Review

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# Climate sensitivity across latitude: scaling physiology to communities

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While we know climate change will impact individuals, populations, and communities, we lack a cross-scale synthesis for understanding global variation in climate change impacts and predicting their ecological effects. Studies of latitudinal variation in individuals' thermal responses have developed primarily in isolation from studies of natural populations' warming responses. Further, it is unclear whether latitudinal variation in temperature-dependent population responses will manifest into latitudinal patterns in community stability. Integrating across scales, we discuss the key drivers of latitudinal variation in climate change effects, with the goal of identifying key pieces of information necessary to predict warming effects in natural communities. We propose two experimental approaches synthesizing latitudinal variability in climate change impacts across scales of biological organization.

#### Climate change impacts across individuals, populations, and communities

Climate change represents one of the most severe threats to species conservation and ecosystem stability. Yet despite decades of research, it remains difficult to predict where climate variation, including climate change, will have the largest impact on biological systems on a global scale. Much of this debate is focused on whether species are more vulnerable to climate change at high or low latitudes, or even whether there are predictable latitudinal gradients in climate change impacts [1-6]. This uncertainty is not due to an absence of theory; rather, there has been a long history of contrasting predictions, from Darwin's suggestion that climate more strongly regulates populations at high latitudes [7] to Janzen's recognition that climate tolerances are narrower in the tropics [8] (Figure 1). Connecting these historical predictions to contemporary and future climate change is further complicated by differential rates of warming and changes in the degree of temperature variability (see Glossary) across latitudes, and the concurrent gradients in species richness make this problem singularly challenging. Empirical tests of individual and population-level responses to climate have yielded mixed results, suggesting that latitudinal trends in climate effects are complex [1,9–11], and few empirical studies have quantified how such processes scale up to affect emergent dynamics of communities such as synchrony and stability.

Clarifying the potential for latitudinal trends in the impacts of climate change requires understanding responses at three scales: individual performance, population dynamics, and communitylevel interactions and stability, and articulating how they are related. Here, we describe hypotheses and empirical evidence for latitudinal trends in climate impacts at each of these scales to address the following questions:

- (i) Do species show systematic latitudinal variation in the position or extent of temperature tolerances for individual performance metrics [i.e., thermal performance curves (TPC)]?
- Do temperature effects on populations mirror patterns in individual performance metrics? (ii)
- (iii) Do we expect the effect of temperature on community dynamics to show latitudinal trends, given concurrent gradients in temperature and species richness?

#### Highlights

Climate change will affect individuals, populations, and communities, but it is unclear whether these cross-scale effects will be larger in tropical versus temperate areas.

Latitudinal variation in the shape and position of thermal performance curves, while better understood than variation in population and community responses, may not scale to population responses to warming, nor is it clear how such effects translate into community stability.

Evidence for latitudinal variation in temperature effects on individual performance and population growth rate is mixed, and there is not enough data to identify latitudinal patterns in community responses to warming.

Effects of warming on populations and communities will be modulated by latitudinal variation in other factors, such as natural selection, seasonal warming rates, species richness, and the impact of species interactions.

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## **Trends in Ecology & Evolution**

# Climate

+ vulnerability - vulnerability

- Greater climate variability
- Greater magnitude warming
- Historically colder, shorter seasons

# Individual performance

- Lower T<sub>opt</sub>
- Greater temperature breadth
- Greater maximum performance
- Greater thermal safety margin

# Population dynamics

- Slower life-cycle
- Lower sensitivity to vital rates that are
- strongly affected by climate

# Community stability

- Lower species richness
- Greater synchrony
- Stronger pairwise interactions

# **Evolutionary potential**

- Lower R<sub>max</sub>
- Greater potential for adaptive gene flow
- Greater genetic variation in temperature response

#### Trends in Ecology & Evolution

Here we summarize the empirical evidence for these three questions, use a simple mathematical model to illustrate how latitudinal trends in temperature impacts on individual species' population dynamics might impact **community stability**, and outline current knowledge gaps and two promising experimental approaches to advance our understanding of climate change impacts across latitudes. Such a synthesis is crucial for moving towards a synthetic understanding of latitudinal variation in climate change impacts given concurrent gradients in diversity and for informing generalizable predictions and land management priorities under projected climate change.

#### How does individual performance respond to temperature across latitudes?

Key to our analysis is a discussion of how current and projected temperature, along with species temperature tolerances, vary across latitudes. We focus on temperature as it shows strong latitudinal variation in both mean and intra-annual current and future temperatures (including both faster absolute rates of warming at high latitudes and faster relative warming rates at low latitudes [12]). By contrast, neither historical mean precipitation nor future change in precipitation

Figure 1. The potential response of organisms, populations, and communities to current and projected future temperatures varies across latitudes. We show hypothesized mechanisms influencing latitudinal variation in climate impacts. Hypothesized changes in temperature, physiological performance, population dynamics, community stability, and evolutionary processes are predicted to increase (red) or decrease (blue) the negative impacts of climate change with increasing (absolute values of) latitudes. Abbreviations: abs, absolute values of; T<sub>opt</sub>, optimal temperature.

#### Glossary

**Community stability:** a measure of the amount of variability in aggregated abundance (e.g., percentage cover, biomass, or number of individuals); often quantified as the ratio of the temporal mean to the standard deviation (the inverse of the coefficient of variation) (see [90,91] for a discussion of metrics of stability).

**Maximum value:** the highest level of performance achieved under optimal temperatures; TPC parameter.

Optimal temperature (Top): the temperature at which some aspect of performance is maximized; TPC parameter.

**Portfolio effect:** a hypothesis for linking species diversity and ecosystem stability, arguing that probabilistically, more diverse communities will be more stable due to high variation in species' abundance fluctuations.

Sensitivity: the change in population growth rate in response to small perturbations in a vital rate or in an environmental driver.

**Temperature variability:** diurnal, seasonal, or interannual variation in temperature.

Thermal performance curve (TPC):

the unimodal response of an aspect of individual performance (i.e., development rate, physiological performance, or fitness component) in response to temperature. TPCs are often defined by their optimal temperature, maximum performance, and breadth.

TPC breadth: the range of temperatures above which species maintain some biologically-relevant level of performance. TPC breadth is often summarized using critical maximum or minimum temperatures, defined as the maximum or minimum temperature beyond which some aspect of performance is negligible; TPC parameter.

Thermal safety margin: difference between an individuals' maximum temperature tolerance and the temperatures it currently experiences; TPC parameter.

Vital rate: survival, growth (including regression), or reproduction (including processes such as seed germination or hatching rates), the three key factors that contribute directly to population growth rate.

vary systematically across latitudes (although precipitation [13], as well as other factors such as topography, oceanic influences, and disturbances will modify climate change impacts in particular regions [12,14]). Throughout, we focus our discussion primarily on terrestrial patterns, synthesizing data from diverse taxa. While outside the scope of our manuscript, we note that marine systems may show distinct latitudinal patterns in temperature effects on individual performance [5,15,16].

#### Temperature-dependent individual performance

Much of the empirical evidence on impacts of temperature variation and of climate changeinduced warming on any scale comes from studies that measure the effect of temperature on individual performance to construct a TPC (Figure 2A). Most commonly, these curves describe fitness-adjacent performance metrics (such as growth rate or running speed) to realistic temperatures (current and/or projected) in a laboratory setting. Commonly measured aspects of TPCs (reviewed by [17]) include: (i) their position, including metrics such as the **optimal temperature**  $(T_{opt})$  at which performance is maximized; (ii) their breadth, or the range of temperatures above which some level of performance is maintained; and (iii) their **maximum value**, or the highest level of performance achieved under optimal temperatures.



Figure 2. How commonly measured aspects of performance derived from thermal performance curve (TPC) studies may differ from intrinsic and stochastic population growth rates measured in natural populations at high (blue) and low (orange) latitudes. Transparent rectangles indicate the historical range of temperature experienced at each latitude. (A) Temperature effects on performance, as commonly measured in TPC curves (e.g., jumping distance, respiration rate), as well as key characteristics of low and high latitude TPCs such as greater breadth, lower Topt, and lower maximum performance of a thermal generalist at high latitude. (B) Shows how these curves may translate into deterministic population growth rates ( $\lambda$ ) reflecting potentially greater buffering at high latitude and higher maximum growth rates at low latitude. Distributions on the vertical axis show how normally-distributed temperature variation may translate into temporal variation in population growth. (C) Shows how variability in temperature may translate into stochastic population growth rates ( $\lambda_s$ ) as a function of mean temperatures. Note that greater temperature variability at higher latitudes results in greater discrepancies between temperature effects on  $\lambda$  versus  $\lambda_s,$  including decreasing maximum  $\lambda_s$  and reducing T<sub>opt</sub>. Abbreviations: T<sub>opt</sub>, optimal temperature.

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Evolutionary theory suggests that lower mean temperature and higher temperature variability at high latitudes should select for certain TPC characteristics. Adaptation to lower mean temperatures should result in lower optimal temperatures at high latitudes (Figure 2A), a pattern found by many studies [18–22]. This is expected despite the fact that TPCs are often asymmetric, favoring optimal temperatures that are higher than the average temperature experienced by an organism, and metabolic theory that predicts increasing rates of reaction with warmer temperature (reviewed by [23]). If populations are perfectly adapted, temperature increases should reduce fitness at any latitude. However, other studies show weak or absent local adaptation, such that high latitude populations have a much higher T<sub>opt</sub> than they currently experience and therefore are likely to benefit (at least initially) from warming [1,5,24,25]. Recent synthetic studies suggest that geographic variation in TPC parameters are variable among taxa and performance metrics [26,27], finding, for example, that T<sub>opt</sub> shows local adaptation for measures of development and locomotion but not for growth or photosynthetic rates. In spite of these disparate findings, one consistent pattern emerging from these studies is that the thermal safety margin is generally either lower in the tropics, or low across all latitudes, due to strong local adaptation ([15,16,28,29]; but see [10]).

Latitudinal patterns in temperature variability also exert strong selective pressure on the shape of TPC curves. Trade-offs between maximum value and breadth (i.e., thermal specialist-generalist trade-offs) [30,31] predict that greater temperature variability at high latitude should select for 'thermal generalists' who have wide **TPC breadth** at the expense of maximum performance (Figure 1) [1,15,24,25,32]. 'Thermal specialists' in the tropics should have narrow TPC breadth but high maximum performance. While some studies find evidence consistent with these patterns [19,33], others find counter-gradient variation in thermal performance where, for a given species, high latitude populations have higher maximum performance than low latitude populations at all temperatures [34–37]. For example, high-latitude medaka fish (*Oryza latipes*) populations grow more rapidly at all temperatures than low-latitude populations [36]. This pattern is inconsistent with a breadth/maximum value tradeoff, as high-latitude fish have high maximum performance with no concomitant reduction in TPC breadth.

The majority of TPC studies quantify temperature effects on particular aspects of individual performance (e.g., photosynthetic rate, jumping distance) rather than fitness [26]. However, temperature effects on fitness may not correlate with these metrics of performance [31]. Some TPC studies do quantify temperature effects on **vital rates** (e.g., survival, growth rate, or germination probabilities), which can be combined to estimate temperature effects on lifetime fitness or population growth rates [1,10]. Studies of vital rates show that they are often strongly linked to temperature, both in experimental manipulations of temperature in laboratory settings and in responses of natural populations to ambient variation in temperature [19–21,38]. While warming experiments with natural populations often show temperature-dependent vital rates [39], these studies almost universally lack the necessary data to quantify whether the effect mirrors that of a TPC curve measured in a controlled lab or greenhouse environment. There are several other challenges for linking results from the TPC literature to temperature-dependent vital rates in natural populations, including the potential for cumulative effects of thermal stress not captured by simple temperature manipulations in the lab [40] and variability in TPC parameters among individuals or developmental stages [41].

#### How sensitive is population growth to temperature across latitudes?

Three key pieces of information are critical for predicting the change in population growth rate under current versus future temperatures at a given latitude: (i) What is the shape of temperature effects on vital rates in natural populations? (ii) How sensitive are populations to those vital rates?



and (iii) How does the effect of other drivers, such as species interactions, vary latitudinally in current versus future climate conditions? There are several demographic and evolutionary processes that could result in disparate effects of temperature on individual performance versus stochastic population growth rate ( $\lambda_s$ ), the gold standard for measuring fitness and predicting extinction [42,43]. Most notably, latitudinal variation in **sensitivity** to vital rates governs the connection between  $\lambda_s$  and temperature-vital rate relationships derived from TPCs [44].

Sensitivity of populations to particular vital rates, and thus to temperature effects on those vital rates, can vary latitudinally, though the direction of the effect is unclear. Two mechanisms are likely to reduce sensitivity to temperature at high latitudes. First, theory suggests that populations should evolve life history mechanisms to buffer themselves from highly variable vital rates, a hypothesis generally supported by empirical studies [45] (but see [46]). Such buffering effects should lead to low temperature sensitivity of high latitude populations. A recent comprehensive test of this hypothesis actually found the opposite: higher sensitivity to abiotic drivers, including temperature, at higher latitudes [9]. In addition to buffering effects, the impact of a given vital rate on population growth rate can vary with life history, because short-lived species (common at low latitudes [47]) are predicted to be more sensitive to current and future temperature variation [48]. Other factors besides temperature could act in the opposite direction, reducing sensitivity to temperature at low latitudes. Namely, latitudinal variation in the frequency, severity, or sensitivity to species interactions could modify sensitivity to temperature (similar to [49]). For example, if growth is limited at low latitudes by high herbivory rates or high herbivore diversity, and temperature also impacts growth, we might expect strong impacts of temperature at low latitudes. The direction of this effect (reduction or increase in low latitude temperature sensitivity) depends on how species interactions and temperature affect vital rates.

#### Evidence for latitudinal trends in temperature sensitivity

We see some support for different directions of temperature effect on population growth across latitudes. The only field-based study that comprises a large enough latitudinal gradient and sufficient data from tropical populations to test for differential temperature effects shows that the effect of temperature on population size is positive at high latitudes and generally negative at low latitudes (in birds) [50]. Note that some studies across smaller latitudinal ranges or without as strong tropical coverage show similar patterns (in birds and mammals) [51], but others show no effect (diverse taxa) [52,53] or even the opposite effect (plants) [54]. Thus, when considering temperature effects on population growth at very broad geographical scales, it seems likely that the breadth of temperature tolerance of population growth rate increases with latitude, and that population growth rates are closer to their thermal optimum in low latitudes (similar to TPC studies of individual performance).

Perhaps the best test of these hypotheses to date, due to their broad representation of tropical and temperate species, come from studies that have estimated temperature effects on intrinsic population growth in controlled laboratory settings [1,10]. These studies show substantial variation in the projected fitness effects of warming across latitudes, ranging from greater negative impacts in tropical [1] or in mid-latitude species [10], depending on assumptions of the models. However, the laboratory-derived intrinsic population growth rates used in these studies may not reflect  $\lambda_s$  of natural populations. Such an effect might arise because sensitivities to particular vital rates change as a function of density [55,56]. Other processes might lead to latitudinal variation in the degree of discrepancy between intrinsic and stochastic population growth rate; both density-dependent processes [57,58] and interspecific species interactions [59] are likely to be more impactful in tropical populations [60] and lead to greater divergence between intrinsic and stochastic population growth always reduces the  $\lambda_s$  (Box 1), meaning that this reduction should be more pronounced at high latitudes [10],



Box 1. Effect of thermal performance curves on current versus future stability across latitudes

We used the thermal performance curve (TPC) from the high- and low-latitude species in Figure 1 of reference [1], combined with associated mean, variance, and projected increase in mean monthly temperatures, to obtain predictions of deterministic population growth rate ( $\lambda$ ) and stochastic population growth rate ( $\lambda_s$ ) in current and future climates (see the supplemental information online for Methods). We found that future declines in  $\lambda_s$  at low latitudes are even more catastrophic than TPC predictions of  $\lambda$  (crosses:  $\lambda$ , open circles:  $\lambda_s$ ; Box 1 Figure IA).

To quantify the impact of temperature increases on metrics of community response, we modified the simulation above to include multiple species that varied in T<sub>opt</sub>. We included latitudinal variation in species richness, as well as realistic variation in species-specific temperature responses; namely, similar levels of across-species variation in Topt across latitudes (see the supplemental information online). In these simulations, we see lower stability in a future climate for high latitudes (blue), but similar levels of stability in current versus future climates in low latitudes (red, Box 1 Figure IC). Such an effect might arise because at low latitudes in current temperatures, species are already responding asynchronously (some increase and some decrease biomass in warm years), and small changes in temperature will have little effect on the relative proportion of species responding with increase versus decrease in biomass. By contrast, at high latitudes, synchrony will increase in a future climate, likely due to the convex shape of the TPC curve below Topt (convexity results in stronger temperature responses under future temperature conditions; Box 1 Figure IC). Exploratory analysis shows that the position of the TPC curve relative to current versus future temperatures is most important for dictating latitudinal variation in community stability, but also the concavity of the curve, reflected in specialist generalist trade-offs, is important (Figure S1 in the supplemental information online). We know little about these parameters in natural populations. These analyses also suggest that no change or increases in stability under climate change are most likely at low latitudes, whereas high latitudes could increase or decrease in stability, depending on parameter estimates (see Figure S1 in the supplemental information online). Abbreviation: Topt, optimal temperature.





assuming similar positions along a TPC [61]. Thus, it is not immediately clear what the shape of the relationship between temperature and  $\lambda_s$  is over future temperature conditions, and we argue this is a fundamental gap in our current understanding of temperature impacts in natural populations.

#### Evolutionary potential under climate change

An additional complexity is that natural selection could change the relationship of population growth and temperature over time with ongoing climate change, with perhaps higher degree and efficacy of natural selection in high latitudes. Studies of rates of climatic niche divergence



[62] are consistent with higher rates of evolution in high versus low latitude populations. High rates of evolution might occur at high latitudes due to gene flow from populations adapted to warm temperatures to historically cooler climates at high latitudes, a phenomenon that would not occur in tropical populations [63]. In addition, it may be that higher intra-annual variability in temperature at higher latitudes has maintained greater genetic variability in individual TPCs within populations [23,64]. Alternatively, any increase in genetic variance with latitude may be offset by potentially longer generation times and lower maximum fecundity, dampening any overall latitudinal effect on rates of evolution [6].

# How does the interplay of temperature, diversity, synchrony, and species interactions shape community level properties across latitudes?

Sensitivity of individual species to temperature will, in the aggregate, determine community-level stability in a future climate (Figure 3A). At the community scale, predictions for how stability might vary across latitudes depend on: (i) the degree of and variation in temperature effects on population growth across species; (ii) the latitudinal diversity gradient; and (iii) the degree of correlation in species' abundance fluctuations and their underlying drivers, such as species interactions.

Higher species richness in tropical communities will likely result in higher stability in both current and future climate conditions, assuming that species differ in their sensitivities to temperature. Many systems show support for a positive effect of species richness on stability, though the shape of the relationship (linear versus saturating) and the many mechanisms that contribute to it are still debated [65]. Namely, high richness can dampen the effects of species-specific fluctuations in population size in response to temperature, as species may respond in non-correlated or even negatively correlated (i.e., asynchronous) manners, a mechanism commonly referred to as the **portfolio effect** [66,67].

Both theory and empirical tests show that community stability is highest when populations respond asynchronously to environmental fluctuations, such as temperature, but it is not clear at



Figure 3. Effects of temperature and species interactions on synchrony. (A) Shows how thermal performance curves (TPCs) may scale to alter community synchrony [assuming similar density dependence across species such that stochastic population growth rate ( $\lambda_{s}$ ) corresponds to observed population sizes]. As temperature increases, communities may become less synchronous or even asynchronous (broken to unbroken lines) due to species' variation in the location and shape of TPCs, as the current temperature nears or even exceeds species' optimal temperatures. However, past a thermal environmental threshold (star), we expect strong synchrony to again occur as all species respond more similarly to fluctuations in temperature. Here, we expect strong synchrony to occur along with extinction events, as thermal thresholds are exceeded. (B) Both species' sensitivity to environmental fluctuations (e.g., temperature, A) and competition jointly contribute to expected synchrony patterns. Therefore, patterns in synchrony and stability across latitudes will depend both on environmental change and latitudinal gradients in species richness.



which latitudes communities should be strongly versus weakly synchronous, or even asynchronous. Here we use 'asynchrony' to denote negative correlations in fluctuations, but note that these negative correlations in changes in species' abundances are uncommon, especially when considering entire communities rather than species pairs [68]. Stability is highest when asynchronous fluctuations occur among the dominant species in the community, particularly when evenness is low [69]. It is not clear whether asynchronous fluctuations (and thus stability) are likely to be most common in high versus low latitudes. Some evidence indicates that asynchrony should be highest in areas with higher mean temperatures [69] and high variation in precipitation [70] (such as the tropics), but others suggest strong asynchrony with a larger range in annual temperatures (such as high latitudes) [69]. In a rigorous experimental test of climate effects on stability, Hallett et al. [70] found increased asynchrony with high precipitation variability across nine grassland sites, but also higher species richness and higher stability with higher mean annual precipitation. Similarly, Valencia et al. [69] found that that increased mean and variability in precipitation promotes stability, while increased mean temperature and temperature ranges decreased stability. Most of these results suggest that stability should be highest in low latitudes, but they also showcase that we know little about how multiple climate drivers that vary with latitude should impact stability, particularly in a changing climate. Supporting this assertion, empirical studies of the effect of experimental warming on stability show conflicting results [71,72].

Interactions among species will likely lead to latitudinal variation in stability. Community theory suggests that high diversity at low latitudes may dilute the probability of strong pairwise interspecific competition by increasing the stochasticity in the patterns of interaction neighborhoods [73,74]. At higher latitudes, strong competition in locations with limited resources [75] could help stabilize ecosystems via stronger asynchrony [76,77], or potentially through niche partitioning among species across environmental variability or limiting resources [75,78]. However, increased asynchrony from competition is often not enough to compensate for increased amplitudes of species' fluctuations that destabilize ecosystem function with increasing competition [79]. Additionally, as climate changes further, we expect that species may cross thresholds where entire communities respond similarly to environmental drivers. In this case, environmental effects will dominate over competitive interactions, causing stronger synchrony and therefore less temporal stability (Figure 3). To date, large-scale evidence for these thresholds is still weak [80], and higher diversity often moderates temperature-driven fluctuations in population sizes from cascading through ecosystems [81]. However, we know much less about how other types of species interactions (e.g., predation, herbivory, and mutualists) affect stability. There is also evidence that the sign of the relationship between species richness and stability varies with aridity [82], suggesting that latitudinal variation in abiotic conditions may interact non-additively with latitudinal variation in species richness.

Overall, these conflicting mechanisms do not give a clear hypothesis for how community stability varies with latitude. In addition, we lack empirical tests of variation in stability across latitudinal gradients, which include temperature as well as species richness or lifespan gradients; Box 2) [70,83,84]. The only study of which we are aware that assesses stability across a relatively broad latitudinal gradient (c. 2°) showed a negative relationship between latitude and stability. Namely, kelp beds in low latitudes had higher stability in the face of canopy removal by storms than did high latitude kelp beds, an effect mediated by changes in intraspecific competition [85]. In this observational study, however, the authors were unable to disentangle the role of temperature versus species richness and other factors across latitudes, all of which likely simultaneously affect stability (Box 2).

Disentangling the effects of latitudinal variation in temperature on stability from those of species richness is a daunting challenge, but will be essential to accurately predict changes in stability



#### Box 2. Additional factors influencing latitudinal variation in current and future stability

The degree of community stability in the face of a changing climate will be further moderated by latitudinal variation in species demography and seasonal warming rates. Slow-growing species characterized by a conservative resource use strategy tend to increase stability [88]. Therefore, community-averaged longer lifespans at high latitudes could act to increase stability [47,89]. Additionally, differential rates of warming across seasons, which is more pronounced at high latitudes (see Figure S2 in the supplemental information online), could contribute to asynchrony in species fluctuations at high latitudes. For example, if species A's population growth rate is very sensitive to winter temperature, species B is somewhat sensitive to winter temperature, and species C is most sensitive to summer temperature, but winters are warming faster than summers, we would expect higher synchrony between A versus B in a future climate, but stronger asynchrony between A versus C, and A versus B (Box 2 Figure II). In the figure, cold winters are shown in blue transparent colors, warm summers are shown in orange, with the level of transparency indicative of the severity. Warming begins at the grey line. Before warming, A versus B are somewhat synchronous, whereas A versus C and B versus C are somewhat asynchronous. After warming, A versus B are very synchronous, whereas A versus C and B versus C are asynchronous. Both of these phenomena (latitudinal variation in lifespan and seasonal warming) should increase stability at high latitudes in a future climate.





in a future climate. While temperature will change dramatically in a future climate, with predictable latitudinal variation in the magnitude of change, changes in precipitation and species richness will be site-specific and/or delayed. This reality means that quantifying the relative impact of climate change on tropical versus temperate systems will require understanding what fraction of the effect is due to temperature changes alone. Thus, articulating the role of temperature *per se* in affecting stability is critical to developing a predictive framework for how stability at high versus low latitudes should change in a future climate.

#### Concluding remarks

We advocate for synthetic studies that use model systems from discipline-specific work to design studies addressing other scales (see Outstanding questions). Namely, we propose three key collaborative efforts: (i) Linking TPC parameters to demographic effects of temperature. Temperature sensitivities in species that have been the subject of long-term stochastic demography work (e.g., *Mimulus cardinalis* or *Plantago lanceolata*) could be compared to TPC studies. At the very least, we suggest that population biologists explicitly test for nonlinear responses to temperature increases. (ii) Constructing population models for species for which there are numerous TPC studies on vital rates (e.g., *Drosophila*), and using these models to quantify latitudinal variation in sensitivity to those vital rates to temperature-dependent vital rates in TPC studies. (iii) Linking temperature effects on stochastic population dynamics to community stability; we advocate for construction of temperature-dependent population models using long-term community level monitoring data (e.g., across Long Term Ecological Research sites or the Nutrient Network). At the very least, we advocate for parsing the drivers of stability, with a particular focus on the role of

#### Outstanding questions

To what degree do TPCs translate into stochastic population growth rate ( $\lambda_s$ ), and how does this vary across latitudes? This question requires quantifying sensitivities of population growth to temperature dependent vital rates, and effects of intra- and interspecific species interactions on the shape and position of TPCs.

What is the shape of the relationship between temperature and  $\lambda_s$  over future temperature conditions? Does the shape differ latitudinally, and do differences arise due to changes in temperature effects on vital rates or in sensitivities to vital rates?

How might natural selection modify the effect of temperature on  $\lambda_s$ ? Are there latitudinal gradients in the strength of selection, degree of local adaptation, or rate of evolution, and will these gradients facilitate adaptative evolution in a changing climate?

How does asynchrony among species in population-level temperature responses vary latitudinally? What fraction of asynchrony is due to divergent temperature responses across broad spatial scales?

What is the role of temperature *per se* in affecting stability across latitudes? This question requires disentangling the concurrent variation in species richness (and other abiotic and biotic factors) from that of current and historical temperature, perhaps with targeted comparisons of temperature effects on stability (e.g., comparing across paleo time periods or species guilds, North versus South hemispheres, marine versus terrestrial systems, or latitudes versus elevations).

How do natural communities respond to warming temperatures, when considering realistic latitudinal variation in warming and concomitant gradients in species richness? Results of community warming experiments may differ from those on component species due to changes in competitor hierarchies or extinctions (e.g., biotic attrition might result in declines in tropical biomass, with sufficient dispersal preventing attrition in higher latitudes).



temperature effects on population growth rate (which may be nonlinear) across many systems to predict shifts in synchrony with temperature increase.

We envision key insights arising from two proposed complementary experimental approaches that aim to disentangle the impact of concurrent latitudinal gradients in historical temperature, future temperature (both mean and seasonal), and species richness. First, we advocate for a globally-distributed warming experiment, similar in scale and scope to the Nutrient Network [86] or Drought-Net [87], perhaps using passive warming experiments in terrestrial plant communities. This approach would include quantification of TPC parameters and simple population modelling for key dominant species. To disentangle the relative contributions of temperature versus species richness, we suggest pairing warming experiments with manipulations of species richness in several sites across a latitudinal gradient. This integrative approach would allow us to determine under what conditions TPC parameters do or do not translate into stochastic population growth rates, inform us whether we can use already-collected TPC data to infer population dynamics, as well as quantify the degree to which sensitivity to temperature manifests into divergent community-level temperature effects across latitudes.

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No interests are declared.

#### **Supplemental Information**

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