Title: Trees have overlapping potential niches that extend beyond their realized niches

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Abstract:

Tree species appear to prefer distinct climatic conditions, but the true nature of these preferences is obscured by species interactions and dispersal, which limit species' ranges. We quantified realized and potential thermal niches of 188 North American tree species to conduct a continental-scale test of the architecture of niches. We found strong and consistent evidence that species occurring at thermal extremes occupy less than three-quarters of their potential niches and species' potential niches overlap at a mean annual temperature of approximately 12 °C. These results clarify the breadth of thermal tolerances of temperate tree species and support the centrifugal organization of thermal niches. Accounting for the non-realized components of ecological niches will advance theory and prediction in global change ecology.

One-Sentence Summary:

Tree species can grow and survive at one common mean annual temperature despite their distinct distributions in nature.

Main Text:

Predicting species' responses to rising global temperatures requires knowledge of their thermal tolerance niches, yet our current understanding is informed primarily by the more limited realized niches. Realized niches are observed distributions of species along environmental gradients that reflect all the forces acting on the distribution including abiotic constraints such as climate, biotic interactions, and dispersal limitation (*1-3*). The realized niche differs from the fundamental niche, which is the complete set of conditions in which a species can sustain itself in the absence of biotic interactions (*2, 4*). Difficulties in measuring the fundamental niche have rendered it one of the most well-known yet least quantified concepts in ecology. Potential niches, on the other hand, are the complete set of conditions that allow species to survive and grow, but where recruitment rate is unknown (*5-7*). Potential niches are measurable and informative for organisms with a slow pace of life because adult survival is a more influential fitness component than fecundity (*8, 9*). If a species' potential niche is larger than its realized niche, then it can tolerate a greater range of environments. Predictions of how species respond to climate change will be biased if based solely on the realized niche.

Competitive interactions are known to contract realized niches into less favorable environments at local spatial scales (*10, 11*), but whether interspecific competition contracts realized distributions at macroecological scales remains an open question. The Eltonian Noise Hypothesis assumes that the importance of competition decreases at broader spatial scales (*12*) and therefore predicts that realized niches are roughly equivalent to potential niches. If true, this would justify current methods in species distribution modeling that use present day realized niches to predict future responses to climate change (*13*). But this assumption of near equivalence is virtually untested and is increasingly contradicted by available evidence: the study of invasions (*14, 15*), experimental transplants of species outside their geographic range (*16*), and cultivation in botanical gardens (*5-7*) all show that many species can grow and survive outside of their current realized niches.

It is increasingly clear that we should reject the simple, convenient assumption of niche equivalence, but we still do not know the most basic architectural relationships between potential and realized niches. Hypotheses about these relationships (*17-21*) have gained new urgency in light of efforts to predict species range shifts in response to climate change (*22, 23*). Such efforts have problematically treated the realized niche of today as if it was the fundamental niche and only possible future realized niche (*24-26*). In this paper we leverage global inventories of arboreta to empirically estimate present day potential niches of 188 tree species to conduct a continental-scale test of the architectures of ecological niches.

Architectures of ecological niches

Potential niches could exhibit three distinct architectures in relation to their corresponding realized niches, each driven by different mechanisms (Fig. 1). Following established terminology, potential niches could exhibit 1) distinct preferences, 2) shared preferences, or 3) centrifugal organization (*1, 18-20*). First, if the potential niche of each species covers distinct environmental conditions, then potential niches would be centered over their realized niches and would likewise inhabit distinct portions of an environmental gradient (Fig. 1A). Second, a trade-off between competitive ability and abiotic tolerance of more stressful conditions could generate distinct realized niches despite all species sharing a preference for one end of the environmental gradient (Fig. 1B). Under these conditions competitive species would dominate the preferred environment at one end and more tolerant species would be relegated to suboptimal environments at the other end (*7, 11, 18, 19, 27, 28*). Third, trade-offs generated by distinct physiological tolerances of two opposing abiotic extremes could also generate distinct realized niches along a gradient. Under these conditions, potential niches would overlap in the central core, yet their realized niches would be pushed toward the peripheries to avoid competition (Fig. 1C). Centrifugal organization was originally proposed for two or more orthogonal gradients that define the same core habitat (*20, 29*), but this third model is a special case of centrifugal organization where trade-offs in tolerating lethal conditions at opposite ends of the same gradient (e.g., cold-tolerant species are not heat-tolerant) can also contract realized niches toward the climate extremes. The idea that differences between potential and realized niches is driven by competition has been the primary hypothesis to date (*18, 20, 21, 29*), although other mechanisms are conceivable. Here we only test for the differences but do not directly test the mechanisms.

These three conceptual models generate testable relationships between temperature and three niche metrics (Fig. 1): i) potential niche width, ii) the ratio of the realized-to-potential niche widths (‘R:P ratio’), and iii) ‘niche contraction’. The R:P ratio ranges from 0 to 1 because the realized niche is contained within the potential niche. Niche contraction measures the directional contraction of the realized niche into different regions of the potential niche and ranges from -1 to 1, where, in this study, positive values indicate contraction of the realized niche from cooler climates into warmer climates, and negative values indicate contraction from warmer climates into cooler climates (Fig. 1). Evidence for each of the three models can be distinguished by unique geometric signatures encoded in the architectures of the potential niches (Fig. 1D-F). First, the distinct preference model would be supported if none of these metrics vary significantly with realized niche positions, *i.e.*, the location of each species along the gradient calculated as the median temperature of the realized niche (Fig. 1G). Second, shared preference of warm temperatures would be supported if potential niche widths decrease with rising temperature, causing the R:P ratio to increase, and causing niche contraction to increase from more negative values to less negative values if realized niches contract from warmer into cooler climates (Fig. 1H). Note that the directions of these relationships and signs of the metrics would differ for other environmental contexts. Third, centrifugal organization would be supported if potential niche width is lowest at an intermediate temperature, causing the R:P ratio to peak at this intermediate temperature, and causing niche contraction to switch sign from negative to positive with increasing temperature (Fig. 1I). A worked example of these niche metrics is illustrated in Fig. 1J-L.

We quantified the empirical support for each of the three hypotheses by estimating realized and potential thermal niches for 188 North American tree species. Realized niches were quantified using natural occurrence records in the Botanical Information and Ecology Network (BIEN 4.1) (*30*) and Little’s species range maps (*31*) (Fig. S1). We quantified potential niches by supplementing native occurrence records with 17,180 occurrence records from 447 arboreta around the world provided to us by Botanic Gardens Conservation International (BGCI) (*32*), including dozens to hundreds of occurrence records for each species (Fig. S2). Arboreta can be used to quantify potential niches because they eliminate dispersal limitation and minimize effects of competition (*5*-*7*). We used CHELSA V.2 (*33*) to determine minimum, mean, and maximum temperatures (1980-2010) for all occurrence records to estimate thermal niches. Both the natural and arboreta occurrence data show broad coverage of a range of current climates for estimating present day potential niches (Fig. S1).

Thermal niches of North American tree species

We found strong and consistent support for centrifugal organization of thermal niches of North American tree species (Fig. 2, Table S1). The R:P ratio for mean annual temperature exhibited large variation among species, ranging from 0.42 to 1.0, with a median value of 0.91 (Fig. 2B). This in itself is a novel finding – that several species occupy less than three-quarters of their potential niche while others occupy nearly 100%. In fact, the R:P ratios were not randomly distributed across the temperature gradient, but rather exhibited a significant hump-shaped relationship with mean annual temperature ($R^2_{\text{adj}} = 0.45$, $F_{2,185} = 76.9$, $P < 0.0001$), reaching a maximum at 10.0 °C (Fig. 2B). Species with realized niches near this maximum exhibited similar realized and potential niche widths (i.e., R:P ratio ~ 1). These central species approximately conform with the predictions of the Eltonian Noise Hypothesis, but species at both temperature extremes contradict the predictions.

The directional niche contraction metric exhibited a strong positive relationship with mean annual temperature ($R^2_{\text{adj}} = 0.71$, $F_{2,185} = 225$; $P < 0.0001$). The switch from niche contraction into cooler sites (blue colors in Fig. 2) to contraction into warmer sites (gold colors in Fig. 2) occurred at 12.0 °C (Fig. 2C). Potential niche width exhibited a significant *u*-shaped relationship with mean annual temperature ($R^2_{\text{adj}} = 0.29$, $F_{2,185} = 37.6$; $P < 0.0001$), where potential niche width reached a minimum at 15.9 °C (Fig. 2D). We estimated the centrifugal center value as the mean of three critical values: the maximum, *x*-intercept, and minimum of the fitted regression models in Figs. 2B, C, and D, respectively. The estimated centrifugal center was 12.6 °C (denoted by the vertical line in Fig. 2A, Table S1). Remarkably, 176 of 188 species (94%) were observed to be growing and surviving in arboreta at 12.6 °C even though only 64% of these species occurred at this temperature in their native ranges (Fig. 2A, Table S1).

Similar results were obtained for maximum temperature of the warmest month and minimum temperature of the coldest month. Centrifugal organization was supported in all three statistical tests of maximum temperature with a center at 25.5 °C (Fig. 3, Fig. S3, Table S1) and 100% of species could tolerate this central maximum temperature (Fig. S3). Centrifugal organization was also supported in two of three statistical tests for minimum temperature (Fig. 3, Fig. S4, Table S1). In the one exception, potential niche width of minimum temperature declined nonlinearly with increasing realized niche position, supporting a shared preference for a higher temperature above freezing. The propensity of evidence indicates that a low temperature center exists at -3.2 °C and 97% of species could tolerate this central minimum temperature.

Overall, these results falsify the model of distinct thermal preferences and support the centrifugal organization of potential thermal niches. They also clarify the true breadth of thermal tolerances of North American temperate tree species, showing that many species occupy only a fraction of their potential niche and confirm that trees can tolerate surprisingly large ranges in temperature (*14, 34*).

Centrifugal organization of thermal niches

Tree species inhabit distinct environments in nature, but two results seem counterintuitive to this observation. First, many species have potential temperature tolerances much greater than where they are observed to occur. Second, North American temperate trees share a single environment with a mean annual temperature around 12 °C where they can grow and survive, even though we can clearly identify tree species that occur in nature only in colder or warmer temperatures.

Why do species have realized niches that span less than three-quarters of their potential niches? Our measurement of potential niches necessarily used data that could involve sampling biases, but these biases are all in the direction of not covering a large enough range of temperatures. Better sampling of potential niches could only expand them, so this cannot explain why species inhabit a small slice of their potential niches. A second possible explanation is that the definition of the potential niche only considers survival and growth of mature trees, not recruitment. Our results cannot prove that populations could indefinitely persist at the central temperatures because the fundamental niche additionally requires an ability to reproduce to maintain positive population growth rates (*4, 35, 36*). This seems unlikely to explain most of the unoccupied parts of the potential niche for two reasons. First, in tree populations that are not growing exponentially but have been in rough equilibrium, such as the trees of North America in recent millennia (*37*), elasticity analyses of population growth rates show that it is the survival of adults that are most important to fitness (*8*). Second, trees only need one or a short sequence of a few years in which successful reproduction and seedling establishment can occur, and this may occur at any point in the temporally variable, multidecadal reproductive phase of a tree (*36, 38*). A third explanation for the failure to fully occupy the potential thermal niche is dispersal limitation. While trees are certainly dispersal limited over even centennial timescales (*39*), and dispersal limitation has been invoked to explain occurrence ‘holes’ found in present-day ranges (*40*), temperatures have been approximately stable for almost 10,000 years in North America. Fat-tailed dispersal kernels suggest that trees have the ability to move rapidly enough that it is unlikely trees are still several °C short of tracking their realized climate niche (*39*). Moreover, trees that now occupy the cold end of their potential thermal niche have clearly already dispersed to reach those colder locations since glaciation, abandoning the warmer locations that now compose the unoccupied portions of their potential thermal niche.

This leaves biotic interactions as the most likely explanation for why species do not fill their potential temperature niches. Although biotic interactions likely play out differently at large scales than they do in the small-scale competition studies that are most commonly used to study them, there is good evidence from closely related species that do not co-occur across part or all of their range that biotic interactions can indeed limit species distributions at regional to continental scales (*41, 42*). The centrifugal niche pattern observed has a clear explanation based in a competition-tolerance trade-off (*7, 18-20*). In such a trade-off, some species allocate resources to being competitively dominant to occupy the central core habitat. Other species allocate resources to being tolerant of lethal environmental conditions, such as frost and drought. But it is likely that all forms of biotic interaction (i.e., competition, herbivory, disease, etc.) play a role.

The second result that requires explanation is the shared tolerance for intermediate temperatures around 12 °C MAT. One explanation could be physiological. Thermal gradients are well-known in biology for generating hump-shaped reaction rates (*43, 44*). For example, C_3 photosynthesis is the dominant pathway in trees, and global average temperature response of photosynthesis peaks at 18 °C (*45*). Moreover, radial growth rates of trees in the northeastern US reach an optimum around 11.5 °C (Fig. S5). The full explanation likely involves temperature interacting with precipitation and CO_2 (*46*).

Evolutionary explanations, at first glance, would seem challenging: selection should quickly evolve potential niches to match realized niches as there is no selection in non-realized regions of the potential niche. A deeper time explanation involving extinction filters and niche conservatism (*47*) is possible. The 12 °C is close to the warmest mean annual temperature found in North America at the last glacial maximum (LGM, Fig. S6) and probably approximately similar to previous glacial maxima over the last 2 Ma. The 12 °C is also close to the coolest temperatures found in the same space 56 Mya in the Paleocene-Eocene Thermal Maximum

(PETM) (*48*), although uncertainties around these estimates are high. One could posit that cold-adapted trees unable to survive temperatures ≥ 12 °C went extinct in the PETM and warm-adapted trees unable to survive temperatures ≤ 12 °C went extinct in one of the glacial maxima. Furthermore, if the warm temperature tolerances of cold-adapted trees were conserved for 56 Ma while the cold temperature tolerances of warm-adapted trees were retained for merely 2 Ma, which follows the documented asymmetry in niche conservatism of warm and cold limits (*49*), then this could explain the present centrifugal organization. But one would have to explain why trees with refugia in Mexico maintained tolerance of 12 °C. Overall, more work would be needed to make this theory rigorous. Our results do provide a plausible explanation for the occurrence of no-analog communities. For example, *Picea* spp. and *Fraxinus* spp. have narrow co-occurrence today, but co-occurred 12,000-17,000 years ago (*37*), which was possible because their potential niches overlap.

We rejected the shared preference model for temperature (Fig. 1B), but this does not preclude the possibility that there could be other non-temperature gradients along which distinct (Fig. 1A) or shared preferences (Fig. 1B) exist (Fig. 1B). In small scale studies, shared preferences are common in co-existing plant species along consumable resource gradients (*19*), and animals have shown a strong propensity for distinct niche preferences along diet gradients (*19*). We note that centrifugal organization is often found when there are multiple dimensions of lethality (*21, 29*), and that temperature effectively achieves this with cold adaptation being very different from heat stress adaptation.

Implications for species responses to a warming world

Centrifugal organization of potential thermal niches has substantial implications for efforts to predict and understand species responses to climate change (*22, 23, 50, 51*). If the potential niche is a representative analog of the fundamental niche, then the fact that many species occupy only a limited subset of their potential niche raises the possibility that their realized niche could change and occupy a different subset of their potential niche when abiotic conditions not present today become available. This breaks a core assumption of species distribution models.

Niche modeling must get serious about the distinction between realized niches and their potential and fundamental counterparts. On the one hand, niche modeling of tree species whose realized niches are centered on 12 °C could be accurate because their realized and potential niches are so similar (i.e., R:P ratio ~ 1; Fig. 2A). On the other hand, the fact that potential niches of cold-adapted species extend to warmer temperatures while potential niches of warm-adapted species extend to cooler temperatures implies differential fates in a warming world. Cold-adapted species may not need to migrate to stay within their potential thermal niche, provided they can survive changing disturbance and competitive regimes, while warm-adapted species will need to migrate to stay within their potential niche under warming temperatures. Trees that are actively shifting their ranges and experiencing exponential growth may flip to conditions where fitness will be most sensitive to the regeneration niche (*36*) because dispersal and recruitment rates drive the advancing range. We should not assume, however, that regeneration niches are identical to realized recruitment patterns based on these results.

The longstanding recognition of the importance of fundamental niches has not been adequately addressed empirically. Our results show that realized niches are not trivial contractions of potential niches. Rather, they differ substantially in a systematic fashion where realized niches contract away from an intermediate temperature into both the hot and cold ends of the thermal spectrum. Our findings challenge existing predictions of how ranges will shift under climate change and suggest a need for deeper exploration of the relationship between potential and realized niches, including the mechanisms driving these differences.

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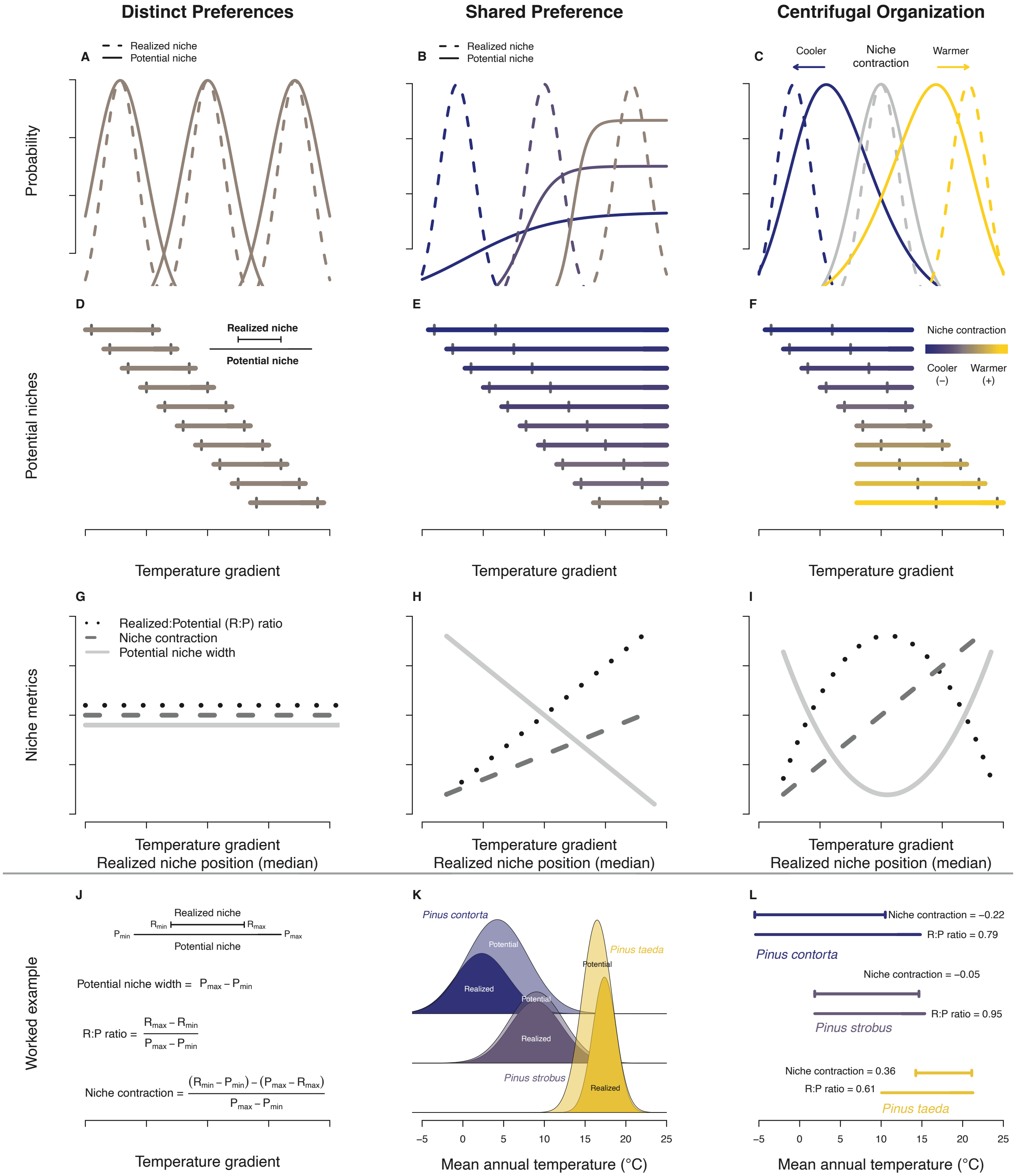

Fig. 1. Three testable models of the architecture of ecological niches.

Realized niches (denoted as dashed lines in A-C) that are distinct and arrayed sequentially along an environmental gradient may differ from potential niches (denoted as solid lines in A-C) even though realized niches are nested inside of potential niches. Potential and realized niches can be organized three different ways. Potential niches will exhibit either (A) distinct preferences among species centered on their realized niches, (B) a shared preference among species where potential niches share the same extreme value, or (C) centrifugal organization where species overlap in the middle despite opposing abiotic tolerances. (D-F) Each model generates distinct geometric signatures in the potential niches while the realized niches remain constant. Consider an idealized set of ten potential niches stacked on top of each other and ordered by increasing realized niche minima: (D) distinct preferences would generate an orderly progression of similar potential width niches along the gradient, (E) shared preferences would generate a set of decreasing potential niche widths along the gradient that all share the same niche maxima, and (F) centrifugal organization would generate a skewed hourglass where potential niche width is lowest at intermediate locations along the gradient. (G-I) These signatures generate unique testable relationships between realized niche position (medians) and three niche metrics: potential niche width (see equations in J), the ratio of the realized-to-potential niche width (‘R:P ratio’), and the directional contraction of the realized niche into cooler or warmer regions of the potential niche (‘niche contraction’). (J-L). Worked example of how niche metrics were computed for three *Pinus* species where we quantified niche widths as the distance between 0.01 and 0.99 quantiles for both realized occurrences (BIEN and Little’s range maps) and potential occurrences (a combination of realized occurrences plus arboreta occurrences). (J) The niche contraction metric is a directional index that quantifies how realized niches are contracted subsets of the potential niches. (K) Probability densities of realized and potential niches using occurrence data along a gradient of mean annual temperature for three *Pinus* species. (L) Note how the realized niche of *Pinus contorta* is contracted into cooler climates, *Pinus strobus* is not noticeably contracted in either direction, and *Pinus taeda* is contracted into warmer climates.

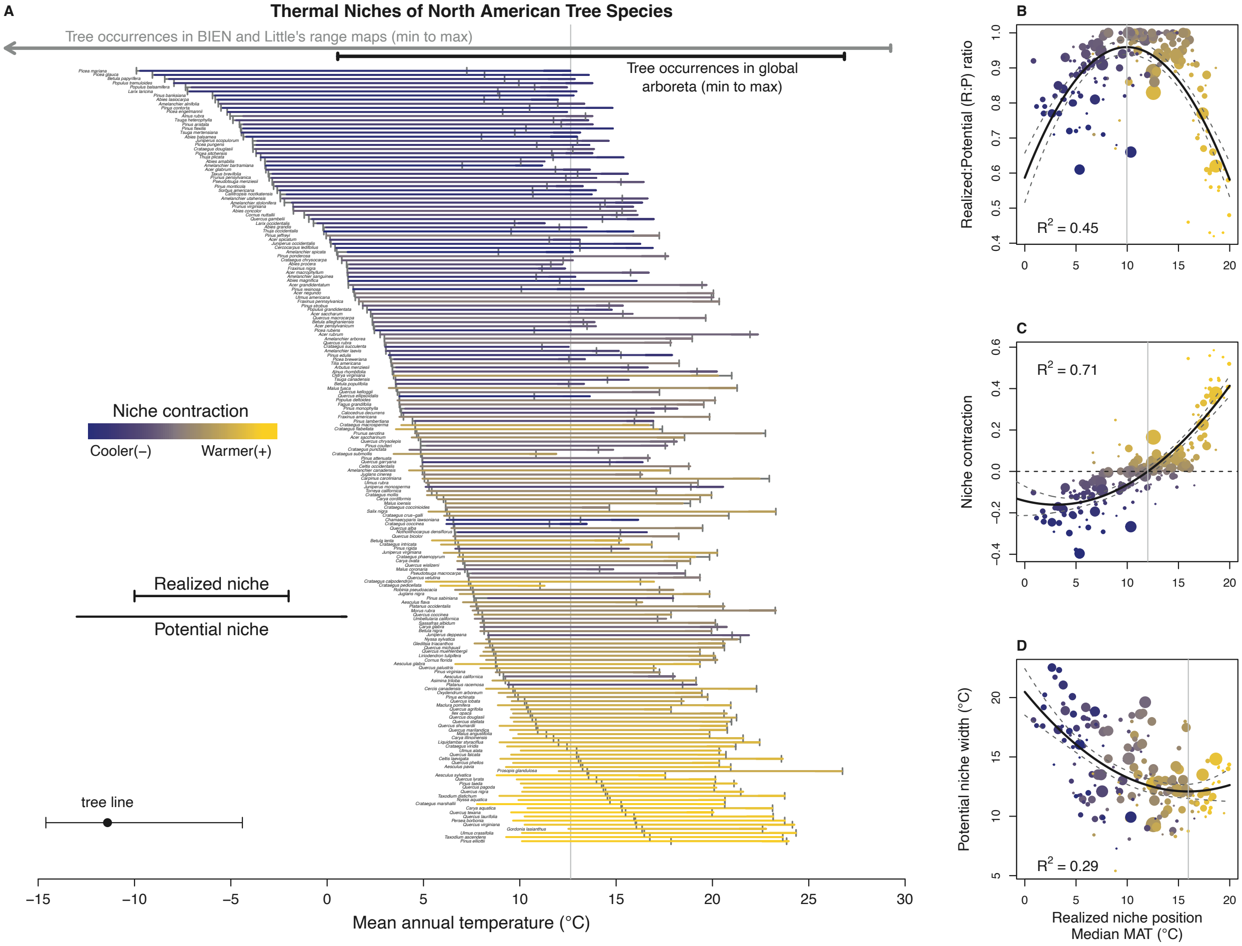

Fig. 2. Realized and potential thermal niches of North American tree species along a gradient of mean annual temperature.

(A) Empirical estimates of realized and potential niches of 188 North American tree species along a mean annual temperature (MAT) gradient. Realized niches (denoted by hash marks) are subsets of potential niches. Species are ordered by increasing realized niche minima from top to bottom. Niche minima and maxima are defined as the 0.01 and 0.99 quantiles of their distributions along MAT to remove effects of extreme outliers. Species with realized niches contracting to cooler temperatures are shown in blue, while species with realized niches contracting to warmer temperatures are shown in gold. Almost all species (94%) have a potential niche that overlaps the central temperature (solid grey vertical line) of 12.6 °C. The grey horizontal line denotes the range of temperatures sampled by BIEN and Little's range maps (note the cold end is cut off and continues further), and the black horizonal line denotes the range of temperatures of the arboreta. (B) Relationship between realized niche position (median MAT) and the realized-to-potential niche width ratio (R:P ratio). (C) Relationship between realized niche position and niche contraction, which is a directional index of contraction of the realized niche into warmer (positive) or cooler (negative) climates. (D) Relationship between realized niche medians and potential niche widths. All three relationships support the centrifugal organization of thermal niches for North American tree species. Symbols in B, C, and D are sized in proportion to the number of occurrences in arboreta, but these were not used to weight observations in the regression analyses. The vertical line in panel A represents the mean value of the estimated maximum, *x*-intercept, and minimum from panels B, C, and D, respectively.

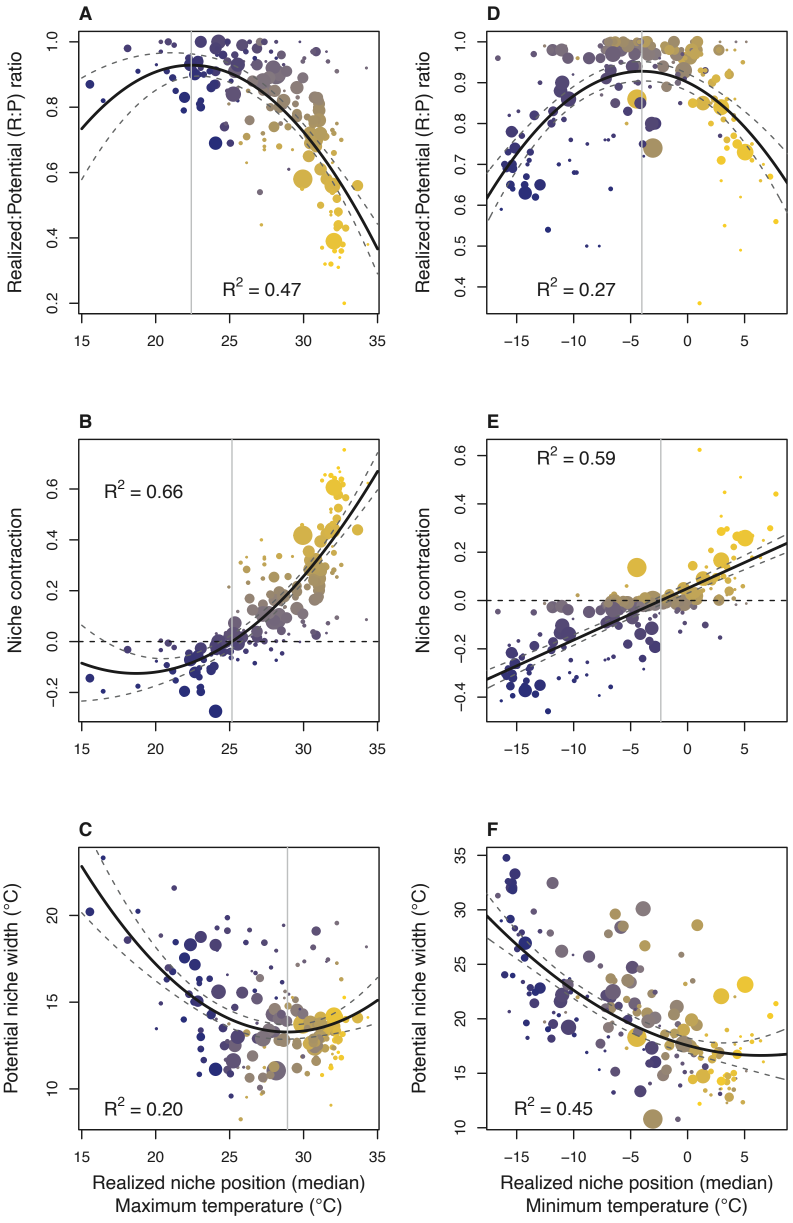

Fig. 3. Relationships between three niche metrics and realized niche position for North American tree species along gradients of maximum and minimum temperatures.

Relationships between realized niche position (median maximum temperature of the warmest month) and (A) the realized-to-potential niche width ratio (R:P ratio), (B) niche contraction, and (C) potential niche width. Niche contraction is a directional index of contraction of the realized niche into warmer (positive) or cooler (negative) climates. Species with realized niches contracting to cooler temperatures are shown in blue colors, while species with realized niches contracting to warmer temperatures are shown in gold colors. Relationships between realized niche position (median minimum temperature of the warmest month) and (D) the realized-to-potential niche width ratio (R:P ratio), (E) niche contraction, and (F) potential niche width. Symbols are sized in proportion to the number of occurrences in arboreta, but these were not used to weight observations in the regression analyses.

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We are grateful to the Botanic Gardens Conservation International (BGCI) for sharing their arboretum inventories with us. We dedicate this paper to the memory of Paul A. Keddy (1953-2023).

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Author contributions:

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Analysis: DCL, BJM

Writing: DCL, BJM

Competing interests: Authors declare that they have no competing interests.

Data and materials availability: All native species distribution data is freely available through the Botanical Information and Ecology Network (BIEN) (*30*) and Little's range maps (*31*). We obtained inventories of arboreta by request from the Botanic Gardens Conservation International (BGCI) (*32*), which is a scientific non-profit, and their data policies prevent us from publishing their location data, but the data may be requested from them at https://www.bgci.org/. R scripts and data (scrubbed of arboretum location information) to reproduce results are available at https://doi.org/10.5061/dryad.0cfxpnw9f (*52*).

Supplementary Material

Materials and Methods
Fig. S1. Geographic and climatic distributions of arboreta and realized tree occurrences in North America.
Fig. S2. Distribution of number of occurrences in botanical gardens for each species.
Fig. S3. Empirical estimates of the potential and realized thermal niches of North American trees along a gradient of maximum temperature of the warmest month.
Fig. S4. Empirical estimates of the potential and realized thermal niches of North American trees along a gradient of minimum temperature of the coldest month.
Fig. S5. Mean radial tree growth rate by species by site.
Fig. S6. Mean annual temperature at present and at the last glacial maximum (LGM).
Fig. S7. Relationship between summer temperature and mean annual temperature.

Table S1. Results of model comparisons for three sets of temperature variables (minimum, mean, maximum) and three sets of niche metrics.
Table S2. Comparison of mean annual temperature (MAT) model results using different random samples.

Supplementary Materials for

Trees have overlapping potential niches that extend beyond their realized niches

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The PDF file includes:

Materials and Methods
Figs. S1 to S7
Tables S1 to S2

Materials and Methods

We estimated empirical realized and potential niches along global temperature gradients using occurrence data for 188 North American tree species. We submitted a data request to Botanic Gardens Conservation International (BGCI) for lists of arboreta in which 298 North American trees were growing and surviving. We received information from 447 arboreta around the world (Fig. S1) (*32*). After taxonomic matching, we analyzed the 188 species that had a minimum of 20 occurrences in arboreta and for which natural occurrence data was available (Fig. S1, S2).

Realized niches for each species were quantified as the range of climate conditions across their native ranges in North America. We downloaded native occurrence data for these species from the Botanical Information and Ecology Network (BIEN 4.1) (*30*). We removed cultivated records from the BIEN data to ensure these were native occurrence records and limited all occurrences to within North America. We supplemented occurrence records in BIEN with point samples from Little's range maps (*31*) to ensure full sampling of species ranges into Canada and Mexico. We used CHELSA V2.1 climate normals (1980-2010) (*33*) to quantify mean annual temperature, maximum temperature of the warmest month, and minimum temperature of the coldest month for each occurrence record (Fig. S1).

Potential niches for each species were quantified as the range of climate conditions across their native ranges in North America in addition to the range of climate conditions across the globally-distributed arboretums (i.e., native occurrences plus arboreta occurrences), because realized niches are subsets of potential niches (*5, 10*). We use the term 'potential niche' to represent the conditions that permit survival (but with no information about reproduction) (*6, 7*), which is equivalent to the 'tolerance niche' (*5*), but differs from the paleoecological concept of a 'potential niche' defined as the intersection between the fundamental niche and realized environmental space at any given time (*26*). Given that natural occurrences outnumbered the arboretum occurrences by several orders of magnitude and would overwhelm the estimates of niche ranges, we randomly sampled occurrences from BIEN and Little's range maps at 10 times the number of occurrences in the arboretums for a total of 165,315 occurrences. Random samples using different starting conditions yielded consistent results (Table S2).

Three niche metrics were computed for each of the 188 species to test the three models of niche architecture. These metrics focus on the ranges of temperatures (including mean annual temperature, minimum temperature of the coldest month, and maximum temperature of the warmest month) in which a species could grow and survive. Quantiles were preferred over absolute minimum and maximum values to prevent biasing metrics toward extreme outliers (*53*). Each metric was calculated using four quantities: the minimum realized niche $R_{\min}$ (0.01 quantile), the maximum realized niche $R_{\max}$ (0.99 quantile), the minimum potential niche $P_{\min}$ (0.01 quantile), and the maximum potential niche $P_{\max}$ (0.99 quantile). First, niche widths were computed as a range of temperatures, where realized niche width = $R_{\max} - R_{\min}$, and potential niche width = $P_{\max} - P_{\min}$. Second, we computed the ratio of the realized niche width -to-potential niche width, where R:P ratio = $(R_{\max} - R_{\min}) / (P_{\max} - P_{\min})$ (Fig. 1). Third, we computed an index of niche contraction (Fig. 1), where niche contraction = $[(R_{\min} - P_{\min}) - (P_{\max} - R_{\max})] / (P_{\max} - P_{\min})$. Positive values of niche contraction indicate contraction of the realized niche into warmer climates and negative values indicate contraction into cooler climates. We regressed each of the three metrics on realized niche positions (medians, 0.5 quantile). We tested for linear and quadratic polynomial relationships and report the model most supported by data assessed using likelihood ratio tests and AIC (Table S1).

The number of occurrences in arboreta for each species ranged from 20 to 268, with a median of 78 occurrences per species (Fig. S2). We tested whether the number of occurrences in arboreta for each species could affect the likelihood of detecting a contraction of the potential niche, by regressing each of the niche metrics on the number of occurrences. The R:P ratio exhibited a positive yet weak ($R^2 = 0.05$) relationship with number of occurrences, but this positive relationship would indicate the opposite of a bias because larger samples of arboreta show potential niches that are most similar to the realized niches, while smaller samples show potential niches much wider than realized niche widths. Potential niche width was positively yet weakly ($R^2 = 0.03$) correlated with number of occurrences in arboreta. Niche contraction was uncorrelated with the number of occurrences in arboreta. Overall, the number of occurrences in arboreta did not systematically bias niche metrics.

The occurrence records of trees in arboreta provide valuable information about whether mature individuals of a species can grow and survive in the conditions of the arboretum. Arboreta occurrences are valuable because they eliminate dispersal limitation and minimize competition. However, these records do not directly measure fundamental niches because no information was available on reproductive rates, failed cultivations, pest and disease control, soil properties, or the demographic data that is needed to quantify the population growth rate of the species (*4, 5, 7*). Analyses of population growth rates would constitute a stronger test of niche theory because they could be used to generate estimates of fitness optima (*2*), but the necessary experiments to generate this data cannot be conducted at continental scales with current resources. Our focus on occurrence data allows us to quantify both realized and potential thermal niches using the same ecological currency: growth and survival, and survival is the most influential fitness component for trees with stable age distributions (*8*). While aspects of the precipitation regime are of great interest, we focused on temperature exclusively because the arboreta could have initially supplemented water, which means that these estimates of thermal niches are best perceived as maximum temperatures in a possibly above-average precipitation regime (*6*).

No arboretums occur below a mean annual temperature of 0 °C (Fig. S1), which could be a potential bias of our estimates of potential niches at the cold end of the gradient. However, it is unlikely that trees will survive at colder temperatures beyond the observed cold limits for physiological reasons. Alpine ecologists have demonstrated that ~ 6 °C average temperature of the growing season is the temperature limit at tree line (*54*). Moreover, a 6 °C average temperature of the growing season corresponds to a MAT of -11.4 °C (confidence interval range: -14.6, -4.4) (Fig. S7), and we observed the coldest realized niche minimum at -10 °C MAT, which closely agrees with the tree line temperature limit (Fig. 2A). Given that neither competition nor dispersal limitation can be invoked to explain tree lines, this lower limit likely represents the cold limit of both realized and potential niches of cold-tolerant species.

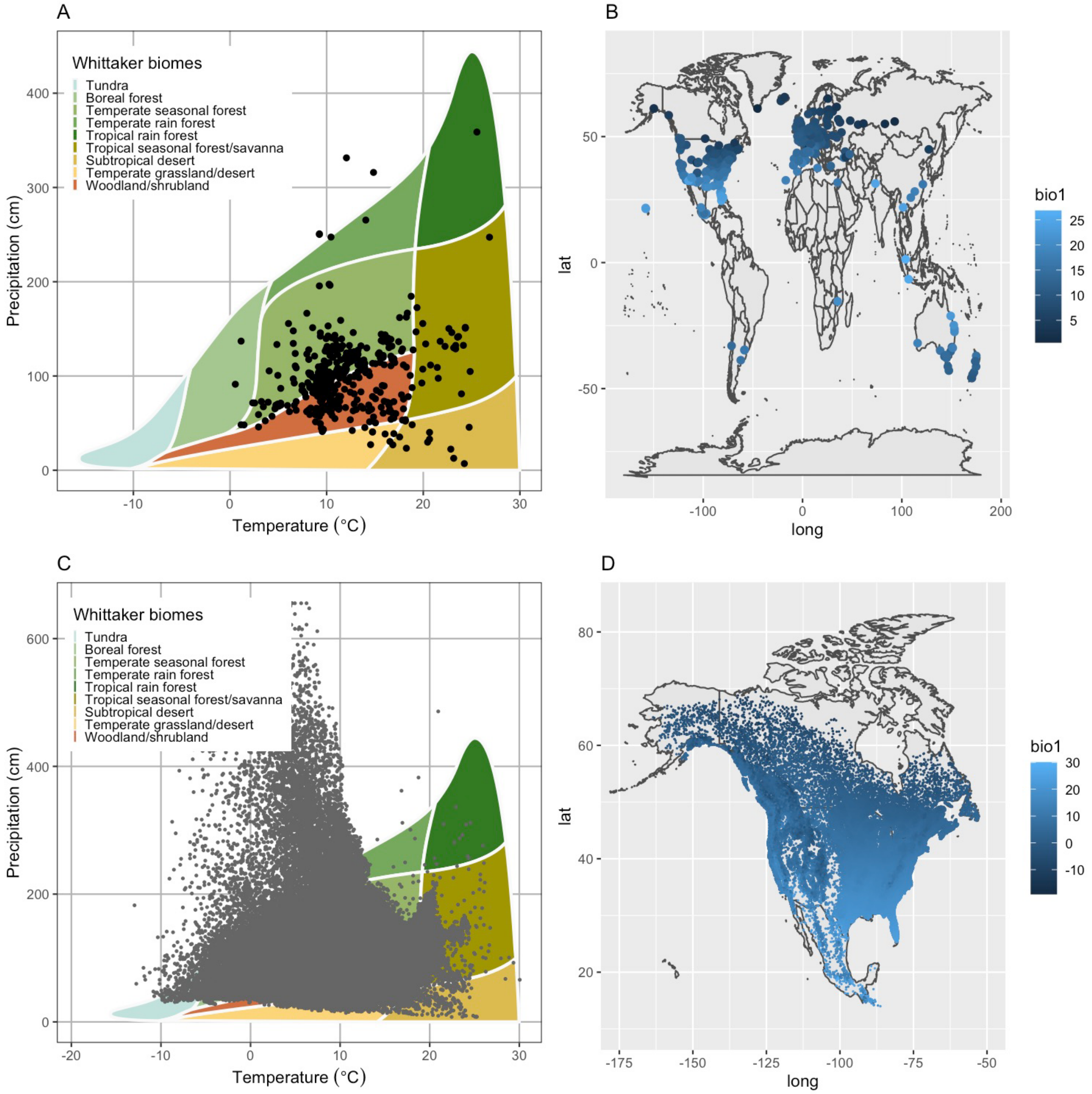

Fig. S1. Geographic and climatic distributions of arboreta and realized occurrences in North America.

Distributions of arboreta around the world in (A) Whittaker biome climate space and (B) geographical space. Distributions of occurrence data using BIEN and Little's range maps in (C) Whittaker biome climate space and (D) geographical space (bio1 = mean annual temperature).

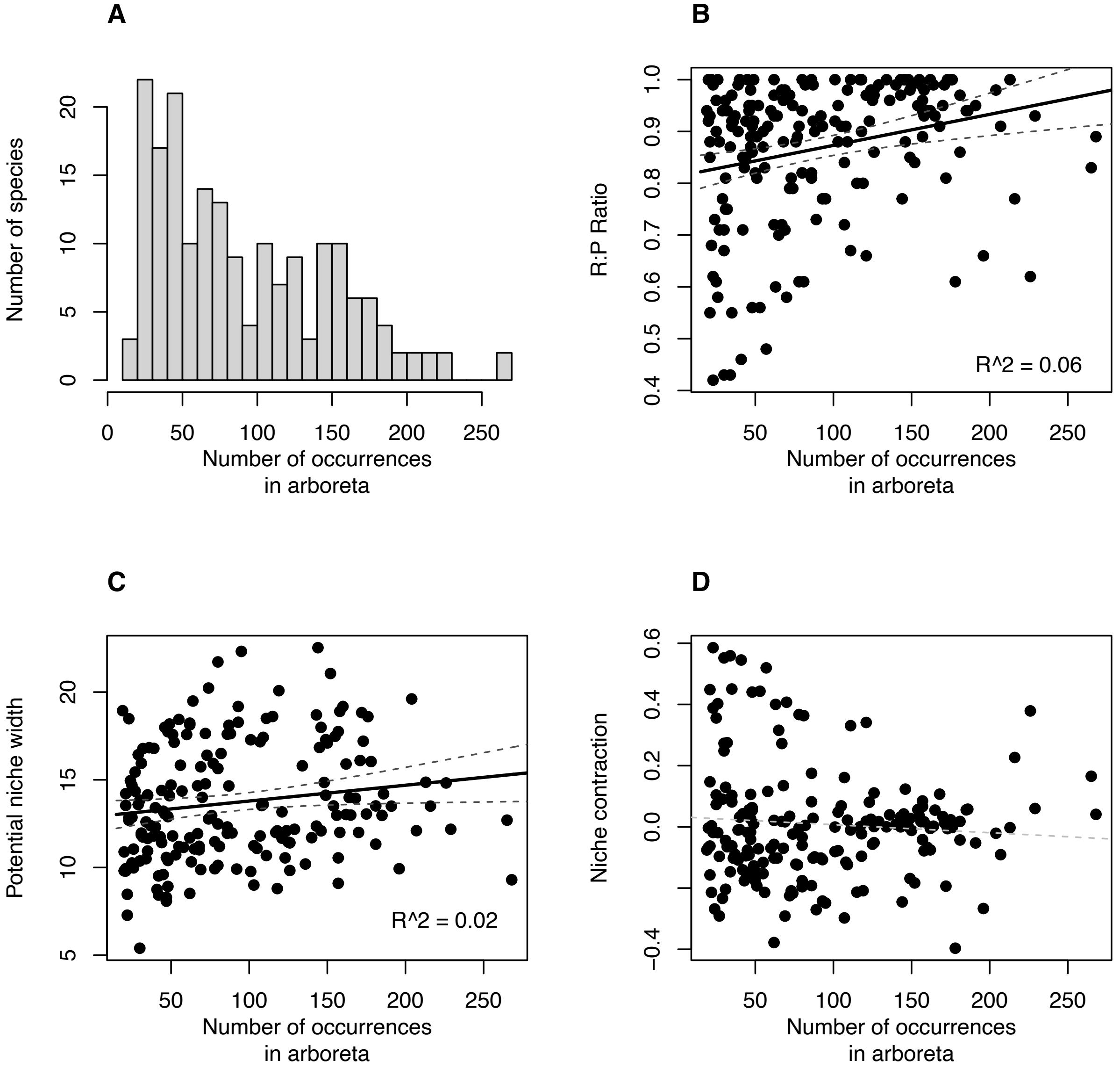

Fig. S2. Distribution of number of occurrences in botanical gardens for each species and their lack of systematic bias on the calculation of niche metrics for mean annual temperature.

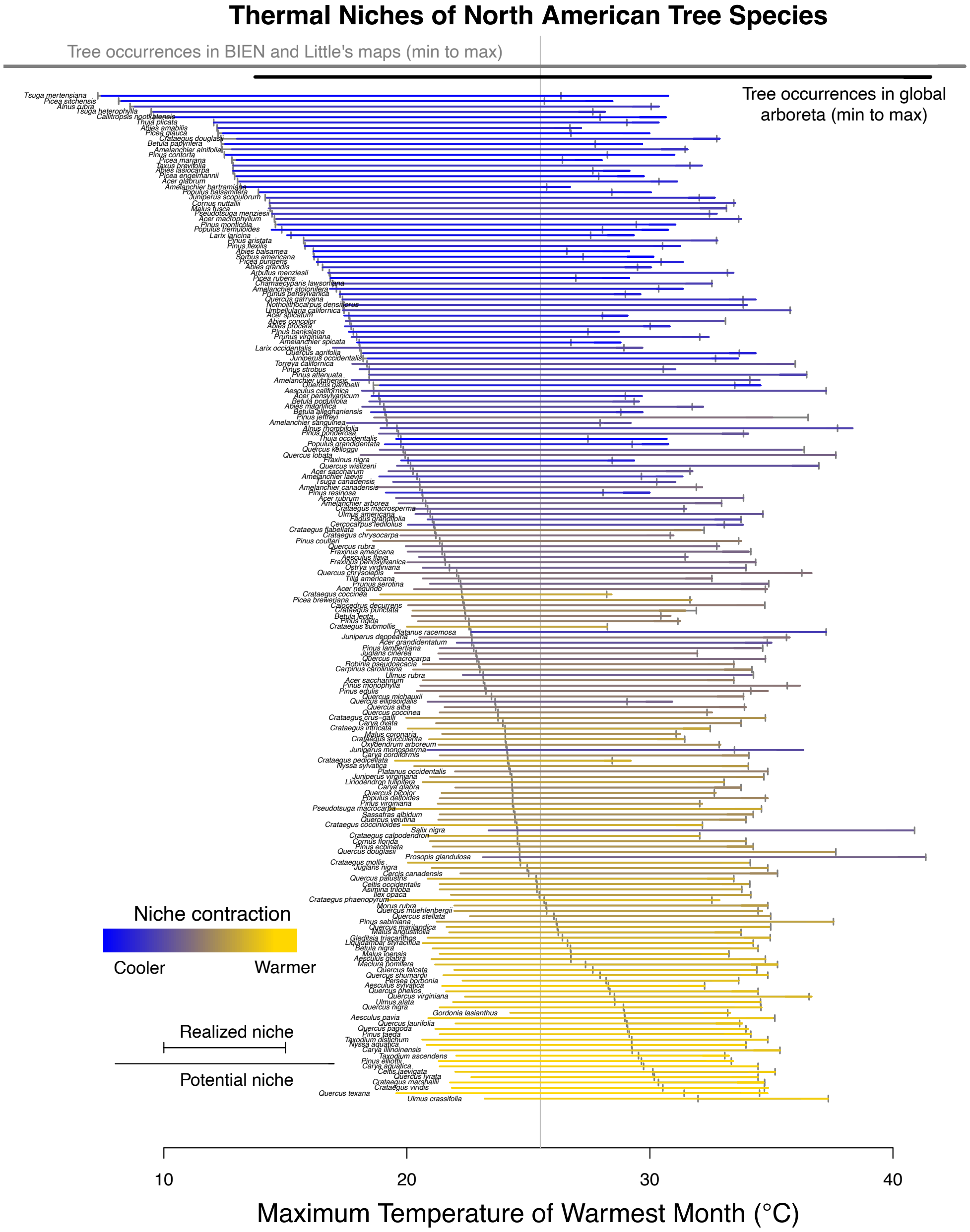

Fig. S3. Empirical estimates of the potential and realized thermal niches of North American trees along a gradient of maximum temperature of the warmest month.

Empirical estimates of realized and potential niches of 188 North American tree species along a gradient of maximum temperature of the warmest month. Realized niches (denoted by hash marks) are subsets of potential niches. Species are ordered by increasing realized niche minima. Niche minima and maxima are defined as the 0.01 and 0.99 quantiles of their distributions to remove effects of extreme outliers. All species have a potential niche that overlaps the central temperature (solid vertical line) of 25.5 °C. The grey horizontal line denotes the range of temperatures sampled by BIEN and Little's range maps, and the black horizonal line denotes the range of temperatures of the arboreta. The vertical line represents the mean value of the estimated maximum, *x*-intercept, and minimum from fitted regression models in Fig. 3 in the main text.

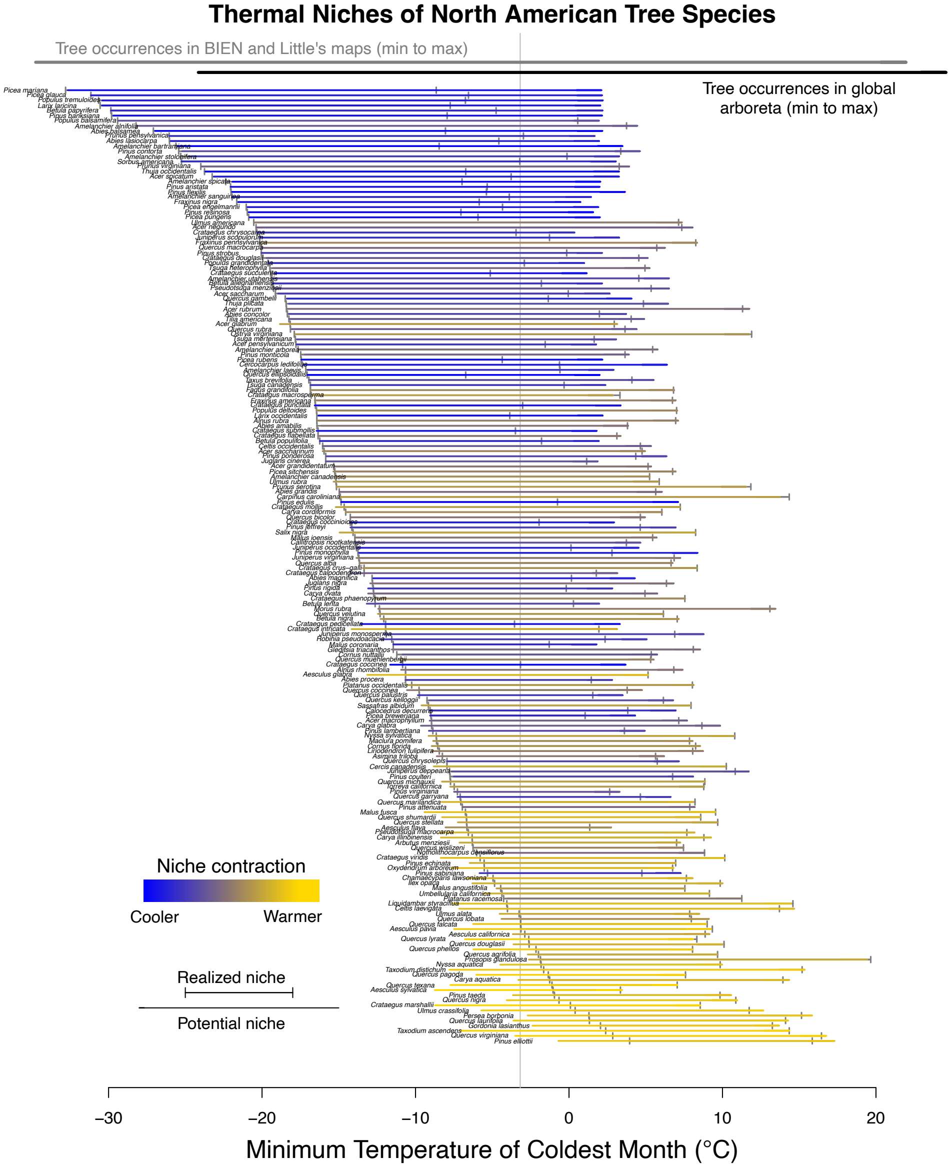

Fig. S4. Empirical estimates of the potential and realized thermal niches of North American trees along a gradient of minimum temperature of the coldest month.

Empirical estimates of realized and potential niches of 188 North American tree species along a gradient of minimum temperature of the coldest month. Realized niches (denoted by hash marks) are subsets of potential niches. Species are ordered by increasing realized niche minima. Niche minima and maxima are defined as the 0.01 and 0.99 quantiles of their distributions to remove effects of extreme outliers. Most species have a potential niche that overlaps the central temperature (solid vertical line) of -3.2 °C. The grey horizontal line denotes the range of temperatures sampled by BIEN and Little's range maps, and the black horizonal line denotes the range of temperatures of the arboreta. The vertical line represents the mean value of the estimated maximum and *x*-intercept from the fitted regression models in Fig. 3 in the main text.

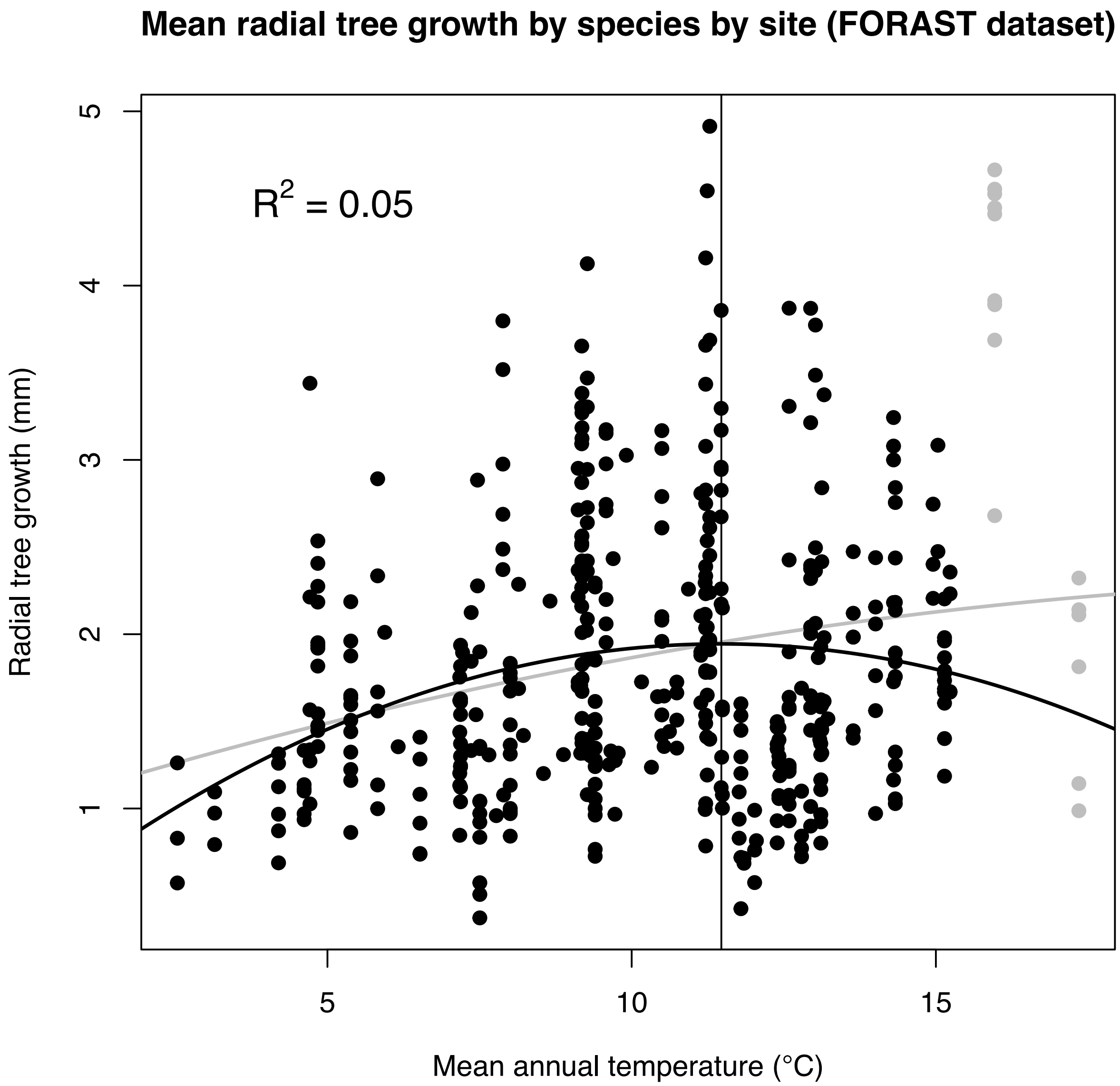

Fig. S5. Mean radial tree growth rate by species by site in the FORAST tree ring dataset from the northeastern United States.

A model fit to all the data is an increasing function, and the second-order term in the quadratic polynomial is not significant (grey line). However, if the two sites with divergent growth rates at the highest mean annual temperatures are removed (one of these sites has extremely fast growth rates for all species and are potential outliers and the warmest site is removed out of an abundance of caution to avoid few points that are highly leveraged), then the quadratic polynomial is highly significant with an optimum temperature for growth at 11.9 °C. Data reanalyzed from based on the FORAST data (*55, 56*).

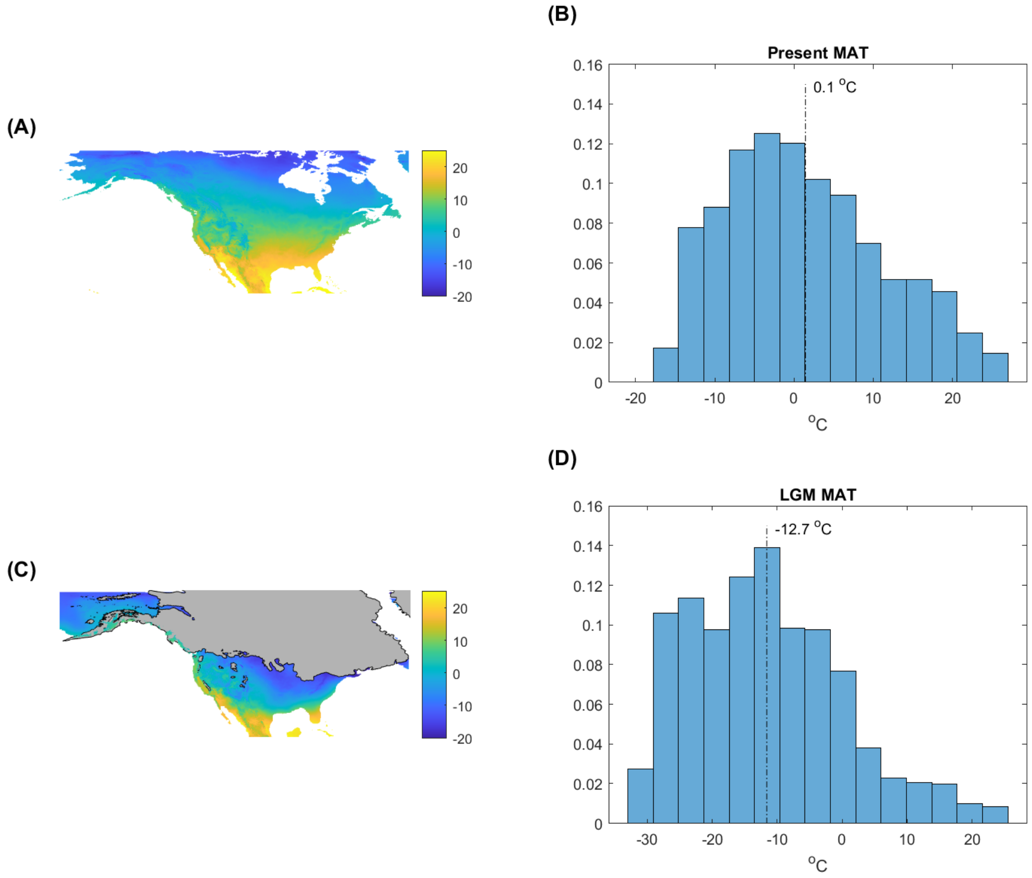

Fig. S6. Mean annual temperature at present and at the last glacial maximum (LGM).

Geographic distribution of mean annual temperatures in North America at present (A) and at the LGM (C) and frequency distributions of mean annual temperatures at the two time periods (B, D). Top row represents the present day. Bottom row represents the LGM. Vertical lines denote medians. Climate data based on WorldClim 1.4 (*57*) and ice sheet data based on Dalton et al. (*58*).

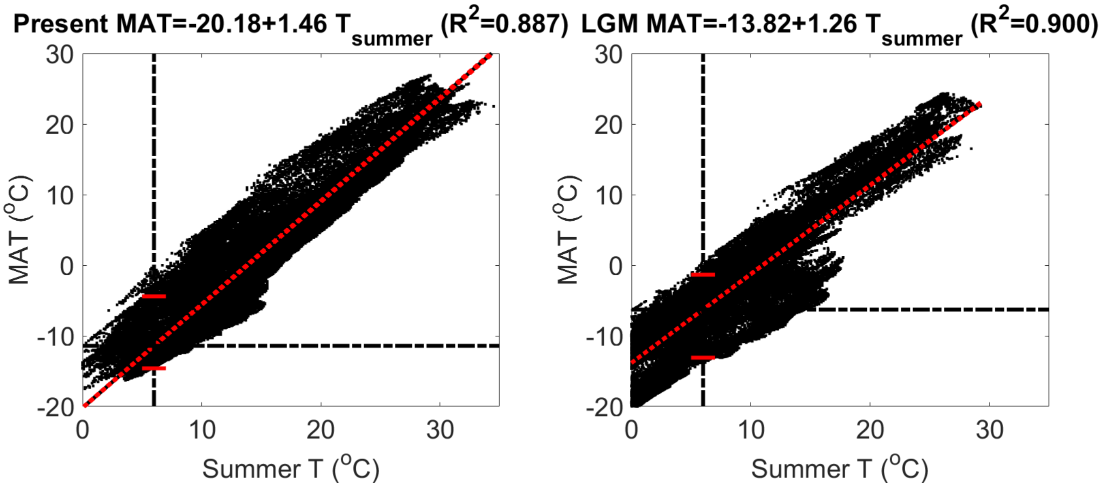

Fig. S7. Relationship between summer temperature (bio10) and mean annual temperature (bio1).

In the present day, a 6 °C summer temperature equates to a -11.4 °C mean annual temperature (MAT) with a 90% confidence interval of (-14.6, -4.4). In the last glacial maximum (LGM) a 6 °C summer temperature equates to a -6.34 °C mean annual temperature (MAT) with a 90% confidence interval of (-13.1, -1.3). Data from WorldClim 1.4 (*57*).

Table S1. Results of model comparisons for three sets of temperature variables (minimum, mean, maximum) and three sets of niche metrics. These results provide details about the test statistics shown in Fig. 2, S3, and S4. Models in bold were selected as the best model using AIC and likelihood ratio tests (LRT).

Temperature variable	Metric	Model	R^2	AIC	LRT	Model rank
Mean annual temperature	R:P ratio	Linear	0.06	-220	*NA*	2nd
		Quadratic	0.45	-320	*F*=134, *P* <0.0001	1st
	Niche contraction	Linear	0.65	-286	*NA*	2nd
		Quadratic	0.71	-318	*F*=38, *P*<0.0001	1st
	Potential niche width	Linear	0.24	940	*NA*	2nd
		Quadratic	0.29	929	*F*=13, *P*=0.0003	1st
Minimum temperature of coldest month	R:P ratio	Linear	0.03	-220	*NA*	2nd
		Quadratic	0.27	-273	*F*=62, *P*<0.0001	1st
	Niche contraction	Linear	0.59	-275	*NA*	1st
		Quadratic	0.60	-275	*F*=2.3, *P*=0.12	2nd
	Potential niche width	Linear	0.42	1045	*NA*	2nd
		Quadratic	0.45	1037	*F*=10.2, *P*=0.0016	1st
Maximum temperature of warmest month	R:P ratio	Linear	0.36	-171	*NA*	2nd
		Quadratic	0.47	-203	*F*=36, *P*<0.0001	1st
	Niche contraction	Linear	0.62	-194	*NA*	2nd
		Quadratic	0.67	-218	*F*=28, *P*<0.0001	1st
	Potential niche width	Linear	0.10	886	*NA*	2nd
		Quadratic	0.20	866	*F*=24, *P*=0.0002	1st

Table S2. Comparison of mean annual temperature (MAT) model results using different random samples from the BIEN and Little's range map data generated from different starting conditions for the random number generator. The three sets sampled from BIEN and Little's range maps using 10 times the number of botanical garden occurrences. Given their high similarity, we report results based on the first sample in the main text.

Sample	**Statistic**	**Sample 1 (reported in paper)**	**Sample 2**	**Sample 3**	**Mean of samples**
R:P ratio	Maximum	9.96	9.93	9.88	9.92
	R^2	0.45	0.48	0.46	0.46
Niche contraction	x-intercept	12.01	11.99	11.82	11.94
	R^2	0.71	0.70	0.70	0.70
Potential niche width	Minimum	15.96	16.51	15.80	16.09
	R^2	0.29	0.24	0.31	0.28
Mean					12.65