

Widespread range expansions shape latitudinal variation in insect thermal limits

Lesley T. Lancaster

Current anthropogenic impacts, including habitat modification and climate change, may contribute to a sixth mass extinction¹. To mitigate these impacts and slow further losses of biodiversity, we need to understand which species are most at risk and identify the factors contributing to current and future declines. Such information is often obtained through large-scale, comparative and biogeographic analysis of lineages or traits that are potentially sensitive to ongoing anthropogenic change—for instance to predict which regions are most susceptible to climate change-induced biodiversity loss^{2–4}. However, for this approach to be generally successful, the underlying causes of identified geographical trends need to be carefully considered⁵. Here, I augment and reanalyse a global data set of insect thermal tolerances, evaluating the contribution of recent and contemporary range expansions to latitudinal variation in thermal niche breadth. Previous indications that high-latitude ectotherms exhibit broad thermal niches and high warming tolerances held only for species undergoing range expansions or invasions. In contrast, species with stable or declining geographic ranges exhibit latitudinally decreasing absolute thermal tolerances and no latitudinal variation in tolerance breadths. Thus, non-range-expanding species, particularly insular or endemic species, which are often of highest conservation priority, are unlikely to tolerate future climatic warming at high latitudes.

Several recent analyses of ectothermic animals' thermal tolerances across latitudes indicate that species inhabiting higher latitudes are often characterized by broader physiological thermal tolerances than organisms from lower latitudes, a trend that reflects a greater ability of high-latitude species to withstand cold exposure (latitudinally decreasing critical or lethal thermal minimum temperatures, T_{\min}), but no latitudinal effects on species' upper thermal limits (T_{\max} ; refs 6–8). Thus, tropical species' relatively narrow thermal tolerance breadths ($T_{\max} - T_{\min}$) are ecologically appropriate to the (low) levels of environmental thermal variation (T_{env}) that they typically experience⁹, although these lineages may not be well prepared to tolerate additional climatic warming^{3,10} (but see ref. 4). Like tropical species, higher-latitude species also often exhibit an adaptive match between values of T_{\min} and T_{env} (ref. 11). However, latitudinal invariance of T_{\max} across species means that high-latitude species often exhibit greater T_{\max} , higher optimal body temperatures (T_{opt}), and greater thermal tolerance breadths ($T_{\max} - T_{\min}$) than are predicted by the T_{env} that they typically experience³. Such surprisingly high upper thermal tolerances of high-latitude organisms result in substantial 'warming tolerance' ($WT = T_{\max} - T_{\text{env}}$) (ref. 3) for many of these species, and it has been suggested that large warming tolerances will enable these species to withstand a greater magnitude of global warming than

tropical or mid-latitude species^{3,4,12}. Increased warming tolerance at high latitudes suggests that tropical and mid-latitude organisms are at greatest risk of warming-induced declines, despite a greater magnitude of warming occurring at higher latitudes^{10,13}.

Despite the robustness of these latitudinal trends, it has not been straightforward to explain latitudinal invariance of species' upper thermal tolerances and the existence of large warming tolerances at high latitudes, and misinterpretation of the underlying causes of these patterns could result in misguided conservation efforts. Previous hypotheses have suggested that latitudinal invariance in T_{\max} may result from physiological constraints on the evolution of T_{\max} (ref. 11) or from latitudinally invariant fitness consequences of T_{\max} (ref. 12). Such hypotheses rest on the assumption that thermal tolerances of both tropical and temperate species are shaped primarily by local adaptation to their current environmental contexts, within their evolvable limits. However, species are in fact often involved in dynamic biogeographic processes, which may also have large, historical effects on shaping current geographical trait variation.

In response to historic and ongoing global warming events, many species have experienced pronounced and rapid range shifts as newly thermally suitable habitat becomes available at higher latitudes¹⁴. Compounding climate change-mediated range shifts are effects of anthropogenic habitat modification and human-assisted long-distance dispersal, which have resulted in an epidemic of global, biological invasions^{15,16}. Such anthropogenic restructuring of global biodiversity is particularly evident in small ectotherms¹⁴, the same group for which latitudinal invariance in T_{\max} and strongly latitudinally dependent thermal tolerance breadths have most often been reported.

Here, I test the hypothesis that latitudinal invariance of T_{\max} and increased thermal tolerance breadths ($T_{\max} - T_{\min}$) at high latitudes within and among insect species are emergent properties of range expansions and invasions, dynamic processes that are rapidly moving species in a net poleward direction^{14,16}. As organisms move to newly suitable but cooler poleward habitats, selection on upper thermal tolerances is relaxed^{17–19}, while selection on lower thermal tolerance is often intensified because of higher climatic variability near the poles^{7,18}. Thus, release from selection on upper thermal tolerances combined with intensifying selection on lower thermal tolerances during a climate change-induced range expansion or a poleward invasion can result in increased thermal tolerance breadths and latitudinally invariant values for T_{\max} , at least for the duration of the current expansion¹⁸.

Increasing thermal tolerance breadth during a poleward range expansion, which results in latitudinal invariance in T_{\max} , has been demonstrated within species¹⁸, but its potential to generate comparative-level trends is previously unknown. To test this

Table 1 | Biogeographic histories of species used in this and previous meta-analyses of insect thermal tolerance and latitude.

| | Range-expanding species | | Non-range-expanding species | |
|--|---------------------------------------|--|-----------------------------|----------------------------------|
| | Invasives, pests and human commensals | Climate change-mediated range expansions | Insular or narrow endemic | Non-endemic, stable or declining |
| Previously compiled latitudinal thermal tolerance data | 16 | 4 | 19 | 2 |
| Expanded data set (this study) | 2 | 2 | 2 | 1 |
| Percentage of total species | 38% | 13% | 44% | 6% |

hypothesis, I expanded on a publicly available compilation of global insect thermal tolerances^{6,8}, a data set that has been used in different versions to identify latitudinal variation in species' thermal tolerances^{6–8,12}. The species in this data set exhibit a wide array of biogeographic histories and geographic range dynamics, from globally invasive pests to narrowly restricted endemics, as summarized in Table 1 (see Supplementary Table 1 for species-specific details and data). I then used linear mixed models to evaluate how differing biogeographic histories and range dynamics might impact previously reported latitudinal trends, to improve understanding of factors predictive of future warming-induced declines. To account for the fact that range expansion status may be imperfectly known or may correlate with other, confounding aspects of the species' ecology (for example, it is easier to assess geographic stasis for insular species), I conducted a second analysis examining range position effects on within-species geographic variation in T_{min} , T_{max} , and thermal tolerance breadths (see Supplementary Table 2 for data), without respect to their range expansion status, testing the hypothesis that latitudinal increases in thermal tolerance breadth should be more likely to be observed near the species' poleward range margin, which is where any poleward range expansions would have most recently occurred.

Results

Among species, insect thermal tolerance breadths increase with latitude, but only for species that are undergoing large-scale, contemporary or post-glacial range expansions (as invasives, pests, or tracking climate change; Fig. 1a, Table 2). In contrast, among non-range-expanding and range-declining species, there was no correlation between latitude and thermal tolerance breadth (Fig. 1b and Table 2).

For range-expanding species, the pattern of increasing thermal tolerance breadths at higher latitudes reflects latitudinally decreasing T_{min} , most likely in response to increased selection on cold tolerance as species spread polewards¹⁸. T_{max} of range-expanding species did not vary with latitude or any other explanatory variable in the model (Fig. 1a and Table 2), supporting the hypothesis that T_{max} is released from selection during poleward range expansions, and thus measured T_{max} values for range-expanding species are not (yet) locally adapted to the latitude at which experimental subjects or lineages were obtained.

In contrast, non-range-expanding species exhibited coupled changes in T_{max} and T_{min} across latitude, with both upper and lower thermal tolerance limits exhibiting parallel, decelerating declines towards the poles (Fig. 1b and Table 2). Thus, for non-range-expanding lineages, local adaptation to (latitudinally variable, cooler at high latitudes) T_{env} is likely to have been the most important factor shaping both upper and lower thermal tolerances in their current locales. T_{min} of non-range-expanding species corresponds to relative range position in addition to latitude (Table 2), indicating that populations closer to their poleward range margin are likely to exhibit stronger adaptations to cold than populations situated closer to their equatorial range margin, irrespective of absolute latitude. An F -test for heterogeneity of variances indicates that T_{min} and T_{max} of non-range-expanding species each have similar

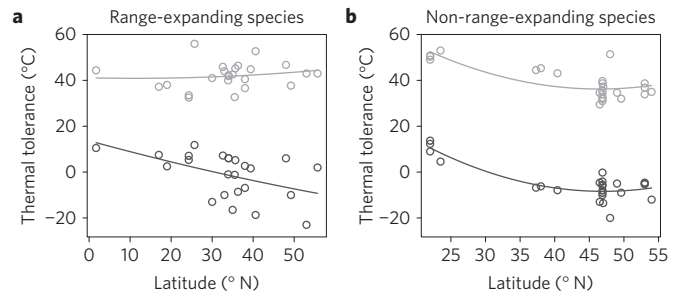


Figure 1 | Latitudinal trends in thermal tolerance for insects with differing biogeographic histories. **a,b**, Latitudinal variation in T_{max} (grey circles and line) and T_{min} (black circles and line) for range-expanding species (**a**), and non-range-expanding species (**b**). As range expansions produce latitudinally invariant T_{max} , thermal tolerance breadth increases with latitude in range-expanding lineages. However, for species with stable or declining geographic ranges, both T_{max} and T_{min} decline with latitude in a highly parallel manner.

levels of among-species variation ($F_{23,23} = 0.85$, $P = 0.69$); thus, it is unlikely that T_{max} is generally more physiologically or evolutionarily constrained than T_{min} .

Within species, thermal tolerance breadths increase with latitude only if the two assessed latitudes are both within the poleward portion of the species range, whereas thermal tolerance does not increase with latitude if assessed in the equatorial portion of the species range, where any phenotypic signatures of past or ongoing poleward range expansions on thermal tolerance breadths would have had the longest time to decay (Pillai's test statistic = 0.08, $F_{1,11} = 0.96$, $P = 0.02$; Supplementary Fig. 1A and Supplementary Table 3). Similarly, T_{max} is more likely to exhibit within-species latitudinal declines if assessed towards the species' equatorial range margin than towards the poleward range margin (Pillai's test statistic = 0.52, $F_{1,11} = 12.21$, $P = 0.005$; Supplementary Fig. 1B and Supplementary Table 3). Latitudinal variation in T_{min} , which is less affected by the species' biogeographic history (Fig. 1), is also unaffected by relative range position within species (Supplementary Table 3).

Discussion

Dynamic range expansions have powerful effects on biogeographic patterns in ecological trait variation¹⁹. The results of this study suggest that evolutionary dynamics attributable to range shifts occurring in the Holocene and increasingly commonly in the Anthropocene may underpin many oft-reported macrophysiological 'rules', such as increases in thermal tolerance breadth with latitude or range size, and latitudinal invariance of upper thermal tolerances. Among species recently or currently undergoing large-scale range expansions, I find that T_{min} responds readily to cooler temperatures at higher latitudes, whereas T_{max} exhibits no latitudinal change (Table 1 and Fig. 1a). This pattern may suggest mild evolutionary constraint on T_{max} , but the equal latitudinal and among-species variation in T_{min} and T_{max} in non-expanding lineages reported here (Table 2 and Fig. 1b) suggests otherwise.

Table 2 | Best-fit models for factors affecting thermal tolerances in range-expanding and non-range-expanding species.

| Thermal trait | Fixed effect | Estimate | s.e.m. | t | P | $R^2_{\text{fixed effects}}$ |
|------------------------------------|---------------------------|----------|--------|-------|---------|------------------------------|
| Range-expanding species | | | | | | |
| $T_{\text{max}}-T_{\text{min}}$ | Intercept | 32.52 | 20.39 | 4.47 | 0.0002 | 0.15 |
| | Latitude | 0.39 | 21.65 | 2.1 | 0.04 | |
| T_{max} | Intercept | 43.84 | 1.42 | 30.98 | <0.0001 | 0 |
| T_{min} | Intercept | 11.43 | 6.01 | 1.90 | 0.07 | 0.18 |
| | Latitude | -0.40 | 0.15 | -2.69 | 0.01 | |
| Non-range-expanding species | | | | | | |
| $T_{\text{max}}-T_{\text{min}}$ | Intercept | 60.43 | 3.92 | 15.44 | <0.0001 | 0.59 |
| | Hemisphere | -18.56 | 4.25 | -4.36 | 0.002 | |
| T_{max} | Intercept | 122.46 | 12.03 | 10.18 | <0.0001 | 0.78 |
| | Hemisphere | -13.88 | 2.17 | -6.40 | 0.002 | |
| | Latitude | -3.45 | 0.62 | -5.60 | <0.0001 | |
| | Latitude ² | 0.04 | 0.008 | 4.90 | 0.0001 | |
| T_{min} | Intercept | 64.24 | 15.93 | 4.03 | 0.001 | 0.60 |
| | Distance to poleward edge | 3.64 | 1.16 | 3.14 | 0.01 | |
| | Latitude | -3.4 | 0.76 | -4.45 | 0.0003 | |
| | Latitude ² | 0.04 | 0.009 | 4.21 | 0.0004 | |
| All species | | | | | | |
| $T_{\text{max}}-T_{\text{min}}$ | Intercept | 62.69 | 9.16 | 6.85 | <0.0001 | 0.23 |
| | Latitude | -0.49 | 0.21 | -2.35 | 0.02 | |
| | Range-expanding? | -30.03 | 11.37 | -2.64 | 0.01 | |
| | Latitude × expanding? | 0.95 | 0.29 | 3.12 | 0.002 | |
| T_{max} | Intercept | 68.22 | 5.31 | 12.84 | <0.0001 | 0.52 |
| | Hemisphere | -7.67 | 2.94 | -2.61 | 0.01 | |
| | Latitude | -0.54 | 0.11 | -4.99 | <0.0001 | |
| | Range-expanding? | -22.82 | 6.52 | -3.50 | 0.001 | |
| | Hemisphere × expanding? | 6.2 | 3.43 | 1.81 | 0.08 | |
| | Latitude × expanding? | 0.51 | 0.15 | 3.50 | 0.001 | |
| T_{min} | Intercept | -12.1 | 6.29 | -1.92 | 0.06 | 0.15 |
| | Distance to poleward edge | 4.92 | 2.03 | 2.42 | 0.03 | |
| | Hemisphere | 1.56 | 1.99 | 0.73 | 0.47 | |
| | Latitude | 0.15 | 0.13 | 1.15 | 0.26 | |
| | Range-expanding? | 16.64 | 7.51 | 2.22 | 0.04 | |
| | Latitude × expanding? | -0.53 | 0.20 | -2.68 | 0.01 | |

These patterns more likely emerge because of unequal changes in the strength of selection on T_{max} versus T_{min} as populations rapidly expand to cooler, poleward locales, such that increasing fitness costs of cold exposure during the expansion are greater than fitness costs of maintaining ancestral T_{max} at cooler, higher latitudes. Equally latitudinally variable T_{max} and T_{min} across non-range-expanding species also suggests that after expanding species become geographically stable and locally adapted, their values for T_{max} may then subsequently decline to values appropriate to their immediate surroundings, especially if maintenance of high values for T_{max} is energetically costly or in physiological trade-off with other traits²⁰. This interpretation is additionally supported by the result that within-species latitudinal increases in thermal tolerance breadths are more commonly observed over the poleward portions of their geographic ranges, where any ongoing or past poleward range expansions would have more recently occurred. Complementarily, I find that within-species latitudinal declines in T_{max} are more commonly observed when thermal tolerances were assessed towards the species' equatorial range margin, where species have had a greater amount of time to locally adapt following any historic poleward expansions.

The role of range expansions in shaping latitudinal variation in thermal tolerances can help explain previous findings that, not only do high-latitude species tend to have unusually high values of T_{max} for their environment (that is, large values of WT),

but their optimal body temperatures (T_{opt}) are also higher than temperatures commonly found in their current environment³. Thus, if T_{max} and T_{opt} are evolutionarily coupled, populations that have recently expanded to higher latitudes may be much more limited to ancestrally favourable thermal microclimates in their new set of habitats, and these lineages may also be limited by the need to behaviourally thermoregulate to maintain optimally high body temperatures¹² than are species that have had a longer period of time to adapt to life at high latitudes.

One question that emerges from these results is whether the ability to adopt broad thermal tolerances at high latitudes is a cause or a consequence of contemporary range expansions. The capacity to undergo rapid, climate-mediated or invasive range expansions is often underpinned by favourable life history and dispersal traits^{21,22}, although effects of T_{min} evolvability on expansion potential have rarely been considered. Ultimately, multiple, synergistic trait shifts probably underpin most rapid range expansion or invasions²³.

Crucially, the results presented here suggest that high warming tolerances may not be properties of high-latitude species per se, but only of high-latitude species that are already undergoing climate-mediated range expansions or biological invasions. Such species are not commonly under conservation watch or at risk of decline under future warming effects. Thus, conservation priorities based on the concept of latitudinal variation in warming tolerance may be flawed. These results also suggest that any predictions of species' responses

to future climate change must incorporate the (often pronounced) effects of climate change or anthropogenic habitat modification that have already occurred. Unfortunately, the results of this study also imply that non-range-expanding species, including insular and endemic species that are often the targets of conservation efforts, are unlikely to be physiologically shielded from warming climates at high latitudes.

Methods

Methods and any associated references are available in the [online version of the paper](#).

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Additional information

Supplementary information is available in the [online version of the paper](#). Reprints and permissions information is available online at www.nature.com/reprints.

Competing financial interests

The author declares no competing financial interests.

Methods

Latitudinal variation in thermal tolerances among species. For the among-species comparison, a literature search was performed to identify insect species for which a measure of T_{\min} and T_{\max} (see below) had been estimated at a single time and place, and for which geographic range information was available, including both the latitudinal extent of the species range and whether the species was currently or recently range expanding (Table 1). Forty-eight species were identified, spanning 1.7°–55.7° absolute latitude, and details on each species are included in Supplementary Table 1.

Range expansion status for each species was diagnosed on the basis of historical records and/or population genetic data and historic niche reconstructions (references in Supplementary Table 1). The hypothesis tested in this study is that range expansions result in latitudinally invariant values of T_{\max} and latitudinally increasing thermal tolerance breadths because as species move polewards, they bring their ancestral values of T_{\max} to higher latitudes, while their T_{\min} adapts to cooler climates at higher latitudes. Thus, to fit with the mechanisms implied in this hypothesis (described further in the main text), a diagnosed range expansion needed to have occurred relatively recently, that is, within the Holocene or Anthropocene, so that ancestral thermal tolerances could be reasonably expected to have been retained in the recently colonized region. The range expansion also must have covered significant latitudinal distance (more than a few degrees latitude), so that the recent latitudinal movement of a species' ancestral T_{\max} value covered a great enough distance to have a measurable effect on global, latitudinal patterns among species in T_{\max} . Species that met these two criteria are listed as range expanders in Supplementary Table 1.

Similarly, it was important to diagnose range stasis, to compare range expanders with species that have not undergone recent and significant range expansions. What is critical when establishing a lineage as non-range-expanding is not whether its range limits have remained utterly static over millennia, a criterion that no species can fulfil, but instead it is important to establish that the species is unlikely to have expanded far enough and recently enough to have transferred its established upper thermal tolerances to a new latitudinal position. Accepted evidence of range stasis for species listed in Supplementary Table 1 included: evidence of *in situ* diversification (speciation) within a restricted, geographic area where the species resides as an endemic alongside its nearest relatives (and this evidence should be combined with evidence of local glacial refugia, if the species has persisted at high latitudes), historical niche reconstructions, often combined with population genetic evidence, demonstrating demographic and geographic stasis since before the Last Glacial Maximum, endemic status combined with evidence of strong local adaptation to a narrowly geographically restricted habitat (examples include: antifreeze proteins, specialization on an endemic host plant, adaptations to extreme desert environments), or patchily distributed populations, often in decline, with a geographic distribution strongly indicative of relict status.

In all cases where species were categorized as non-range-expanding, there was no evidence of recent spread (no conflicting evidence was found). All species in the data set categorized as range-expanding have undergone recent (Holocene or Anthropocene), documented poleward expansions resulting in changes of >10° latitude (Supplementary Table 1 column: Latitudinal extent of documented portion of expansion), with the exception of *Merizodus soledadinus*, which has undergone a documented poleward expansion of only ~3° latitude in the Anthropocene. It is unknown whether this distance is significantly large to contribute to latitudinal invariance of T_{\max} . However, given that this species is known to be an aggressive invader (listed in the Global Invasive Species Database www.issg.org, and expanding at a rate of 3 km yr⁻¹ in the invaded region²⁴), and its pre-1900s expansion history is unknown, I chose to include this species as a range expander in the analysis. Removal of this species does not alter the reported results.

Upper and lower thermal tolerances are abbreviated here as T_{\min} and T_{\max} . In some included studies, thermal limits were estimated as critical thermal limits (T_{crit} in Supplementary Table 1), representing the temperature at which individuals lose critical motor function, whereas other studies estimated lethal temperatures (temperatures at which 50% or 100% of subjects died). The endpoint used (loss of function versus death) can affect the reported values, because lethal temperatures are usually more extreme than critical temperatures. However, differences between critical and lethal temperatures are not always large, and these values are usually highly positively correlated within species¹¹. Furthermore, other aspects of experimental non-standardization such as variation in ramping protocol can have even greater effects on reported thermal limits²⁵. In previous meta-analyses of latitudinal variation in thermal tolerances, critical and lethal temperatures have often been lumped together^{8,11}, and a covariate for the endpoint used may sometimes be included¹². Where these measures have not been lumped together, they each show similar patterns of latitudinal variation⁸, and conclusions reached are similar regardless of whether critical limits are considered together or separately from lethal limits^{8,11}. Here, to deal with this issue, I first examined whether the measure for upper and lower thermal tolerances (critical versus lethal) was significantly correlated with latitude or with species' range expansion status.

None of these relationships was significant. I also examined whether including a covariate for critical/lethal affected the reported models, and found that the results and conclusions remain fundamentally unchanged. Furthermore, despite the fact that thermal tolerance measurements are not methodologically well standardized among studies, models reported here explain a large proportion of variation in T_{\min} , T_{\max} and $(T_{\max} - T_{\min})$ ($R^2_{\text{fixed+random effects}} = 0.81 \pm 0.14$ s.d., for models reported in Table 2). The substantial proportion of variation explained suggests that differences in experimental approach do not have large effects on latitudinal variation in thermal phenotypes, relative to the effect sizes of biogeographic variables. This is reassuring and supports the validity of thermal tolerance meta-analysis using existing data from a variety of sources.

Using this data set, I used linear mixed models in the lme4/lmerTest package for R v.3.0.2 (refs 26–28) to explain variation in T_{\min} , T_{\max} and $(T_{\max} - T_{\min})$. For each of these response variables, I included explanatory fixed effects of: latitude (at which thermal tolerance was measured), latitude², the species' latitudinal range extent, the relative range position at which thermal tolerance was measured (proportional distance to the species' poleward range margin), and the hemisphere in which thermal tolerance was measured. Each of these factors was also considered in interaction with the species range expansion status (yes/no), to identify differences in the effects of latitude or range size on thermal tolerances, depending on whether species are undergoing or have recently undergone range expansions. Similar models were also run separately for range-expanding versus non-range-expanding lineages. For the full analysis and in range-expanding lineages, I also evaluated whether the type of range expansion (climate-mediated expansion versus invasion) impacted latitudinal variation in thermal tolerance. For the full analysis and in non-range-expanding lineages, I examined effects of insularity and endemism status. As a suitably resolved insect phylogeny is not available at present, phylogenetic effects on thermal tolerances were controlled by including order and family as random effects, following refs 6,12. Mixed-effects model R^2 was estimated using the method of ref. 29, implemented in the rsquared.glm package for R (ref. 30), and model selection was made on the basis of AICc, implemented in the AICcmodavg package for R (ref. 31).

Latitudinal variation in thermal tolerances within species. For within-species comparisons, I identified from a previous meta-analysis⁶ insect species for which thermal tolerances had been measured at multiple latitudes (Supplementary Table 2), and I conducted a Type III repeated-measures multivariate analysis of variance³² to assess effects of latitude, hemisphere, taxonomy and relative range position on within-species variation in thermal tolerances (Supplementary Table 3). Relative range position was broadly categorized using occurrence data and atlas information available from www.gbif.org, and was considered equatorial if any of the latitudes at which thermal tolerance was measured fell within the equatorial portion of the species latitudinal range (where the equatorial portion of the range is defined as the extent between the range's latitudinal midpoint and the location within the species' distribution that is closest to the Equator). If the two measurement locations were both located in the poleward portion of the species range, the relative range position was considered to be poleward.

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