

## Supplementary Information

### Global variation in the thermal tolerances of plants

Lesley T. Lancaster and Aelys M. Humphreys

*Proceedings of the National Academy of Sciences, USA (2020)*

#### Contents:

*i. Taxonomic and spatial patterns in plant cold and heat tolerances*

**Table S1:** Representation of species in the dataset by taxonomic group

**Figure S1:** Distribution of thermal tolerances among families

*ii. Effect of growth form on thermal tolerances*

**Figure S2:** Distribution of thermal tolerances among growth forms, with trees and shrubs plotted separately

*iii. Effect of experimental approach on thermal tolerances*

*a.* Experimental approaches to estimating  $T_{min}$  and  $T_{max}$

*b.* Experimental approaches to hardening

**Figure S3:**  $T_{max}$  and  $T_{min}$  values plotted according to experimental approach

*iv. Plant thermal tolerance strategies (and in comparison to animals)*

*v. Whole-plant and leaf-trait syndromes and potential correlations with  $T_{min}$  and  $T_{max}$*

*a.* Energetic and physiological trade-offs, ecological and life history strategies

*b.* Precipitation and water availability

*c.* Conclusions

*vi. Fitting of phylogenetic models*

*vii. Phylogenetic supplementary results*

**Table S2.** Fit of phylogenetic models

**Table S3.** Parameter estimates under OU models

**Figure S4.** Phylogenetic distribution of measured heat and cold tolerance limits

*viii. Testing for type I errors in fitting OU models*

**Figure S5.** Fit of BM and OU models to data simulated under a BM

process

*ix. Spatial autocorrelation of thermal tolerances*

**Figure S6.** Spatial autocorrelation in heat and cold tolerance

*x. Additional latitudinal patterns*

a. Frequentist results

b. Latitudinal patterns in the context of climate extremes

**Figure S7.** Tmin and Tmax, and local extreme temperatures, across latitudes

*xi. Model comparisons (Global variation in thermal tolerances: Intrinsic, biogeographic, and environmental drivers)*

**Table S4.** Variance explained under full and reduced Bayesian mixed models explaining heat and cold tolerance

**Figure S8.** Gradients in heat and cold tolerance related to environmental variables

*xii. Our results in the context of previous studies that have examined global patterns in thermal tolerance*

**Table S5.** Overview of synthesis studies of global variation in thermal tolerances with latitude

*xiii. Supplementary references*

### *i. Taxonomic and spatial patterns in cold and heat tolerances*

The distribution of thermal tolerance records across major taxonomic groups is depicted in Table S1. For angiosperms, records are distributed across  $n=132$  families, which is fewer than half of all described. Despite overall broad taxonomic and geographic coverage (Figure S1), our data capture only a small fraction of total plant diversity, and several major gaps were identified. In particular, we identified the worst gaps for Africa, Asia and the Southern Hemisphere, especially for non-seed plants. Moreover, cold tolerance estimates for angiosperms and heat tolerance estimates for gymnosperms were underrepresented— thus there could be a research bias toward measuring heat tolerance for relatively heat tolerant (e.g. *Aloë*) and cold tolerance for relatively cold tolerant (e.g. Pinaceae) taxa. We note that the higher proportion of data we found for gymnosperms is all for conifers, with no data for cycads or Gnetales and only a single estimate for *Ginkgo* (Figure S1). These taxa are known to have high extinction risk (1), but without knowledge about their inherent thermal tolerances our ability to predict to what extent this risk is exacerbated by ongoing climate change is limited. Nonetheless, we greatly expand on previously compiled data on plant thermal tolerances (e.g., (2)), and our sampling is higher than other equivalent studies in animals (Table S5). Filling additional gaps in available thermal tolerance data for plants will be an important task for future research. Crucially, future studies should focus on the extent to which hardening (acclimation) increases tolerance of thermal extremes and how, and how often, hardening ability has evolved across land plants.

Such knowledge gaps notwithstanding, our data suggest that ferns, lycophytes and bryophytes are much less tolerant of thermal extremes than seed plants, although only few studies reported to have measured these in their hardened state (some for ferns, which were not much different from non-hardened ferns; Figures 1, S1). Our data indicate the lowest (best) cold tolerances overall for Pinaceae (Figure S1), followed by the birch and willow families (Betulaceae and Salicaceae; all in the hardened state). These families are abundant at high altitudes and latitudes. Extreme heat tolerances have been measured for drought-adapted taxa such as Cactaceae, *Aloë* (Asparagaceae), Amaranthaceae and Zygophyllaceae, and other tropical families including Moraceae (figs) and Phyllanthaceae (Figure S1).

**Table S1:** Representation of species in the dataset by taxonomic group (and as a percentage of total diversity).

	<u><i>Tmin</i></u>	<u><i>Tmax</i></u>
Total observations:	769	966
Total species:	510 (0.15%)	691 (0.21%)
Gymnosperms	62 (5.8%)	25 (2.3%)
Angiosperms	327 (0.11%)	614 (0.21%)
Ferns	93 (0.88%)	27 (0.26%)
Lycophytes	4 (0.31%)	1 (0.08%)
Bryophytes	24 (0.10%)	24 (0.10%)

**Figure S1.** (following pages) Distribution of thermal tolerances among families, separately for (A) angiosperms, (B) gymnosperms, (C) ferns and horsetails, and (D) lycophytes, liverworts, and mosses. Minimum thermal tolerances (*Tmin*, cold tolerance) are plotted in blues and maximum thermal tolerances (*Tmax*, heat tolerance) in reds; measurements on hardened plants are shown in dark hues and non-hardened (including those with no information on hardening status) in light hues. Vertical dashed lines denote the standard deviation across all data for each of heat and cold tolerance (n=769 for *Tmin*, n=966 for *Tmax*).

Figure S1A:

### Thermal tolerance of angiosperms

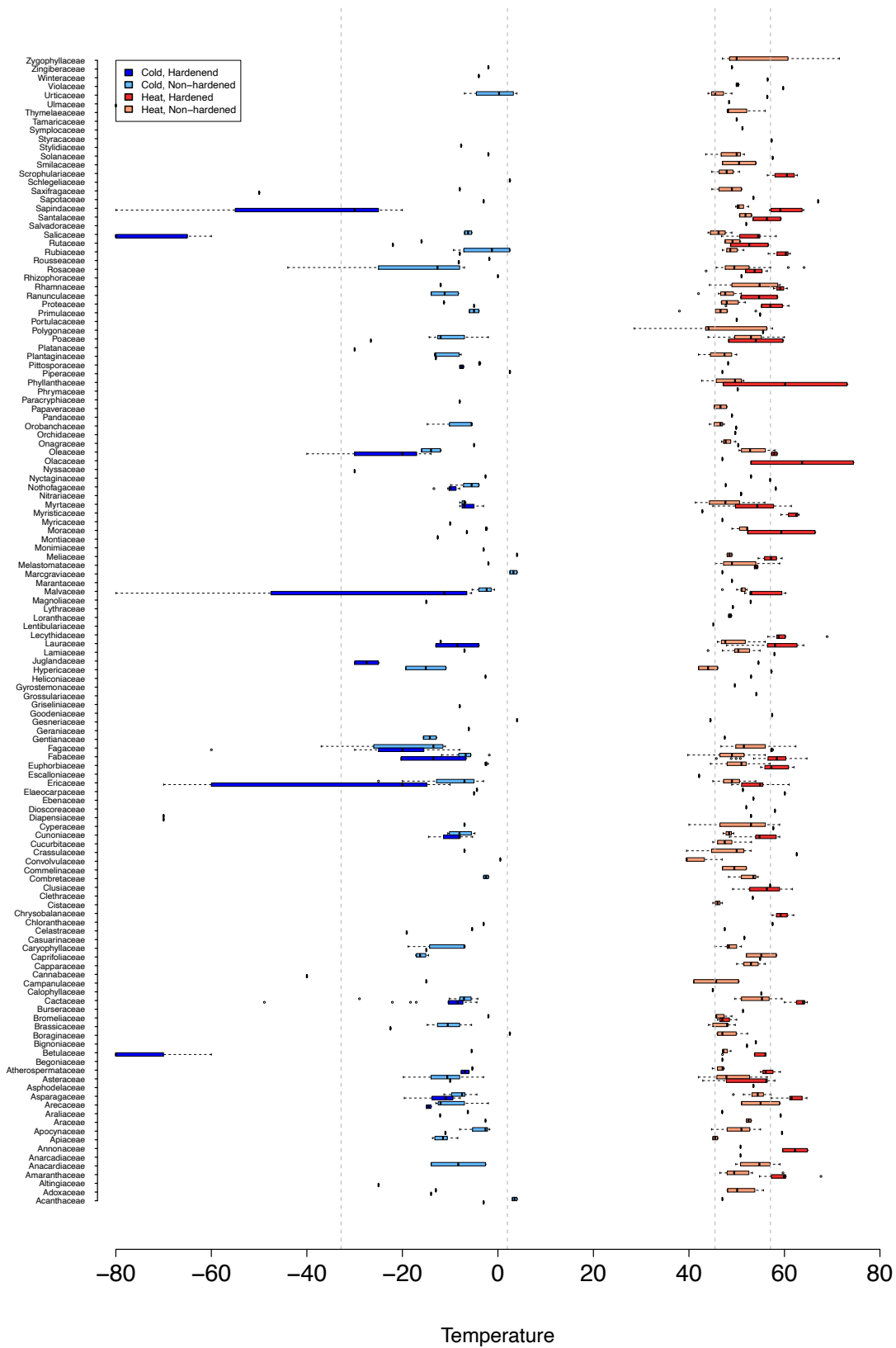


Figure S1B:

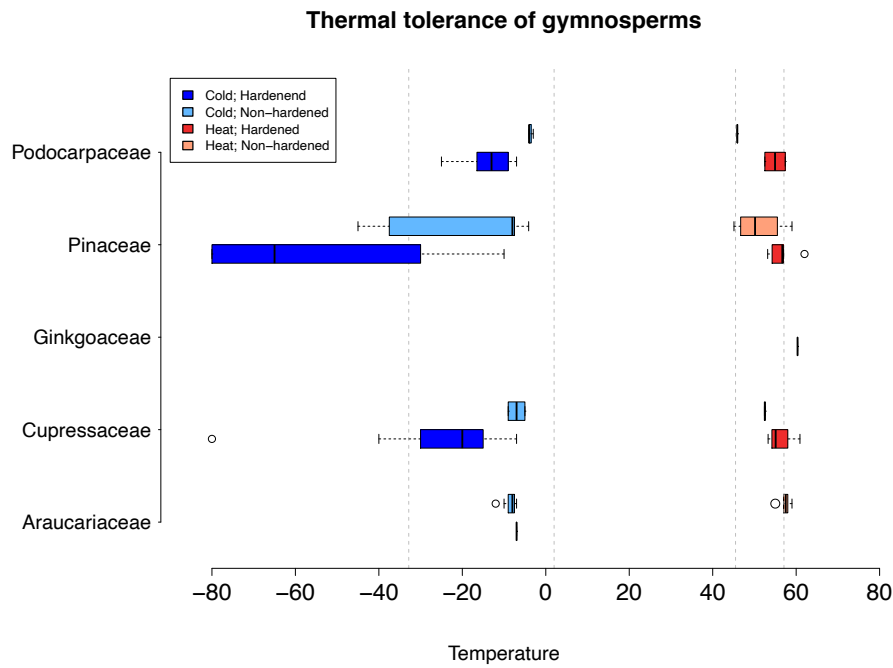


Figure S1C:

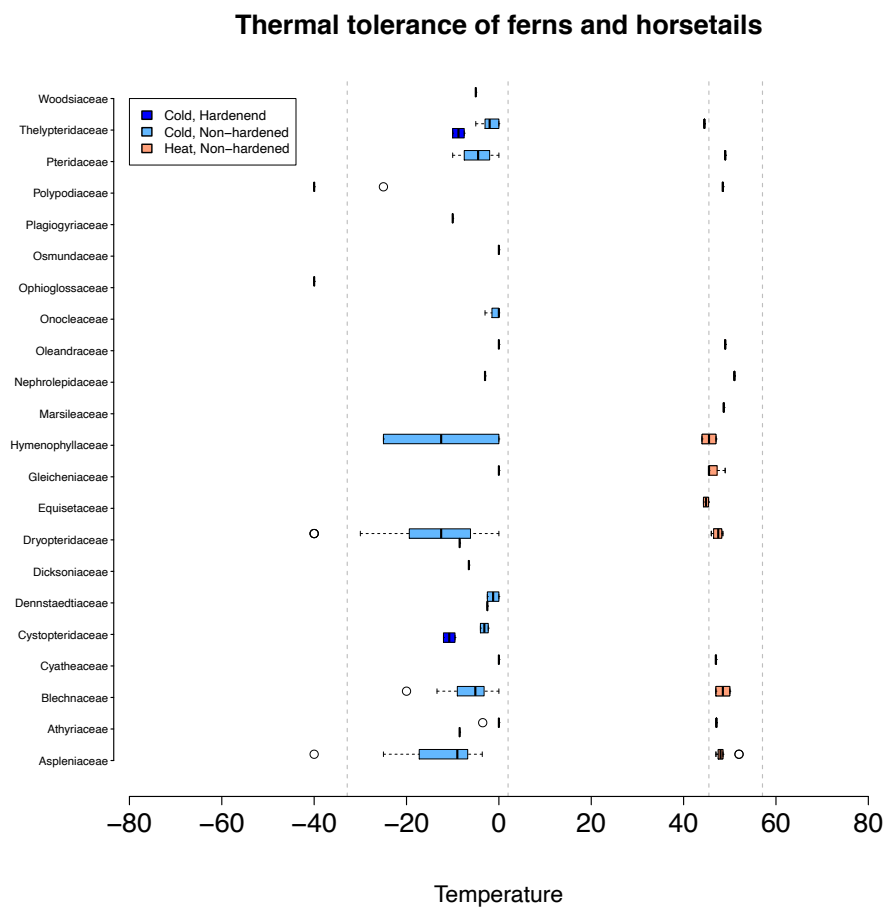
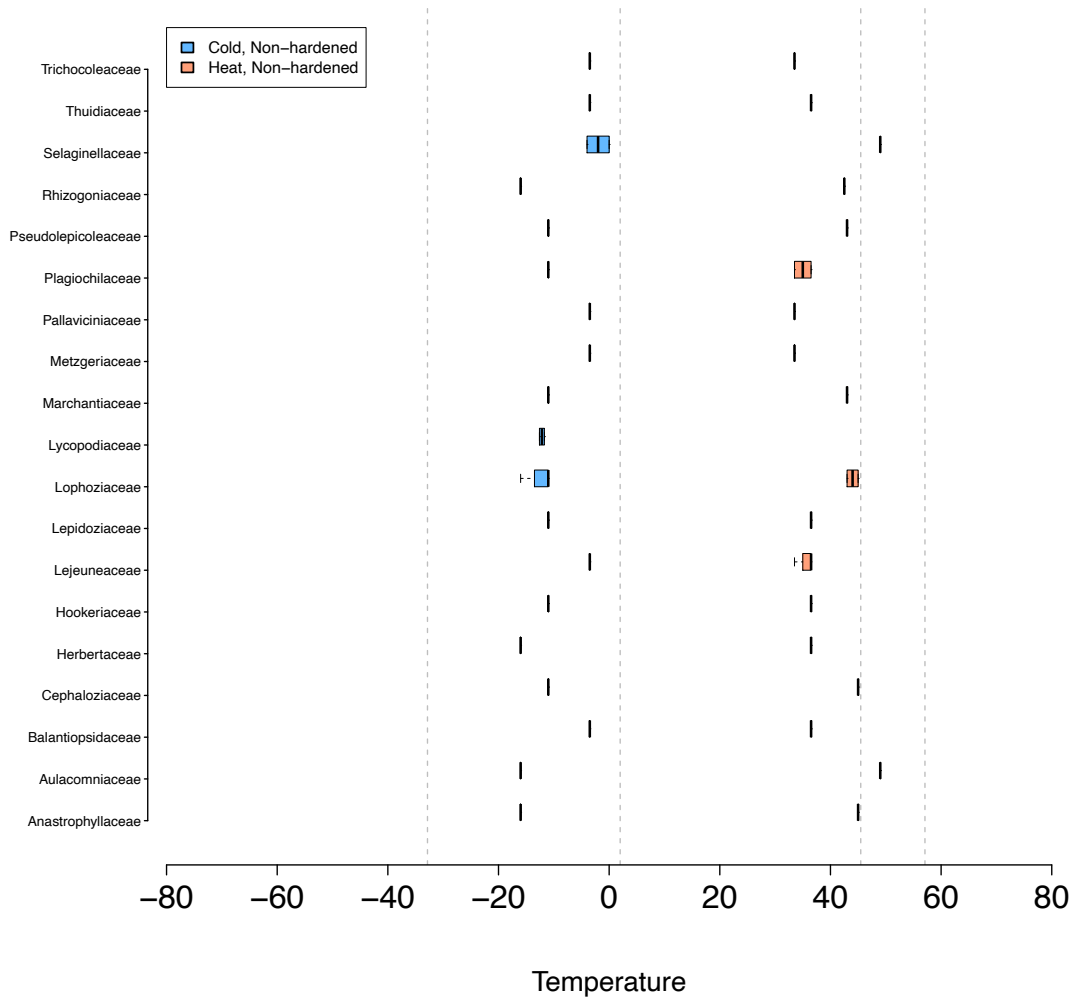


Figure S1D:

### Thermal tolerance of lycophytes, liverworts and mosses



## *ii. Effect of growth form on thermal tolerances*

Among growth form categories, the database includes thermal tolerance records for herbaceous annuals (n=39; all of which are angiosperms), herbaceous perennials (n=420; including herbaceous angiosperms, ferns, horsetails and lycophytes; and all monocots except palms [Arecaceae]), woody perennials (n=1167; including shrubs, n=537, trees, n=630 and palms), cushion plants (n=65; all of which are angiosperms) and bryophytes (n=49; for liverworts and true mosses).

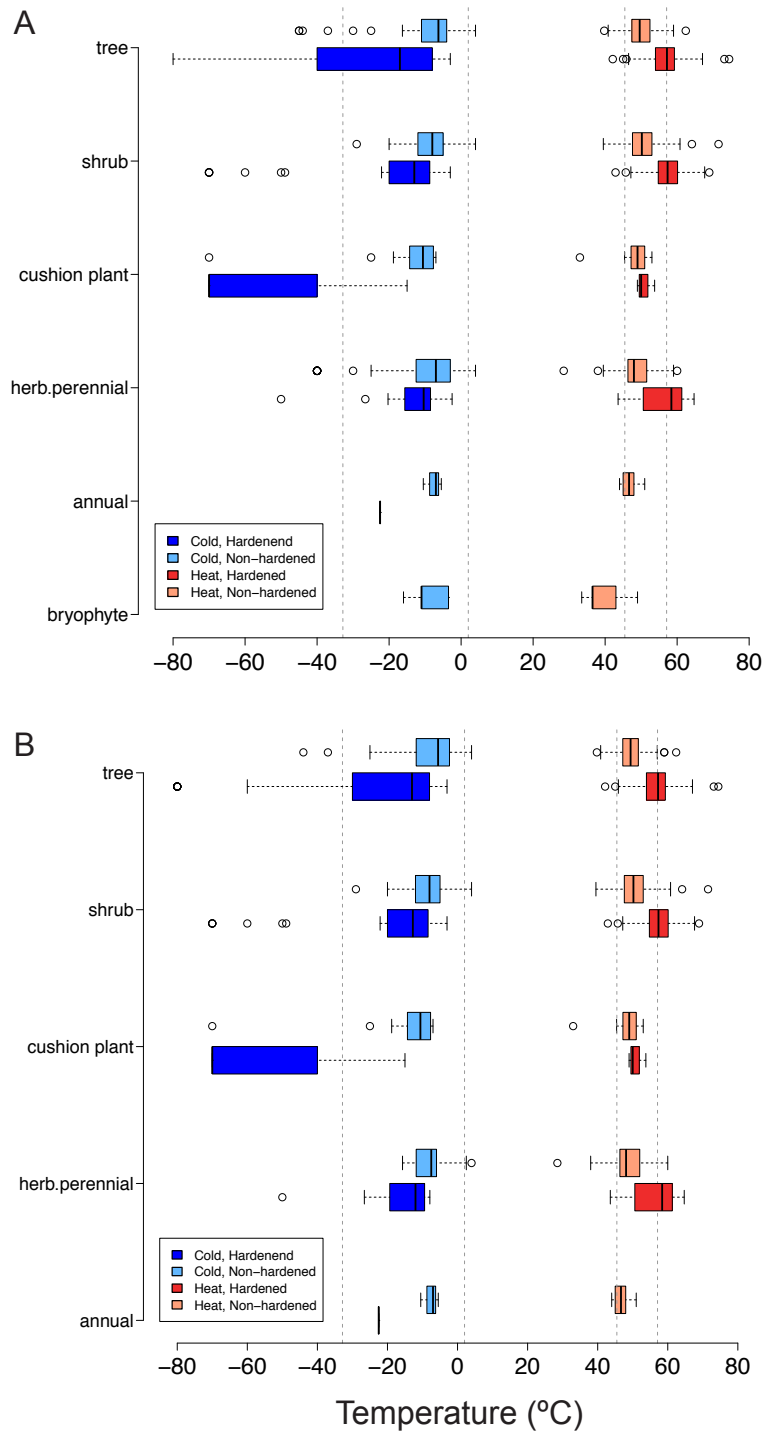
Cushion plants are the most cold tolerant overall, followed by woody perennials (Figure 1d, main text). Of the woody perennials, hardened trees appear more cold tolerant than shrubs (Figure S2A). This is surprising, because taller plants (trees) are generally considered less cold tolerant than shorter plants, a growth form difference that is thought to lead to the establishment of tree lines (e.g. (3)), and expressed on a global scale as a latitudinal gradient in plant height (decreasing height with increasing latitude), in part attributed to a shift in the proportions of trees, shrubs and herbs at different latitudes (4, 5). However, most of the difference in cold tolerance between trees and shrubs in our data is likely driven by taxonomic differences related to extreme cold resistance of certain trees, especially conifers (see Figure S1). Among angiosperms only there is less of a difference in cold tolerance between trees and shrubs (Figure S2B).

Herbaceous perennials are the most heat tolerant but, overall, there is less variation among growth forms for heat tolerance compared to cold tolerance (figures 1D, S2). Bryophytes are the most sensitive to both high and low temperatures, with no measurements in the hardened state being reported. Most thermal tolerance data for bryophytes are for liverworts and these are known to inhabit extreme environments, such as thermal springs; the lack of any extreme measures for these plants is therefore surprising. Clearly, many important gaps exist in the available plant thermal tolerance data.

Despite the variation described above, growth form explained only a fraction of the global variation in thermal tolerances of land plants (Figure 3, main article).



**Figure S2.** Distribution of thermal tolerances among growth forms, with trees and shrubs plotted separately for (A) all land plants, and (B) angiosperms only.



### *iii. Effect of experimental approach on thermal tolerances*

#### (a) Experimental approaches to estimating T<sub>min</sub> and T<sub>max</sub>

The included studies used a variety of measures to test physiological tolerances of plant tissues to temperature extremes. For T<sub>max</sub>, this was typically accomplished by pursuing one of the following measurements: T<sub>crit</sub>, the temperature at which photosynthetic and respiratory machinery begin to sustain damage (6); T<sub>max</sub>, the maximum temperature at which photosynthetic and respiratory machinery can function; and lethal temperatures LT (0,50,100 % of tissue or population), temperatures at which the leaf tissue begins to die, typically assessed via visual inspection of plant tissue, electrolyte leakage (indicating levels of membrane disruption), or stain uptake (i.e., by still living cells). For T<sub>min</sub>, measures included: Freezing resistance (FR; the lowest temperature at which the plant tissue resisted freezing, i.e., via upregulation of sugars to reduce freezing points or anti-nucleating agents to promote supercooling); Freezing tolerance (FT; the lowest temperature at which plant tissue could tolerate intracellular ice crystallization (i.e., via adaptive cellular dehydration; (7))); and LT (0,50,100; assessed as described above). While the measure used can affect the resulting T<sub>max</sub> or T<sub>min</sub> estimate, these values tend to be strongly positively correlated with each other within individuals or populations (6, 8), or reflect alternative physiological mechanisms that may vary across species (e.g., freezing resistance vs. tolerance; (7)).

In general, as expected, T<sub>max</sub> measures which record more advanced states of tissue damage (i.e., LT<sub>100</sub>) were recorded at more extreme temperatures than those measures which record more mild disruption to physiological processes or adaptive response to temperature extremes (i.e., FR). This effect was more pronounced for heat tolerance than for cold tolerance, and the effect of experimental approach was also affected by whether the plant was observed in the hardened state (Figure S3A,C). Nonetheless, the tolerance measure employed to assess physiological limits explained very little variation in T<sub>min</sub> and T<sub>max</sub> overall, in comparison to the other, underpinning phylogenetic, spatial, and local environmental patterns and processes (Figure 3, main text).

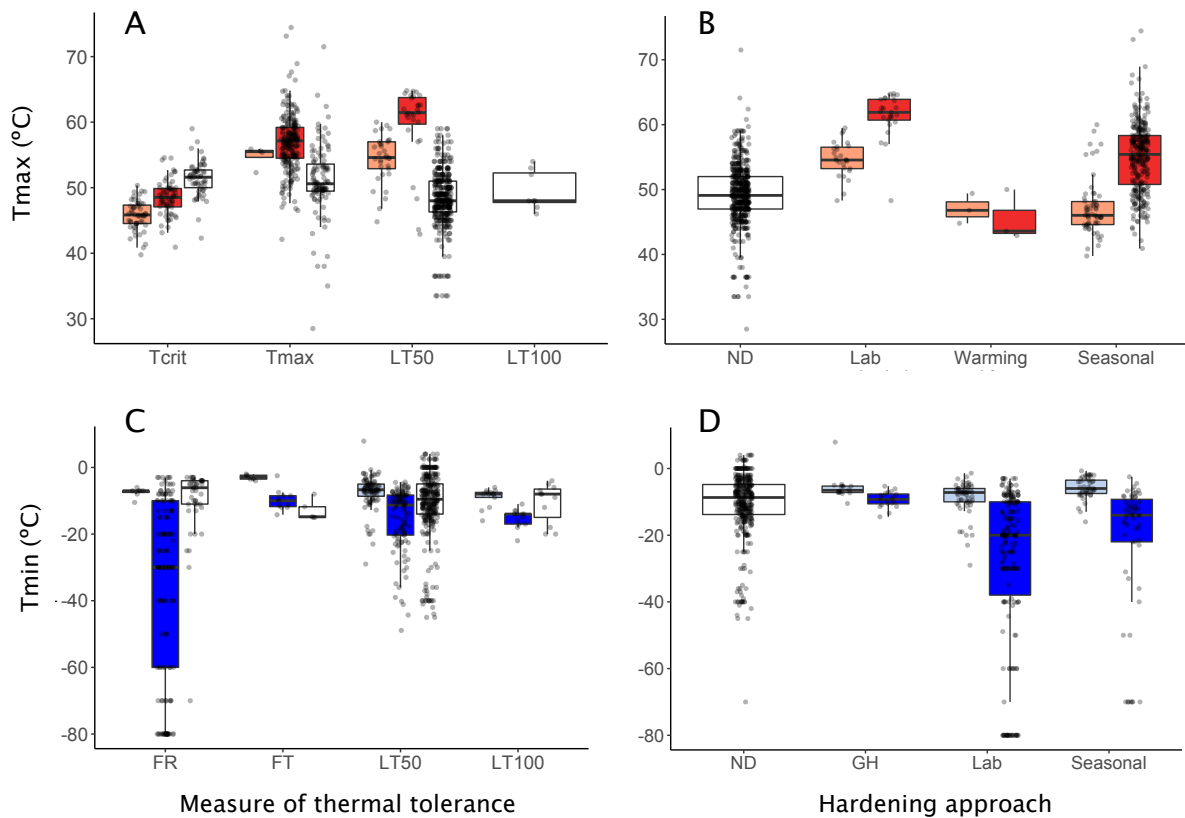
## (b) Experimental approaches to hardening

Where reported, acclimation (or de-acclimation) of plant subjects was typically either induced under laboratory (Lab;  $n= 51$  heat,  $n= 249$  cold) or greenhouse (GH;  $n=36$  cold de-acclimation) conditions, or reported as variation in thermal tolerances under salient variation in seasonal climatic conditions in the field ( $n= 356$  heat,  $n= 106$  cold). A very small minority of two studies ( $n=6$  records overall) used artificial warming in the field to induce hardening, although this approach was rarely effective (Figure S3, Dataset S1 references). Where hardening status was not explicitly considered, measures were typically, but not always, made during a time of year that would appear reasonable (i.e., assessing heat tolerance from spring to autumn, and cold tolerance from autumn to spring). However, without explicit knowledge of the particular regions, yearly variation, and study system under consideration in each case, we conservatively avoided making assumptions about hardening status in cases where it was not assessed in the primary studies. Moreover, the particular temperatures chosen for laboratory acclimation varied among studies, and in each case reflected the authors' natural history knowledge of their study species and region (see Dataset S1 references).

Laboratory acclimation was associated with overall higher values of  $T_{max}$  and lower values of  $T_{min}$  than seasonal acclimation in the wild, and this was again more pronounced for heat than for cold tolerance (Figure S3B,D). This may occur because laboratory acclimation reduces the number of additional stressors imposed by natural environments (i.e., drought, herbivory, or nutrient stress), or involves less realistic thermal regimes. Alternatively, differences in age between laboratory and field individuals may in part explain such variation.

Because acclimation regime (i.e., laboratory vs. field) could only be assessed on the individuals for which hardening status was known, inclusion of this factor in our reported analyses of  $T_{min}$  and  $T_{max}$  resulted in wider confidence intervals and longer time to model convergence. Nonetheless, inclusion of this additional random term did not affect the relative contribution of other variables in the model, nor the magnitude and significance of main effects. Moreover, the effect of hardening approach per se on  $T_{min}$  or  $T_{max}$ , in comparison to other factors in the model, was very low (mean proportion of variance in  $T_{min}$  which was due to hardening approach = 0.02 [0.0006 – 0.07 HPD];  $T_{max}$ , mean proportion of variance due to hardening approach = 0.07 [0.002 – 0.28 HPD]).

**Figure S3:** Tmax (A,B) and Tmin (C,D) values plotted according to experimental approach to measuring thermal tolerance (A,C) and inducing hardening (B,D). Darker colors: hardened individuals; lighter colors: non-hardened individuals. White: individuals lacking explicit information on hardening status.



#### *iv. Plant thermal tolerance strategies (and in comparison to animals)*

Plants have evolved a range of architectural, behavioral, phenological and physiological adaptations to withstand the stress imposed by both high and low temperatures (e.g. (8–11)). In particular, plant adaptations act to regulate photosynthetic and respiratory metabolism and reproduction and minimize any structural damage that could be lethal. In fact, plants and animals share a number of ancient cellular structural and physiological thermal stress protection mechanisms, but their evolutionary divergence has led to completely different regulation and coordination of these mechanisms (12).

The highly modular development of plants allows for short-term physiological and morphological adjustments in response to prevailing abiotic conditions, including dormancy, leaf taxis behavior (13), changes in overall investments into leaf development (reflecting quality and quantity), shedding leaves and shoots, leaf orientation and stomatal closure behaviors, and phenological regulation of development and reproduction (9–11, 14, 15).

Further temperature adaptations in plants include: architectural ones, such as hairiness to protect sensitive organs (e.g. buds or petals) against thermal extremes or minimize water loss by evapotranspiration, and the cushion habit, which provides insulation against extreme cold; physiological adaptations to heat, such as production of heat shock proteins to stabilize tissues (e.g. membranes) and succulence and photosynthetic changes to minimize water loss; physiological adaptations to cold, such as supercooling and restriction of ice formation (7); and, finally, a variety of leaf traits have been implicated in thermal adaptation and thermoregulation (see below).

Thus while plants lack the more complex behaviors of animals, they can compensate by a variety of morphological and physiological responses generally unavailable to animals. In addition, stressed plants must protect complex photosynthetic and respiratory metabolic pathways, with photosynthetic pathways being more thermally sensitive of the two (12). Despite this, plants can tolerate both extreme cold and heat, and, due to their advanced physiological and morphological response capabilities, exhibit thermal acclimation beyond levels typically sustainable by animals (16).

Our macrophysiological results for plants add generality to established rules of thermal macrophysiology, and suggest that thermal physiological or behavioural processes unique to animals are not required to generate the expected global patterns.

#### *v. Whole-plant and leaf-trait syndromes and potential correlations with $T_{min}$ and $T_{max}$*

Several plant traits show a latitudinal gradient and correlate broadly with temperature and each other, e.g. plant height, wood density and several leaf and life history traits (e.g. (4, 17–20) and many references therein). Plant height (and other size-related traits) and leaf traits represent two different major axes of multidimensional trait space (17) that often covary with

both temperature and precipitation (5, 21, 22); we might therefore expect these traits to correlate with the thermal traits analyzed here as well. However, predicting the exact nature of such a relationship is not straightforward, due to the different ways trade-offs among these trait syndromes might be resolved, ecology and life history, and interactions with precipitation. Each of these is discussed below.

(a) Energetic and physiological trade-offs, ecological and life history strategies

Energetic and physiological trade-offs among different whole-plant and leaf traits are likely to limit the convergence of all plants on any one particular trait strategy for coping with thermal stress; for instance, trade-offs among traits that promote thermal stability vs. photosynthetic ability allow plants to alternatively resolve thermal adaptations along a fast-slow continuum (23, 24), depending on whether growth, size, productivity, or fitness is strategically maximized by the plant species (25). Our dataset captures only those traits that maximize survival at acutely stressful temperatures, which may differ from the leaf traits that promote growth, size, or reproductive output under different climate regimes. Accordingly, O'Sullivan et al. (8) found no correlation between the heat tolerance of leaves and other leaf traits. Although we did not explicitly consider leaf characteristics in our analysis, we observed the greatest thermal tolerance for diverse taxa, exhibiting highly divergent leaf characteristics and habitat affinities (Figure S1, SI sections *i,ii*).

Latitudinal change in whole-plant traits such as height itself is, at least partly, attributed to shifting proportions of trees, shrubs and herbs with latitude (4). Such variation in whole-plant traits is likely to reflect selection on growth or reproductive rates, rather than acute stress tolerance. However, taller plants also have wider vessels more prone to embolism; thus smaller stature in plants is also a freezing and drought resistance strategy (5). In our data, growth form explained only a fraction of the overall global variation in thermal tolerance (Figure 3). Previous studies have also found that stand and canopy structure exert a strong effect on canopy temperature (13) and productivity, where the effect of stand characteristics on productivity outweighed effects of climate (26).

Different ecological strategies may also be expected to alter some trait-climate relationships. Deciduous and herbaceous plants tend to increase in prevalence in cool and dry areas (27, 28), enduring the unfavorable season in a (semi)dormant state after shedding

their leaves or senescing all above-ground tissue. It has therefore been suggested that variation in those traits themselves account for other trait-climate correlations (e.g.(19)). Indeed, Wright et al. (21) found the tightest relationships between leaf sizes and growing season conditions for woody as opposed to herbaceous plants, and for woody species the relationship was stronger for evergreen than deciduous leaves. We did not observe a difference in thermal tolerance between herbaceous and woody flowering plants (across all land plants trees appear more cold tolerant than herbaceous plants [Figure 1], but this is largely a taxon effect, driven by several highly tolerant conifers, not growth form differences *per se*; Figure S2). Furthermore, the flowering plant families Salicaceae and Betulaceae are deciduous trees and shrubs that grow in high altitude and latitude environments, but they were still found to be among the most cold tolerant of plants, withstanding at least the same level of freezing as evergreen conifers and cushion plants (Figures S1,S2). Similarly, O’Sullivan et al. (8) found no difference in the heat tolerance of deciduous and evergreen leaves. The explanation for a lack of effect of deciduousness on leaf thermal tolerance might be that high altitude and latitude plants can be exposed to freezing temperatures throughout the growing season. Consistently with this, Wright et al. (21) found nighttime temperatures to be the most important determinant of leaf sizes in cold habitats, i.e. the coldest temperatures the leaves are exposed to during the growing season.

Finally, we might expect annual plants to be less tolerant of thermal extremes, adopting the stress-avoidance strategy of spending the harsh season as seed. The annuals included in our analyses certainly appeared to be among the least tolerant of both high and low thermal extremes; however, our dataset included too few annuals to assess this properly (n=39, almost all in their non-hardened state; Figure 1).

#### (b) Precipitation and water availability

Alternative leaf and whole-plant thermal tolerance strategies may vary according to moisture gradients (5, 21), both because moisture can increase freezing damage, and because some thermal strategies are prohibitively water-intensive under drought conditions (e.g., thermoregulation via transpirational water loss). We did not find any effect of precipitation variables on thermal tolerances, either alone or after accounting for effects of temperature, potentially because the moist-adapted vs. dry-adapted species in our dataset deploy different

strategies to achieve similar levels of thermal stress protection. For example, several of the most heat tolerant species belonged to generally drought-adapted flowering plant families, such as Amaranthaceae, Asparagaceae (*Alöe*) and Cactaceae, however some families inhabiting primarily the wet tropics (e.g. figs, Moraceae) exhibited similar heat tolerances (Figure S1). We might expect traits associated with aridity, such as C4 and CAM photosynthesis or succulence, to correlate with heat tolerance but we did not include such information here. Another reason we found no effect of precipitation might be because rainfall is only one factor affecting the amount of water available to plants, with other important factors being vegetation cover, soil depth and type, access to groundwater, temperature (evapotranspiration, which is also affected by vegetation and canopy cover and height) and the root systems themselves.

Plants adapted to both high and low thermal extremes are often adapted to physiological drought because of high rates of evapotranspiration in hot environments and low availability of (liquid) water in freezing ones, and both high and low temperatures will be handled differently at different levels of water availability. However, it is particularly difficult to separate the effects of heat and drought and, in the field, high temperature stress is frequently, but not always, associated with reduced water availability (8, 29). While molecular or tissue-level responses to damaging temperatures, such as assessed in this analysis, may depend less on drought-avoidance strategies, other (growth or reproductive) responses to temperature are likely closely linked with water use strategies.

### (c) Conclusions

In summary, we expect thermal tolerance traits to correlate with other plant traits but resolving how will require detailed study. The fact that O'Sullivan et al. (8) found no correlation between leaf heat tolerance and other leaf traits (and therefore could not explain why plants from a single site differed in their heat tolerance) and Bruelheide et al. (30) found that trait-trait and trait-environment relationships differed at global and local scales (but could not explain why the same trait combinations were found in many environments and the same environment accommodated many different trait combinations), suggests that other, hitherto unconsidered factors must be important too. Overall, temperature tends to be a stronger predictor of plant trait variation than precipitation (19), but climate generally



does not explain very much of that variation overall ((4, 30–33); this study). We anticipate that increased understanding of trait-trait and trait-climate relationships will come from a holistic view incorporating effects of evolutionary and biogeographic histories. Such a view will provide not only a more complete picture of how plant trait variation is structured globally but allow for more accurate predictions of responses to ongoing climate change as well.

#### *vi. Fitting of phylogenetic models*

For fitting phylogenetic models, each species was represented only once in the tree (in contrast to the MCMCglmm models, where every observation was fitted). Species with multiple thermal tolerance measurements were represented by their minimum cold tolerance and/or maximum heat tolerance in the phylogenetic analyses. Phylogenetic signal was determined by comparing the fit of Pagel's  $\lambda$  (34, 35) and Brownian Motion (BM; equivalent to  $\lambda = 1$ ) and a model with  $\lambda = 0$  ('white') using 'fitContinuous' in the R package Geiger (36). Values approaching 1 indicate that trait variances are correlated with phylogenetic distances.

Next, we tested whether there was evidence for a signature of constrained evolution for heat tolerance, as suggested by some authors (37, 38). One way in which traits may display constraint is if they are being pulled back to their ancestral state (sometimes referred to as 'stabilising selection' toward an "optimum" value; (39, 40)). We tested this using a single-optimum Ornstein-Uhlenbeck (OU) model (39, 40), with the expectation that it might be a good fit for the heat tolerance data but not cold tolerance. For cold tolerance, a model of punctuated evolution ( $\kappa$ , kappa model) might be expected to be a better fit, if extreme cold tolerance is conferred by an ability to substantially increase tolerance of freezing extremes via hardening (cold acclimation) and that ability evolves only rarely (27, 41, 42). We therefore compared the fit of BM, white,  $\lambda$ ,  $\kappa$  and OU models for both cold and heat tolerance data. All models were fitted using the 'fitContinuous' function in Geiger and their fit compared using AICc values.

### *vii. Phylogenetic supplementary results*

The results of the model fitting are presented in Table S2 and the parameter estimates under the best-fitting OU models are shown in Table S3. The OU model could not be rejected for any of the analyses (Table S2). However, for most heat tolerance analyses and non-hardened cold tolerance, this model was not statistically distinguishable from the second best-fitting model, lambda ( $\lambda$ ). In contrast, for most cold tolerance analyses, the second best model was the kappa ( $\kappa$ ) model of punctuated evolution, but this model was not statistically supported.

Parameter estimates for the OU model suggest that it may be a good model for describing heat tolerance evolution (a low stationary variance, i.e. a strong pull toward the trait optimum) but not cold tolerance evolution (a high stationary variance, indicating a very weak pull toward the central value, meaning the model essentially becomes equivalent to a BM model; Table S3; but this is unlikely to be caused by a type I statistical error, see below and Figure S5). Thus, our results are consistent with a model of constrained evolution for heat tolerance, expressed as an OU model with a central tendency. However, we caution against over-interpreting this result due to the lower explanatory power of phylogeny for heat tolerances overall (Figure 3); other mechanisms are more important for explaining how plant heat tolerances are structured globally (see Main Article).

For cold tolerance, the combined findings of only a weak pull toward an optimal level of cold tolerance (Table S3), the repeated inference of the pulsed ( $\kappa$ ) model as the second best model (even though it was not statistically supported; Table S2), and the high proportion of the overall variance in cold tolerance accounted for by phylogenetic distance (Figure 3) suggest a strong role of evolutionary history in determining interspecific differences in cold tolerance across land plants. Determining the precise evolutionary processes involved requires further research.

**Table S2.** Fit of phylogenetic models, based on AICc values.

	HEAT				COLD			
	All	Hardened	Non-hardened	No.info	All	Hardened	Non-hardened	No.info
n (species)	653	252	82	419	455	187	76	284
BM ( $\lambda=1$ )	4241.00	1628.64	480.70	2443.02	4035.32	1733.56	432.62	2187.16
LAMBDA	<b>4029.10*</b>	<u>1518.23*</u>	<b>456.75*</b>	<u>2353.79</u>	3943.13	1716.27	<u>413.65*</u>	2167.94
WHITE ( $\lambda=0$ )	4129.93	1539.85	500.11	2394.29	3998.93	1741.47	419.55	2118.64
KAPPA	4120.26	1571.38	461.16	2386.93	<u>3892.47</u>	<u>1673.81</u>	426.37	<u>2115.79</u>
OU	<b>4026.39*</b>	<b>1515.39*</b>	<u>458.58*</u>	<b>2320.58*</b>	<b>3858.02*</b>	<b>1669.29*</b>	<b>410.65*</b>	<b>2084.28*</b>

Lowest AICc score shown in bold; second best model underlined; asterisks denote significantly best model(s) overall (based on  $\Delta AICc \geq 3$ ).

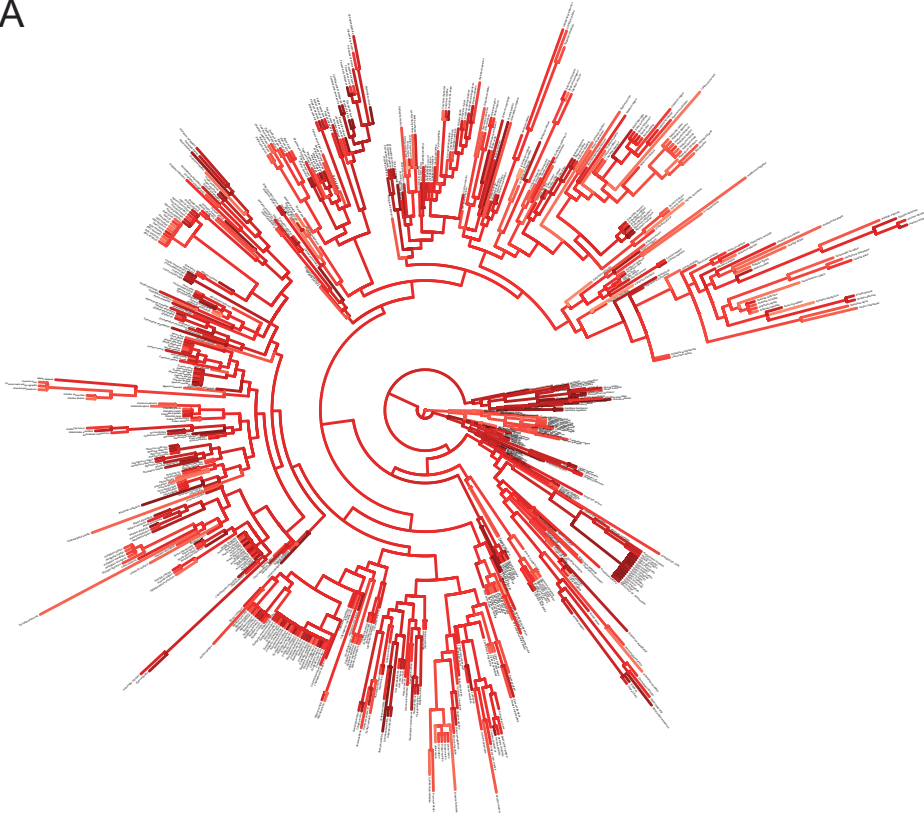
**Table S3.** Parameter estimates under OU models.

	HEAT				COLD			
	All	Hardened	Non-hard	No.info	All	Hardened	Non-hard	No.info
$Z_0$ ( $^{\circ}C$ )	52.2	56.8	48.7	49.7	-13.9	-22.0	-7.10	-9.04
$\alpha$	0.30	0.42	0.14	0.23	0.32	0.24	0.19	0.31
$\sigma^2$	20.2	22.2	6.85	8.19	220.34	271.93	6.36	66.1
$\sigma^2/2\alpha$	33.7	26.4	24.5	17.8	344.28	566.52	16.7	106.5

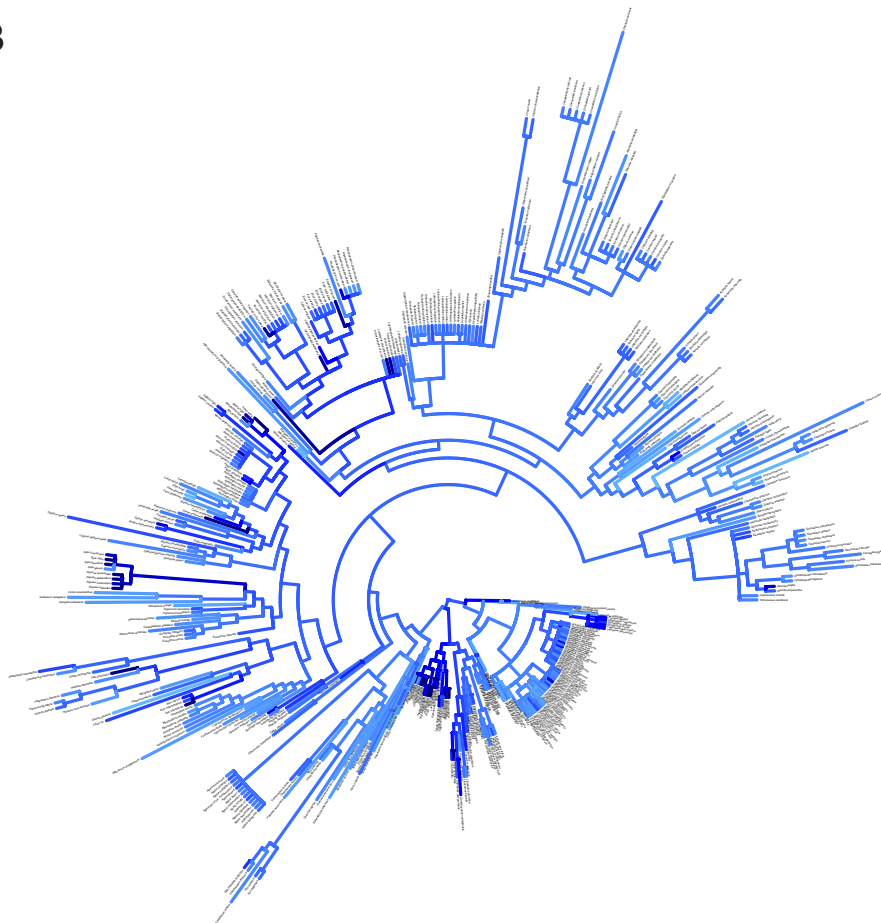
$Z_0$  = ancestral state, here equivalent to the 'trait optimum';  $\sigma^2$  = rate of change through random walk process (stochastic change);  $\alpha$  = strength of pull toward central/optimal value;  $\sigma^2/2\alpha$  = stationary variance, a measure of strength of the pull toward the trait optimum compared to the rate of stochastic change (lower values mean relatively stronger pull).

**Figure S4.** (following page) Phylogenetic distribution of measured (A) heat and (B) cold tolerance limits. The phylogenetic signal,  $\lambda$ , is 0.65 for heat tolerance and 0.67 for cold tolerance, based on analysis of n=653 species for heat tolerance (maximum temperature recorded per species) and n=455 species for cold tolerance (minimum temperature recorded per species) for which both thermal tolerance and phylogenetic data were available. Darker shades of red/blue indicate more extreme values of heat or cold tolerance.

A



B

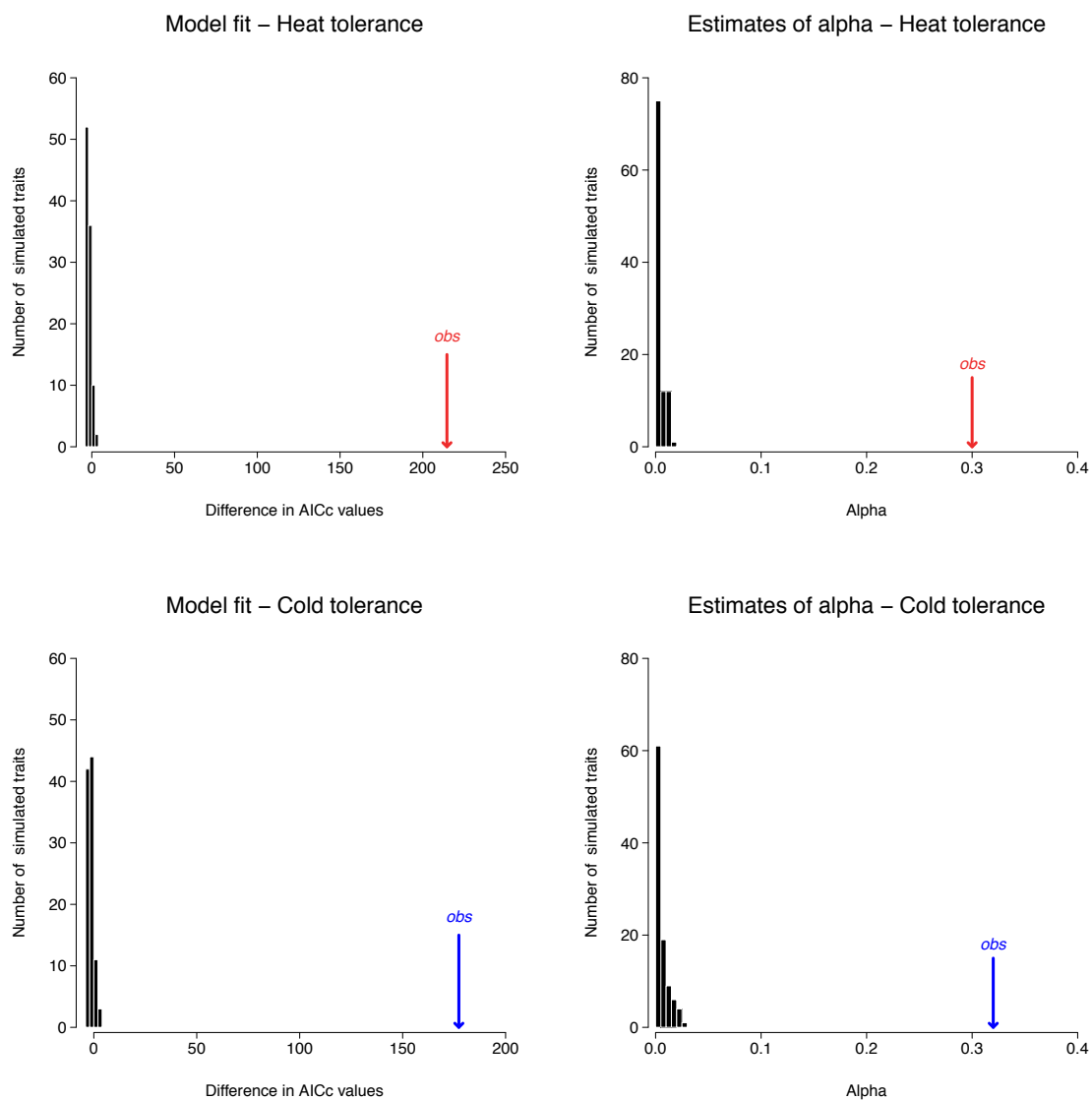


### *viii. Testing for type I errors in fitting OU models*

We tested for a known tendency of high rates of type I statistical errors (false rejection of the null; (43)) associated with the OU model by simulating 100 traits each across the heat and cold tolerance trees under BM and comparing the fit of BM and OU models for each simulated trait. Traits were simulated using ‘sim.char’ in Geiger (36).

We found that the difference in fit between OU and BM was much stronger for observed heat and cold tolerance data (heat:  $\Delta\text{AICc} = 214.6$ , cold:  $\Delta\text{AICc} = 177.0$ ) than for simulated data (heat:  $-1.41$  [ $-2.02$ – $1.69$ ], cold:  $-1.26$  [ $-2.03$ – $2.43$ ]; Figure S5). The low  $\Delta\text{AICc}$  values for simulated traits suggest that the BM and OU models were mostly statistically indistinguishable for these data, and although BM was erroneously rejected in some cases (positive  $\Delta\text{AICc}$  values; heat: 12% of traits, cold: 14%), this was only ever on weak statistical grounds. Similarly, estimates of  $\alpha$  were also much higher for observed (heat: 0.30, cold: 0.32) than simulated (heat: 0.0030 [0–0.014], cold: 0.0050 [0–0.0021]; Figure S5) data. Rejection of BM in favor of OU for our observed data is therefore unlikely to be a result of statistical error.

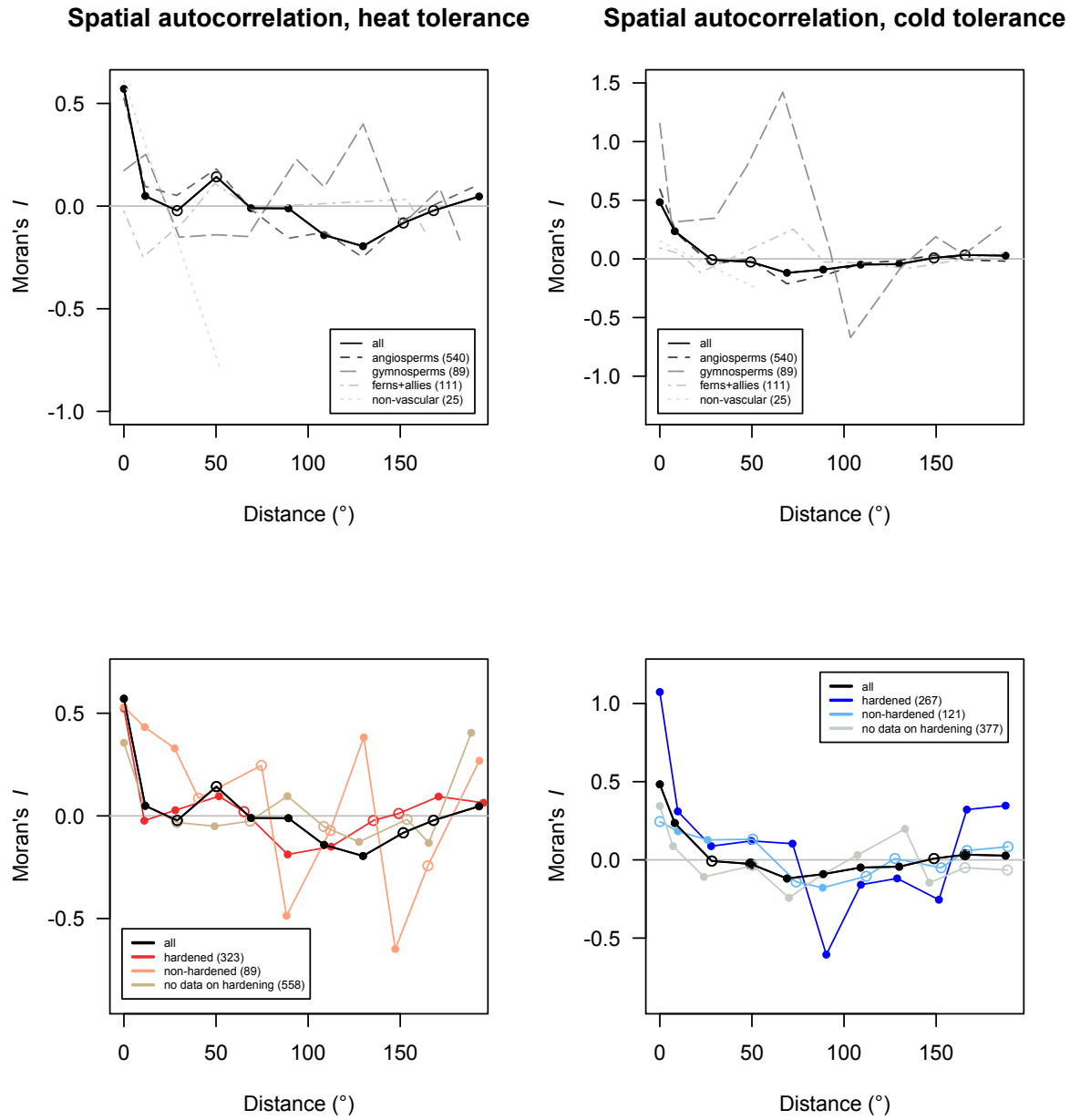
**Figure S5.** Fit of BM and OU models to data simulated under a BM process. Model fit (difference in AICc scores, left column) and estimates of the parameter alpha (right column) for 100 traits simulated under BM on the trees for heat (upper row) and cold tolerance (lower row). Analysis of observed data (colored arrows) give very different results compared to simulated data; thus, results for observed heat and cold tolerance data are unlikely to be an artefact of type I statistical error.



### *ix. Spatial autocorrelation of thermal tolerances*

Heat and cold tolerance exhibit remarkably similar spatial patterns overall (compare solid line in left vs. right panels, Figure S6). Both exhibit some spatial autocorrelation at relatively close geographic distances (Moran's  $I \sim 0.5$  at distances of less than 20° Latitude and/or Longitude), with only hardened cold tolerances exhibiting stronger patterns of spatial autocorrelation at this short spatial scale. This pattern bolsters our conclusion that evolution of cold hardiness is important for shaping land plant distributions. Gymnosperms and unhardened heat tolerances exhibit the most erratic patterns of spatial autocorrelation, likely in part representing low sample sizes, but also possibly suggesting idiosyncratic patterns of dispersal and local adaptation in this group / trait. Bryophytes and lycophytes exhibited the steepest decline in autocorrelation as a function of distance, perhaps reflecting the strongly limited dispersal of many taxa, but also potentially reflecting the patchy nature of the data for bryophytes.

**Figure S6.** Spatial autocorrelation in heat (left column) and cold (right column) tolerance, overall and also separated by taxonomic group (upper row) and by hardening status (lower row).





## *x. Additional latitudinal patterns*

### (a) Frequentist results

In the context of REML mixed models accounting for taxonomy, growth form, and methodology of  $T_{min}$  assessment, the best model describing latitudinal effects on cold tolerance included significant interactions of both latitude and hemisphere with hardening status: effect of latitude x hardening status on cold tolerance =  $-0.29 \pm 0.11$ ,  $t = -3.14$ ,  $P = 0.002$ ; effect of hemisphere x hardening status =  $11.80 \pm 2.24$ ,  $t = 5.26$ ,  $P < 0.0001$ ).

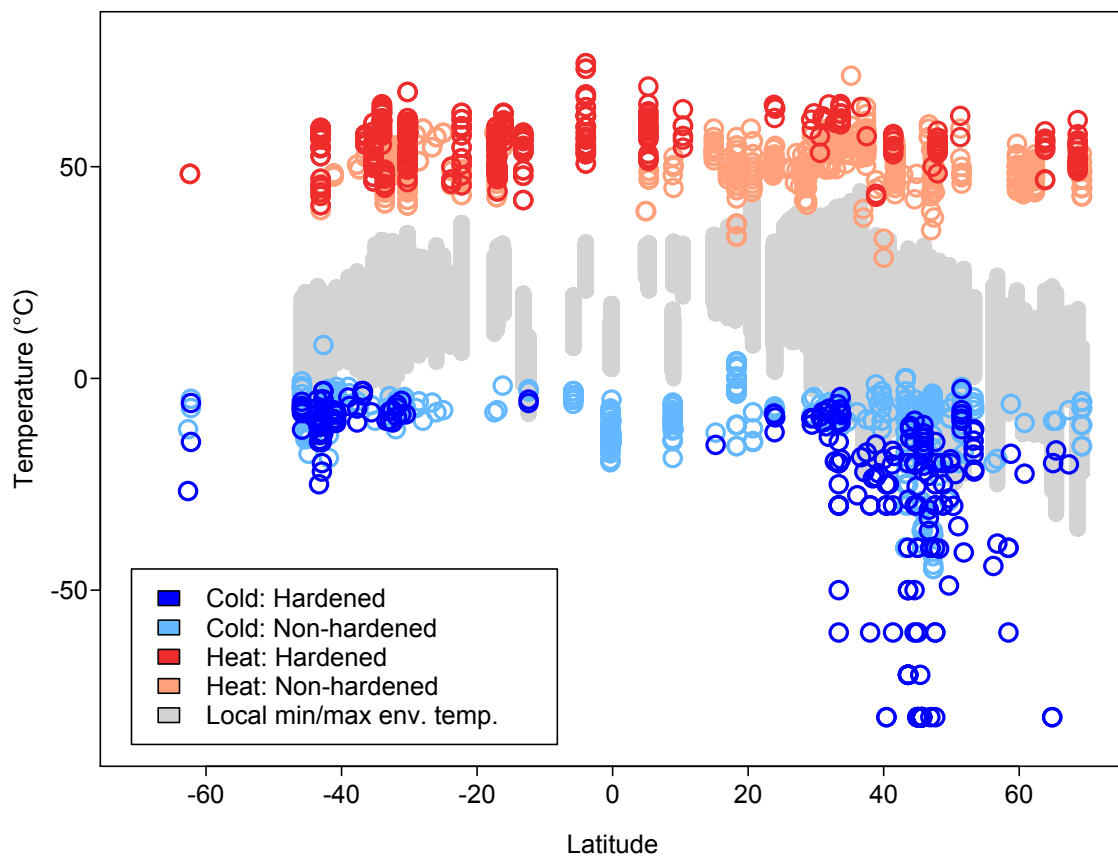
The best REML mixed model explaining latitudinal effects on heat tolerance included a significant 3-way interaction among latitude, hemisphere, and hardening status, as well as significant 2-way interactions among each of these variables: effect of latitude x hemisphere x hardening status =  $0.42 \pm 0.09$ ,  $t = 4.95$ ,  $P < 0.0001$ ; effect of latitude x hardening status =  $-0.42 \pm 0.08$ ,  $t = -5.96$ ,  $P < 0.0001$ ; effect of hemisphere (S) x hardening status =  $-16.48 \pm 2.99$ ,  $t = -5.50$ ,  $P < 0.0001$ ; effect of latitude x hemisphere (S) =  $-0.40 \pm 0.09$ ,  $t = -4.62$ ,  $P < 0.0001$ .

### (b) Latitudinal patterns in the context of climate extremes

We found that  $T_{max}$  measures were closest to local environmental heat extremes at mid latitudes and in the Northern Hemisphere, with unhardened heat tolerances often being exceeded by local thermal maxima (Figure S7). Previous studies have showed the highest vulnerabilities to warming at middle latitudes (ca.  $20^{\circ}$ - $40^{\circ}$  lat) for both animals and plants (8, 44, 45), whereas others have found the highest vulnerabilities at tropical latitudes ( $<23^{\circ}$  lat; e.g. (37, 46)). Mid-latitude areas are home to savannahs and Mediterranean climate regions, which support a sparse, low-canopy vegetation (at least seasonally), providing less shade and moisture for cooling, increasing heat exposure. Dry summers are characteristic of large portions of this latitudinal zone and if coupled with reduced transpiration would further elevate leaf temperature. Heat waves are likely to become more common in the future. In contrast,  $T_{min}$  appear to be at greatest risk for increasing cold snaps at high latitudes in both hemispheres, where estimated  $T_{min}$  values, especially unhardened, already often fail to protect individuals against extremes of local environments (Figure S7). Even for hardened plants, ongoing warming during winter months at high latitudes is exposing them to new

winter conditions, including reduced snow cover (47). This increases exposure to cold and freeze-thaw cycles and challenges the survival of all plants, even those adapted to high latitudes and altitudes.

**Figure S7.** Tmin and Tmax (colored points) and local extreme temperatures (grey bars) across latitudes. Grey bars represent local environmental maximum and minimum temperatures (Bioclim Bio5 and Bio6; (48)) at sampling locations where plants or plant materials in our dataset were obtained for testing; where Tmin or Tmax values fall near or within the shaded regions, there is likely higher potential for climate-induced mortality; therefore reliance on thermal microrefugia may be higher, or phenological processes are more critically important for maintaining survival. These regions are likely at greatest risk for further plant extinctions (49).

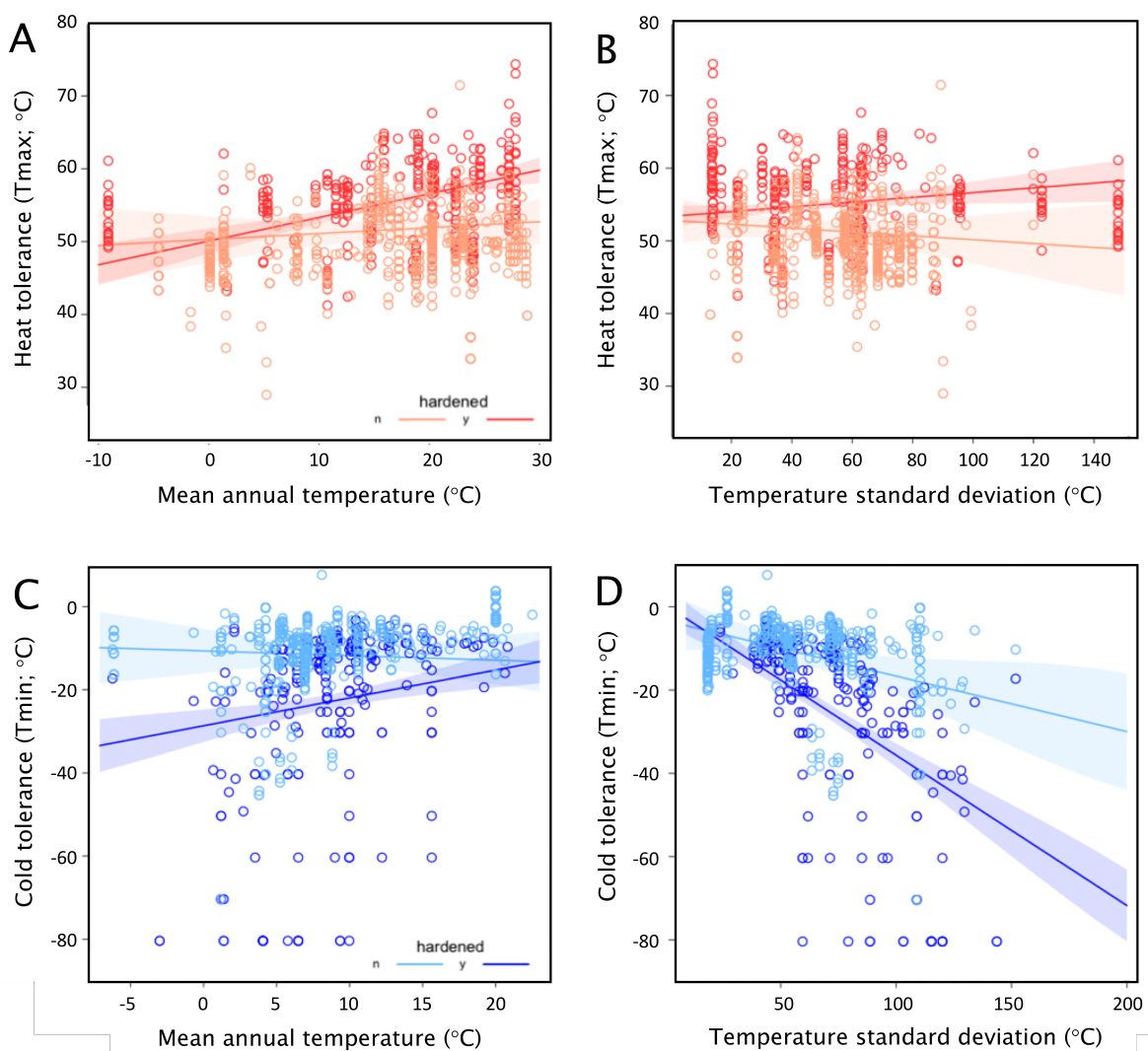


*xi. Model comparisons (Global variation in thermal tolerances: Intrinsic, biogeographic, and environmental drivers).*

**Table S4.** Proportional variance explained under full and reduced Bayesian mixed models for heat and cold tolerance. Comparison of the full model (as reported in the main text) to models which considered only a) geographic distance, b) phylogenetic distance, or c) environmental variables. Experimental method was retained in all models to account for variation in how  $T_{min}$  and  $T_{max}$  were assessed, but growth form was omitted from the reduced models as this explained very little variation overall (and omitting it sped up the model fitting procedure). When failing to account for geographical, phylogenetic, and environmental factors in predicting drivers of global distributions, we see both (i) a loss of predictive power overall (proportion of variance explained decreases; residual variation increases), and (ii) an inflation in the relative importance of the modelled effect. Thus simpler models are likely to lead to erroneous conclusions about the importance of modelled effects (see SI section *xiii*, Table S5). Presented values are mean estimates and Highest Posterior Density (HPD) intervals of the proportional variance explained by each factor, calculated using ((50, 51); see main text Methods for details).

	Full model	Geography only	Phylogeny only	Environment only
<b>Cold tolerance</b>				
Env. x hardening	0.23 [0.16-0.31]	–	–	<b>0.37 [0.22-0.50]</b>
Hardening only	–	<b>0.03 [0.02-0.05]</b>	<b>0.03 [0.02-0.05]</b>	–
Experimental	0.10 [0.03-0.26]	0.18 [0.03-0.45]	0.12 [0.03-0.28]	0.25 [0.05-0.56]
Geographical	0.12 [0.06-0.21]	<b>0.55 [0.32-0.77]</b>	–	–
Phylogenetic	0.34 [0.23-0.48]	–	<b>0.66 [0.53-0.78]</b>	–
Growth form	0.01 [0.00-0.06]	–	–	–
Residual	0.19 [0.14-0.27]	0.24 [0.14-0.35]	0.19 [0.12-0.25]	<b>0.38 [0.21-0.48]</b>
<b>Heat tolerance</b>				
Env. x hardening	0.14 [0.05-0.22]	–	–	<b>0.25 [0.14-0.32]</b>
Hardening only	–	<b>0.09 [0.04-0.15]</b>	<b>0.03 [0.01-0.04]</b>	–
Experimental	0.25 [0.07-0.47]	0.21 [0.06-0.48]	0.28 [0.11-0.53]	0.23 [0.08-0.50]
Geographical	0.41 [0.20-0.57]	<b>0.57 [0.33-0.72]</b>	–	–
Phylogenetic	0.11 [0.04-0.18]	–	<b>0.53 [0.34-0.68]</b>	–
Growth form	0.01 [0.00-0.05]	–	–	–
Residual	0.08 [0.05-0.11]	0.13 [0.07-0.18]	0.16 [0.07-0.02]	<b>0.52 [0.36-0.65]</b>

**Figure S8.** Gradients in heat (A and B) and cold (C and D) tolerance related to interactions between hardening status and environmental variables of mean annual temperature (A and C) and temperature seasonality (B and D). Plotted are marginal effects of hardening x climate in the context of the reported models. Minimum temperatures (Tmin, cold tolerance) are plotted in blues and maximum temperatures (Tmax, heat tolerance) in reds; measurements on hardened plants are shown in dark hues and non-hardened (including those with no information on hardening status) in light hues.



*xii. Our results in the context of previous studies that have examined global patterns in thermal tolerance.*

Although several studies synthesize an impressive amount of data, it is clear from Table S5 that our collective knowledge of physiological limits to withstanding thermal extremes is restricted to a tiny fraction of all species. Despite low overall sampling, some of the global patterns in thermal tolerance variation are by now well established across studies and taxa. For instance, there is a tendency for  $T_{min}$  to correlate more strongly with climate than  $T_{max}$  (e.g. (38, 44, 52)) – in that respect our findings for plants reflect those for other ectotherms. However, we also show that not accounting for the variance explained by geographic or phylogenetic distance can inflate the variance attributed to (and thus the perceived importance of) climate (see Main Text; SI section *xi*; Table S4).

Another example of a well-established pattern is that  $T_{min}$  is more variable overall and declines more steeply with latitude than  $T_{max}$  (e.g. (38, 53, 54); this study). However, the opposite has also been found, with  $T_{max}$  being more variable than  $T_{min}$  for ants and lizards (52, 55). It is therefore likely that taxon or habitat specific patterns also exist (e.g. (45, 54)). For example, several studies have found high phylogenetic signal or invoke ‘phylogenetic conservatism’ in  $T_{max}$  (37, 38) but, for lizards and plants, similar (high) phylogenetic signal has been measured for  $T_{max}$  and  $T_{min}$  ((44); this study). Furthermore, for both these groups spatial distance is more important than phylogeny for explaining the overall variance in  $T_{max}$  ((55); this study). Finding phylogenetic signal therefore does not in itself say anything about how well phylogeny accounts for overall trait variance relative to other factors (see also (56–58)). More research is needed to determine the contribution of generalities versus taxon or habitat specific idiosyncrasies. This will be essential for improving our understanding of the processes driving global variation in thermal tolerances.

Perhaps the strongest message from Table S5 is that it is difficult to compare findings across the studies performed to date. First, it is impossible to infer the relative importance of evolutionary history (phylogeny), biogeographic processes (spatial distance) and adaptation (local climate), unless all three factors have been taken into account simultaneously. Even in cases where this has been done, different analytical approaches (50, 56) prohibit direct comparison of the results, especially as the former approach does not incorporate intraspecific spatial variation, which can be quite significant (59). Furthermore, differences in

sample sizes, as well as geographic and phylogenetic scope, can also confound inference of the relative importance of the factors included (e.g. narrower phylogenetic scope would be expected to reduce the variance attributed to phylogeny, all else being equal). For these reasons, we caution against over-interpreting the similarities and differences among the findings of the studies listed here.

**Table S5.** Overview of synthesis studies of global variation in thermal tolerances with latitude

Study	Taxon sampling (n species)	Approach	Findings	Predictor(s) of Tmax <sup>1,2</sup>			Predictor(s) of Tmin <sup>1,2</sup>			Implications
				Spatial distance	Phylo. distance	(Local) climate	Spatial distance	Phylo. distance	(Local) climate	
Addo-Beddiako et al. 2000 (53)	Insects (n=250 for Tmin; n for Tmax not given but fewer than for Tmin)	Test climatic variability hypothesis by plotting latitudinal change in Tmin and Tmax.	Tmin declines with increasing latitude; Tmax less variable overall and with latitude.	NA	NA	NA	NA	NA	NA	Upper thermal limits show less variation overall and less geographical variation than lower ones. Authors suggest this supports climatic variability hypothesis.
Sunday et al. 2011 (54)	Metazoan ectotherms (n=341; terrestrial = 239, marine=102) <sup>3</sup>	Test latitudinal relationship for Tmin and Tmax; and the effect of acclimation, hemisphere and marine/ terrestrial systems.	<u>Terrestrial</u> : Stronger latitudinal decrease for Tmin than Tmax, especially in the Northern Hemisphere. <u>Marine</u> : Less latitudinal decline overall and no difference between slopes for Tmin and Tmax.	NA	NA	NA	NA	NA	NA	Different macrophysiological rules may apply in terrestrial and marine systems. Authors suggest terrestrial Tmin/Tmax patterns mirror change in environmental temperature with latitude; or thermoregulatory behavior decouples body temperatures from environmental temperatures; or upper thermal limits are evolutionarily conserved and do not reflect requirements at high latitudes.
Kellerman et al. 2012 (37)	<i>Drosophila</i> (n=94)	Correlate Tmax with ambient temperature, precipitation and spatial proximity; calculate phylogenetic signal for Tmax.	Tmax correlates with maximum temperature and annual precipitation of species' ranges; only weakly with spatial distance. There is phylogenetic signal to Tmax.	(+)	(+)	(+/-)	NA	NA	NA	Authors suggest low variation in upper thermal limits reflect weak selection pressures or strong evolutionary constraints (they favor 'constraints').
Araujo et al. 2013 (38)	Endotherms (n=697), Ectotherms (n=227), Plants (n=520) <sup>4</sup>	For a subset (n=306; no plants) thermal tolerances plotted against ambient temperature across species ranges.	Tmin more variable than Tmax in all groups. Stronger (positive) relationship of Tmin with environmental temperature than for Tmax.	NA	NA	+/0/-	NA	NA	+	Authors suggest cold tolerances are the result of local adaptation and heat tolerances physiologically constrained.
Grigg & Buckley 2013 (55)	Lizards (Tmax n=68, Tmin n=60)	Partition variance in Tmax and Tmin between phylogenetic and geographic distance (expressed as spatial distance or difference in ambient temperature; Freckleton & Jetz 2009).	Variance in Tmax is <i>greater</i> than in Tmin. Tmax and Tmin: more variance explained by spatial than phylogenetic distance but variance in Tmin is almost entirely (92%) unexplained. Replacing spatial distance with 'temperature distance' increases relative importance of phylogeny (Tmax) or 'temperature' (Tmin).	++	+	NA	+	+	NA	Both phylogenetic and geographic distances required for explaining heat tolerances in lizards. Cold tolerances are poorly explained by either effect.

Hoffmann et al. 2013 (44)	Insects (Tmin n=264, Tmax n=210), Lizards and Snakes (Tmin n=130, Tmax n=238); across fewer species	(Phylogenetic) generalized least squares regression against ambient temperature. Calculated phylogenetic signal in Tmax and Tmin.	Tmin more variable overall, more plastic and more strongly correlated with ambient temperature than Tmax. <u>Insects</u> : higher phylogenetic signal for Tmax than Tmin. <u>Reptiles</u> : similarly high phylogenetic signal for both Tmax and Tmin.	NA	(+)	(+/0)	NA	(+)	(+)	Differences apparent between taxonomic groups regarding patterns of interspecific variation in plasticity and phylogenetic signal to Tmin and Tmax.
Sunday et al. 2014 (45)	Terrestrial ectotherms (n=300) <sup>5</sup>	Compare thermal tolerance limits to air temperatures and modelled operative body temperatures.	On average, Tmax higher than maximum air temperatures but lower than modelled body temperatures (details differ among taxa). Tmin slightly lower than both air and body temperatures.	NA	NA	NA	NA	NA	NA	Authors suggest ectothermic animals unlikely to survive thermal extremes through physiological thermal tolerances alone; implies thermoregulatory behavior important (e.g. seeking out more favorable microsites).
Khalilq et al. 2014 (60)	Endotherms (birds n= 161, mammals = 297) <sup>6</sup>	Test climatic variability hypothesis with phylogenetic generalized least squares regressions for TNZ <sup>6</sup> and climate variability; assess species' vulnerability to predicted climate change.	Thermal tolerance breadth increases with increasing latitude and climate variability for birds but not mammals. Lower TNZ limits correlated with minimum ambient temperatures for birds but not mammals.	NA	NA	NA	NA	NA	+/-	The climatic variability hypothesis supported for birds but not mammals. Authors suggest that birds' thermal physiology may be more directly linked to ambient temperatures than for mammals; and many endotherms may tolerate projected temperature increases but tropical species are the most vulnerable.
Lancaster 2016 (59)	Insects (n=48)	Examine role of poleward range shifts for driving latitudinal variation in Tmin, Tmax and thermal tolerance breadth.	Tmax declines with latitude for stable-ranged species but shows no latitudinal trend for range expanding species. Tmin declines with latitude for both expanding and stable-ranged species.	NA	NA	NA	NA	NA	NA	Author suggests that range shifts have moved Tmax values far from where they originated, while Tmin values undergo adaptive evolution during poleward range expansion. Thus biogeographic processes are important for explaining latitudinal increases in thermal niche breadth.
O'Sullivan et al. 2017 (8)	Seed plants (n=218)	Leaf heat tolerances correlated with latitude and various measures of the thermal environment.	Leaf Tmax decreases with latitude but by less than the decrease in ambient temperature; Tmax correlates with the warmest environmental temperatures; including site aridity did not improve models.	NA	NA	+	NA	NA	NA	Leaf upper thermal tolerances decrease with latitude but less sharply than decrease in ambient temperature. Leaf Tmax can exceed ambient temperatures by up to 20 °C.
Diamond & Chick 2018 (52)	Ants (n=148)	Partition variance in Tmax and Tmin between phylogenetic and geographic distance; correlate variance independent of either with local climate (56).	Variance in Tmax is <i>greater</i> than in Tmin and is mainly explained by phylogeny. Variance in Tmin is mainly independent of both spatial and phylogenetic distances. Climate (temperature) correlates more strongly with Tmin than Tmax.	0	++	+	0	+	NA	Authors suggest different relative effects of evolutionary history and local climate on Tmax and Tmin; and suggest heat tolerance is phylogenetically constrained but cold tolerance is not. <sup>7</sup>



Sunday et al. 2019 (61)	Ectothermic and endothermic animals (n= ca. 1700; all data from Bennett et al. (2) excluding plants)	Assess support for the Climate Extremes Hypothesis by correlating Tmax and Tmin with extreme daily temperatures, while accounting for thermal tolerance assessment method.	Both Tmax and Tmin are positively correlated with extreme daily temperatures at collection locality. Previously found latitudinal patterns are not an artefact of thermal tolerance assessment method.	NA	NA	+	NA	NA	+	Climate extremes explain some of the variation in Tmin and Tmax. Authors suggest lower overall variation in Tmax (with latitude) may, at least in part, be due to less latitudinal variation in episodic extreme heat events.
This study	Land plants (n=1028)	Partition variance in Tmax and Tmin between phylogenetic and geographic distances and local environment (MCMCglmm (50); see <i>Methods</i> ).	Several known patterns in animals found for plants as well (see main text). Variance in Tmax explained by geography > climate > phylogeny. Variance in Tmin explained by phylogeny > climate > geography.	+++	+	++	+	+++	++	The local environment, phylogenetic and spatial distances are all needed to explain global variation in both Tmax and Tmin of plants but the relative importance of each factor differs between Tmax and Tmin. Excluding spatial or geographic distances (or both) inflates the variance attributed to climate.

<sup>1</sup>NA = Not tested; 0 = no relationship; + = positive relationship (more pluses = relatively stronger relationship); - = negative relationship (more minuses = relatively stronger relationship); brackets mean effects tested separately so relative importance cannot be assessed; more than one type of symbol means different results for different taxa tested separately.

<sup>2</sup>Tmax=heat tolerance (various measures, including upper critical temperature limit, CTmax; upper lethal temperature, ULT); Tmin=cold tolerance (various measures, including lower critical temperature limit, CTmin; lower lethal temperature, LLT).

<sup>3</sup>Terrestrial: reptiles, arthropods and amphibians; Marine: fish, molluscs and arthropods.

<sup>4</sup>Ectotherms: reptiles, amphibians, spiders, insects; Endotherms: birds, mammals; Plants: no further information provided. Cold tolerance (“cold hardiness” and frost tolerance) data for an additional n=1296 plant species provided in supplement only.

<sup>5</sup>Terrestrial ectotherms: insects, amphibians and reptiles.

<sup>6</sup>Data are for the thermoneutral zone (TNZ), i.e. the temperature range where only minimal energy is needed to compensate for the difference between body and ambient temperatures; or, where the metabolism of an endotherm is lowest and almost independent of ambient temperature. Data for an additional 94 species of migratory birds were excluded from analyses.

<sup>7</sup>It is clear that phylogeny explains more variance than climate for Tmax (phylogeny > ‘independent’). For Tmin, however, it is unclear how much of the ‘independent’ variance (not explained by either phylogenetic or spatial distances) is explained by climate and how much remains unexplained overall (residual variance)

### xiii. Supplementary references

1. IUCN (2016) The IUCN Red List of Threatened Species. *Version 3.1*.
2. Bennett JM, et al. (2018) GlobTherm, a global database on thermal tolerances for aquatic and terrestrial organisms. *Sci Data* 5:180022.
3. Körner C (2012) Treelines will be understood once the functional difference between a tree and a shrub is. *Ambio* 41 Suppl 3:197–206.
4. Moles AT, et al. (2009) Global patterns in plant height. *J Ecol* 97(5):923–932.
5. Olson ME, et al. (2018) Plant height and hydraulic vulnerability to drought and cold. *Proc Natl Acad Sci U S A* 115(29):7551–7556.
6. O’Sullivan OS, et al. (2013) High-resolution temperature responses of leaf respiration in snow gum (*Eucalyptus pauciflora*) reveal high-temperature limits to respiratory function. *Plant, Cell Environ* 36(7):1268–1284.
7. Vitasse Y, Lenz A, Körner C (2014) The interaction between freezing tolerance and phenology in temperate deciduous trees. *Front Plant Sci* 5(OCT):1–12.
8. O’Sullivan OS, et al. (2017) Thermal limits of leaf metabolism across biomes. *Glob Chang Biol* 23(1):209–223.
9. Sakai A, Larcher W (1987) *Frost Survival of Plants : Responses and Adaptation to Freezing Stress* (Springer Berlin Heidelberg).
10. Bitá CE, Gerats T (2013) Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. *Front Plant Sci* 4:273.
11. Körner C (2016) Plant adaptation to cold climates. *F1000Research* 5:1–5.
12. Nievola CC, Carvalho CP, Carvalho V, Rodrigues E (2017) Rapid responses of plants to temperature changes. *Temp (Austin, Tex)* 4(4):371–405.
13. Leuzinger S, Körner C (2007) Tree species diversity affects canopy leaf temperatures in a mature temperate forest. *Agric For Meteorol* 146(1–2):29–37.
14. Garrett TY, Huynh C-V, North GB (2010) Root contraction helps protect the “living rock” cactus *Ariocarpus fissuratus* from lethal high temperatures when growing in rocky soil. *Am J Bot* 97(12):1951–1960.
15. Menzel A, Seifert H, Estrella N (2011) Effects of recent warm and cold spells on European plant phenology. *Int J Biometeorol* 55(6):921–932.
16. Strimbeck GR, Schaberg PG, Fossdal CG, Schröder WP, Kjellsen TD (2015) Extreme low temperature tolerance in woody plants. *Front Plant Sci* 6:884.
17. Díaz S, et al. (2016) The global spectrum of plant form and function. *Nature* 529(7585):167–171.
18. Moles AT, et al. (2007) Global patterns in seed size. *Glob Ecol Biogeogr* 16(1):109–116.
19. Moles AT, et al. (2014) Which is a better predictor of plant traits: Temperature or precipitation? *J Veg Sci* 25(5):1167–1180.
20. Wright IJ, et al. (2004) The worldwide leaf economics spectrum. *Nature* 428(6985):821–827.
21. Wright IJ, et al. (2017) Global climatic drivers of leaf size. *Science (80- )* 357(6354):917–921.
22. Bjorkman AD, et al. (2018) Plant functional trait change across a warming tundra biome. *Nature* 562(7725):57–62.

23. Michaletz ST, et al. (2016) The energetic and carbon economic origins of leaf thermoregulation. *Nat Plants* 2:16129.
24. Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: Global convergence in plant functioning. *Proc Natl Acad Sci U S A* 94(25):13730–13734.
25. Michaletz ST, et al. (2015) Plant Thermoregulation: Energetics, Trait–Environment Interactions, and Carbon Economics. *Trends Ecol Evol* 30(12):714–724.
26. Michaletz ST, Cheng D, Kerkhoff AJ, Enquist BJ (2014) Convergence of terrestrial plant production across global climate gradients. *Nature* 512(1):39–43.
27. Zanne AE, et al. (2014) Three keys to the radiation of angiosperms into freezing environments. *Nature* 506(7486):89–92.
28. Judd WS, Sanders RW, Donoghue MJ (1994) Angiosperm family pairs: preliminary phylogenetic analyses. *Harvard Pap Bot* 1(5):1–51.
29. Wahid A, Gelani S, Ashraf M, Foolad MR (2007) Heat tolerance in plants: An overview. *Environ Exp Bot* 61(3):199–223.
30. Bruelheide H, Dengler J, Purschke O, Al. E (2018) Global trait–environment relationships of plant communities. *Nat Ecol Evol* 2:1906–1917.
31. Moles AT, et al. (2005) Factors that shape seed mass evolution. *Proc Natl Acad Sci U S A* 102(30):10540–10544.
32. Wright IJ, et al. (2005) Assessing the generality of global leaf trait relationships. *New Phytol* 166(2):485–496.
33. Kumarathunge DP, et al. (2019) Acclimation and adaptation components of the temperature dependence of plant photosynthesis at the global scale. *New Phytol* 222(2):768–784.
34. Pagel M (1999) Inferring the historical patterns of biological evolution. *Nature* 401(6756):877–884.
35. Pagel M (1997) Inferring evolutionary processes from phylogenies. *Zool Scr* 26(4):331–348.
36. Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W (2008) GEIGER: investigating evolutionary radiations. *Bioinformatics* 24(1):129–131.
37. Kellermann V, et al. (2012) Upper thermal limits of *Drosophila* are linked to species distributions and strongly constrained phylogenetically. *Proc Natl Acad Sci U S A* 109(40):16228–33.
38. Araújo MB, et al. (2013) Heat freezes niche evolution. *Ecol Lett* 16(9):1206–19.
39. Hansen TF (1997) Stabilizing selection and the comparative analysis of adaptation. *Evolution (N Y)* 51(5):1341–1351.
40. Butler MA, King AA (2004) Phylogenetic Comparative Analysis: A Modeling Approach for Adaptive Evolution. *Am Nat* 164(6):683–695.
41. Wiens JJ, Donoghue MJ (2004) Historical biogeography, ecology and species richness. *Trends Ecol Evol* 19(12):639–644.
42. Kerkhoff AJ, Moriarty PE, Weiser MD (2014) The latitudinal species richness gradient in New World woody angiosperms is consistent with the tropical conservatism hypothesis. *Proc Natl Acad Sci* 111(22):8125–8130.
43. Cooper N, Thomas GH, Venditti C, Meade A, Freckleton RP (2016) A cautionary note on the use of Ornstein Uhlenbeck models in macroevolutionary studies. *Biol J Linn Soc* 118(1):64–77.
44. Hoffmann AA, Chown SL, Clusella-Trullas S (2013) Upper thermal limits in terrestrial ectotherms: how constrained are they? *Funct Ecol* 27(4):934–949.

45. Sunday JM, et al. (2014) Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proc Natl Acad Sci U S A* 111(15):5610–5.
46. Deutsch CA, et al. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proc Natl Acad Sci U S A* 105(18):6668–72.
47. Pimm SL Review Climate Disruption and Biodiversity. *Curr Biol* 19:R595–R601.
48. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25(15):1965–1978.
49. Román-Palacios C, Wiens JJ (2020) Recent responses to climate change reveal the drivers of species extinction and survival. *Proc Natl Acad Sci* 117(8):201913007.
50. Hadfield JD (2010) MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCgmm R Package. *J Stat Softw* 33(2):1–22.
51. Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142.
52. Diamond SE, Chick LD (2018) The Janus of macrophysiology: stronger effects of evolutionary history, but weaker effects of climate on upper thermal limits are reversed for lower thermal limits in ants. *Curr Zool* 64(2):223–230.
53. Addo-Bediako A, Chown SL, Gaston KJ (2000) Thermal tolerance, climatic variability and latitude. *Proc Biol Sci* 267(1445):739–45.
54. Sunday JM, Bates AE, Dulvy NK (2011) Global analysis of thermal tolerance and latitude in ectotherms. *Proc Biol Sci* 278(1713):1823–30.
55. Grigg JW, Buckley LB (2013) Conservatism of lizard thermal tolerances and body temperatures across evolutionary history and geography. *Biol Lett* 9(2):20121056–20121056.
56. Freckleton RP, Jetz W (2009) Space versus phylogeny: Disentangling phylogenetic and spatial signals in comparative data. *Proc R Soc B Biol Sci* 276(1654):21–30.
57. Cooper N, Freckleton RP, Jetz W (2011) Phylogenetic conservatism of environmental niches in mammals. *Proc R Soc B Biol Sci* 278(1716):2384–2391.
58. Humphreys AM, Linder HP (2013) Evidence for recent evolution of cold tolerance in grasses suggests current distribution is not limited by (low) temperature. *New Phytol* 198(4):1261–1273.
59. Lancaster LT (2016) Widespread range expansions shape latitudinal variation in insect thermal limits. *Nat Clim Chang* 6(6):618–621.
60. Khaliq I, Hof C, Prinzing R, Böhning-Gaese K, Pfenninger M (2014) Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proc R Soc B Biol Sci* 281(1789):20141097.
61. Sunday J, et al. (2019) Thermal tolerance patterns across latitude and elevation. *Philos Trans R Soc B Biol Sci* 374(1778):20190036.