Trends in
Ecology & Evolution

CellPress

Review

# Climate sensitivity across latitude: scaling physiology to communities

Allison M. Louthan, [1,4,*,@] Megan L. Peterson, [2,5,7] and Lauren G. Shoemaker[3,6,7,@]

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.

## 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.

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

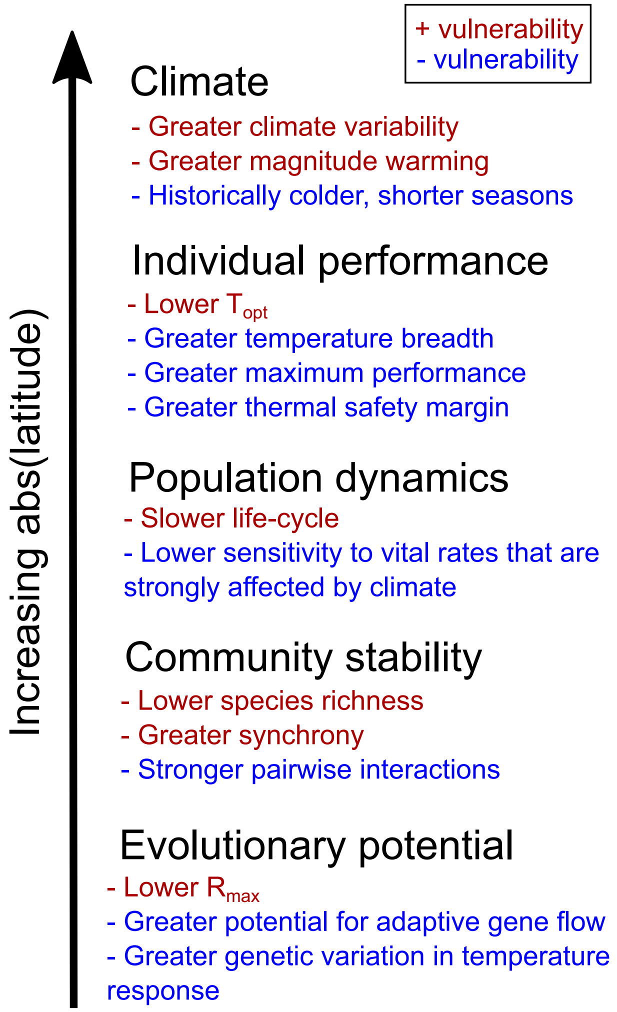
Climate change represents one of the most severe threats to species conservation and ecosystem stability. Yet despite decades of research, it remains difficult to predict where climate variation, including climate change, will have the largest impact on biological systems on a global scale. Much of this 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 community-level 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)**]?
(ii) Do temperature effects on populations mirror patterns in individual performance metrics?
(iii) Do we expect the effect of temperature on community dynamics to show latitudinal trends, given concurrent gradients in temperature and species richness?

[1]Division of Biology, Kansas State University, Manhattan, KS, 66506, USA
[2]Plant Biology Department, University of Georgia, Athens, GA, 30602, USA
[3]Botany Department, University of Wyoming, Laramie, WY 82071, USA
[4]http://www.louthanlab.com
[5]http://meganlpeterson.weebly.com
[6]https://laurenshoemaker.weebly.com
[7]These authors contributed equally to this work

*Correspondence:
amlouthan@ksu.edu (A.M. Louthan).
@Twitter: @allisonmlouthan (A.M. Louthan) and @LG_Shoemaker (L.G. Shoemaker).



Trends in Ecology & Evolution

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; $T_{opt}$, optimal temperature.

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

## 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 ($T_{opt}$):** 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 change-induced 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.

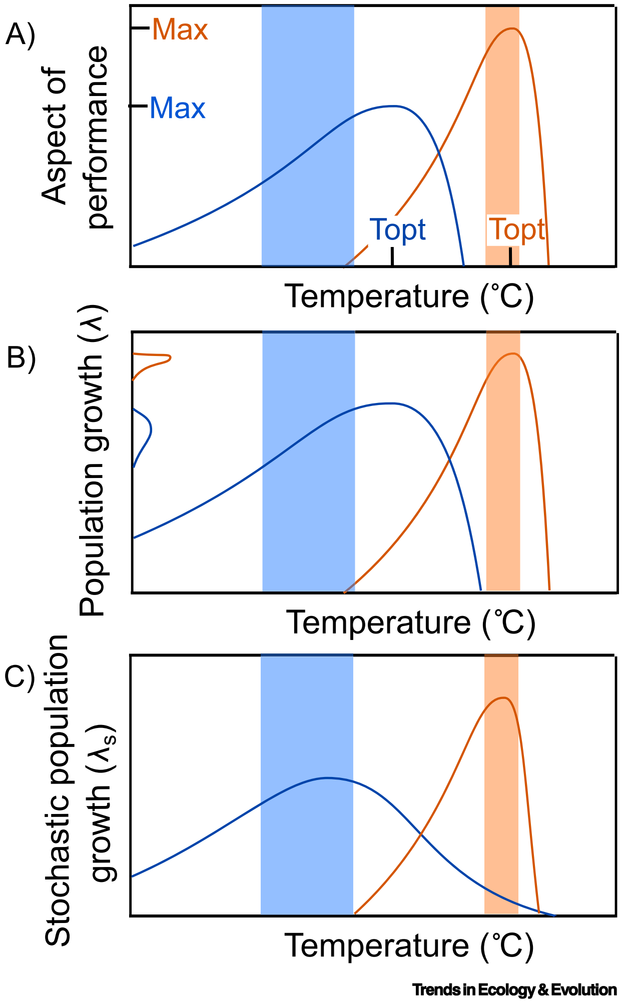


Figure 2. How commonly measured aspects of performance derived from thermal performance curve (TPC) studies may differ from intrinsic and stochastic population growth rates measured in natural populations at high (blue) and low (orange) latitudes. Transparent rectangles indicate the historical range 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 $T_{opt}$, and lower maximum performance of a thermal generalist at high latitude. (B) Shows how these curves may translate into deterministic population growth rates (λ) 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 λ versus $\lambda_s$, including decreasing maximum $\lambda_s$ and reducing $T_{opt}$. Abbreviations: $T_{opt}$, optimal temperature.

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 $T_{opt}$ 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 $T_{opt}$ 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

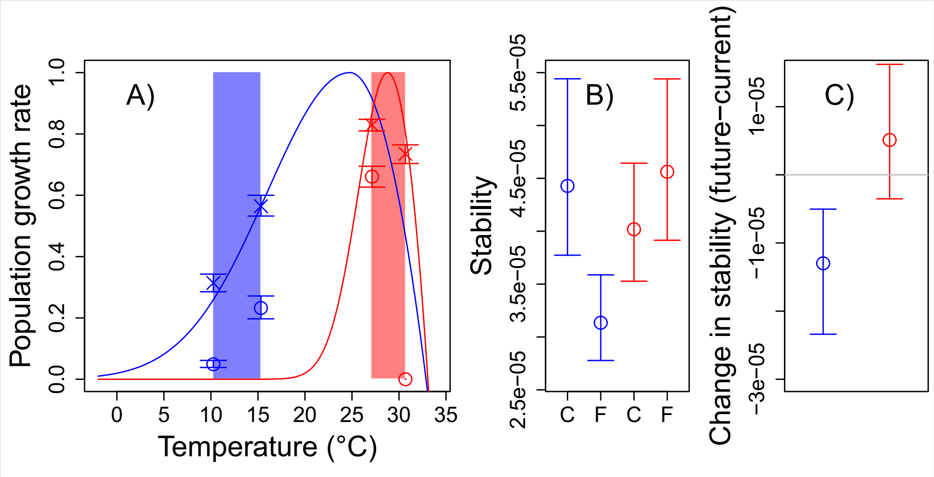
We see some support for different directions of temperature effect on population growth across latitudes. The only field-based study that comprises a large enough latitudinal gradient and sufficient data from tropical populations to test for differential temperature effects shows that the effect of temperature 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. Alternatively, high variability in 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 $T_{opt}$. 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 $T_{opt}$ 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 $T_{opt}$ (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: $T_{opt}$, optimal temperature.



Trends in Ecology & Evolution

Figure I. Deterministic (crosses) and stochastic (open circles) population growth rates predicted by thermal performance curves (TPCs, (A), modified from [1]), stability (B) and changes in stability (C) in a future ('F') versus current ('C') climate at low (red) and high (blue) latitudes.

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

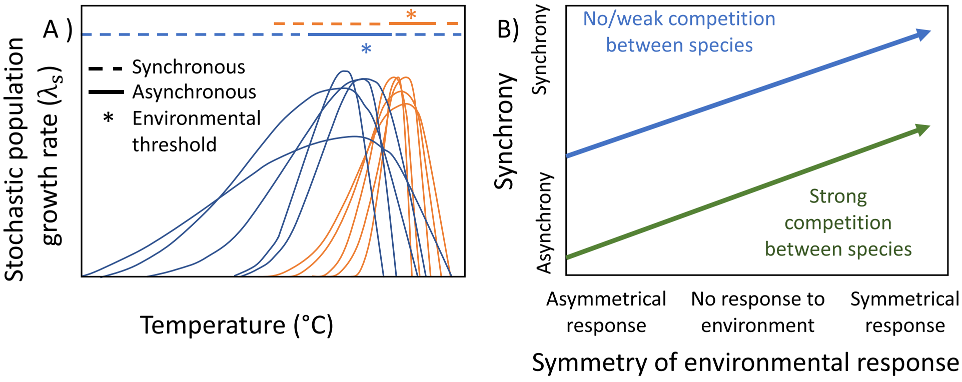


Figure 3. Effects of temperature and species interactions on synchrony. (A) Shows how thermal performance curves (TPCs) may scale to alter community synchrony [assuming similar density dependence across species such that stochastic population growth rate ($\lambda_s$) corresponds to observed population 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.

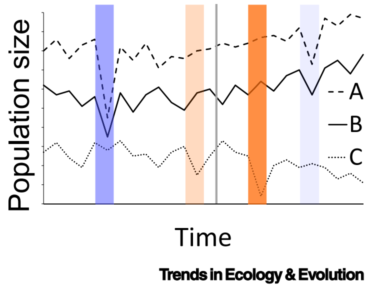


Figure II. Population dynamics of three hypothetical high-latitude species in the face of seasonal warming under climate change (beginning at grey line). Harsh winters are shown by deep blue transparent colors, warm summers are shown by deep orange.

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. At minimum, we advocate for explicit consideration of the sensitivity of population growth 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.

## Acknowledgments

We thank multiple anonymous reviewers, Riley Thoen, and Meredith Zettlemoyer for their comments, and acknowledge funding from National Science Foundation 2033292, 2019528, Division of Environmental Biology 1753980, and the US Department of Agriculture National Institute of Food and Agriculture, Hatch project 1016746. This manusucript is contribution number 21-314-J from the Kansas Agricultural Experiment Station.

## Declaration of interests

No interests are declared.

## Supplemental Information

Supplemental information associated with this article can be found online at https://doi.org/10.1016/j.tree.2021.05.008.

## References

1. Deutsch, C.A. *et al.* (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl. Acad. Sci.* 105, 6668–6672
2. Gonzalez, P. *et al.* (2010) Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. *Glob. Ecol. Biogeogr.* 19, 755–768
3. Iwamura, T. *et al.* (2010) A climatic stability approach to prioritizing global conservation investments. *PLoS One* 5, e15103
4. Corlett, R.T. (2012) Climate change in the tropics: the end of the world as we know it? *Biol. Conserv.* 151, 22–25
5. Sunday, J.M. *et al.* (2012) Thermal tolerance and the global redistribution of animals. *Nat. Clim. Chang.* 2, 686–690
6. Walters, R.J. *et al.* (2012) Forecasting extinction risk of ectotherms under climate warming: an evolutionary perspective. *Funct. Ecol.* 26, 1324–1338
7. Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection, or, the Preservation of Favoured Races in the Struggle for Life*, J. Murray, London
8. Janzen, D.H. (1967) Why mountain passes are higher in the tropics. *Am. Nat.* 101, 233–249
9. Morris, W.F. *et al.* (2020) Biotic and anthropogenic forces rival climatic/abiotic factors in determining global plant population growth and fitness. *Proc. Natl. Acad. Sci.* 117, 1107–1112
10. Kingsolver, J.G. *et al.* (2013) Heat stress and the fitness consequences of climate change for terrestrial ectotherms. *Funct. Ecol.* 27, 1415–1423
11. Lancaster, L.T. (2016) Widespread range expansions shape latitudinal variation in insect thermal limits. *Nat. Clim. Chang.* 6, 618–621
12. IPCC (2014) *Climate Change 2014: Impacts, Adaptation, and Vulnerability*, Cambridge University Press
13. Clusella-Trullas, S. *et al.* (2011) Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. *Am. Nat.* 177, 738–751
14. Loarie, S.R. *et al.* (2009) The velocity of climate change. *Nature* 462, 1052–1055
15. Sunday, J.M. *et al.* (2011) Global analysis of thermal tolerance and latitude in ectotherms. *Proc. R. Soc. B Biol. Sci.* 278, 1823–1830
16. Sunday, J. *et al.* (2019) Thermal tolerance patterns across latitude and elevation. *Philos. Trans. R. Soc. B Biol. Sci.* 374, 20190036
17. Angilletta, M.J. (2009) *Thermal Adaptation: A Theoretical and Empirical Synthesis*, Oxford University Press
18. Hoffman, A.A. *et al.* (2002) Opposing clines for high and low temperature resistance in *Drosophila melanogaster*. *Ecol. Lett.* 5, 614–618
19. Angert, A.L. *et al.* (2011) Incorporating population-level variation in thermal performance into predictions of geographic range shifts. *Integr. Comp. Biol.* 51, 733–750
20. Kelly, M.W. *et al.* (2012) Limited potential for adaptation to climate change in a broadly distributed marine crustacean. *Proc. R. Soc. B Biol. Sci.* 279, 349–356
21. Peterson, M.L. *et al.* (2018) Both life-history plasticity and local adaptation will shape range-wide responses to climate warming in the tundra plant *Silene acaulis*. *Glob. Chang. Biol.* 24, 1614–1625
22. Latimer, C.A.L. *et al.* (2011) Quantitative genetic variation for thermal performance curves within and among natural populations of *Drosophila serrata*. *J. Evol. Biol.* 24, 965–975

23. Huey, R.B. and Kingsolver, J.G. (1989) Evolution of thermal sensitivity of ectotherm performance. *Trends Ecol. Evol.* 4, 131–135
24. Compton, T.J. *et al.* (2007) Thermal tolerance ranges and climate variability: a comparison between bivalves from differing climates. *J. Exp. Mar. Biol. Ecol.* 352, 200–211
25. Diamond, S.E. *et al.* (2012) Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. *Glob. Chang. Biol.* 18, 448–456
26. Sørensen, J.G. *et al.* (2018) A widespread thermodynamic effect, but maintenance of biological rates through space across life's major domains. *Proc. R. Soc. B Biol. Sci.* 285, 20181775
27. Rezende, E.L. and Bozinovic, F. (2019) Thermal performance across levels of biological organization. *Philos. Trans. R. Soc. B Biol. Sci.* 374, 20180549
28. Bennett, S. *et al.* (2019) Integrating within-species variation in thermal physiology into climate change ecology. *Philos. Trans. R. Soc. B Biol. Sci.* 374, 20180550
29. Bennett, J.M. *et al.* (2021) The evolution of critical thermal limits of life on Earth. *Nat. Commun.* 12, 1198
30. Huey, R.B. and Hertz, P.E. (1984) Is a jack-of-all-temperatures a master of none? *Evolution* 38, 441–444
31. Angilletta, M.J. *et al.* (2003) Tradeoffs and the evolution of thermal reaction norms. *Trends Ecol. Evol.* 18, 234–240
32. MacLean, H.J. *et al.* (2019) Evolution and plasticity of thermal performance: an analysis of variation in thermal tolerance and fitness in 22 *Drosophila* species. *Philos. Trans. R. Soc. B Biol. Sci.* 374, 20180548
33. Phillips, B.L. *et al.* (2014) Do evolutionary constraints on thermal performance manifest at different organizational scales? *J. Evol. Biol.* 27, 2687–2694
34. Conover, D.O. and Present, T.M.C. (1990) Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia* 83, 316–324
35. Laugen, A.T. *et al.* (2003) Latitudinal countergradient variation in the common frog (*Rana temporaria*) development rates–evidence for local adaptation. *J. Evol. Biol.* 16, 996–1005
36. Yamahira, K. *et al.* (2007) Inter- and intrapopulation variation in thermal reaction norms for growth rate: evolution of latitudinal compensation in ectotherms with a genetic constraint. *Evolution* 61, 1577–1589
37. Conover, D.O. *et al.* (2009) The covariance between genetic and environmental influences across ecological gradients: reassessing the evolutionary significance of countergradient and cogradient variation. *Ann. N. Y. Acad. Sci.* 1168, 100–129
38. Zettlemoyer, M.A. *et al.* (2017) The effect of a latitudinal temperature gradient on germination patterns. *Int. J. Plant Sci.* 178, 673–679
39. Reed, P.B. *et al.* (2020) Climate manipulations differentially affect plant population dynamics within versus beyond northern range limits. *J. Ecol.* 109, 664–675
40. Rezende, E.L. *et al.* (2020) Predicting temperature mortality and selection in natural *Drosophila* populations. *Science* 369, 1242–1245
41. Dahlke, F.T. *et al.* (2020) Thermal bottlenecks in the life cycle define climate vulnerability of fish. *Science* 369, 65–70
42. Lewontin, R.C. and Cohen, D. (1969) On population growth in a randomly varying environment. *Proc. Natl. Acad. Sci.* 62, 1056–1060
43. Morris, W.F. and Doak, D.F. (2002) *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*, Sinauer Associates
44. Caswell, H. (2000) *Matrix Population Models: Construction, Analysis, and Interpretation* (2nd edition), Sinauer Associates Inc
45. Hilde, C.H. *et al.* (2020) The demographic buffering hypothesis: evidence and challenges. *Trends Ecol. Evol.* 35, 523–538
46. Koons, D.N. *et al.* (2009) Is life-history buffering or lability adaptive in stochastic environments? *Oikos* 118, 972–980
47. Locosselli, G.M. *et al.* (2020) Global tree-ring analysis reveals rapid decrease in tropical tree longevity with temperature. *Proc. Natl. Acad. Sci.* 117, 33358–33364
48. Morris, W.F. *et al.* (2008) Longevity can buffer plant and animal populations against changing climatic variability. *Ecology* 89, 19–25
49. Louthan, A.M. *et al.* (2018) Aridity weakens population-level effects of multiple species interactions on *Hibiscus meyeri*. *Proc. Natl. Acad. Sci.* 115, 543–548
50. Amano, T. *et al.* (2020) Responses of global waterbird populations to climate change vary with latitude. *Nat. Clim. Chang.* 10, 959–964
51. Spooner, F.E.B. *et al.* (2018) Rapid warming is associated with population decline among terrestrial birds and mammals globally. *Glob. Chang. Biol.* 24, 4521–4531
52. Pearce-Higgins, J.W. *et al.* (2015) Geographical variation in species' population responses to changes in temperature and precipitation. *Proc. R. Soc. B Biol. Sci.* 282, 20151561
53. Bose, A. *et al.* (2020) Growth and resilience responses of Scots pine to extreme droughts across Europe depend on pre-drought growth conditions. *Glob. Chang. Biol.* 26, 4521–4537
54. Peterson, M.L. *et al.* (2021) Latitudinal gradients in population growth do not reflect demographic responses to climate. *Ecol. Appl.* 31, e2242
55. Feldman, T.S. and Morris, W.F. (2011) Higher survival at low density counteracts lower fecundity to obviate Allee effects in a perennial plant. *J. Ecol.* 99, 1162–1170
56. Gornish, E.S. (2013) Effects of density and fire on the vital rates and population growth of a perennial goldenaster. *AoB PLANTS* 5, 1–11
57. LaManna, J.A. *et al.* (2016) Negative density dependence is stronger in resource-rich environments and diversifies communities when stronger for common but not rare species. *Ecol. Lett.* 19, 657–667
58. Comita, L.S. *et al.* (2014) Testing predictions of the Janzen–Connell hypothesis: a meta-analysis of experimental evidence for distance-and density-dependent seed and seedling survival. *J. Ecol.* 102, 845–856
59. Luhring, T.M. and DeLong, J.P. (2016) Predation changes the shape of thermal performance curves for population growth rate. *Curr. Zool.* 62, 501–505
60. Louthan, A.M. *et al.* (2015) Where and when do species interactions set range limits? *Trends Ecol. Evol.* 30, 780–792
61. Bernhardt, J.R. *et al.* (2018) Nonlinear averaging of thermal experience predicts population growth rates in a thermally variable environment. *Proc. R. Soc. B Biol. Sci.* 285, 20181076
62. Jezkova, T. and Wiens, J.J. (2016) Rates of change in climatic niches in plant and animal populations are much slower than projected climate change. *Proc. R. Soc. B Biol. Sci.* 283, 20162104
63. Walters, R.J. and Berger, D. (2019) Implications of existing local (mal)adaptations for ecological forecasting under environmental change. *Evol. Appl.* 12, 1487–1502
64. Berger, D. *et al.* (2013) Quantitative genetic divergence and standing genetic (co)variance in thermal reaction norms along latitude. *Evolution* 67, 2385–2399
65. Craven, D. *et al.* (2018) Multiple facets of biodiversity drive the diversity–stability relationship. *Nat. Ecol. Evol.* 2, 1579–1587
66. Doak, D.F. *et al.* (1998) The statistical inevitability of stability-diversity relationships in community ecology. *Am. Nat.* 151, 264–276
67. Tilman, D. *et al.* (1998) Diversity-stability relationships: statistical inevitability or ecological consequence? *Am. Nat.* 151, 277–282
68. Houlahan, J.E. *et al.* (2007) Compensatory dynamics are rare in natural ecological communities. *Proc. Natl. Acad. Sci.* 104, 3273–3277
69. Valencia, E. *et al.* (2020) Synchrony matters more than species richness in plant community stability at a global scale. *Proc. Natl. Acad. Sci.* 117, 24345–24351
70. Hallett, L.M. *et al.* (2014) Biotic mechanisms of community stability shift along a precipitation gradient. *Ecology* 95, 1693–1700
71. Shi, Z. *et al.* (2016) Dual mechanisms regulate ecosystem stability under decade-long warming and hay harvest. *Nat. Commun.* 7, 11973
72. Ma, Z. *et al.* (2017) Climate warming reduces the temporal stability of plant community biomass production. *Nat. Commun.* 8, 15378
73. Wiegand, T. *et al.* (2012) Testing the independent species' arrangement assertion made by theories of stochastic geometry of biodiversity. *Proc. R. Soc. B Biol. Sci.* 279, 3312–3320

74. Wang, X. *et al.* (2016) Stochastic dilution effects weaken deterministic effects of niche-based processes in species rich forests. *Ecology* 97, 347–360
75. Tilman, D. (1982) *Resource Competition and Community Structure*, Princeton University Press
76. Loreau, M. and de Mazancourt, C. (2008) Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *Am. Nat.* 172, E48–E66
77. Gonzalez, A. and Loreau, M. (2009) The causes and consequences of compensatory dynamics in ecological communities. *Annu. Rev. Ecol. Evol. Syst.* 40, 393–414
78. Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* 31, 343–366
79. Loreau, M. and de Mazancourt, C. (2013) Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecol. Lett.* 16, 106–115
80. Hillebrand, H. *et al.* (2020) Thresholds for ecological responses to global change do not emerge from empirical data. *Nat. Ecol. Evol.* 4, 1502–1509
81. Sousa-Silva, R. *et al.* (2018) Tree diversity mitigates defoliation after a drought-induced tipping point. *Glob. Chang. Biol.* 24, 4304–4315
82. García-Palacios, P. *et al.* (2018) Climate mediates the biodiversity–ecosystem stability relationship globally. *Proc. Natl. Acad. Sci.* 115, 8400–8405
83. Blüthgen, N. *et al.* (2016) Land use imperils plant and animal community stability through changes in asynchrony rather than diversity. *Nat. Commun.* 7, 10697
84. Lepš, J. *et al.* (2018) Stabilizing effects in temporal fluctuations: management, traits, and species richness in high-diversity communities. *Ecology* 99, 360–371
85. Wernberg, T. *et al.* (2010) Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. *Ecol. Lett.* 13, 685–694
86. Borer, E.T. *et al.* (2014) Finding generality in ecology: a model for globally distributed experiments. *Methods Ecol. Evol.* 5, 65–73
87. Smith, M.D. *et al.* (2016) Drought-Net: a global network merging observations, experiments, and modeling to forecast terrestrial ecosystem sensitivity to drought. *AGU Fall Meet.* Published online December 2016. https://adsabs.harvard.edu/abs/2016AGUFM.B11J..06S
88. Májeková, M. *et al.* (2014) Plant functional traits as determinants of population stability. *Ecology* 95, 2369–2374
89. Munch, S.B. and Salinas, S. (2009) Latitudinal variation in lifespan within species is explained by the metabolic theory of ecology. *Proc. Natl. Acad. Sci. U. S. A.* 106, 13860–13864
90. Donohue, I. *et al.* (2013) On the dimensionality of ecological stability. *Ecol. Lett.* 16, 421–429
91. Lemoine, N.P. (2021) Unifying ecosystem responses to disturbance into a single statistical framework. *Oikos* 130, 408–421