Global variation in the thermal tolerances of plants

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

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Significance Statement

Knowledge of how thermal tolerances are distributed across major clades and biogeographic regions is important for understanding biome formation and climate change responses. However, most research has concentrated on animals, and we lack equivalent knowledge for other organisms. Here we compile global data on heat and cold tolerances of plants, showing that many, but not all, broad-scale patterns known from animals are also true for plants. Importantly, failing to account simultaneously for influences of local environments, and evolutionary and biogeographic histories, can mislead conclusions about underlying drivers. Our study unravels how and why plant cold and heat tolerances vary globally, and highlights that all plants, particularly at mid-to-high latitudes and in their non-hardened state, are vulnerable to ongoing climate change.

Abstract

Thermal macrophysiology is an established research field that has led to well-described patterns in the global structuring of climate adaptation and risk. However, since it was developed primarily in animals we lack information on how general these patterns are across organisms. This is alarming if we are to understand how thermal tolerances are distributed globally, improve predictions of climate change, and mitigate effects. We approached this knowledge gap by compiling a geographically and taxonomically extensive database on plant heat and cold tolerances, and used this dataset to test for thermal macrophysiological patterns and processes in plants. We found support for several expected patterns: cold tolerances are more variable and exhibit steeper latitudinal clines and stronger relationships with local environmental temperatures than heat tolerances overall. Next, we disentangled the importance of local environments and evolutionary and biogeographic histories in generating these patterns. We found that all three processes have significantly contributed to variation in both heat and cold tolerances but that their relative importance differs. We also show that failure to simultaneously account for all three effects overestimates the importance of the included variable, challenging previous conclusions drawn from less comprehensive models. Our results are consistent with rare evolutionary innovations in cold acclimation ability structuring plant distributions across biomes. In contrast, plant heat tolerances vary mainly as a result of biogeographical processes and drift. Our results further highlight that all plants, particularly at mid-to-high latitudes and in their non-hardened state, will become increasingly vulnerable to ongoing climate change.

Keywords: acclimation, cold, hardening, heat, hemisphere, latitude, macrophysiology, temperature

Introduction

As our global climate continues to change, there is a need to increase understanding of the ecological and evolutionary processes that cause variation in temperature tolerances across organisms and biomes. Improved knowledge of how individuals cope with novel extreme thermal conditions can lead to better predictions of how species and communities will respond to climate change, and aid development of mitigation strategies (1, 2). Moreover, knowledge of how thermal tolerances are distributed geographically and phylogenetically sheds light on the fundamental biogeographic and evolutionary processes that shape inherent physiological limits (3, 4), with important implications for how and why species' range limits and biodiversity gradients are formed (5, 6). As a consequence, the past decade has seen a reinvigoration of the field of macrophysiology (4, 7–9), and several global analyses of physiological thermal limits have been conducted for different animal groups (3, 10–13). However, equivalent in-depth studies for non-animal systems are lacking, limiting the generality of our understanding and ability to predict biotic responses to climate change.

Previous work on the global distribution of thermal tolerances in animals has led to the recognition of several major patterns, including (a) cold tolerances are more phenotypically variable and exhibit greater acclimation response than heat tolerances, for a similar set of organisms (11, 14), (b) cold tolerances exhibit stronger latitudinal clines than heat tolerances (3, 10), (c) the extent to which acclimation improves thermal tolerance increases with latitude (4, 15), and (d) signatures of local adaptation in thermal tolerances are stronger under more extreme conditions (i.e., under strong directional selection (16–19)).

Multiple hypotheses have been developed to explain these patterns, in particular, the lower latitudinal variability and acclimation capacity of heat tolerances. Hypotheses include lower evolvability of heat tolerance (11, 14), lower spatial variability in extreme heat than extreme cold environmental conditions themselves, limiting the magnitude of divergence in local adaptation for heat tolerance (3), and/or stronger mechanistic or scaling-related associations between metabolic optima and heat tolerance (12, 20). However, biogeographic processes, such as range shifts and endemism, may also play critical roles in driving the global distribution of heat or cold tolerances, both because limited dispersal between speciation events can constrain the phylogenetically-determined rate of thermal tolerance evolution (21), and because large-scale dispersal events, e.g. during post-glacial and contemporary range shifts, can transport thermal tolerance limits far from where they evolved (19). Species movement processes can also produce asymmetrical variability in heat vs. cold tolerances, depending on whether net migration is to colder or warmer regions (19).

Here we test the diverse patterns and hypotheses developed for animals in a previously overlooked group: land plants. Plant thermal tolerances have been extensively studied in a mechanistic context (22, 23), but they have rarely been used to test fundamental macrophysiological hypotheses (but see discussions in *12–14*). Latitudinal gradients have also been discovered for several ecologically important plant traits (e.g. (27–29)) but latitudinal gradients in plant thermal tolerances remain undescribed (but see (25)). This is surprising given that plants cover every terrestrial surface of Earth, and that their distribution is strongly spatially and climatically structured, with temperature being considered one of the strongest determinants of plant distribution patterns globally (30, 31). The spatial structuring of plants is reflected in the major biomes of the world (e.g. broadleaf forest, coniferous forest and grassland), and is the result of biogeographical and evolutionary processes over thousands to millions of years (32–34). Contemporary range shifts in response to changing climates have been documented for plants (35, 36), but migration through anthropogenically fragmented landscapes may be too slow for many species to keep pace with geographically shifting climate niches (37); the already elevated rates of plant extinction in the Anthropocene (38) are therefore likely to increase.

To increase understanding of global patterns of plant thermal tolerances, and how such patterns evolve, we compiled a new database of thermal tolerances from the literature (SI Dataset), examined latitudinal patterns, and tested for the importance of local climate, phylogeny, and geographic distance in explaining those patterns, taking into account hardening status and method, measurement method, and hemisphere. We further fitted phylogenetic trait evolution models to test for a potential constraint in heat and cold tolerance evolution. Given the large variation in lifespan, growth form, and dispersal ability across land plants, the associated myriad of ways in which they avoid or tolerate thermal stress might lead to new patterns, and confirm or refute existing macrophysiological hypotheses developed for (ectothermic) animals.

Results

Geographic and taxonomic coverage of plant thermal tolerance data

We searched the literature for published estimates of georeferenced physiological thermal limits for land plants, focussing on both heat tolerance (Tmax) and cold tolerance (Tmin). These estimates represent a set of measures for assessing the environmental temperatures under which plants lose function physiologically (see below). We found 70 books, monographs, and articles, which provided n = 1732 thermal tolerance data points with geographical information for n = 1028 plant species (SI Dataset). The thermal tolerance data were gathered from 246 unique locations (149 for cold and 138 for heat tolerance; Fig. 1a,b). In addition, n=806 records included confirmed information on hardening or acclimation status.

Across all data, there is more variation in cold than heat tolerance (Tmin: mean -15.4 ± 17.4 ºC standard deviation, Tmax: 51.3 ± 5.8 ºC). Most of the variation in cold tolerance comes from hardened plants in the Northern Hemisphere, especially cushion plants and gymnosperms (Fig. 1c,d). There are very few data for Southern Hemisphere bryophytes, lycophytes and ferns. (See SI Appendix, sections *i-v*, Figs. S1-S3, Table S1, for further analysis and discussion of thermal tolerances in the context of taxonomic group, growth form, experimental approach, other plant traits and plant thermal tolerance strategies.)

Phylogenetic signal and evolutionary mode of heat and cold tolerance

To estimate phylogenetic signal and test how cold and heat tolerances are evolving across land plants, we obtained phylogenetic information (39) for n = 653 and 455 species for heat and cold tolerance, respectively, representing 95% and 89% of the total dataset, respectively, with a bias against retention of non-vascular plants (SI Appendix, Fig. S4). Heat and cold tolerances exhibited similar phylogenetic signal, being significantly different from both 0 and 1 (cold: $\lambda = 0.67$, $\Delta AICc \geq 55$; heat: $\lambda = 0.65$, $\Delta AICc \geq 100$; SI Appendix, Table S2). Further, we tested whether there was support for heat tolerance being evolutionarily constrained, as expressed by an Ornstein-Uhlenbeck (OU (40)) model, in which species' heat tolerances are pulled to an optimal value, and whether there was support for punctuated evolution for cold tolerance, as expressed by a 'kappa' (κ) model (41), and as expected if extreme cold tolerance is conferred by hardening ability and that ability evolves only rarely ((42); SI Appendix, sections *vi-viii*, Tables S2-S3, Figs. S4-S5).

The OU model could not be rejected in any of the analyses for either heat or cold tolerance (based on ΔAICc ≥ 3.0; SI Appendix, Table S2); it was the best model in all cases except non-hardened heat, where the λ model had a slightly better fit (ΔAICc = 1.83). Nevertheless, parameter estimates suggest that the OU model is a better explanation for change in heat tolerances than cold tolerances: the stationary variance ($\sigma^2/2\alpha$), which measures the rate of stochastic change (or 'drift', as described by BM, σ^2) relative to the strength of the adaptive pull (α) towards the optimal value, is much higher for cold tolerance (344.3 [overall], 566.5 [hardened-only]) than heat tolerance (33.7 [overall], 26.4 [hardened-only]; SI Appendix, Table S3). This suggest a much weaker pull toward a globally optimal thermal state for cold tolerance than for heat tolerance.

Spatial autocorrelation

Both heat and cold tolerance exhibited significant spatial autocorrelation, calculated using Moran's *I*, particularly at short to moderate spatial scales (i.e., within 50° Latitude or Longitude, corresponding to approximately 5000 km; SI Appendix, Fig. S6), both within and across taxonomic groups (SI Appendix, section *ix*). There is a clearer distance-decay relationship in cold tolerance than in heat tolerance. For cold tolerance, spatial autocorrelation is stronger in hardened than in non-hardened individuals, whereas for heat tolerance hardened and non-hardened individuals show similar levels of spatial autocorrelation (SI Appendix, Fig. S6).

Global variation in thermal tolerances: Latitudinal trends

We tested for latitudinal variation in thermal tolerance using a Bayesian mixed modelling approach (43), further testing whether latitudinal effects on Tmin or Tmax were impacted by hemisphere and hardening status, and correcting for effects of phylogeny, sampling location, growth form, and the experimental approach used to assess tolerance. For heat tolerance, the best fit model included a significant 3-way interaction among latitude, hemisphere, and hardening status, as well as significant 2-way interactions between each of these variables: effect of latitude x hemisphere x hardening status = 0.27 [0.12 – 0.45 C.I.], *P* < 0.005; effect of latitude x hardening status = -0.32 [-0.44 – -0.16 C.I.], *P* < 0.005; effect of hemisphere (S) x hardening status = -12.39 [-16.95 – -6.28 C.I.], *P* < 0.005; effect of latitude x hemisphere (S) = -0.23 [-0.42 – -0.03], *P* = 0.01 (Fig. 2a,b). Heat tolerance declines with latitude, but, this is primarily observed in hardened individuals, and the difference in latitudinal patterns between hardened and non-hardened individuals was also driven primarily by Northern Hemisphere plants.

The best Bayesian mixed model describing latitudinal effects on cold tolerance included significant fixed effect interactions of both latitude and hemisphere with hardening status, but not a 3-way interaction among all 3 of these variables: effect of latitude x hardening status = -0.29 [-0.46 – -0.09 95% C.I.], *P* < 0.005; effect of hemisphere (S) x hardening status = 9.96 [6.58 – 13.95 C.I.], *P* < 0.005 (Fig. 2c,d). In essence, the global distribution of cold tolerance in plants exhibits the predicted latitudinal variation (better tolerance at higher latitudes), but this pattern only holds for hardened individuals. For non-hardened individuals, there is no apparent latitudinal variation in cold tolerance. Moreover, latitudinal variation in hardened individuals is driven largely by Northern Hemisphere plants, as hardening status has negligible effects on cold tolerance in the Southern Hemisphere.

As is typically found in ectothermic animals and has previously been reported in plants (25, 44), Tmax was closest to local environmental heat extremes at mid latitudes and in the Northern Hemisphere, with unhardened heat tolerances often being exceeded by local environmental thermal maxima there (SI Appendix, section x, Fig. S7). In contrast, Tmin was at greatest risk for increasing cold snaps at high latitudes in both hemispheres, where estimated Tmin values, especially unhardened, already often fail to protect individuals against extremes of local environments (SI Appendix, section *x*, Fig. S7).

Environmental predictors of cold and heat tolerances

After correcting for phylogeny, geographic distance, growth form, and experimental approach, the best Bayesian mixed model describing environmental effects on Tmax included significant interactions of mean annual temperature and temperature seasonality with hardening status (effect of mean temperature x hardening status = 0.24 [0.13 – 0.37 C.I.], *P* < 0.005; effect of seasonality x hardening status = 0.53 [0.13 – 0.90 C.I], *P* < 0.005). Hardened heat tolerance increased at higher values of temperature mean and seasonality, but non-hardened heat tolerance was not positively affected by these environmental variables (SI Appendix, Fig. S8). However, combined fixed effects of environment and hardening status explained very little of the variation in heat tolerance overall (Fig. 3).

The best Bayesian mixed model describing environmental effects on Tmin included significant interactions between fixed effects of mean annual temperature and temperature seasonality of the site, with hardening status (effect of mean temperature x hardening status = 0.88 [0.50 – 1.31 C.I.], $P < 0.005$; effect of seasonality x hardening status = -0.26 [-0.32 – -0.19 C.I.], $P < 0.005$; SI Appendix, Fig. S8). In effect, these environmental factors predicted variation in hardened cold tolerance (hardened Tmin was positively correlated with mean temperature, and negatively correlated with temperature seasonality), but, as for Tmax, hardening and environmental variation explained only a small proportion of the overall variance in Tmin (Fig. 3), and none at all for non-hardened Tmin, which exhibited less correlation with environmental variables (no correlation with mean temperatures, shallower correlation with temperature seasonality; SI Appendix, Fig. S8).

Global variation in thermal tolerances: Intrinsic, biogeographic, and environmental drivers

In the context of our Bayesian mixed models, we further partitioned the variance in cold and heat tolerance among fixed effects of local climate variables x hardening status, geographic and phylogenetic distances, growth form, and experimental method (Fig. 3). The total variance in heat tolerance explained by the model was 92% [36 - 149% HPD], with spatial distance having the largest effect (41% [20 – 57%]), followed by measurement method (25% [7-47%]), fixed effects of local environment and acclimation (14% [5-22%]), phylogeny (11% [4-18%]), and growth form (only 1% [0.01-5%]; Fig. 3A).

The total variance explained for cold tolerance was 81% [48% - 126% HPD], with the largest proportion of the total variance attributed to phylogeny (34% [23-48% HPD]), followed by the fixed effects of local environmental variables and hardening status (23% [16-31%]), geographic distance (12% [6-21%]), measurement method (10% [3-26%]), and very little variance explained by growth form (1% [0-5%]; Fig. 3A).

Differences in the proportional contribution of each of these factors to heat vs. cold tolerance arise in part due to differences in the total variance in these traits (greater for cold than for heat, see above and Fig. 1). The *total* variance explained by environmental factors is 11 [5-18] for heat tolerance vs. 76 [55-107 HPD] for cold; geographic distance: 32 [18-55] for heat vs. 41 [22-73] for cold; phylogeny: 9 [4-13] heat vs. 111 [61-163] cold; growth form: 1 [0.1-4] for heat vs. 5 [1-18] cold; measurement method: 21 [4-47] heat vs. 36 [2-92] cold; leaving a residual variance of 6 [5-7] for heat vs. 62 [53-71] for cold (Fig. 3B). It is evident that geographical distance, measurement method, and growth form explain similar amounts of the absolute variance for heat and cold tolerance. The larger total variance in cold tolerance is in addition explained by phylogenetic distance and local environmental factors (as well as a larger residual variance). Thus the higher phenotypic variance in cold tolerance is largely explained by phylogenetic distance and more extreme acclimation processes.

Discussion

Our knowledge of the thermal tolerance of plants is extremely limited; we found data for 1028 land plant species overall, which amounts to a mere 0.31% of the ca. 330,200 species recognised (45). This acute lack of information on the intrinsic thermal tolerances of most plants implies we have limited ability to incorporate such information in realistic predictions about how specific plant lineages will fare under future climates and how plant distributions might be altered. However, the dataset is taxonomically and geographically broad (SI Appendix, Table S5), spanning a large latitudinal rage (Fig. 1), allowing for analysis of how thermal tolerances vary globally and what might be driving this variation.

The generality of macrophysiological rules developed in animals

Overall, we found several expected macrophysiological patterns, including: greater overall and latitudinal variability in cold than heat tolerance (Janzen’s rule; Figs. 1&2; (4, 11, 14, 46)); greater acclimation potential at higher latitudes (Vernberg’s rule; Fig. 2 (4, 15)); greater effect of acclimation on cold than heat tolerance and greater acclimation ability under more extreme climatic conditions (Payne’s rule; SI Appendix, Fig. S8; (4, 47, 48)). These patterns are in agreement with previous macrophysiological “rules” primarily generated from the study of ectothermic animals.

However, we also found significant departures from the expected macrophysiological patterns. We found similar phylogenetic signal in heat and cold tolerance, but higher variance explained by phylogeny for cold than heat tolerance (Fig. 3; see SI Appendix, Table S5 for how this compares to results from animals). Variation in heat tolerance in plants was instead better explained by geographic distance, a finding that has received mixed support in animals ((7, 8, 11, 17) SI Appendix, section *xii*, Table S5). In addition, we found a stronger hemisphere effect on macrophysiological patterns, and weaker (often non-existent) evidence for the macrophysiological drivers of unhardened thermal tolerances of plants compared to animals (10, 14) (Fig. 3). We discuss our findings in detail below but, overall, differences among studies (SI Appendix, Table S5) suggest more work is required to understand what aspects of ecology, physiology, and biogeography result in different phylogenetic, spatial or hemispherical signals in heat or cold tolerance distributions across major divisions of life, as well as to establish the robustness of these differences to varying geographic and/or phylogenetic scales (and modelling approaches) of different study systems (see also SI Appendix, sections *iv* and *xii*).

Evolutionary, ecological, and biogeographical drivers of global variation in plant thermal tolerances

Our comprehensive mixed modelling approach led to a number of important conclusions. First, our models explained almost all variation in thermal tolerance for plants (81% for cold tolerance; 92% for heat tolerance). This suggests plant thermal tolerances can be understood with just a few parameters, making predictions more straightforward. Second, our findings are not an artefact of measurement method (cf. (48)). Third, our models show that phylogeny, geography and the local environment are *all* needed to explain global variation in thermal tolerances (Fig. 3). Failure to incorporate one or more of these variables decreased the explanatory power of the models overall and overestimated the importance of the factors included (SI Appendix, Table S4). For example, including only phylogenetic or geographic information inflated the importance of the included random effect, while models including neither phylogenetic nor geographic information enormously inflated the apparent importance of the local environment and acclimation status (fixed effect; SI Appendix, Table S4). This occurs partly because of spatial autocorrelation in climates, meaning that environmental effects can be confounded with effects of spatial or phylogenetic processes, if gene flow or biogeographic events produce patterns of trait variance that correlate with, but are not caused by, environmental gradients (19, 49). Our results can also be explained by the tendency of closely related lineages to occur in greater spatial proximity to each other, and thus may also inhabit more similar environments by chance, compared to more distantly related species; failing to account for direct environment effects *and* spatial distance can therefore inflate the phylogenetic signal in thermal traits (21, 50, 51). Our results clearly demonstrate that incomplete models that do not account for all potential drivers simultaneously can yield erroneous conclusions about the importance of local adaptation, evolutionary legacies, or biogeographical drivers of global variation in thermal tolerances.

At first glance, our resulting models were strikingly similar for heat and cold tolerances: similar phylogenetic signal; similar support for an evolutionary model with a central tendency (OU model); similar importance of hardening and a Northern Hemisphere distribution; similar levels of spatial autocorrelation; similar relationships with latitude (direction, not magnitude), similar environmental temperature variables ranking highest in importance and a conspicuous lack of any relationship with any precipitation variable (see SI Appendix, section *v*). However, there were major differences in the relative importance of each factor for explaining variation in heat versus cold tolerance (Fig. 3), and the parameter estimates of the OU models suggest different underlying evolutionary processes (SI Appendix, Table S3). Taken together, these results suggest that evolutionary history, particularly transitions to and within cold hardening capacity, strongly structure how plant cold tolerances are distributed globally. This is consistent with evolutionary innovations in hardened cold tolerances playing a critical role in determining plant distributions across biomes, and tropical-to-temperate transitions being key evolutionary events (30, 42). In contrast, plant heat tolerances and non-hardened cold tolerances are primarily structured spatially, likely reflecting effects of gene flow or colonisation history. The magnitude of spatial drift in heat tolerance and non-hardened cold tolerance may, however, be limited (14, 19), as indicated by the relatively strong strength of pull back to ancestral values for these traits (SI Appendix, section *vii*, Table S3). Thus, our results suggest strongly divergent underlying processes structuring global variation in heat and (hardened) cold tolerances of plants.

Implications for climate change

The importance of hardening in our data has implications for plant responses to climate change. Throughout, hardening status was found to be an important mediator of patterns of both heat and cold tolerances; we found no relationship of non-hardened thermal tolerances with latitude (Fig. 2), and weaker or no relationships with the local environment (SI Appendix, Fig. S8). Yet, non-hardened tolerances may become increasingly important under less predictable temperature fluctuations, which increase the exposure of unhardened plants to extreme weather. Particular risks suggested by our data are unseasonal cold snaps at high latitudes, and unseasonal heat waves at mid-latitudes (SI Appendix, Fig. S7, section *x*); such events are predicted to increase under future climate scenrios (52). An inability of plants to cope with higher or unseasonable temperatures under future warning can affect the functioning of entire ecosystems (53, 54). These changes have consequences not only for the future survival and distributions of plants, but for the animals and people that depend on them too. For example, substantial losses to winegrowing areas have been predicted from even modest warming (55), and freezing damage to grain crops due to changing weather patterns is already a serious economic problem (56). Understanding the ecological role of thermal safety margins must therefore focus on thermal tolerance traits, as well as how they interact with and trade off against traits that influence other aspects of plant survival, productivity and reproduction.

Methods

Dataset construction

Suitable literature was identified using Web of Science and Google Scholar, employing search strings including combinations of: “heat”, “cold”, “temperature”, “limits”, “tolerance”, “metabolic”, “respiration”, “photosynthesis”, “physiological”, “chill”, “freeze”, “critical” and “lethal”. We also searched citing and cited references of relevant articles. The search was carried out between October 2017 and January 2018. For reviewing articles, e.g. (24), we referred to the original study where possible. For articles not written in English, we used Google Translate (https://translate.google.com) to extract relevant methodological details. Across studies, thermal tolerances were estimated on a variety of scales, but mostly included

LT50 under heat or cold stress, assessed visually via stain uptake or electrolyte leakage assessments (n= 439 heat, n = 512 cold), LT100 (n= 8 heat, n=37 cold), Tcrit (n=177 heat), Tmax (n=340 heat), freezing resistance (n=183 cold), freezing tolerance (n=22 cold), or unknown, i.e. where the methods were insufficiently recorded (n=14). We also recorded hardening status (heat/cold acclimation; n=594 hardened vs. n=212 non-hardened and n=928 records where no information was provided). Where stated, we also separated whether hardening was induced in the lab (n= 51 heat, n= 249 cold), field (warming: n= 6 heat), or greenhouse (n=36 cold) or was the result of natural seasonal variation (n= 356 heat, n= 106 cold). Additional data exploration with respect to experimental approach is provided in the SI Appendix (section *iii*).

Environmental variables

Climatic data for the spatial coordinates of the collection localities for each thermal tolerance estimate were extacted using the bioclim environmental layers (58) at the 10' resolution using the raster package for R (59, 60). Elevational data for each point were extracted from the USGS GMTED2010 digital elevation model at the 30" resolution (61). Where the elevation of a sampling location was reported in the original report, we used this value. We further extracted distance from the nearest coastline from the NASA oceancolor dataset, at the 0.01° resolution (62).

Growth form, taxonomic and phylogenetic information

Taxonomic designations at the family, genus and species levels were updated using the taxize package for R, based on the TNRS and NCBI databases (63–65). The taxonomy was further verified using the World Checklist of Selected Plant Families (WCSP, http://wcsp.science.kew.org), Tropicos (www.tropicos.org) and The Plant List (http://www.theplantlist.org/). Broad classifications were then assigned as follows: bryophytes (liverworts and mosses), lycophytes, 'ferns' (ferns and horsetails), gymnosperms, and angiosperms. Using online floras and the WCSP we further recorded the growth form of each species as woody perennial (including trees [>10m height] and shrubs [< 10m]), cushion plant (herbaceous or woody), herbaceous perennial (including facultative angiosperm annuals, ferns, horsetails and lycophytes), herbaceous annual, or bryophyte (including liverworts and mosses).

Phylogenetic information was obtained from Slik et al. (39) using the Phylomatic query tool (66). For fitting phylogenetic trait evolution models, branch lengths were set to 1. For fitting phylogenetic mixed models, an ultrametric tree of unit height was generated with a default smoothing parameter of 1, under a correlated substitution model, using the chronos() function in ape (67).

Statistical Analyses

Phylogenetic signal and trait evolution analyses for heat and cold tolerance

Phylogenetic signal and the best evolutionary model for cold and heat tolerances were assessed using several models founded in Brownian motion (BM; SI Appendix, sections *vi-viii*). Models were fitted on the complete dataset and separately for hardened and non-hardened subsets using Geiger (68) and compared using AICc (69). To visualise the phylogenetic distribution of each trait (SI Appendix, Fig. S4), each tree was rescaled with the estimated phylogenetic signal (λ) in Geiger and then ancestral states were reconstructed on the rescaled tree using 'fastAnc' in Phytools (60, 70).

Spatial autocorrelation in heat and cold tolerance

Spatial autocorrelation was tested using Moran's *I* and a randomization test to determine the significance of spatial autocorrelation at each distance class, using ncf (71). We evaluated spatial autocorrelation separately for each broad taxonomic group, as well as a combined estimate across all of our data. We also examined spatial autocorrelation of hardened vs. non-hardened tolerances separately (SI Appendix, section *ix*). Significance of spatial autocorrelation at each distance class was assessed using a Bonferroni correction for the number of distance classes tested (n=10 distance classes, α = 0.005). Further testing for effects of geographic distance on thermal tolerance was conducted in a mixed model framework simultaneously accounting for phylogeny and local environments (see below).

Global variation in thermal tolerances: Latitudinal trends

Bayesian linear mixed effects models were fit using MCMCglmm (43), fitting either Tmin or Tmax as the response variable, and including latitude, hemisphere, hardening status (and hardening method; see SI Appendix, section *iii*, Fig. S3) and all interactions as fixed effects. An inverse phylogenetic similarity matrix was fit as a random effect to account for autocorrelation due to phylogenetic distance, and additional random effects were included to account for growth form, effects of shared sampling locations (concatenated Lat/Long), and the methodological approach used to estimate Tmin or Tmax. We used an Inverse Wishart prior for random and residual terms with V=1 and nu=1.002, and a normal prior for fixed effects. We also assessed model outputs for qualitatively similar outcomes after specifying a prior to account for potential correlations among fixed effects and using parameter-expanded priors for random effects. All MCMC chains were run with a length of 1,000,000, burnin of 50,000 and thinning interval of 5000. This was sufficient to achieve model convergence and avoid temporal autocorrelation among the posteriors. DIC was used to select the best combination of fixed effects.

To address the lack of non-vascular plants in the Slik et al. phylogeny, we replicated these analyses on the full dataset using a maximum likelihood approach in lme4 and lmerTest R packages (72, 73). A taxonomic correction was applied, with separate random effects for higher-order taxonomic group (e.g. class or unranked higher clade), family, genus, and species, and additional random effects for growth form, location, and thermal tolerance assessment methodology as described above. AICc was used for model comparison. Results of these models were similar to those from the Bayesian models (SI Appendix, section *x*).

We further plotted latitudinal variation in Tmin and Tmax against local values of maximum and minimum environmental temperatures (BioClim Bio5 and Bio6), to visually assess latitudinal variation in tolerance to climate extremes in plants (SI Appendix, Fig. S7).

Global variation in thermal tolerances: Intrinsic, biogeographic, and environmental drivers

We next partitioned the variation in each of heat and cold tolerance among factors representing the local environment versus phylogenetic or spatial distance. Models were run in MCMCglmm, implementing fixed effects of environmental variables and hardening status, plus phylogenetic and geographic similarity matrices, and additional random effect terms for tolerance measurement method and growth form. For the geographic similarity matrix, we calculated great circle distances using geosphere (74). We then constructed a Gaussian spatial kernel of the distances, $K=\mathrm{e}^{-h\text{*distance\^{}2}}$ (75), with the value of the tuning parameter (h) determined via optimisation (76). For both heat and cold tolerance the optimal value for h was 9e-13. To identify climatic drivers of thermal tolerances, we included temperature (bio1 – mean temperature, bio2 – diurnal temperature range, and bio4 – temperature seasonality) and precipitation (bio12 – annual precipitation, and bio15 – precipitation seasonality) as fixed effect variables, as well as effects for elevation and distance from the coast, which might capture elements of alpine or maritime climates not reflected in extracted temperature and precipitation qualities. Interactions of these with hardening status were also tested. The best combination of these environmental covariates was determined using DIC and significance of effects. Priors and chain lengths were established as described above. The proportion of variance in heat or cold tolerance explained by fixed effects versus each random effect in the final models was calculated using the Nakagawa and Schielzeth approach (77).

Data availability:

The global dataset of gplant thermal tolerances generated for and analysed within this study is appended to Supplementary Information (SI Dataset).

Acknowledgments:

We thank Mark Adams for providing code to optimise spatial distance kernels, and Jake Alexander, Per-Ola Karis, members of the BES Macroecology SIG, and members of the Bolin Centre for Climate Research (Research Area 8) for helpful discussions.

Supplementary Information:

SI Appendix
SI Dataset

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Figures and Tables

Figure 1. Global variation in plant thermal tolerances – distribution of data. (A and B) Geographic distribution of (A) heat and (B) cold tolerance measurements (n=769 for Tmin, n=966 for Tmax). The size of the circles is proportional to the number of data points it represents and ranges from 1 to 114 measurements at the same location for heat and cold tolerance together. Colour hues are used for visibility but do not indicate hardening status (c.f. C and D). Most thermal tolerance data are from North America, Europe, Australia and New Zealand with virtually no records from Africa or Asia. (C and D) Variation in thermal tolerance among (C) major groups (gymnosperms, angiosperms, ferns, lycophytes and bryophytes) and (D) growth forms (woody perennials, herbaceous perennials, cushion plants, annuals and bryophytes). 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. In (C) data for Northern (black frame) and Southern (grey frame) Hemispheres are plotted separately. Vertical dashed lines denote the standard deviation across all data for each of heat and cold tolerance, which is wider for cold than heat tolerance.

Figure 2. Latitudinal clines in plant thermal tolerances. Latitudinal clines are largely driven by Northern Hemisphere plants in the hardened state, and likely reflect the combined influences of phylogenetic, biogeographic, and local adaptation processes (see Fig. 3; SI Appendix, Figs. S4-S6 for graphical depictions of these contributing factors). 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. Plotted relationships are

marginal effects of climate x hardening status from reported models (see Main text).

Figure 3. Variance partitioning of heat and cold tolerance among environmental effects (including hardening status), geographical distance, phylogenetic distance, growth form, experimental protocol, and residual variance (dots and whiskers represent mean values ± HPD from the reported Bayesian analyses). (A) *Proportional* variance in heat (red) and cold (blue) tolerance explained by each factor. (B) *Total* variance in heat (red) and cold (blue) tolerance explained by each factor. Geographical, experimental and growth form effects account for similar amounts of the total variance in heat and cold tolerance, with the higher total variance in cold tolerance (Fig. 1) largely being explained by environmental and phylogenetic effects (plus a higher residual variance). However, a significantly higher *proportion* of the overall variance in heat tolerance is explained by geography, with a significantly higher *proportion* of the variance in cold tolerance being explained by phylogeny (plus residual variance). Other factors account for a similar proportion of the variance in both heat and cold tolerance. Thus, the single most important factor for explaining global variation in heat tolerance among land plants is geographical proximity, while the single most important factor for explaining variation in cold tolerance is phylogenetic relatedness.

Figure 1:

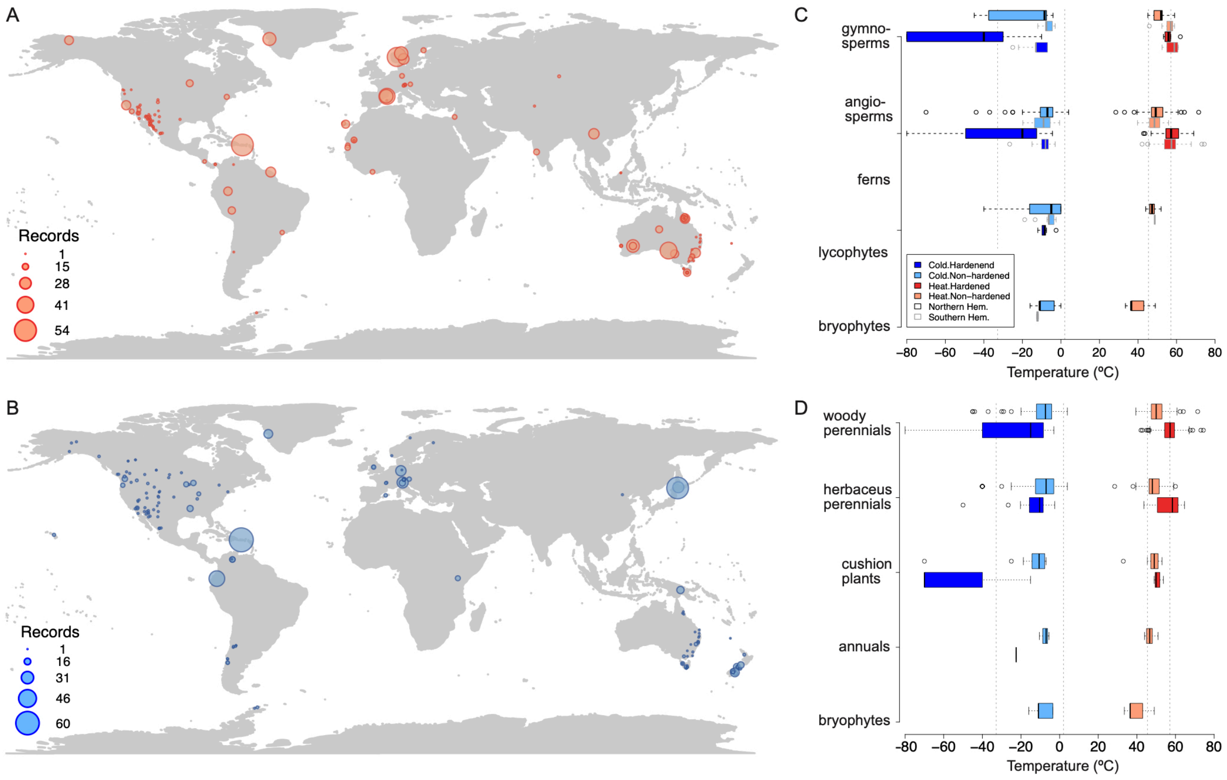

A
Records
1
15
28
41
54
B
Records
1
16
31
46
60
C
gymno-
sperms
angio-
sperms
ferns
lycophytes
bryophytes
Cold.Hardenend
Cold.Non–hardened
Heat.Hardened
Heat.Non–hardened
Northern Hem.
Southern Hem.
−80
−60
−40
−20
0
20
40
60
80
Temperature (ºC)
D
woody
perennials
herbaceus
perennials
cushion
plants
annuals
bryophytes
−80
−60
−40
−20
0
20
40
60
80
Temperature (ºC)

Figure 2:

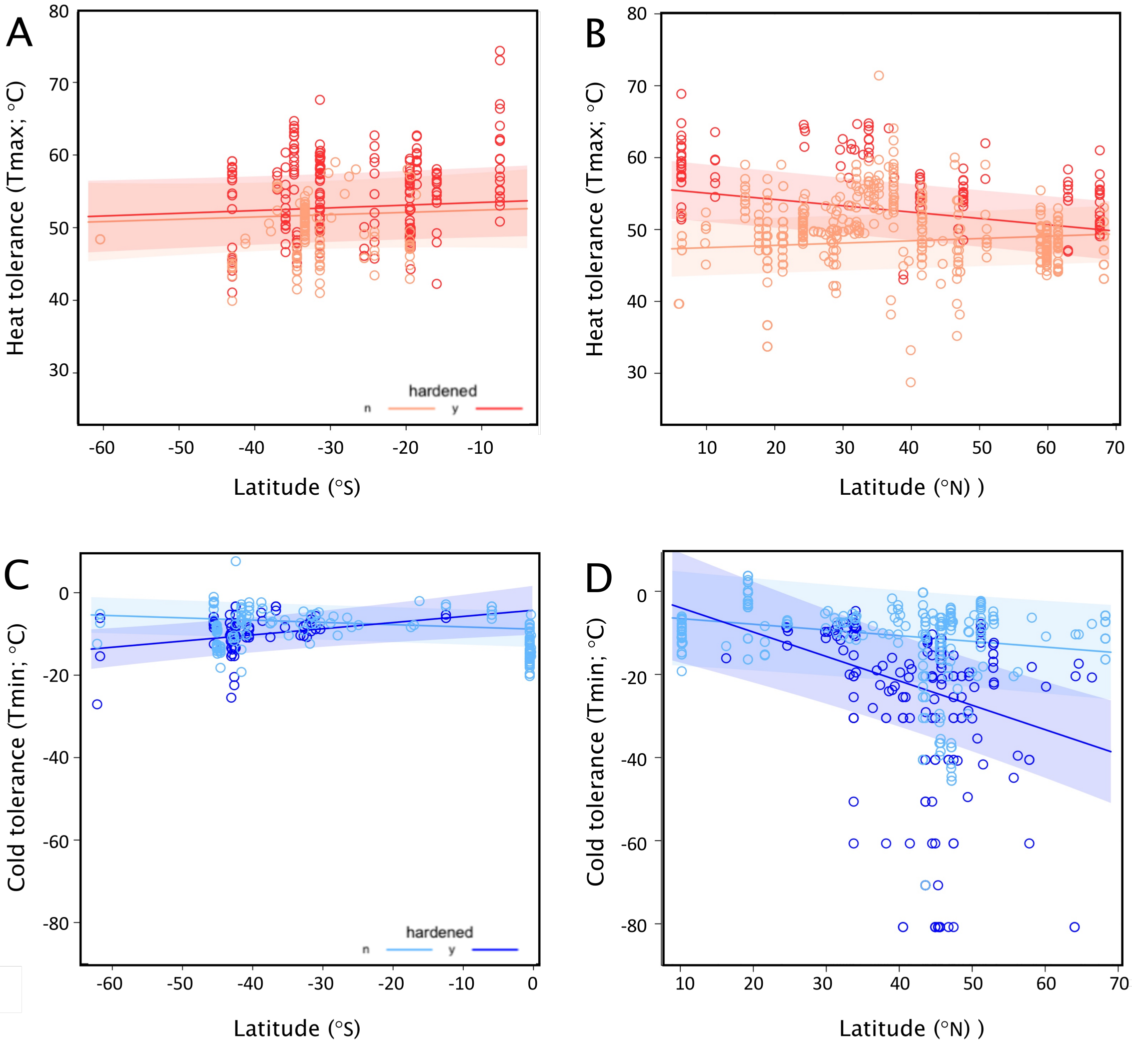
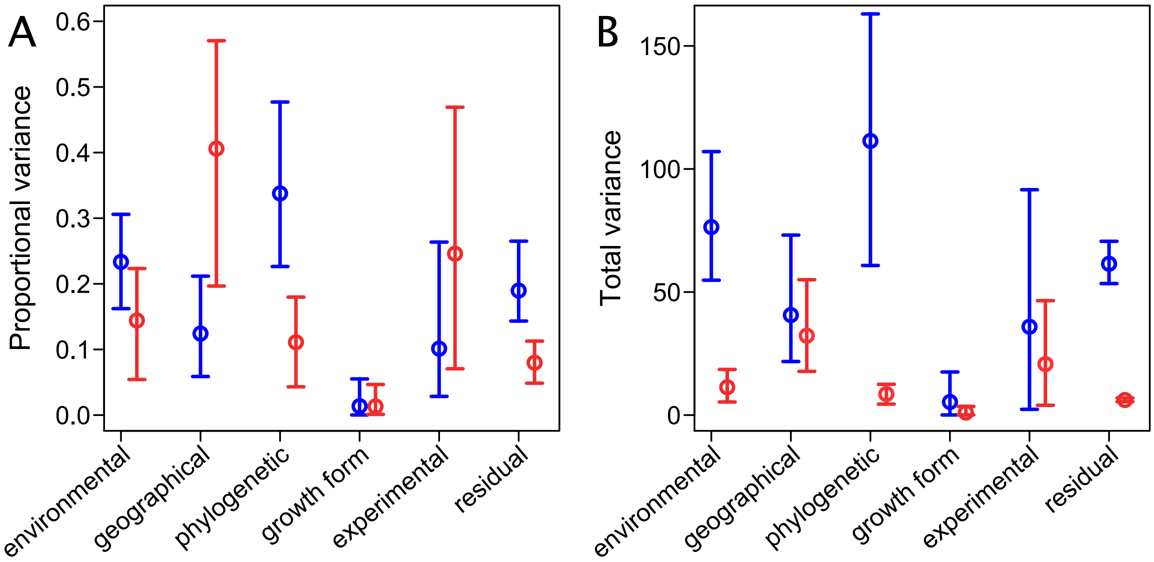

A
Heat tolerance (Tmax; °C)
80
70
60
50
40
30
hardened
n
y
-60
-50
-40
-30
-20
-10
Latitude (°S)
B
Heat tolerance (Tmax; °C)
80
70
60
50
40
30
10
20
30
40
50
60
70
Latitude (°N))
C
Cold tolerance (Tmin; °C)
0
-20
-40
-60
-80
hardened
n
y
-60
-50
-40
-30
-20
-10
0
Latitude (°S)
D
Cold tolerance (Tmin; °C)
0
-20
-40
-60
-80
10
20
30
40
50
60
70
Latitude (°N))

Figure 3:


A
B
Proportional variance
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Total variance
0
50
100
150
environmental
geographical
phylogenetic
growth form
experimental
residual

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 cold and heat tolerances

The distribution of 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 overall (Figure S1), our data captures 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 that 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 massively 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 in future research. Crucially, future studies should focus on the extent to which hardening increases tolerance of thermal extremes and how, and how often, this 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). The dataset indicates 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. The 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).

	Tmin	*Tmax*
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:

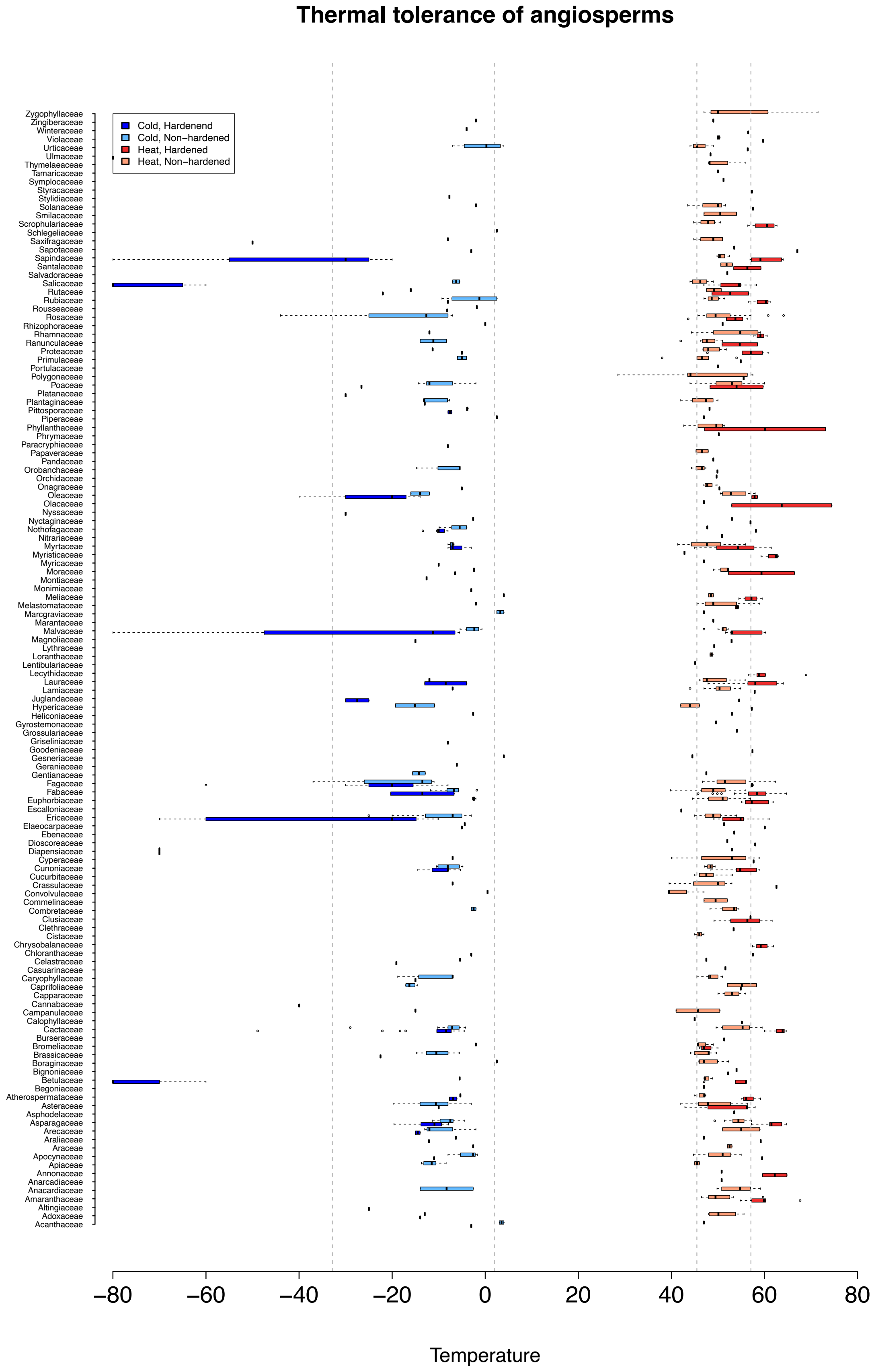

Thermal tolerance of angiosperms
Cold, Hardenend
Cold, Non–hardened
Heat, Hardened
Heat, Non–hardened
Zygophyllaceae
Zingiberaceae
Winteraceae
Violaceae
Urticaceae
Ulmaceae
Thymelaeaceae
Tamaricaceae
Symplocaceae
Styracaceae
Stylidiaceae
Solanaceae
Smilacaceae
Scrophulariaceae
Schlegeliaceae
Saxifragaceae
Sapotaceae
Sapindaceae
Santalaceae
Salvadoraceae
Salicaceae
Rutaceae
Rubiaceae
Rousseaceae
Rosaceae
Rhizophoraceae
Rhamnaceae
Ranunculaceae
Proteaceae
Primulaceae
Portulacaceae
Polygonaceae
Poaceae
Platanaceae
Plantaginaceae
Pittosporaceae
Piperaceae
Phyllanthaceae
Phrymaceae
Paracryphiaceae
Papaveraceae
Pandaceae
Orobanchaceae
Orchidaceae
Onagraceae
Oleaceae
Olacaceae
Nyssaceae
Nyctaginaceae
Nothofagaceae
Nitrariaceae
Myrtaceae
Myristicaceae
Myricaceae
Moraceae
Montiaceae
Monimiaceae
Meliaceae
Melastomataceae
Marcgraviaceae
Marantaceae
Malvaceae
Magnoliaceae
Lythraceae
Loranthaceae
Lentibulariaceae
Lecythidaceae
Lauraceae
Lamiaceae
Juglandaceae
Hypericaceae
Heliconiaceae
Gyrostemonaceae
Grossulariaceae
Griseliniaceae
Goodeniaceae
Gesneriaceae
Geraniaceae
Gentianaceae
Fagaceae
Fabaceae
Euphorbiaceae
Escalloniaceae
Ericaceae
Elaeocarpaceae
Ebenaceae
Dioscoreaceae
Diapensiaceae
Cyperaceae
Cunoniaceae
Cucurbitaceae
Crassulaceae
Convolvulaceae
Commelinaceae
Combretaceae
Clusiaceae
Clethraceae
Cistaceae
Chrysobalanaceae
Chloranthaceae
Celastraceae
Casuarinaceae
Caryophyllaceae
Caprifoliaceae
Capparaceae
Cannabaceae
Campanulaceae
Calophyllaceae
Cactaceae
Burseraceae
Bromeliaceae
Brassicaceae
Boraginaceae
Bignoniaceae
Betulaceae
Begoniaceae
Atherospermataceae
Asteraceae
Asphodelaceae
Asparagaceae
Arecaceae
Araliaceae
Araceae
Apocynaceae
Apiaceae
Annonaceae
Anarcadiaceae
Anacardiaceae
Amaranthaceae
Altingiaceae
Adoxaceae
Acanthaceae
−80
−60
−40
−20
0
20
40
60
80
Temperature

Figure S1B:

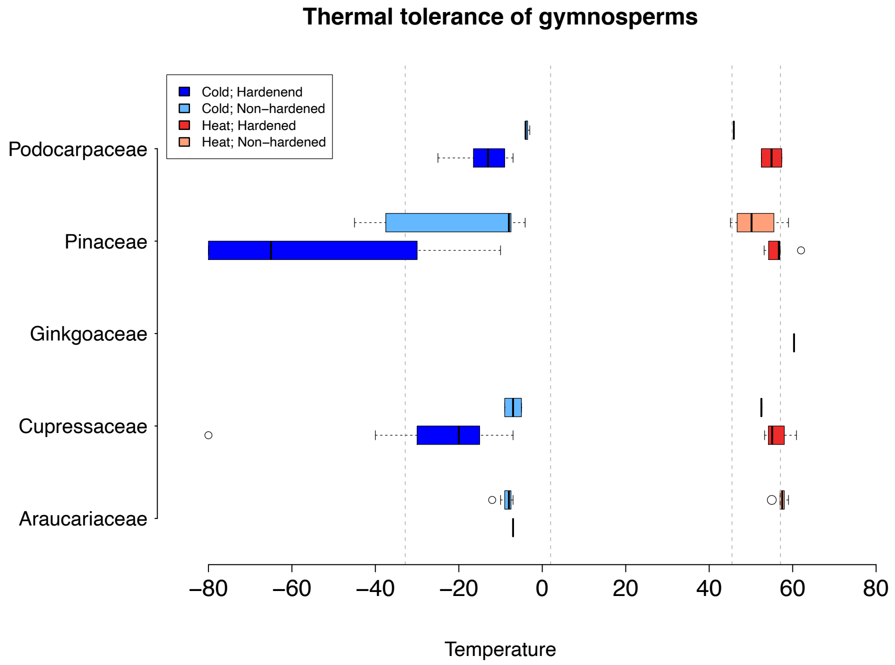


Figure S1C:

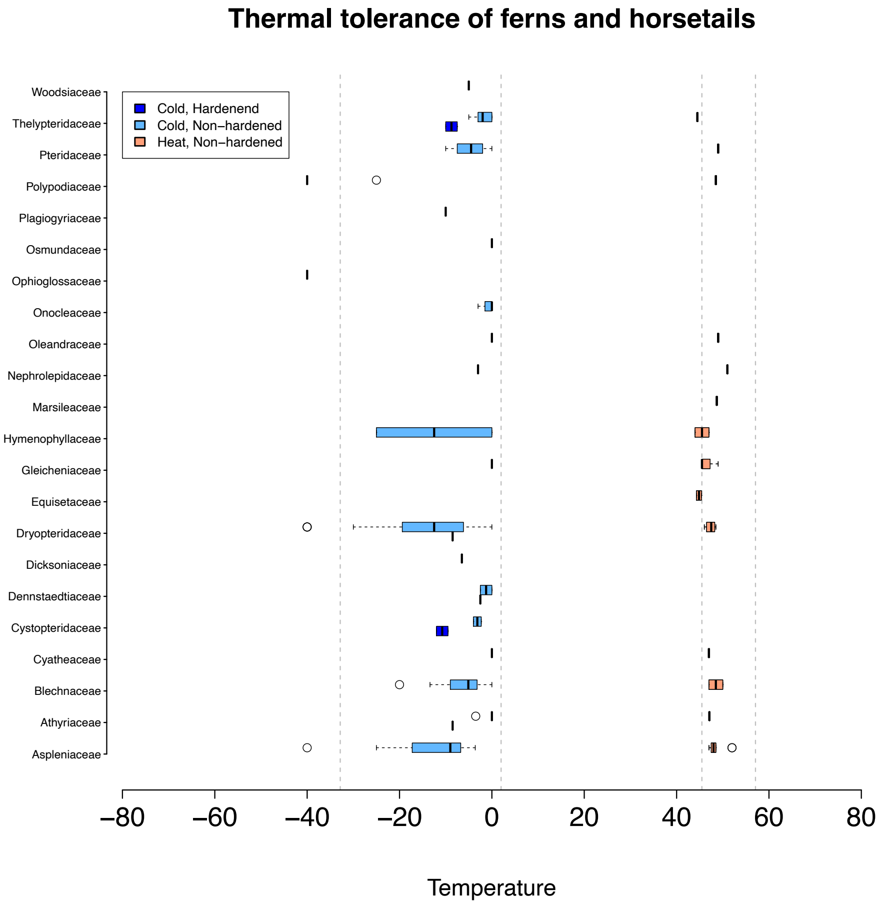
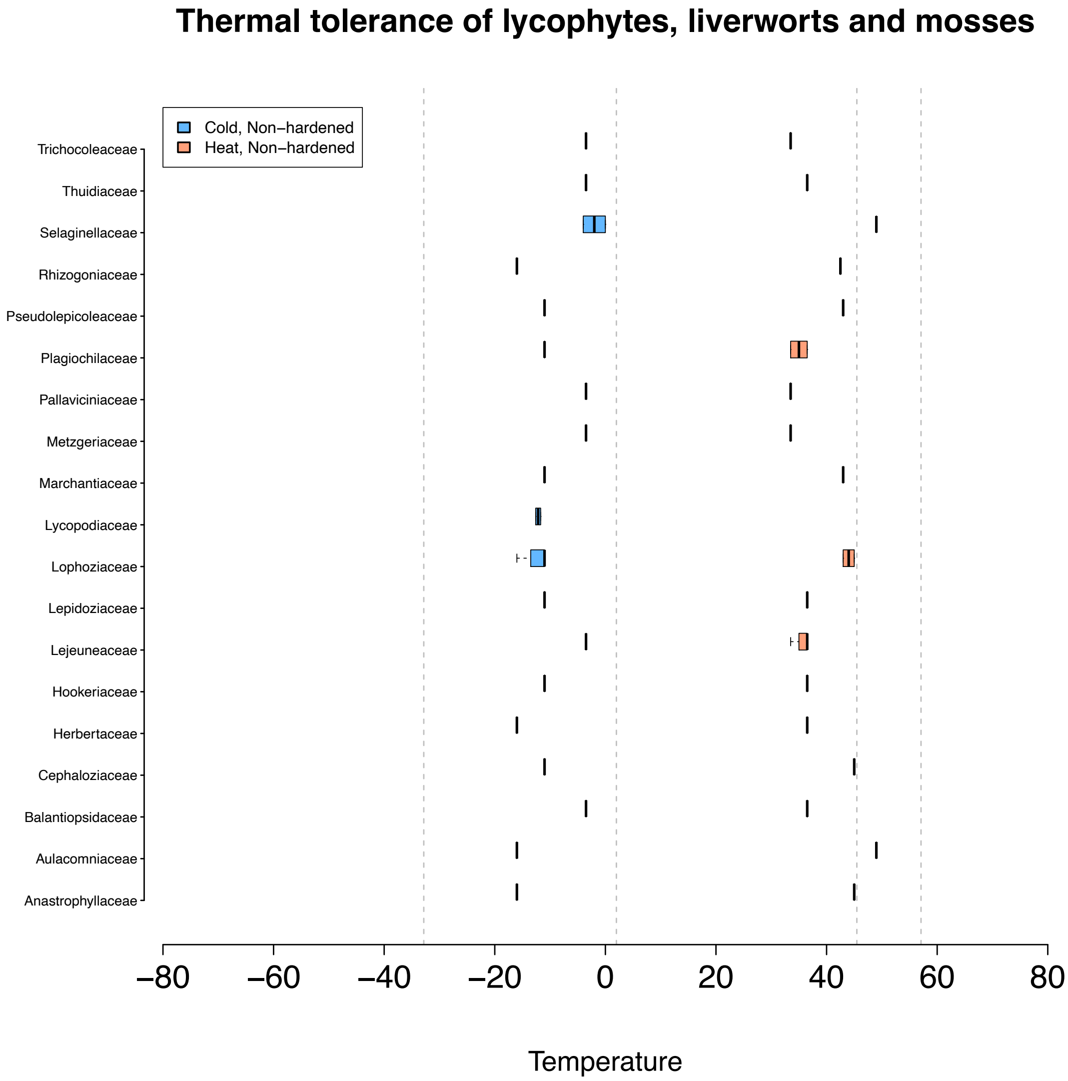


Figure S1D:


Thermal tolerance of lycophytes, liverworts and mosses
Cold, Non−hardened
Heat, Non−hardened
Trichocoleaceae
Thuidiaceae
Selaginellaceae
Rhizogoniaceae
Pseudolepicoleaceae
Plagiochilaceae
Pallaviciniaceae
Metzgeriaceae
Marchantiaceae
Lycopodiaceae
Lophoziaceae
Lepidoziaceae
Lejeuneaceae
Hookeriaceae
Herbertaceae
Cephaloziaceae
Balantiopsidaceae
Aulacomniaceae
Anastrophyllaceae
−80
−60
−40
−20
0
20
40
60
80
Temperature

ii. Effect of growth form on thermal tolerances

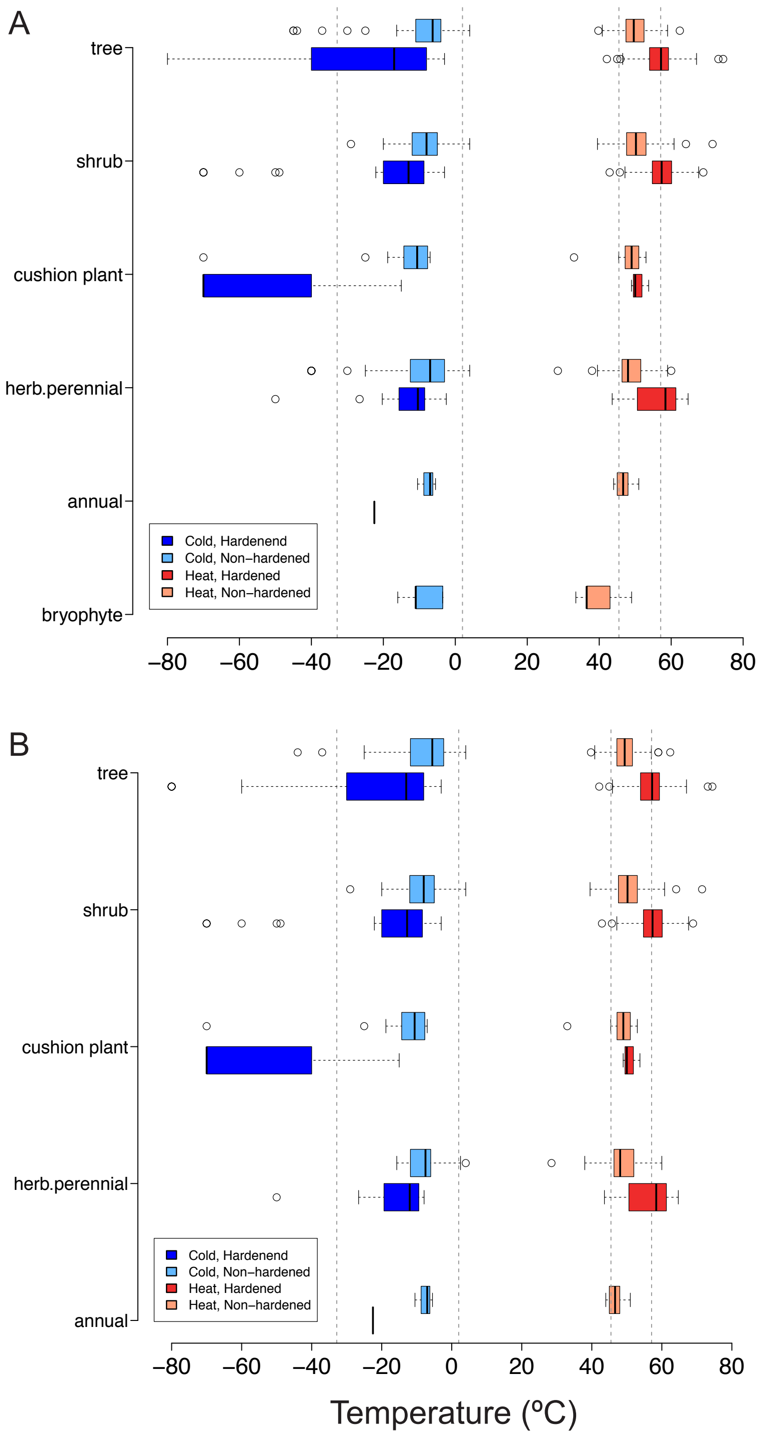
Among growth form categories, the database includes thermal tolerance records for herbaceous annuals (n=39; all of which are angiosperms), herbaceous perennials (n=420; including herbaceous angiosperms, ferns, horsetails and lycophytes; and all monocots except palms [Arecaceae]), woody perennials (n=1167; 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 Tmin and Tmax:

The included studies used a variety of measures to test physiological tolerances of plant tissues to temperature extremes. For Tmax, this was typically accomplished by pursuing one of the following measurements: Tcrit, the temperature at which photosynthetic and respiratory machinery begin to sustain damage (6); Tmax, 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 Tmin, 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 Tmax or Tmin 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, Tmax measures which record more advanced states of tissue damage (i.e., LT100) 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 Tmin and Tmax overall, in comparison to the other, underpinning phylogenetic, spatial, and local environmental patterns and processes (Main text Figure 3).

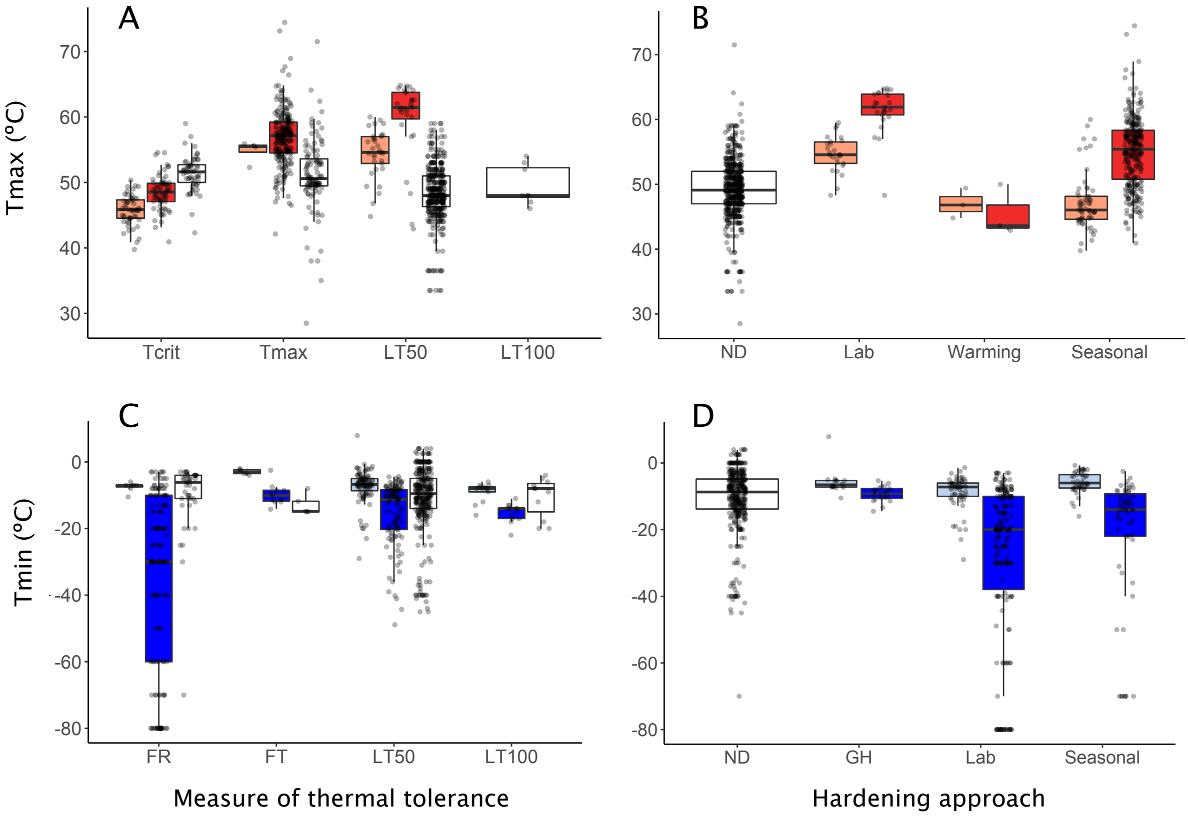
(b) Experimental approaches to hardening:

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, supplemental data 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 study region (see supplemental data references).

Laboratory acclimation was associated with overall higher values of Tmax and lower values of Tmin 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 Tmin and Tmax 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 Tmin or Tmax, in comparison to other factors in the model, was very low (mean proportion of variance in Tmin which was due to hardening approach = 0.02 [0.0006 – 0.07 HPD], for Tmax, 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 hardening approach (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, short term 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 Tmin and Tmax

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 found that the greatest tolerance was observed among diverse taxa, exhibiting highly divergent leaf characteristics and habitat affinities (Figure S1).

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 temperate 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 the 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). 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 λ (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 (κ, 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, λ, κ and OU-1 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-1 models are shown in Table S3. The OU1 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 (λ). In contrast, for most cold tolerance analyses, the second best model was the kappa (κ) model of punctuated evolution, but this model was not statistically supported. Parameter estimates for the OU1 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 (κ) 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. Phylogenetic model fit comparison, 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 (λ=1)	4241.00	1628.64	480.70	2443.02	4035.32	1733.56	432.62	2187.16
LAMBDA	4029.10*	1518.23*	**456.75***	2353.79	3943.13	1716.27	413.65*	2167.94
WHITE (λ=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	3892.47	1673.81	426.37	2115.79
OU-1	**4026.39***	**1515.39***	458.58*	**2320.58***	**3858.02***	**1669.29***	**410.65***	**2084.28***

Lowest AICc score shown in bold; second best model underlined; asterisks denote significantly best model(s) overall (based on ΔAICc ≥ 3).

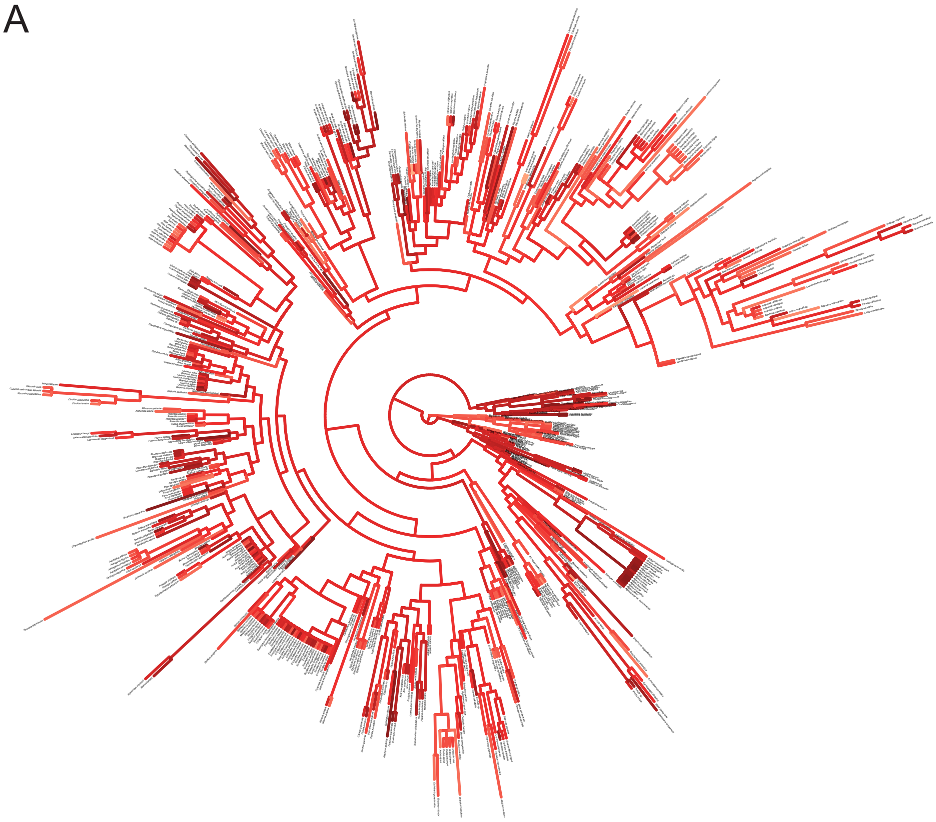
Table S3. Parameter estimates under OU models.

		HEAT				COLD		
	All	Hardened	Non-hard	No.info	All	Hardened	Non-hard	No.info
Z_0 (ºC)	52.2	56.8	48.7	49.7	-13.9	-22.0	-7.10	-9.04
α	0.30	0.42	0.14	0.23	0.32	0.24	0.19	0.31
σ^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'; σ^2 = rate of change through random walk process (stochastic change); α = 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, λ, 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



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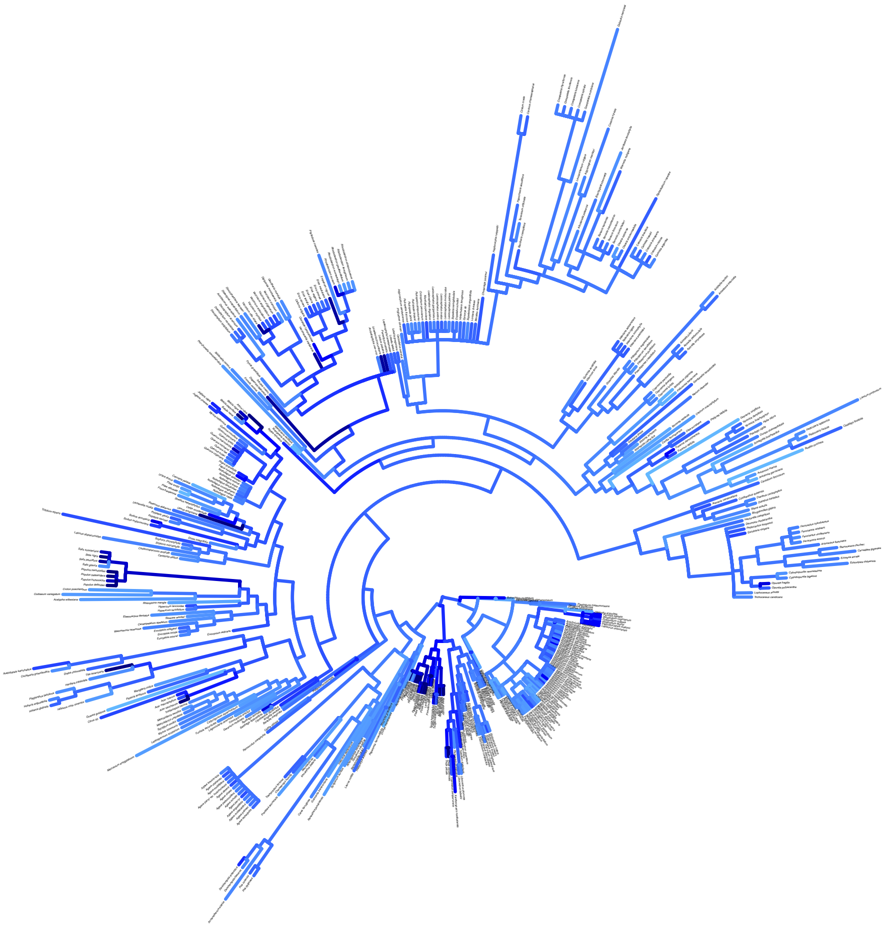
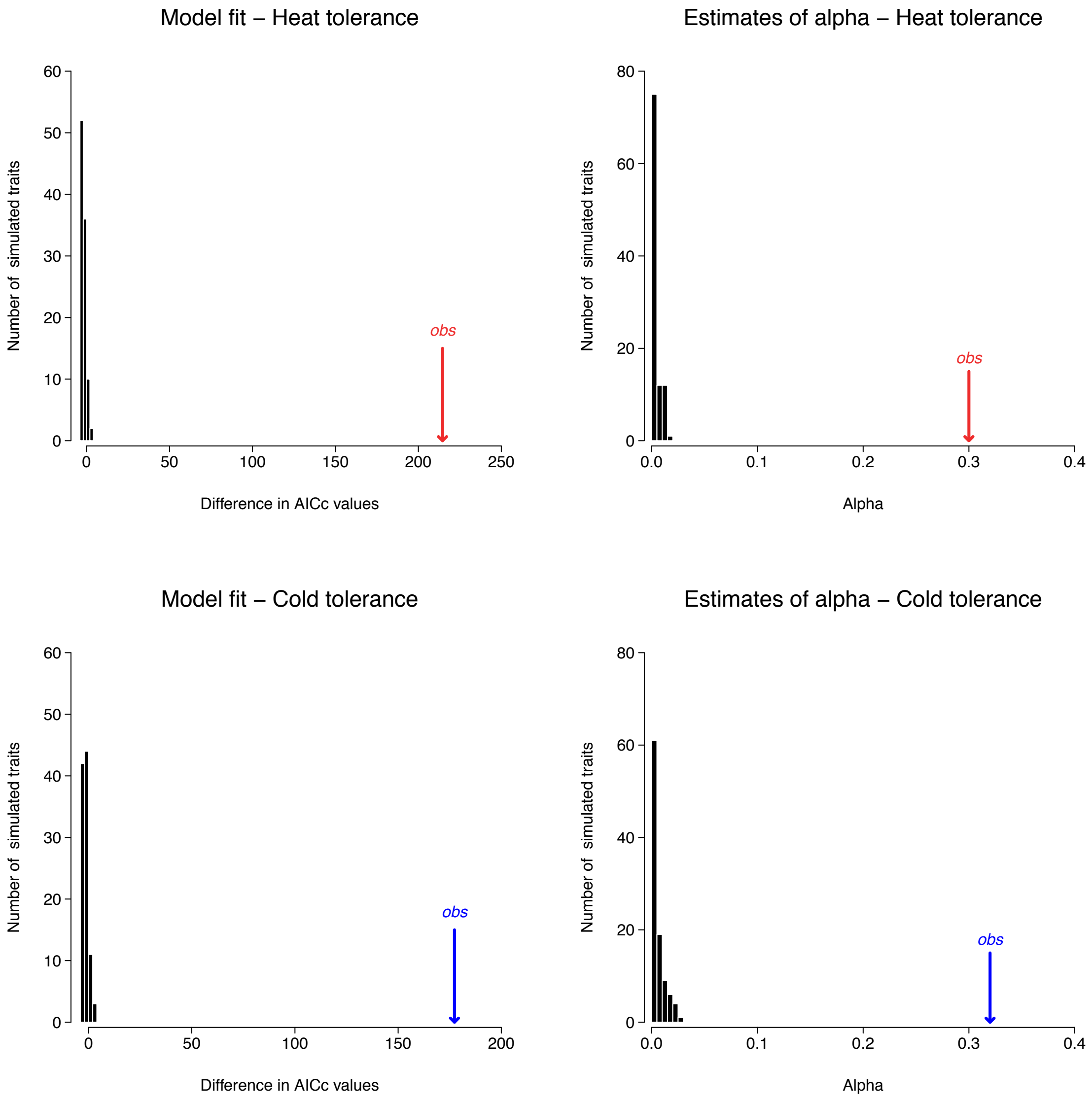


viii. Testing for type I errors in fitting OU models

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: ΔAICc = 214.6, cold: ΔAICc = 177.0) than for simulated data (heat: -1.41 [-2.02–1.69], cold: -1.26 [-2.03–2.43]; Figure S5). The low ΔAICc 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 ΔAICc values; heat: 12% of traits, cold: 14%), this was only ever on weak statistical grounds. Similarly, estimates of α 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 data is therefore unlikely to be a result of statistical error.

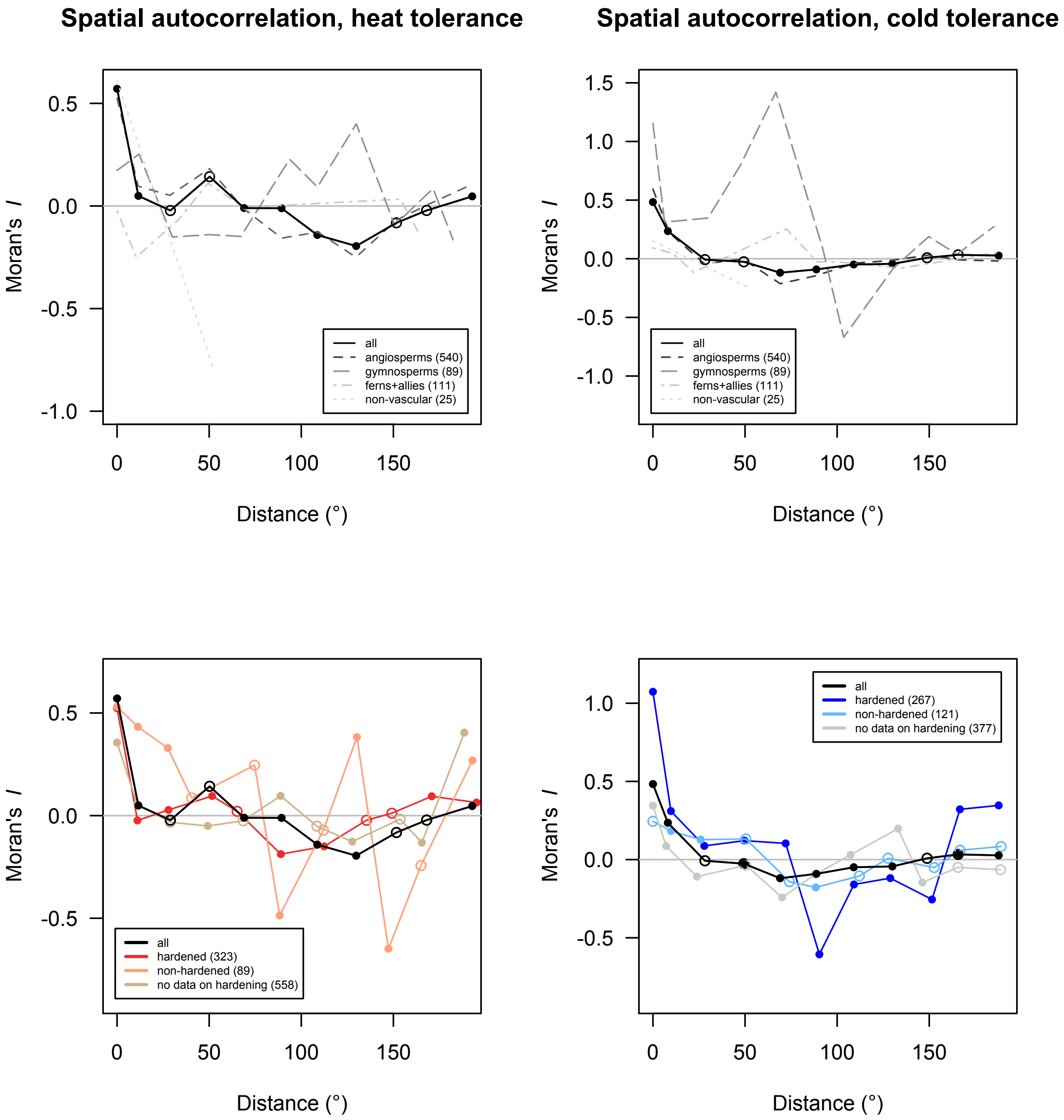
Figure S5. Model fit (difference in AICc scores, left column) and estimates of the parameter alpha (right column) for 100 traits simulated under BM on the trees for heat (upper row) and cold tolerance (lower row). Analysis of observed data (coloured arrows) give very different results compared to simulated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



ix. Patterns of 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 ~ 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

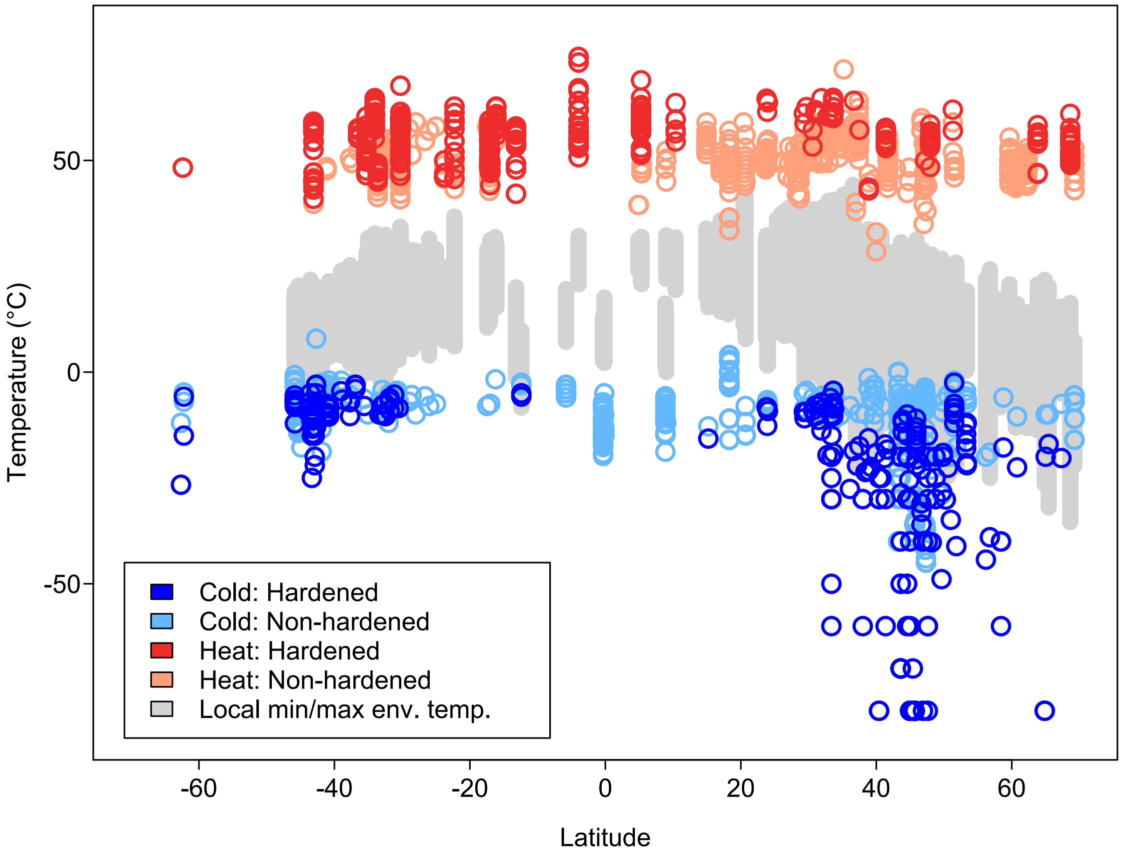
In the context of REML mixed models accounting for taxonomy, growth form, and methodology of Tmin assessment, the best model describing latitudinal effects on cold tolerance included significant interactions of both latitude and hemisphere with hardening status: effect of latitude x hardening status on cold tolerance = -0.29±0.11, t = -3.14, $P = 0.002$; effect of hemisphere x hardening status = 11.80±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±0.09, t = 4.95, $P < 0.0001$; effect of latitude x hardening status = -0.42±0.08, t = -5.96, $P < 0.0001$; effect of hemisphere (S) x hardening status = -16.48±2.99, t = -5.50, $P < 0.0001$; effect of latitude x hemisphere (S) = -0.40±0.09, t = -4.62, $P < 0.0001$.

(b) Latitudinal patterns in the context of climate extremes

We found that Tmax 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. 20º-40º lat) for both animals and plants (8, 44, 45), whereas others have found the highest vulnerabilities at tropical latitudes (<23º 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 available 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, Tmin appear to be at greatest risk for increasing cold snaps at high latitudes in both hemispheres, where estimated Tmin 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 (coloured 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).

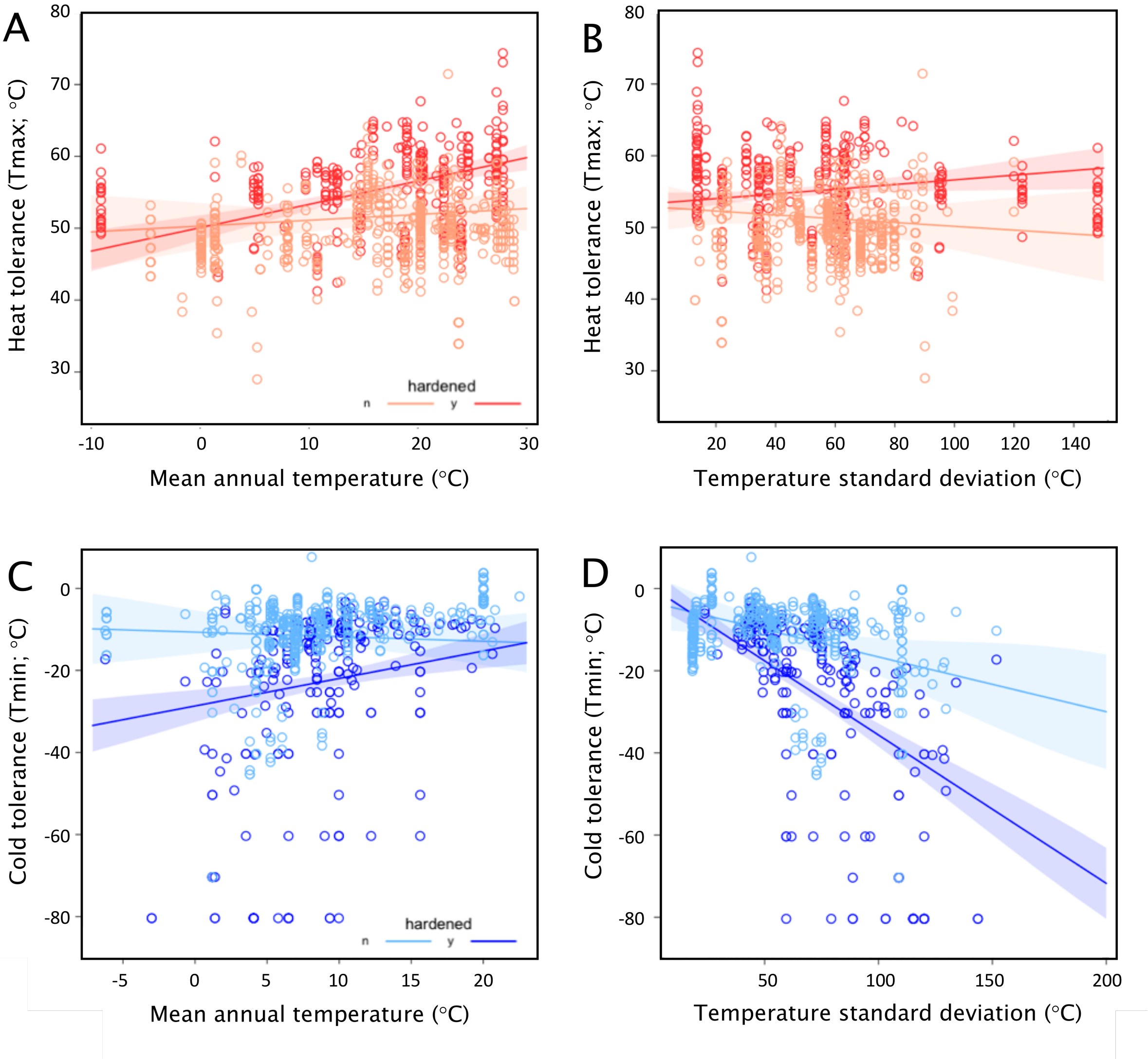


xi. Model comparisons (Global variation in thermal tolerances: Intrinsic, biogeographic, and environmental drivers).

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 Tmin and Tmax 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 Text *xii*, Table 5). Presented values are mean estimates and Highest Posterior Density (HPD) intervals of proportional variance explained by each factor, calculated using (50, 51), see main text methods for details.

	Full model	Geography only	Phylogeny only	Environment only
Cold tolerance				
Env. x hardening	0.23 [0.16-0.31]			**0.37 [0.22-0.50]**
Hardening only		**0.03 [0.02-0.05]**	**0.03 [0.02-0.05]**	
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]	**0.55 [0.32-0.77]**	–	–
Phylogenetic	0.34 [0.23-0.48]	–	**0.66 [0.53-0.78]**	–
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]	**0.38 [0.21-0.48]**
Heat tolerance				
Env. x hardening	0.14 [0.05-0.22]			**0.25 [0.14-0.32]**
Hardening only		**0.09 [0.04-0.15]**	**0.03 [0.01-0.04]**	
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]	**0.57 [0.33-0.72]**		
Phylogenetic	0.11 [0.04-0.18]		**0.53 [0.34-0.68]**	
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]	**0.52 [0.36-0.65]**

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 Tmin to correlate more strongly with climate than Tmax (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 Text *xi*; Table S4).

Another example of a well-established pattern is that Tmin is more variable overall and declines more steeply with latitude than Tmax (e.g. (38, 53, 54); this study). However, the opposite has also been found, with Tmax being *more variable* than Tmin 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 Tmax (37, 38) but, for lizards and plants, similar (high) phylogenetic signal has been measured for Tmax and Tmin ((44); this study). Furthermore, for both these groups *spatial distance* is more important than phylogeny for explaining the overall variance in Tmax ((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, 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

				Predictor(s) of Tmax[1,2]			Predictor(s) of Tmin[1,2]			
Study	**Taxon sampling (n species)**	**Approach**	**Findings**	**Spatial distance**	**Phylo. distance**	**(Local) climate**	**Spatial distance**	**Phylo. distance**	**(Local) climate**	**Implications**
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)[3]	Test latitudinal relationship for Tmin and Tmax; and the effect of acclimation, hemisphere and marine/ terrestrial systems.	Terrestrial: Stronger latitudinal decrease for Tmin than Tmax, especially in the in Northern Hemisphere. Marine: Less latitudinal decline overall and no difference between slopes for Tmin and Tmax.	NA	NA	NA	NA	NA	NA	Different macrophysical 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)	*Drosophila* (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)[4]	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 *greater* 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=474 measures), Lizards and Snakes (Tmin	(Phylogenetic) generalized least squares regression against	Tmin more variable overall, more plastic and more strongly correlated with ambient temperature than Tmax.	NA	(+)	(+/0)	NA	(+)	(+)	Differences apparent between taxonomic groups regarding patterns of

	n=368 measures); across fewer species	ambient temperature. Calculated phylogenetic signal in Tmax and Tmin.	Insects: higher phylogenetic signal for Tmax than Tmin. Reptiles: similarly high phylogenetic signal for both Tmax and Tmin.							interspecific variation in plasticity and phylogenetic signal to Tmin and Tmax.
Sunday et al. 2014 (45)	Terrestrial ectotherms (n=300)[5]	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).
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 ºC.
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 (Freckleton & Jetz 2009)	Variance in Tmax is *greater* 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.[6]
Sunday et al. 2019 (60)	Ectothermic and endothermic animals (n= ca. 1700; all data from Bennett et al. (2018) 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	Several known patterns in animals found for plants as well (see main text). Variance in Tmax explained by	+++	+	++	+	+++	++	The local environment, phylogenetic and spatial distances are all needed to explain global variation in both Tmax

		geographic distances and local environment (MCMCglmm, Hadfield 2010; see *Methods*).	geography > climate > phylogeny. Variance in Tmin explained by phylogeny > climate > geography.							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.

[1] 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.

[2] 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).

[3] Terrestrial: reptiles, arthropods and amphibians; Marine: fish, molluscs and arthropods.

[4] 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.

[5] Terrestrial ectotherms: insects, amphibians and reptiles.

[6] 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

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