



Universiteit
Leiden
The Netherlands

Convergent strategies for leaf traits in tree species from divergent habitats

Xu, H.; Song, Y.; Tan, Y.H.; He, D.; Yang, Y.; Bodegom, P.M. van; ... ; Chen, L.

Citation

Xu, H., Song, Y., Tan, Y. H., He, D., Yang, Y., Bodegom, P. M. van, ... Chen, L. (2025). Convergent strategies for leaf traits in tree species from divergent habitats. *Global Change Biology*, 31(3). doi:10.1111/gcb.70108

Version: Publisher's Version

License: [Licensed under Article 25fa Copyright Act/Law \(Amendment Taverne\)](#)

Downloaded from: <https://hdl.handle.net/1887/4309796>

Note: To cite this publication please use the final published version (if applicable).

RESEARCH ARTICLE

Convergent Strategies for Leaf Traits in Tree Species From Divergent Habitats

Hanfeng Xu^{1,2,3}  | Yu Song⁴  | Yun-Hong Tan⁵ | Dashan He² | Yuchuan Yang² | Peter M. van Bodegom⁶  | Josep Peñuelas^{7,8}  | Yingji Pan^{1,3}  | Lei Chen² 

¹State Key Laboratory of Black Soils Conservation and Utilization, Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun, China | ²Key Laboratory of Bio-Resource and Eco-Environment of Ministry of Education, College of Life Sciences, Sichuan University, Chengdu, China | ³Key Laboratory of Wetland Ecology and Environment, Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun, China | ⁴Key Laboratory of Ecology of Rare and Endangered Species and Environmental Protection (Ministry of Education) & Guangxi Key Laboratory of Landscape Resources Conservation and Sustainable Utilization in Lijiang River Basin, Guangxi Normal University, Guilin, China | ⁵Southeast Asia Biodiversity Research Institute & Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, China | ⁶Institute of Environmental Sciences, Leiden University, Leiden, the Netherlands | ⁷CSIC, Global Ecology Unit CREAF-CSIC-UAB, Barcelona, Spain | ⁸CREAF, Cerdanyola del Vallès, Barcelona, Spain

Correspondence: Yingji Pan (panyingji@iga.ac.cn) | Lei Chen (lei.chen1029@gmail.com)

Received: 18 December 2024 | **Accepted:** 3 February 2025

Funding: This work was supported by the Chinese Academy of Sciences E429S10101 (Y.P.), the Innovation Team Project of Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences 2023CXTD03 (Y.P.), the National Natural Science Foundation of China 32271833 (L.C.) and 32260060 (Y.S.).

Keywords: botanical garden | climate change | consistent alteration in trait–trait relationships | long-term acclimation | trait trade-offs | transplantation

ABSTRACT

Plant trait expressions and their trade-offs reflect the responses and long-term ecological adaptation to environmental gradients. However, how such expressions and trade-offs help plants to acclimate to a new environment remains poorly understood, which is a fundamental preset for plants' survival under a global change scenario. By comparing the trait–trait relationships of 4403 tree species from different climatic regions and the variation in trait trade-offs of 746 tree species that have been transplanted to a tropical botanical garden for several decades, our results reveal convergent but consistent alteration in trait–trait relationships of trees transplanted from different climatic regions to a common environment. The convergent trends enhance the capability of tree species in buffering the impacts of climate change through allocating more resources to growth and tolerance. We propose that altered trait–trait relationships may be the key mechanisms that underlie the long-term ecological stability and resilience of tree species.

1 | Introduction

Plant functional traits are pivotal for growth and survival because they can indicate the efficiency of acquiring resources, the rate of growth, and overall fitness (Pérez-Harguindeguy et al. 2013; Sporbert et al. 2022; Violle et al. 2007). Plant

functional traits also play important roles in ecosystem functions, including the sequestration of carbon, the cycling of nutrients, and the regulation of water (Díaz et al. 2016; Maynard et al. 2022). In particular, the leaf economic spectrum describes the strategies for resource acquisition and allocation in plants, from the so-called quick-return end with high photosynthetic

Hanfeng Xu and Yu Song should be considered joint first author; Yingji Pan and Lei Chen should be considered joint senior author.

capacity (A_{mass}) and dark respiration rates (R_{mass}), high leaf nitrogen concentration (LNC), low leaf mass per area (LMA), and short leaf lifespan (LL) to the slow-return end with low A_{mass} and R_{mass} , low LNC, high LMA, and long LL (Díaz et al. 2016; Maynard et al. 2022; Messier et al. 2017; Pan et al. 2020; Thomas et al. 2020; Wright et al. 2004).

The consequences of global change, such as increased frequencies of heatwaves (Jacquemyn et al. 2012; Rybicki and Hanski 2013), droughts (Aldea et al. 2022; Young et al. 2017), wildfires (Rodman et al. 2021; Taber and Mitchell 2023), and frosts (Pardee et al. 2018), can profoundly alter the expression of plant functional traits and their trait–trait trade-offs, leading to modified strategies across diverse climatic regions. Combinations of traits in response to climate change may render some plants more viable in emerging climatic regimens, whereas other plants could become less competitive or go extinct. In addition to ambient environmental change, trait trade-offs in plants are also influenced by genetic constraints and ecological filtering (Cadotte et al. 2013; Liu et al. 2022; Messier et al. 2017; Umaña and Swenson 2019).

Plants in their natural environments tend to select the most appropriate combinations of traits based on their habitats (Díaz et al. 2016; E-Vojtkó et al. 2022; Maynard et al. 2022; Reich 2014; Umaña and Swenson 2019). For example, plants in tropical humid forests, where hydrothermal conditions are always favorable, often adopt resource-acquisition strategies characterized by increased rates of photosynthesis and growth, indicated by a high specific leaf area (SLA) and LNC and a large leaf area (Hodgson et al. 2011; Liu et al. 2023; Wright et al. 2004, 2017). In contrast, plants in temperate and cold regions often endure harsh environmental conditions, including low temperatures and nutrient scarcity (Liu et al. 2023). They consequently allocate more resources to carbon storage and physical resistance, which leads to thick leaves with a high leaf dry-matter content (LDMC) and a low SLA (Backhaus et al. 2021; Liu et al. 2023; Reich 2014; Thomas et al. 2020; Wright et al. 2017). By comparing the variations in plant traits and their interrelationships across different climatic conditions, we can infer the ecological strategies that plants may employ in response to climate change (Lavorel and Garnier 2002; Messier et al. 2017). For instance, by examining the differences in trait trade-offs between tropical and temperate

species, we can predict the ecological strategies plants might adopt under ongoing climate warming (Tian et al. 2016).

Previous studies have explored trade-offs for plant traits in various climatic regions (Backhaus et al. 2021; Liu et al. 2023; Májeková et al. 2021; Poorter 2009; Umaña and Swenson 2019), but the critical question of how these trade-offs change under climate change remains unresolved. Given that plants can adapt to different habitats through variations in functional traits (Backhaus et al. 2021; Kraft et al. 2015; Messier et al. 2017; Umaña and Swenson 2019) and regulation of trait coordination (Cadotte et al. 2013; Messier et al. 2017; Pan et al. 2020), we hypothesize that the species that have been transplanted to a new environment for decades would have convergent strategies of trait trade-offs for acclimating to a common habitat (Figure 1). Botanical gardens have vast collections of species that have been transplanted from diverse habitats in a shared environment for decades (Primack et al. 2021). Botanical gardens thus provide an ideal venue for identifying the impacts of climate change on plant trait trade-offs by allowing comparisons between trait–trait relationships in natural habitats and botanical gardens.

We focused on the trait–trait relationships of leaf economic spectrum traits and leaf structural traits, including leaf carbon concentration (LCC), LNC, SLA, and LDMC (see details in Table S1). To reveal whether long-term acclimation of plants to a new environment causes the convergent trait–trait relationships, we examined the trait trade-offs between species inhabiting different climatic regions based on the site-species dataset generated from the TRY database (Kattge et al. 2020) and those species that had been transplanted to a tropical botanical garden—the Xishuangbanna Tropical Botanical Garden (XTBG) in China. We first compared the differences in the trait–trait relationships of 1576 species from temperate habitats and 3045 species from tropical habitats as a baseline to demonstrate how trait–trait relationships vary in species of different climatic origins. We then examined the long-term acclimation of 746 species that have been transplanted from temperate and tropical regions into a tropical botanical garden for several decades. The pattern was further validated by categorizing the 746 species into native and non-native species based on their distribution records. This research provides a basis for understanding the plant responses to long-term climate change.

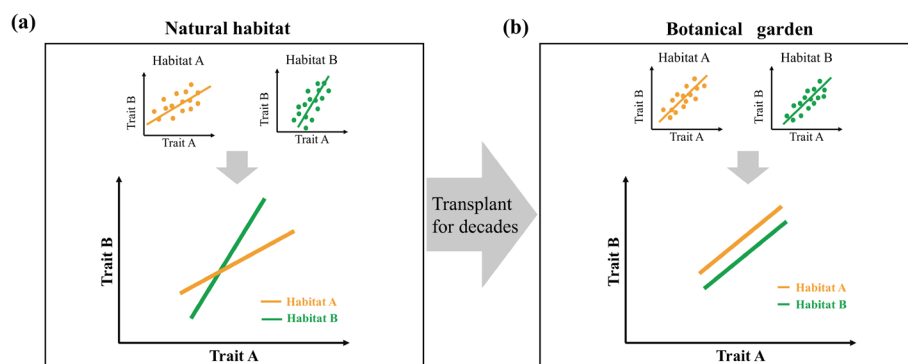


FIGURE 1 | Tree species from different habitats have consistent trait trade-offs after transplantation to the tropical botanical garden for decades. Different slopes between traits A and B imply that the trait trade-offs are differently expressed between habitat A and habitat B, as is the case in natural habitats (a). They have consistent trait trade-offs after their transplantation to the botanical garden (b).

2 | Materials and Methods

2.1 | Collection of Trait Data for Tropical and Temperate Tree Species in Their Natural Habitats

We extracted leaf-trait data for tropical and temperate tree species in their natural habitats from the TRY 6.0 database (Kattge et al. 2020). We used global data for the tropical and temperate species based on the sampling sites (Beck et al. 2018). The species names were standardized using The Plant List database and the “plantlist” R package (Zhang et al. 2021). We filtered the data sets of the TRY database based on their descriptions and excluded data sets that did not represent natural habitats, e.g., glasshouses, greenhouses, and controlled and uncontrolled climatic chambers, to ensure that the trait data set comprised records from natural habitats as much as possible. We designated tree species based on the BGCI GlobalTreeSearch database (BGCI 2022), finally matching 6439 species.

We filtered outliers following the approach by Díaz et al. (2016) to exclude errors or incorrect measurements. Specifically, we removed trait records with more than four standard deviations from the means of corresponding species, genera, and families. Trait records with more than three standard deviations from the means of corresponding species, genera, and families were also checked for plausibility. We excluded all records of gymnosperms to maintain uniformity with the species in the botanical garden. We calculated the average species traits for each site of each climatic region and generated a site-species dataset for the subsequent analyses. Totals of 3045 tropical species in 136 families and 1576 temperate species in 137 families (4403 species in total, 218 species in both tropical and temperate regions) were used for the subsequent analyses.

2.2 | Trait Data for the Botanical Garden

The Xishuangbanna Tropical Botanical Garden (XTBG) (101.25°N, 21.92°E) was established in 1959, covers an area of 1125 ha, and is the most renowned botanical garden with the largest area and richest living collections of plants in China. The garden has a tropical monsoon climate with three distinct seasons: a dry hot season (March to April), a wet hot season (May to October), and a foggy cool season (November to February). The mean annual temperature (MAT) is 21.8°C, and the mean annual precipitation is 1492.9 mm. The leaf traits were sampled between late December 2020 and early January 2021.

We sampled leaves from all available tree species in XTBG, including gymnosperms and angiosperms. These species have lived in the botanical garden for at least 10 to about 60 years. The gymnosperms were not included in the analysis due to the small sample size (13 species) compared to angiosperms (746 species). The species selected covered the main phylogenetic clades of angiosperms (The Angiosperm Phylogeny Group 2016).

2.3 | Measurements of Functional Traits and the Original Habitats

At least three healthy and mature individuals of each species were sampled in the botanical garden. All individuals of a species were sampled if the number of individuals was < 3. We sampled a total of 2120 trees and measured four leaf traits, LCC, LNC, SLA, and LDMC, following the method described by Pérez-Harguindeguy et al. (2013). At least 10 “sun leaves” (outer canopy leaves growing under relatively optimal conditions) per individual were collected for measuring the leaf traits. We collected 3–5 leaves if the leaves were extremely large, e.g., *Carica papaya*. Leaves were collected from the outer canopy and were then immediately placed in sealed moist plastic bags. Leaf fresh weight (LFW) was measured in the laboratory on the same day of sampling. We scanned the leaves after weighing and determined leaf area (LA) using ImageJ (Schneider et al. 2012). The leaves were then oven-dried at 65°C for 48 h, and their dry mass (DM) was weighed. LDMC and SLA were calculated as $LDMC = DM/LFW$ and $SLA = LA/DM$. The dry leaves were grained and analyzed using an elemental analyzer (UNICUBE trace, Germany) for determining the nutrient traits.

The climatic regions of the species were defined based on their original habitats before they were transplanted to the botanical garden. Obtaining relevant information about their original habitats, however, is currently impossible due to the lack of detailed information about the transplantation site for most species in the botanical garden. As an alternative, we categorized the climatic regions of the species in the botanical garden based on species occurrence records of their global distribution from the Global Biodiversity Information Facility (GBIF, <https://www.gbif.org/>). If the species occurrence records on GBIF were sparse or absent, we determined the climatic regions of the species based on floras, including the List of Plants in Xishuangbanna (Li et al. 1996), Flora of China (<http://www.floraofchina.org/>), and eFloras (<http://www.efloras.org/>). Species names were standardized using the “plantlist” R package (Zhang et al. 2021) before the analyses.

The classification of climatic regions followed the criteria proposed by Beck et al. (2018). Species in the botanical garden were categorized into tropical, temperate, and widespread species. In this study, for each species with more than 30 species occurrence records in GBIF, a climate is designated as the primary climatic region for a species if it occurs in more than 70% of the species' occurrence records. For example, if more than 70% of a species' occurrence records are in a tropical climatic region, the species is considered primarily distributed in that climatic region (tropical species). Conversely, a species is considered widespread (widespread species) if the frequency of its occurrence in any one climatic region is less than 70%, and it occurs in at least two climatic regions, each comprising more than 20% of its records. We used the descriptions of distribution area in floras to determine the climatic regions for species with < 30 records of geographic coordinates. Species from arid and cold regions were excluded due to their low species numbers (i.e., only two species respectively).

We also checked the effects of defining different thresholds in occurrence frequency (80%, 90%, and 100%) to identify the climatic regions of a given species, ensuring consistent and valid results. We categorized species as native and non-native based on the records in the List of Plants in Xishuangbanna (Li et al. 1996).

Unlike in the botanical garden, the categorization of the climatic region of species in the natural habitats was based on the climate of the sampling sites. Species in arid, cold, and polar regions were excluded. Species in natural habitats were categorized into tropical and temperate species, as in the botanical garden. To address the potential inconsistencies caused by using different methods for categorizing climate, we also allocated the species to different climatic regions when applying the procedure outlined for the species in the botanical garden (for all thresholds of occurrence frequency: 70%, 80%, 90%, and 100%) and reran the analysis on trade-offs.

2.4 | Statistical Analyses

Compared with traditional linear regression, standardized major-axis regression (SMA) considers errors in the measurement of variables and does not assume any direction that one variable affects another (Májeková et al. 2021). SMA has therefore been frequently applied to estimate bivariate relationships and trait–trait trade-offs (Cui et al. 2020; Pan et al. 2020; Sporbett et al. 2022; Wright et al. 2004). We performed SMA using the “smatr” R package (Warton et al. 2012) to identify leaf trait–trait associations (leaf economic spectrum traits, leaf structural traits) for trees in their natural habitats and the botanical garden from different climatic regions. We calculated mean trait values for the species in the botanical garden. All trait values were $\log_{10}$ -transformed for all analyses. SMA was then used to identify the trait–trait relationships for the various climatic regions of the species in natural habitats and the botanical garden. The slope of the bivariate traits of SMA represents the fundamental trait trade-offs, and the elevation (intercept) of the bivariate traits of SMA indicates the resource-use efficiency (Cui et al. 2020). We identified the differences in the slopes and elevations of pairwise leaf traits for trees from different climatic regions in natural habitats and the botanical garden. We calculated and compared the differences in the slopes and the shifts in elevation when the slope was common among the climatic regions (Warton et al. 2006, 2012). Both similar slopes and elevations indicate that the trait–trait relationships remained consistent across climatic regions. In contrast, a significantly changed slope indicates that the trait–trait relationships had sufficiently adapted to different climatic regions. A consistent slope but a shifted elevation indicates different expressions of specific traits, while the trait–trait relationships remain consistent across the climatic regions. Finally, we compared the trait–trait relationships between species from different climatic regions that had been transplanted to the botanical garden and the trait–trait relationships of native species to determine the adaptability of non-native species. We also analyzed the trait–trait relationships among different climatic regions for species in natural habitats and in the botanical garden when using a different threshold occurrence frequency (70%, 80%, 90%, and 100%) to

assign species to different climatic regions. All statistical analyses were performed in R version 4.1.1 (R Core Team 2024). The data and code that support the findings of this study can be accessed in the Figshare repository (Xu et al. 2024).

3 | Results

3.1 | Trait–Trait Relationships of Tree Species in Natural Habitats

The tree species living in the different climatic regions showed inconsistent trait trade-offs (Figure 2; Table S2). LDMC in the natural habitats was negatively correlated with LNC and SLA for both tropical and temperate species ($p < 0.05$). An SMA analysis identified significant differences in the slopes of the LNC–LDMC and LDMC–SLA relationships between the tropical and temperate species (Figure 2a,b). Specifically, LDMC decreased faster as LNC increased in the tropical species compared with the temperate species, indicating a lower investment in leaf dry matter with increasing LNC in tropical species. In contrast, the slope for the LDMC–SLA relationship was steeper for the temperate species, indicating a larger decrease in SLA as LDMC increased, suggesting that the temperate species decreased their investment in capturing light as the investment in leaf dry matter increased. The LCC–LDMC and LNC–SLA relationships were significantly positively correlated in both tropical and temperate species ($p < 0.05$), and LCC and LDMC were more significantly positively correlated in tropical than temperate species, indicated by a steeper slope (Figure 2c). The slope for the LNC–SLA relationship did not differ significantly between the tropical and temperate species, but elevation did (Figure 2d). Elevation was notably higher for the temperate species, suggesting that they tended to have a higher SLA than the tropical species at a given LNC.

3.2 | Trait–Trait Relationships of Tree Species in the Botanical Garden

The tropical and temperate species exhibited consistent trade-offs decades after being transplanted to the tropical botanical garden (Figure 3; Table S3). The slopes and elevations of the LNC–SLA, LCC–LDMC, LNC–LDMC, and LDMC–SLA relationships did not differ significantly between the tropical and temperate species in the botanical garden ($p > 0.05$, Figure 3). These findings suggest that the trees from tropical and temperate regions have flexible but consistent changes in the trait–trait relationships toward a similar resource use efficiency in the tropical botanical garden. We also determined whether the trait trade-offs were consistent for widespread species in both tropical and temperate regions and found no significant differences in the slopes and elevations of the pairwise traits among the tropical, temperate, and widespread species mentioned above (Figure 4), suggesting that the widespread species adopted trade-off strategies similar to the tropical and temperate species in the botanical garden.

We categorized the tree species in the botanical garden as native and non-native species based on the local flora to test the robustness of our results (Figure 5; Table S3). We also compared the

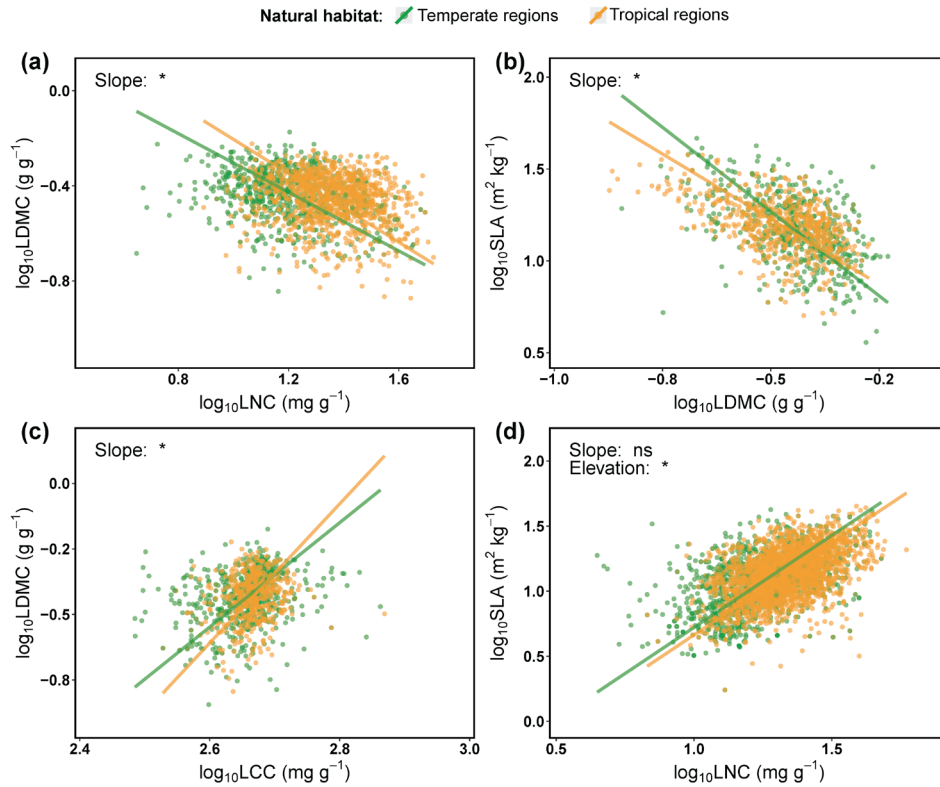


FIGURE 2 | Leaf-trait relationships between the tropical and temperate tree species in natural habitats. The solid lines represent standardized major-axis regressions of pairwise trait relationships. The notation “Slope” and/or “Elevation” identifies significant differences in the slopes or elevations of pairwise traits between the tropical and temperate species. Changes in elevations cannot be detected if the slopes differ significantly. LCC, leaf carbon concentration; LDMC, leaf dry-matter content; LNC, leaf nitrogen concentration; SLA, specific leaf area; ns, $p > 0.05$; *, $p < 0.05$.

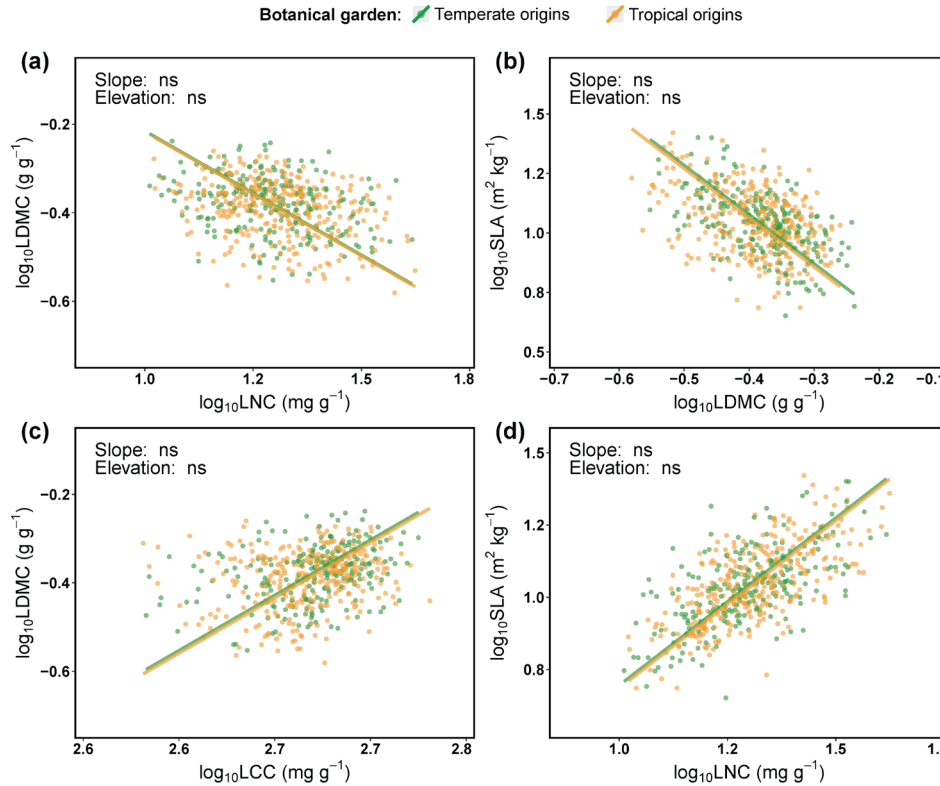


FIGURE 3 | Leaf-trait relationships between the tropical and temperate tree species in the botanical garden. The solid lines represent standardized major-axis regressions of pairwise trait relationships. The notation “Slope” and/or “Elevation” identifies significant differences in the slopes or elevations of pairwise traits between the tropical and temperate species. Changes in elevation cannot be detected if the slopes differ significantly. LCC, leaf carbon concentration; LDMC, leaf dry-matter content; LNC, leaf nitrogen concentration; SLA, specific leaf area; ns, $p > 0.05$; *, $p < 0.05$.

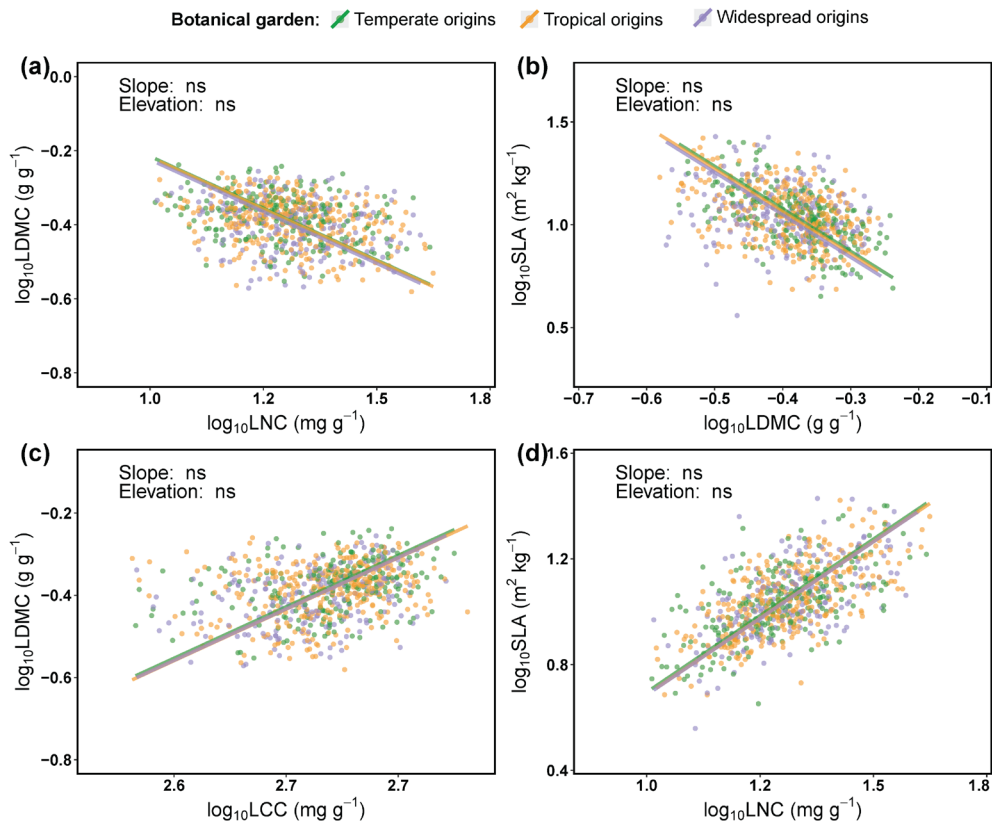


FIGURE 4 | Leaf-trait relationships among the tropical, temperate, and widespread tree species in the botanical garden. The solid lines represent standardized major-axis regressions of pairwise trait relationships. The notation “Slope” and/or “Elevation” identifies significant differences in the slopes or elevations of pairwise traits among tropical, temperate, and widespread species. Changes in elevation cannot be detected if the slopes differ significantly. LCC, leaf carbon concentration; LDMC, leaf dry-matter content; LNC, leaf nitrogen concentration; SLA, specific leaf area; ns, $p > 0.05$; *, $p < 0.05$.

changes in the slopes and elevations of pairwise traits between the native and non-native species. The slopes and elevations of these pairwise traits did not differ significantly between the native and non-native species (Figure 5). These findings suggest that the non-native species adapt to the local climate in the botanical garden by adjusting their trade-offs for the leaf traits and have trade-off strategies consistent with those for the native species.

To test the robustness of our results, we also re-examined the trait-trait relationships by more strictly defining the threshold in the frequency of occurrence for allocating a species to a temperate or tropical climatic region versus a widespread species (see details in Section 2) and obtained similar results. There are significant differences in the slopes of pairwise traits among the tropical, temperate, and widespread species for all different thresholds of occurrence frequency (Figures S1–S4), but the slopes and elevations of pairwise traits did not differ significantly among the tropical, temperate, and widespread species that had been transplanted to the botanical garden (Figures S5–S7). These results further verified the reliability of our results.

4 | Discussion

Our study explored the variations in trade-offs for leaf traits in tree species transplanted from their natural habitats to a tropical

botanical garden several decades ago. Tropical and temperate species had different trade-offs in their natural environments. The slopes and elevations of pairwise traits for temperate, tropical, and widespread species that had been transplanted to a common tropical garden for decades, however, converged, indicating consistent resource allocation strategies of the species after transplantation.

Trees in their natural habitats may encounter diverse habitat selection pressures, such as frost (Pardee et al. 2018; Primack et al. 2021), drought (Aldea et al. 2022; Yang et al. 2023; Young et al. 2017), and wind (Gardiner et al. 2016). Trees thus need to allocate their resources not only for photosynthesis and growth, but also for structural construction and protection (Messier et al. 2017; Osnas et al. 2013; Prieto et al. 2018; Wang et al. 2022; Wright et al. 2004). Tropical regions tend to have higher biodiversity and a greater availability of resources (John et al. 2007; Liu et al. 2023), leading to greater competition and pressures from herbivores than in temperate regions (Backhaus et al. 2021; Liu et al. 2023; Poorter and Rozendaal 2008). Tropical species consequently tend to develop fast-return strategies with enhanced photosynthetic capacities (Díaz et al. 2016; Reich 2014; Wright et al. 2004). In contrast, temperate trees may have a greater risk of cold extremes, such as late spring frost (Augspurger 2009; Vitra et al. 2017; Zohner et al. 2019), leading to a higher allocation of resources to construct better leaf mechanical structures and

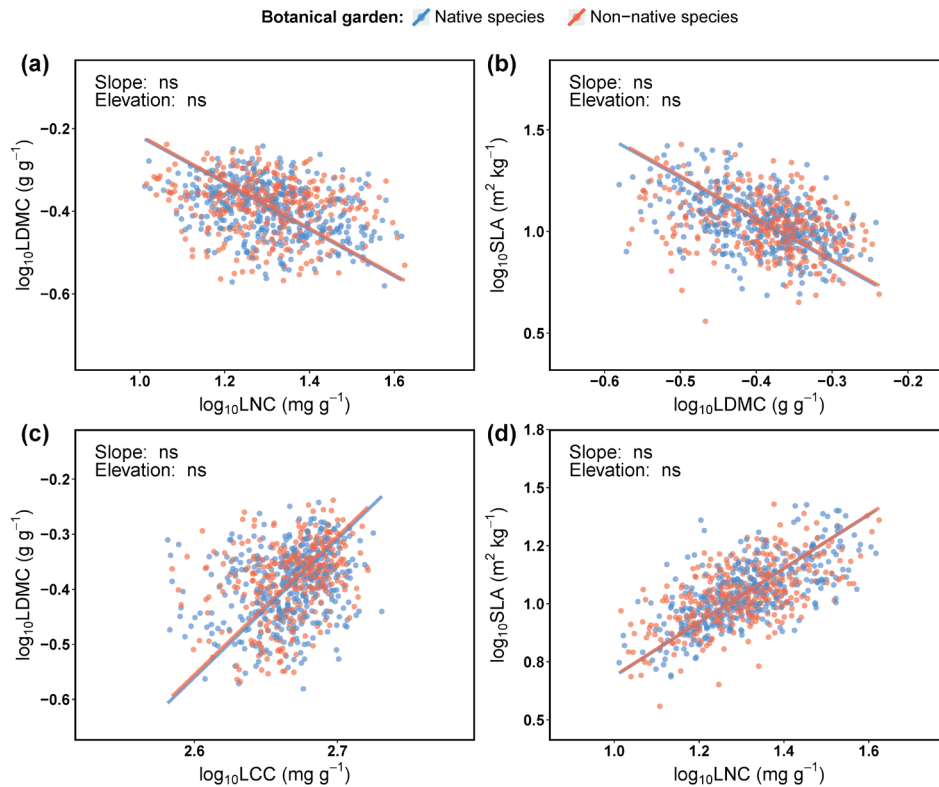


FIGURE 5 | Leaf-trait relationships between native and non-native tree species in the botanical garden. The solid lines represent standardized major-axis regressions of pairwise trait relationships. The notation “Slope” and/or “Elevation” identifies significant differences in the slopes or elevations of pairwise traits between native and non-native species in the botanical garden. Changes in elevation cannot be detected if the slopes differ significantly. LCC, leaf carbon concentration; LDMC, leaf dry-matter content; LNC, leaf nitrogen concentration; SLA, specific leaf area; ns, $p > 0.05$; *, $p < 0.05$.

to increase tolerance (Hodgson et al. 2011; Onoda et al. 2011). Changes in investment in growth and tolerance are represented by altered trait–trait relationships (Pan et al. 2020; Wright et al. 2004). We found that temperate tree species in their natural habitats reduced their investment in photosynthesis and allocated more resources to the tolerance of harsh environmental conditions, such as low-temperature stress. For example, temperate species allocated more carbon to enhance mechanical resistance compared to tropical species as investment in LDMC increased, while simultaneously reducing investments in LNC and SLA to decrease photosynthetic capacity (Figure 2). Thus, divergent growth strategies lead to distinct trade-offs between tropical and temperate trees in their natural habitats.

In contrast, species in a botanical garden experience consistent environmental conditions and are not constrained by cold extremes. So, trees from different climatic regions can reallocate resources to photosynthesis and growth that were originally used for tolerance. Species from different climatic origins consequently acquire convergent trade-offs for leaf traits in the botanical garden after decades of acclimation. This is expressed in the consistent investments in growth and tolerance of species from tropical and temperate regions after being transplanted to the botanical garden to adapt to their common environment: the slopes and elevations of pairwise traits did not differ significantly (Figure 3). The trait trade-offs among the tropical, temperate, and widespread species (Figure 4) and between native

and non-native species were consistent (Figure 5). These results collectively indicate that species from different habitats have convergent strategies of trait trade-offs when in a common environment.

The shift from divergent trait trade-offs for trees in natural habitats of different climatic regions to convergent trait trade-offs in the tropical botanical garden demonstrates that environmental conditions are the dominant driver of trait expression, more than genetics or some hardwired strategies. Based on our findings, we predict that trees from different climatic regions are likely to have convergent patterns in their leaf trait trade-offs after being introduced to a new environment. Trees may adjust their allocation of resources to growth and tolerance, establishing consistent trade-offs to better adapt to the altered climate. Indeed, widespread species, due to their intrinsic high adaptability, may have more variable trait correlations but may ultimately also adopt trait trade-offs consistent with those of the tropical and temperate species. These findings provide evidence for convergent plant ecological strategies to prolonged climate change.

Our study primarily focused on long-term effects from one to several decades and excluded short-term effects. How quickly the trade-offs for leaf traits adapt after trees have been transplanted to a botanical garden remains to be investigated and would provide crucial insights into the initial stages of adaptation and the potentiality for rapid phenotypic plasticity.

Additionally, future research is needed to expand our findings to varied climatic regions and more combinations of functional traits to better generalize our findings.

In summary, our findings indicate that tree species from diverse climatic conditions may develop convergent trade-off strategies after decades of acclimation in the botanical garden, as demonstrated by changes in their leaf trait–trait relationships. This convergence may also lead to crucial losses in functional diversity, despite the potentially enhanced adaptation to climate through the alteration of trait trade-offs (Ensslin et al. 2015; Sun et al. 2022). These insights suggest that prolonged climate change, such as extended drought or warming (Chen et al. 2019; Trenberth et al. 2014), could drive convergences in plant trait–trait trade-offs across different regions. Understanding these patterns is essential for developing effective ex-situ conservation practices and resilient management practices for biodiversity protection in the face of ongoing climate change.

Author Contributions

Hanfang Xu: data curation, formal analysis, investigation, methodology, software, validation, visualization, writing – original draft, writing – review and editing. **Yu Song:** funding acquisition, investigation, resources, writing – review and editing. **Yun-Hong Tan:** resources, writing – review and editing. **Dashan He:** investigation, writing – review and editing. **Yuchuan Yang:** investigation, visualization, writing – review and editing. **Peter M. van Bodegom:** methodology, visualization, writing – review and editing. **Josep Peñuelas:** methodology, writing – review and editing. **Yingji Pan:** conceptualization, formal analysis, funding acquisition, methodology, project administration, supervision, writing – review and editing. **Lei Chen:** conceptualization, formal analysis, funding acquisition, methodology, project administration, supervision, writing – review and editing.

Acknowledgments

We thank Lei Zhang for his help in species identification. We also thank many students for their help in field data collection. We thank the Department of Gardening and Horticulture, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, for providing plant resources and sampling help. We thank the Life Science Core Facilities, College of Life Sciences, Sichuan University, for providing the elemental analyzer. This work was supported by the Chinese Academy of Sciences E429S10101 (Y.P.), the Innovation Team Project of Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences 2023CXTD03 (Y.P.), the National Natural Science Foundation of China 32271833 (L.C.) and 32260060 (Y.S.).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supported the findings of this study are openly available in Figshare at <https://doi.org/10.6084/m9.figshare.27918429>. Tree leaf trait data of species inhabiting different climatic regions is available from the TRY plant database at <https://www.try-db.org/> (version 6.0).

References

Aldea, J., R. Ruiz-Peinado, M. Del Río, et al. 2022. “Timing and Duration of Drought Modulate Tree Growth Response in Pure and Mixed Stands

of Scots Pine and Norway Spruce.” *Journal of Ecology* 110, no. 11: 2673–2683. <https://doi.org/10.1111/1365-2745.13978>.

Augsburger, C. K. 2009. “Spring 2007 Warmth and Frost: Phenology, Damage and Refoliation in a Temperate Deciduous Forest.” *Functional Ecology* 23, no. 6: 1031–1039. <https://doi.org/10.1111/j.1365-2435.2009.01587.x>.

Backhaus, L., G. Albert, A. Cuchietti, et al. 2021. “Shift From Trait Convergence to Divergence Along Old-Field Succession.” *Journal of Vegetation Science* 32, no. 2: e12986. <https://doi.org/10.1111/jvs.12986>.

Beck, H. E., N. E. Zimmermann, T. R. McVicar, N. Vergopolan, A. Berg, and E. F. Wood. 2018. “Present and Future Köppen-Geiger Climate Classification Maps at 1-Km Resolution.” *Scientific Data* 5, no. 1: 180214. <https://doi.org/10.1038/sdata.2018.214>.

BGCI. 2022. *GlobalTreeSearch Online Database*. Botanic Gardens Conservation International. https://tools.bgci.org/global_tree_search.php.

Cadotte, M., C. H. Albert, and S. C. Walker. 2013. “The Ecology of Differences: Assessing Community Assembly With Trait and Evolutionary Distances.” *Ecology Letters* 16, no. 10: 1234–1244. <https://doi.org/10.1111/ele.12161>.

Chen, L., J. Huang, Q. Ma, H. Hänninen, F. Tremblay, and Y. Bergeron. 2019. “Long-Term Changes in the Impacts of Global Warming on Leaf Phenology of Four Temperate Tree Species.” *Global Change Biology* 25, no. 3: 997–1004. <https://doi.org/10.1111/gcb.14496>.

Cui, E., E. Weng, E. Yan, and J. Xia. 2020. “Robust Leaf Trait Relationships Across Species Under Global Environmental Changes.” *Nature Communications* 11, no. 1: 2999. <https://doi.org/10.1038/s41467-020-16839-9>.

Díaz, S., J. Kattge, J. H. C. Cornelissen, et al. 2016. “The Global Spectrum of Plant Form and Function.” *Nature* 529, no. 7585: 167–171. <https://doi.org/10.1038/nature16489>.

Ensslin, A., O. Tschöpe, M. Burkart, and J. Joshi. 2015. “Fitness Decline and Adaptation to Novel Environments in Ex Situ Plant Collections: Current Knowledge and Future Perspectives.” *Biological Conservation* 192: 394–401. <https://doi.org/10.1016/j.biocon.2015.10.012>.

E-Vojtkó, A., R. R. Junker, F. de Bello, and L. Götzenberger. 2022. “Floral and Reproductive Traits Are an Independent Dimension Within the Plant Economic Spectrum of Temperate Central Europe.” *New Phytologist* 236, no. 5: 1964–1975. <https://doi.org/10.1111/nph.18386>.

Gardiner, B., P. Berry, and B. Moulia. 2016. “Review: Wind Impacts on Plant Growth, Mechanics and Damage.” *Plant Science* 245: 94–118. <https://doi.org/10.1016/j.plantsci.2016.01.006>.

Hodgson, J. G., G. Montserrat-Martí, M. Charles, et al. 2011. “Is Leaf Dry Matter Content a Better Predictor of Soil Fertility Than Specific Leaf Area?” *Annals of Botany* 108, no. 7: 1337–1345. <https://doi.org/10.1093/aob/mcr225>.

Jacquemyn, H., L. de Meester, E. Jongejans, and O. Honnay. 2012. “Evolutionary Changes in Plant Reproductive Traits Following Habitat Fragmentation and Their Consequences for Population Fitness: Habitat Fragmentation and Plant Trait Evolution.” *Journal of Ecology* 100, no. 1: 76–87. <https://doi.org/10.1111/j.1365-2745.2011.01919.x>.

John, R., J. W. Dalling, K. E. Harms, et al. 2007. “Soil Nutrients Influence Spatial Distributions of Tropical Tree Species.” *Proceedings of the National Academy of Sciences of the United States of America* 104, no. 3: 864–869. <https://doi.org/10.1073/pnas.0604666104>.

Kattge, J., G. Bönsch, S. Díaz, et al. 2020. “TRY Plant Trait Database Enhanced Coverage and Open Access.” *Global Change Biology* 26, no. 1: 119–188. <https://doi.org/10.1111/gcb.14904>.

Kraft, N. J. B., P. B. Adler, O. Godoy, E. C. James, S. Fuller, and J. M. Levine. 2015. “Community Assembly, Coexistence and the Environmental Filtering Metaphor.” *Functional Ecology* 29, no. 5: 592–599. <https://doi.org/10.1111/1365-2435.12345>.

- Lavorel, S., and E. Garnier. 2002. "Predicting Changes in Community Composition and Ecosystem Functioning From Plant Traits: Revisiting the Holy Grail." *Functional Ecology* 16, no. 5: 545–556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>.
- Li, Y., S. Pei, Z. Xu, et al. 1996. *List of Plants in Xishuangbanna*. 2nd ed. Nationalities Publishing House of Yunnan.
- Liu, H., Q. Ye, K. J. Simpson, E. Cui, and J. Xia. 2022. "Can Evolutionary History Predict Plant Plastic Responses to Climate Change?" *New Phytologist* 235, no. 3: 1260–1271. <https://doi.org/10.1111/nph.18194>.
- Liu, Z., M. Zhao, H. Zhang, T. Ren, C. Liu, and N. He. 2023. "Divergent Response and Adaptation of Specific Leaf Area to Environmental Change at Different Spatio-Temporal Scales Jointly Improve Plant Survival." *Global Change Biology* 29, no. 4: 1144–1159. <https://doi.org/10.1111/gcb.16518>.
- Májeková, M., T. Hájek, Á. J. Albert, et al. 2021. "Weak Coordination Between Leaf Drought Tolerance and Proxy Traits in Herbaceous Plants." *Functional Ecology* 35, no. 6: 1299–1311. <https://doi.org/10.1111/1365-2435.13792>.
- Maynard, D. S., L. Bialic-Murphy, C. M. Zohner, et al. 2022. "Global Relationships in Tree Functional Traits." *Nature Communications* 13, no. 1: 3185. <https://doi.org/10.1038/s41467-022-30888-2>.
- Messier, J., B. J. McGill, B. J. Enquist, and M. J. Lechowicz. 2017. "Trait Variation and Integration Across Scales: Is the Leaf Economic Spectrum Present at Local Scales?" *Ecography* 40, no. 6: 685–697. <https://doi.org/10.1111/ecog.02006>.
- Onoda, Y., M. Westoby, P. B. Adler, et al. 2011. "Global Patterns of Leaf Mechanical Properties: Global Patterns of Leaf Mechanical Properties." *Ecology Letters* 14, no. 3: 301–312. <https://doi.org/10.1111/j.1461-0248.2010.01582.x>.
- Osnas, J. L. D., J. W. Lichstein, P. B. Reich, and S. W. Pacala. 2013. "Global Leaf Trait Relationships: Mass, Area, and the Leaf Economics Spectrum." *Science* 340, no. 6133: 741–744. <https://doi.org/10.1126/science.1231574>.
- Pan, Y., E. Cieraad, J. Armstrong, et al. 2020. "Global Patterns of the Leaf Economics Spectrum in Wetlands." *Nature Communications* 11, no. 1: 4519. <https://doi.org/10.1038/s41467-020-18354-3>.
- Pardee, G. L., D. W. Inouye, and R. E. Irwin. 2018. "Direct and Indirect Effects of Episodic Frost on Plant Growth and Reproduction in Subalpine Wildflowers." *Global Change Biology* 24, no. 2: 848–857. <https://doi.org/10.1111/gcb.13865>.
- Pérez-Harguindeguy, N., S. Díaz, E. Garnier, et al. 2013. "New Handbook for Standardised Measurement of Plant Functional Traits Worldwide." *Australian Journal of Botany* 61, no. 3: 167. <https://doi.org/10.1071/BT12225>.
- Poorter, L. 2009. "Leaf Traits Show Different Relationships With Shade Tolerance in Moist Versus Dry Tropical Forests." *New Phytologist* 181, no. 4: 890–900. <https://doi.org/10.1111/j.1469-8137.2008.02715.x>.
- Poorter, L., and D. M. A. Rozendaal. 2008. "Leaf Size and Leaf Display of Thirty-Eight Tropical Tree Species." *Oecologia* 158, no. 1: 35–46. <https://doi.org/10.1007/s00442-008-1131-x>.
- Prieto, I., J. I. Querejeta, J. Segrestin, F. Volaire, and C. Roumet. 2018. "Leaf Carbon and Oxygen Isotopes Are Coordinated With the Leaf Economics Spectrum in Mediterranean Rangeland Species." *Functional Ecology* 32, no. 3: 612–625. <https://doi.org/10.1111/1365-2435.13025>.
- Primack, R. B., E. R. Ellwood, A. S. Gallinat, and A. J. Miller-Rushing. 2021. "The Growing and Vital Role of Botanical Gardens in Climate Change Research." *New Phytologist* 231, no. 3: 917–932. <https://doi.org/10.1111/nph.17410>.
- R Core Team. 2024. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. <https://www.R-project.org/> [Computer software].
- Reich, P. B. 2014. "The World-Wide 'Fast-Slow' Plant Economics Spectrum: A Traits Manifesto." *Journal of Ecology* 102, no. 2: 275–301. <https://doi.org/10.1111/1365-2745.12211>.
- Rodman, K. C., T. T. Veblen, R. A. Andrus, et al. 2021. "A Trait-Based Approach to Assessing Resistance and Resilience to Wildfire in Two Iconic North American Conifers." *Journal of Ecology* 109, no. 1: 313–326. <https://doi.org/10.1111/1365-2745.13480>.
- Rybicki, J., and I. Hanski. 2013. "Species-Area Relationships and Extinctions Caused by Habitat Loss and Fragmentation." *Ecology Letters* 16: 27–38. <https://doi.org/10.1111/ele.12065>.
- Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. "NIH Image to ImageJ: 25 Years of Image Analysis." *Nature Methods* 9, no. 7: 671–675. <https://doi.org/10.1038/nmeth.2089>.
- Sporbert, M., D. Jakubka, S. F. Bucher, et al. 2022. "Functional Traits Influence Patterns in Vegetative and Reproductive Plant Phenology—A Multi-Botanical Garden Study." *New Phytologist* 235, no. 6: 2199–2210. <https://doi.org/10.1111/nph.18345>.
- Sun, Q., L. Lai, J. Zhou, et al. 2022. "Differences in Ecological Traits Between Plants Grown In Situ and Ex Situ and Implications for Conservation." *Sustainability* 14, no. 9: 5199. <https://doi.org/10.3390/su14095199>.
- Taber, E. M., and R. M. Mitchell. 2023. "Rapid Changes in Functional Trait Expression and Decomposition Following High Severity Fire and Experimental Warming." *Forest Ecology and Management* 541: 121019. <https://doi.org/10.1016/j.foreco.2023.121019>.
- The Angiosperm Phylogeny Group. 2016. "An Update of the Angiosperm Phylogeny Group Classification for the Orders and Families of Flowering Plants: APG IV." *Botanical Journal of the Linnean Society* 181, no. 1: 1–20. <https://doi.org/10.1111/boj.12385>.
- Thomas, H. J. D., A. D. Bjorkman, I. H. Myers-Smith, et al. 2020. "Global Plant Trait Relationships Extend to the Climatic Extremes of the Tundra Biome." *Nature Communications* 11, no. 1: 1351. <https://doi.org/10.1038/s41467-020-15014-4>.
- Tian, M., G. Yu, N. He, and J. Hou. 2016. "Leaf Morphological and Anatomical Traits From Tropical to Temperate Coniferous Forests: Mechanisms and Influencing Factors." *Scientific Reports* 6, no. 1: 19703. <https://doi.org/10.1038/srep19703>.
- Trenberth, K. E., A. Dai, G. van der Schrier, et al. 2014. "Global Warming and Changes in Drought." *Nature Climate Change* 4, no. 1: 17–22. <https://doi.org/10.1038/nclimate2067>.
- Umaña, M. N., and N. G. Swenson. 2019. "Does Trait Variation Within Broadly Distributed Species Mirror Patterns Across Species? A Case Study in Puerto Rico." *Ecology* 100, no. 8: e02745. <https://doi.org/10.1002/ecy.2745>.
- Violle, C., M. Navas, D. Vile, et al. 2007. "Let the Concept of Trait Be Functional!" *Oikos* 116, no. 5: 882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>.
- Vittra, A., A. Lenz, and Y. Vitasse. 2017. "Frost Hardening and Dehardening Potential in Temperate Trees From Winter to Budburst." *New Phytologist* 216, no. 1: 113–123. <https://doi.org/10.1111/nph.14698>.
- Wang, Z., P. A. Townsend, and E. L. Kruger. 2022. "Leaf Spectroscopy Reveals Divergent Inter- and Intra-Species Foliar Trait Covariation and Trait–Environment Relationships Across NEON Domains." *New Phytologist* 235, no. 3: 923–938. <https://doi.org/10.1111/nph.18204>.
- Warton, D. I., R. A. Duursma, D. S. Falster, and S. Taskinen. 2012. "Smatr 3—An R Package for Estimation and Inference About Allometric Lines." *Methods in Ecology and Evolution* 3, no. 2: 257–259. <https://doi.org/10.1111/j.2041-210X.2011.00153.x>.
- Warton, D. I., I. J. Wright, D. S. Falster, and M. Westoby. 2006. "Bivariate Line-Fitting Methods for Allometry." *Biological Reviews* 81, no. 2: 259–291. <https://doi.org/10.1017/S1464793106007007>.

Wright, I. J., N. Dong, V. Maire, et al. 2017. "Global Climatic Drivers of Leaf Size." *Science* 357, no. 6354: 917–921. <https://doi.org/10.1126/science.aal4760>.

Wright, I. J., P. B. Reich, M. Westoby, et al. 2004. "The Worldwide Leaf Economics Spectrum." *Nature* 428, no. 6985: 821–827. <https://doi.org/10.1038/nature02403>.

Xu, H., Y. Song, Y.-H. Tan, et al. 2024. "Convergent Strategies for Leaf Traits in Tree Species From Divergent Habitats." Figshare. <https://doi.org/10.6084/m9.figshare.27918429>.

Yang, H., W. Tao, Q. Ma, et al. 2023. "Compound Hot Extremes Exacerbate Forest Growth Decline in Dry Areas but Not in Humid Areas in the Northern Hemisphere." *Agricultural and Forest Meteorology* 341: 109663. <https://doi.org/10.1016/j.agrformet.2023.109663>.

Young, D. J. N., J. T. Stevens, J. M. Earles, et al. 2017. "Long-Term Climate and Competition Explain Forest Mortality Patterns Under Extreme Drought." *Ecology Letters* 20, no. 1: 78–86. <https://doi.org/10.1111/ele.12711>.

Zhang, J., B. Liu, S. Liu, Z. Feng, and K. Jiang. 2021. "Plantlist: Looking Up the Status of Plant Scientific Names Based on the Plant List Database, Search the Chinese Names and Making Checklists of Plants (Version R package version 0.7.2) [Computer software]." <https://github.com/helixcn/plantlist/>.

Zohner, C. M., A. Rockinger, and S. S. Renner. 2019. "Increased Autumn Productivity Permits Temperate Trees to Compensate for Spring Frost Damage." *New Phytologist* 221, no. 2: 789–795. <https://doi.org/10.1111/nph.15445>.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.