experience fast speeds.

When niche size is variable (Figure 3, right column), the maximum population abundance and range can still exceed the corresponding values without fluctuations, but the minimum does not. When climatic fluctuations are fast compared to the species' life cycle (blue curves), abundance and range remain close to their values without fluctuations. When climatic fluctuations are slow (green curve), abundance and range vary much more: the maximum exceeds the value without fluctuation significantly, but the minimum drops below that value even more. Hence, short-lived species are predicted to show much stronger response to fluctuations than long-lived species. Their maximum abundance increases more but since their minimum abundance also decreases more, their extinction risk in troughs increases. The relative increase over the scenario without fluctuations is quite similar for the

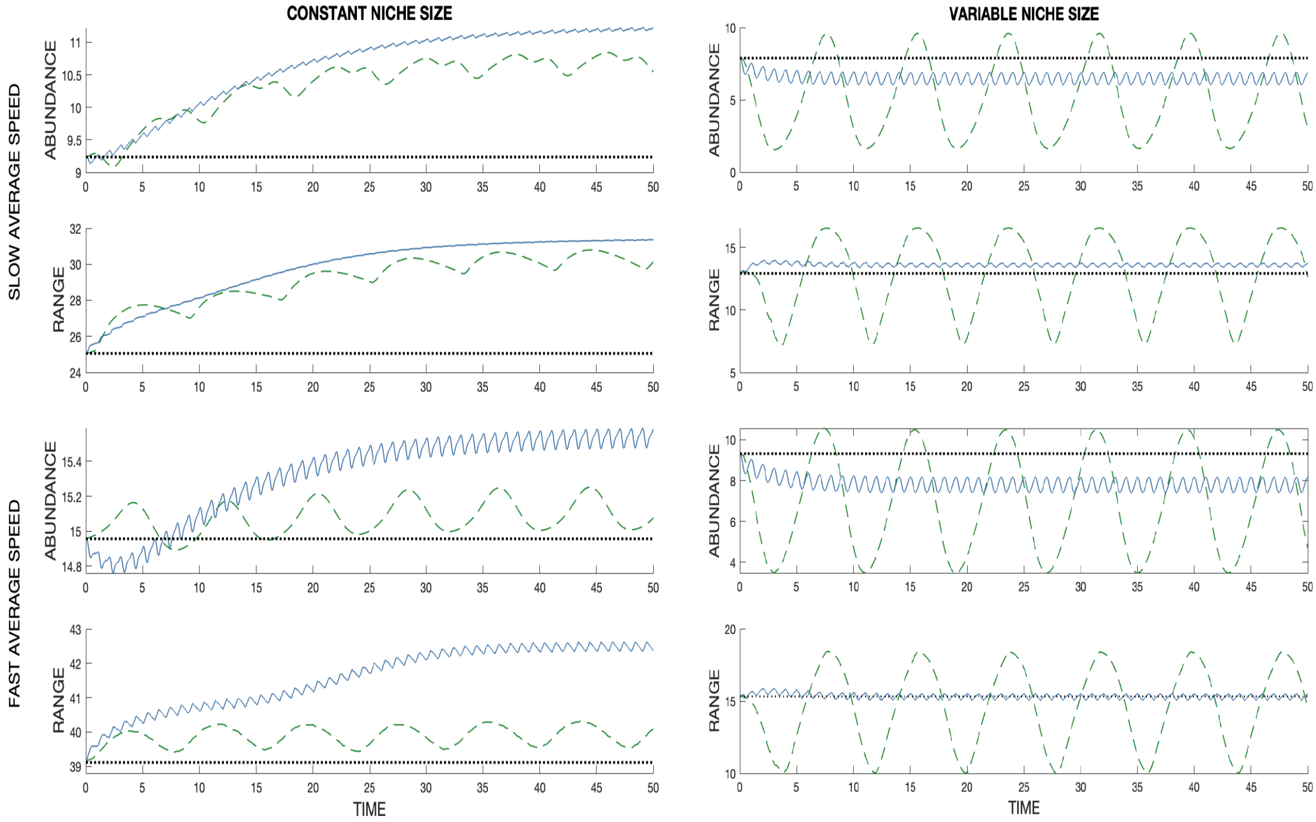

FIGURE 3 Total population abundance and population range with constant (left) and variable (right) niche size and slow (top half) versus fast (bottom half) average speed of climate change. Climatic fluctuations are fast compared to the species' life cycle (short period $T=1$, blue solid) or slow (long period $T=8$, green dashed). The amplitude of climate change differs: constant niche size (left) has $A=5$ (blue solid) and $A=1$ (green dashed); variable niche size has $A=2.5$ (blue solid) and $A=4$ (green dashed). Mortality is low at constant niche size ($m=0.1$) and higher at variable niche size ($m=1$). The average shifting speed is $c=1$ (fast) and $c=0.5$ (slow). The horizontal dotted line indicates the quantity in the absence of fluctuations. Please note that the scales on the vertical axes differ between plots as to best illustrate the relevant points.

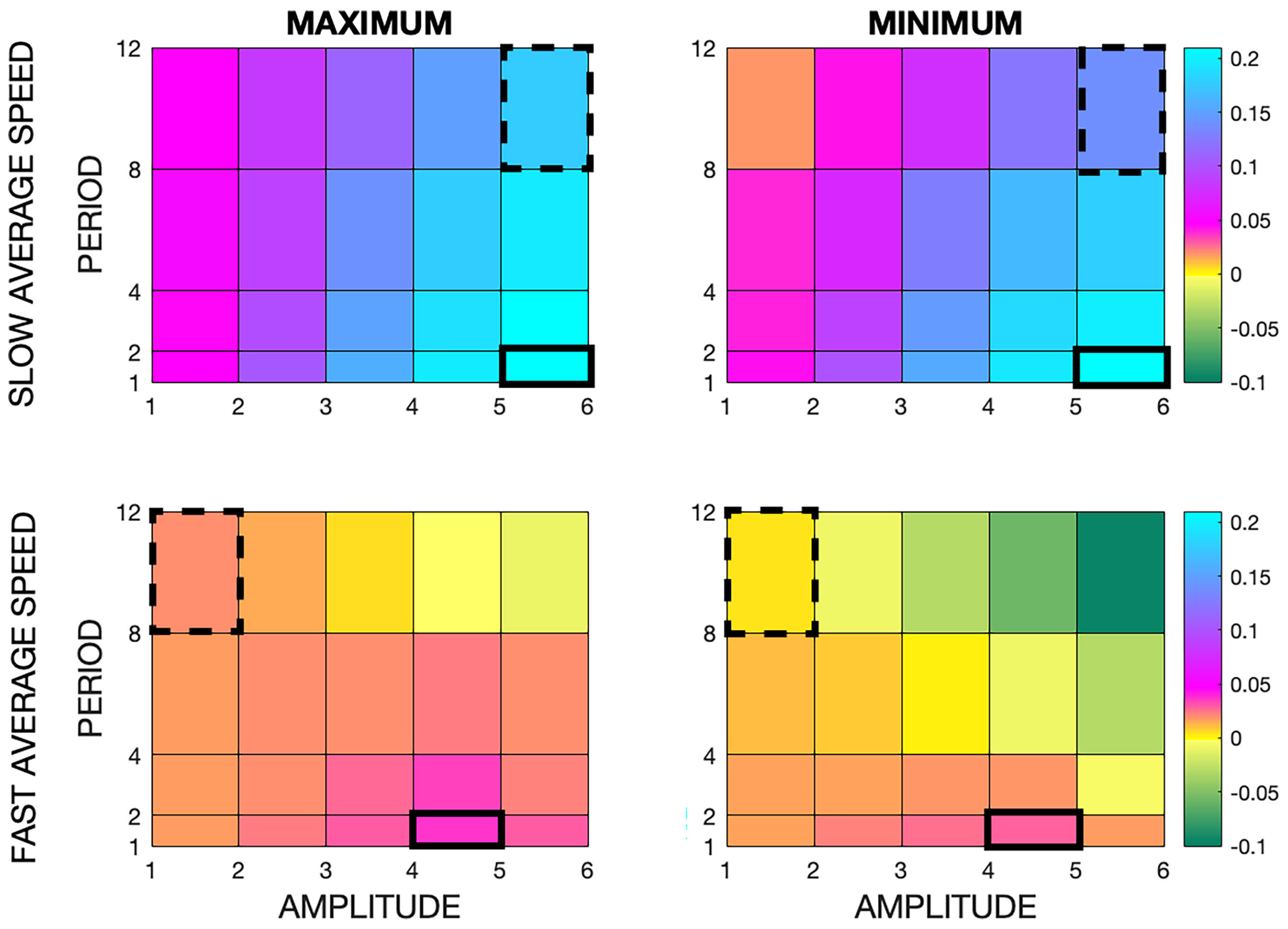

FIGURE 4 Effect of climate fluctuations on total population abundance for constant niche length. Colours indicate the percent increase or decrease of abundance with versus without fluctuations for slower ($c = 0.5$, top panels) and faster ($c = 1$, bottom panels) average speeds. Comparison of the maximum abundance over one period (left panels) and minimum abundance (right panels). Mortality rate is $m = 0.1$. Solid (dashed) boxes correspond to blue (green) lines of Figure 3.

higher and lower shift speeds (see also Figure 4). In the variable niche-size scenario (right column), the population can persist at much higher mortality outside their niche than at constant niche size (left column).

We explore how relative population abundance depends on the interplay between frequency (period) and strength (amplitude) of climatic fluctuations for constant (Figure 4) and variable (Figure 5) niche size. In all cases, population abundance with intermediate climate fluctuations can exceed abundance without. When niche length is constant (Figure 4), the greatest increases in population abundance occur at intermediate amplitudes and short periods. When the average shift speed is high (bottom panels), the relative increase is small, but even small amplitudes lead to an increase in maximum and minimum abundance. By contrast, when the average shift speed is low (top panels), the relative increase can be an order of magnitude larger, but small amplitude fluctuations decrease maximum and minimum abundance. Increasing the period while keeping the amplitude fixed generally has negative effects on abundance and range, as we already saw in Figure 3, left column.

With variable niche length (Figure 5), the greatest increases of population abundance still occur at intermediate amplitude, but in contrast to the constant niche-size scenario above, they occur at longer periods, when climatic fluctuations are slow compared to the life cycle of the species. Only the maximum abundance shows an increase over the case without fluctuations, not the minimum, as in Figure 3, right column. The effect size is of the same order of magnitude for lower (top panels) and higher (bottom panels) average shift speeds.

Averages, break-ups and bottlenecks

When the life cycle is long compared to environmental fluctuations, the population experiences some average conditions and the dynamics are similar to those in the absence of such fluctuations (Figure 6a). The peak of the population is, however, situated at the low altitude/latitude end of their range and not at the average; it is cold-skewed *sensu* Hurford et al. (2019). Without fluctuations, most individuals could not contribute to population

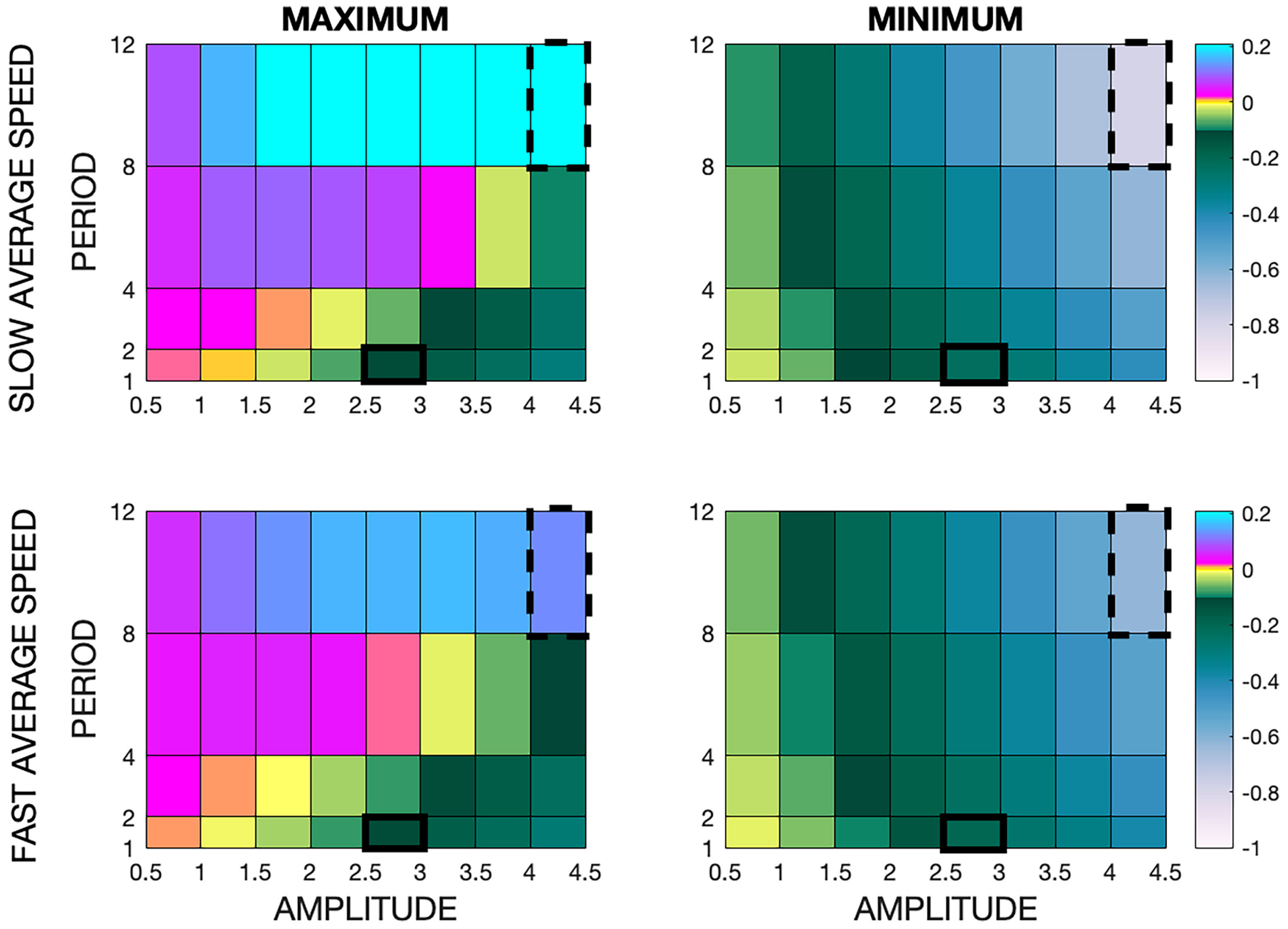

FIGURE 5 Effect of climate fluctuations on total population abundance for variable niche length. Colours indicate the percent increase or decrease of abundance with versus without fluctuations for slower ($c = 0.5$, top panels) and faster ($c = 1$, bottom panels) average speeds. Comparison of the maximum abundance over one period (left panels) and minimum abundance (right panels). Mortality rate is $m = 1$. Solid (dashed) boxes correspond to blue (green) lines of Figure 3.

growth because they are located behind the trailing edge (extinction debt). With fluctuations, these individuals repeatedly experience favourable growth conditions and help maintain the population at a higher level. The population never reaches the high altitude/latitude regions; hence, the colonization credit is large.

When the life cycle is short compared to environmental fluctuations, population densities fluctuate more while their spatial patterns depend on the configuration of the climatic niche. With a constant niche size, the population periodically breaks up: the bulk gets left behind the trailing edge and disappears (extinction debt), while few individuals at the front establish new populations where and when conditions become sufficiently favourable (Figure 6b). This leads to metapopulation-like dynamics of sequential colonization and local extinction. For some part of this cycle, the bulk of the population is located at the leading edge, which is retreating at that time due to fluctuations. Hence, the distribution switches between cold- and warm-skewed. The total population abundance shows two peaks during every period (Figure 3, top left).

By contrast, when the niche size is variable, we observe bottlenecks where the population is concentrated in a very small area (Figure 6c). After a bottleneck, the population spreads in both directions as the niche expands. Spreading towards higher altitude/latitude is limited by dispersal. A travelling front establishes temporarily inside the fast growing niche; its speed is approximately the Fisher speed; see chapter 4.4 in MacDonald (2022).

DISCUSSION

The rapid pace of climate change makes it difficult for species to follow their climatic niche (Loarie et al., 2009; Schloss et al., 2012). While theory and empirical work have made progress on the effects of average climate change on populations, understanding and predicting how fluctuations around this average fluctuations species remains a challenge (Garcia et al., 2014). According to Littlefield et al. (2019): 'Ecologists have a long history of focusing on equilibria and ignoring dynamism, but doing so when addressing climate change is particularly

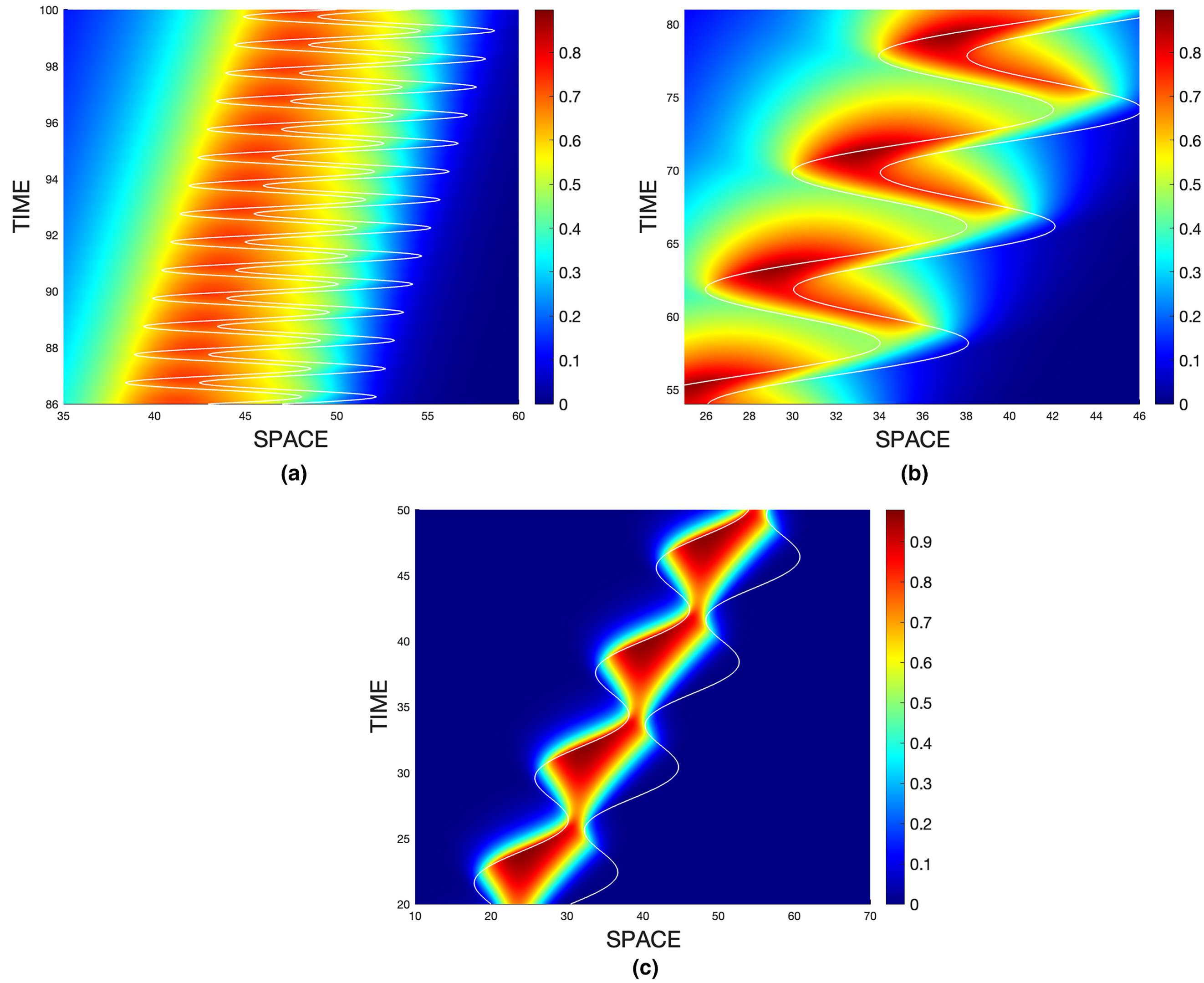

FIGURE 6 Population density (colour bar on the side) in relation to the fundamental thermal niche (white curves) for different scenarios. (a) A long life cycle can buffer against environmental fluctuations: with short period ($T=1$) and low average speed of climate change ($c=0.5$), the population fluctuation is low. (b) A short life cycle can lead to metapopulation-like dynamics: with long period ($T=8$) and low average speed of climate change ($c=0.5$), the population breaks into localized populations. (c) Bottlenecks arise as niche size is variable: with long period ($T=8$) and intermediate average speed of climate change ($c=1$), the population becomes highly concentrated periodically. The amplitude is $A=5$ in (a) and (b) but $A=4$ in (c).

problematic'. Our theoretical work advances our understanding of this issue and provides a tool for exploring further scenarios.

Our moving-habitat model predicts that if a species is already close to extinction due to the average effects of climate change, then fluctuations will be detrimental and push it over the edge; see also Shen et al. (2022). This result is consistent with the long-standing expectation that extinction rates increase with temporal environmental fluctuations (Schreiber, 2010). However, when the niche of the species is large and mortality outside the niche is low, then intermediate fluctuations in climate change can increase the total density and the spatial range of the species. This contrasts the Cushing–Henson conjecture that temporal fluctuations always decrease average population density (Stevic, 2006). But our results are more subtle: Long-lived species increase in abundance and range more from fluctuations at constant niche width whereas short-lived species do so more from variability of the niche width (with constant averages). Long-lived species, such as trees or large mammals, cannot as easily recover after habitat contraction, but do well when a large enough core habitat is available somewhere and periodically. In this case, the maximum and minimum population abundance can exceed that of a constant average shift scenario. The positive effect of the 'zombie' population behind the trailing edge on population spread (Decker et al., 2021) is amplified by the recurrent shift of the favourable niche into this 'zombie' population. Individuals behind the trailing edge repeatedly contribute to population growth. By contrast, short-lived mobile species can react more quickly to an expanding niche and manage to survive during contraction. They become boom and bust populations taking advantage of the best conditions, wherever they may be. Examples include certain (irruptive) bird populations with several clutches per year who are highly vagile and track patterns of environmental fluctuations (Widick et al., 2023). The ability to temporarily persist in unfavourable conditions is crucial for these effects to occur (Early & Sax, 2011; see Supporting Information).

While our results are based on relatively few scenarios, they reveal general principles, so that we expect these effects to occur broadly. The combination of release from intraspecific competition inside the fundamental niche and availability of new habitat because of niche movement, combined with sufficiently low mortality outside the niche, can already increase population abundance from a stationary niche to one moving at constant speed (Berestycki et al., 2009; MacDonald et al., 2021). We show that fluctuations in niche movement can compound this effect even more. The effect size increases with niche size and vanishes when the niche size is the minimal viable size. The effect size also increases when mortality outside the niche decreases. This is intuitively clear since individuals outside the niche can only benefit from the niche returning to them if they are still alive when that happens. It can also be observed in figs 4.5 and 4.12 in MacDonald (2022) and, without fluctuations, in MacDonald et al. (2021).

It is simultaneously a strength and a limitation of analytical models that they consider only a small set of mechanisms acting in nature. While they cannot capture the full complexity of the observed and expected behaviour of species under climate change, they allow us to explore and better understand basic processes in isolation. We considered two scenarios of how a climate niche can move in time (constant vs. variable size) and found that these two scenarios interact with life cycle characteristics of the species under consideration, in particular with the time scale of turn-over relative to the time scale of fluctuations. While the importance of relative time scales in ecology is well documented (Hastings, 2012), more realistic scenarios are likely a combination of the two extreme cases that we chose and will need to consider stochastic variability, which relatively few models currently include; see Bouhours and Lewis (2016) and Reimer et al. (2017). Similarly, our findings are limited to the range of parameter values we chose.

We considered only ‘passive’ dispersers whose dispersal rate is independent of habitat quality and who show no movement bias towards more favourable habitat conditions, even though it is clear that many species disperse more actively and that their activity patterns can greatly affect their ability to persist and spread in heterogeneous landscapes (Crone et al., 2019; Lutscher & Musgrave, 2017). In our previous work that included active dispersal in a moving-habitat model but not temporal variability (MacDonald et al., 2021; MacDonald & Lutscher, 2018), we found that active dispersal can substantially increase the likelihood of persistence and that the behaviour that aids persistence differs between the leading and the trailing edge. Whereas it is helpful to have a strong movement bias towards favourable habitat conditions at the trailing edge (the warm end of the niche, $L_2(t)$, left end in Figure 1), strong bias towards the niche at the leading edge (the cold end of the niche, $L_1(t)$, right end in Figure 1) has little effect. Similarly, high dispersal rates behind the trailing edge support population persistence whereas low dispersal rates ahead of the leading edge are more beneficial (MacDonald & Lutscher, 2018). We expect that with temporal variability as considered here, these differences between the optimal behaviour at the warm and cold end of the niche may decrease. For example, individuals who get left behind the trailing edge need not necessarily catch up with the climate niche by dispersal, they might also find themselves back within the climate niche simply because the niche returns to them. Similarly, higher movement rates at the leading edge might be beneficial to the population as strong dispersers can take advantage of the times when temporal variability moves the niche forward faster than on average and establish at high latitude/altitude conditions as soon as they become habitable, if only for short periods.

We chose a continuous-time model, whereas discrete-time models better represent the life cycle of species with temporally synchronized reproductive and dispersal events. Two new effects could occur in such systems. First, populations with synchronized reproductive events respond to changes with some delay, namely at reproduction. This could buffer against short-term fluctuations that happen between reproductive events. Second, if reproduction occurs during a very short time window, then the environmental conditions during that window might play an overly large role, for example, the loss of arctic sea ice in 2022 that is thought to have led to an almost complete loss of penguin offspring in that year. The analytical models that correspond to such life cycles (integrodifference equations) are well developed and used in the context of moving habitats (Harsch et al., 2014, 2017). Zhou and Fagan (2017) studied integrodifference equations on expanding and contracting habitats, but the combination of these with moving-habitat models is still open.

Several simulation studies explored how dispersal and other traits evolve under shifting climate niches (Gilbert et al., 2018; Henry et al., 2013; Hillaert et al., 2015; Weiss-Lehman & Shaw, 2020). Hargreaves et al. (2015) showed that higher dispersal probabilities evolved at the leading edge, but details depended on the shift speed and the width of the range margin. All the studies that we know consider a climate niche of fixed width moving at constant speed. While we do not study evolutionary aspects, our results allow us to speculate on the effect of climate variability on the evolution of dispersal. At constant niche width, we expect intermediate dispersal rates to evolve. Dispersal is required to keep pace with the shifting niche, but high dispersal carries the cost of loss through the leading and trailing edge into unsuitable habitat. Hargreaves et al. (2015) may not have seen this effect because they evolved dispersal probability rather than distance. Closely related analytical results in a different context show the emergence of an intermediate optimal dispersal distance when loss into unsuitable habitat is possible (Lou & Lutscher, 2014). More interestingly, the two scenarios of fluctuation show a fundamental difference in how a species tracks its niche, and this difference can have evolutionary consequences (compare Figure 6b and c). In the constant niche-size scenario, two subsequent spatio-temporal sub-populations are connected by the furthest forward individuals who establish the new sub-population near the cold edge of the niche, from where it expands as the niche expands backwards (Figure 6b). By contrast, in the variable niche-size scenario, two subsequent sub-populations are connected by individuals from the middle of the range where the population density is relatively high, and the new sub-population expands in both directions from there (Figure 6c). In particular, individuals at the front of the population bulk suddenly find themselves outside the niche (at the cold edge). Hence, while some dispersal ability is required for the species to expand and fill the niche in the variable-size scenario, high dispersal is not useful since it incurs significant loss during phases of niche contraction. Future research will show whether and how fluctuations in climate can affect evolutionary trajectories as species try to track their fundamental thermal niche through time and space.

Our work is a first step in improving our understanding of how climate variability affects populations. We focused on the size and location of the fundamental thermal niche, but temperature affects individuals in many ways, such as metabolism, developmental rates or dispersal propensity. Mechanistic models (Amarasekare & Savage, 2012) could be integrated with our approach to consider the interaction between individual response and niche availability. For example, Hurford et al. (2019) found that, in contrast to classical belief, populations with warm-skewed net reproductive rate (R_0) could benefit from climate change in a moving-habitat model with constant speed, in that their range and abundance may increase over time. This effect occurs since warm-skewed species have a high potential for colonization of habitats ahead of the niche. We conjecture that climate fluctuations could enhance this effect since it leads to bouts of rapid northern extensions of the niche, which a warm-skewed species can capitalize on.

While our deterministic periodic model is a significant advance towards understanding the effects of environmental fluctuations in the context of climate change, future models will be stochastic to capture the predicted increase in temporal autocorrelation ('reddening') and the occurrence of extreme climate events (Field et al., 2012). While there is agreement that the 'colour' of environmental noise can substantially alter population dynamics (Hastings et al., 2021), the exact mechanisms are subtle and depend on model details, such as over- or undercompensation (Petchey et al., 1997), or demographic damping (Tuljapurkar & Haridas, 2006). While stochastic models would be more realistic, they are also much harder to analyse, for example, our approach allows us to use the period map to study persistence, which reduces computational effort considerably. We expect that autocorrelation could lead to even stronger population responses, for example when there are several years of higher than average advances of the niche in a row. An increase in extreme events can be particularly hurtful to a species in the variable niche-size scenario. Extreme events can lead to extremely small niche sizes, which, in turn, carry a high extinction probability. Stochasticity in niche size could also represent landscape features that may arise as the niche moves upward in latitude and/or altitude, for example large bodies of water or mountain ranges.

We consider logistic growth of the species, and we expect qualitatively similar results for all growth functions without Allee effect. When there is a strong demographic Allee effect, that is a negative growth rate at low density, the persistence conditions in Section 3.1 do not apply. With regards to abundance and range, we expect that species with a strong Allee effect behave similarly to species without Allee effects in the constant niche-size scenario, but are much more vulnerable in the varying niche-size scenario. This is because the maximum and minimum densities in the former scenario may remain above those at constant speed of climate change (Figure 3, left plots), while those in the latter scenario show large variations where the density falls to very low levels periodically (Figure 3, right plots). With a strong Allee effect, the latter is detrimental as the population will not be able to recover from below the Allee threshold. With or without Allee effect, our modelling approach considers only the net growth rate of a population and does not distinguish whether reproduction decreases outside the niche or mortality increases or both. When such detailed information is available, a process model could replace the logistic growth function, for example based on reaction kinetics (Amarasekare & Savage, 2012). This will likely lead to a more gradual niche boundary than in our case but also require much larger amounts of data to parameterize, including movement preference data.

AUTHOR CONTRIBUTIONS

The project was conceptualized through discussions of all three authors. JSM wrote the code and ran the simulations. All authors discussed the results. FL wrote the initial draft of the manuscript. All authors discussed and edited the manuscript.

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DATA AVAILABILITY STATEMENT

Model code and instructions for use are available on GitHub (https://github.com/jane-creator/fluct-moving-habitat-model). No data were used in this study.

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SUPPORTING INFORMATION

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