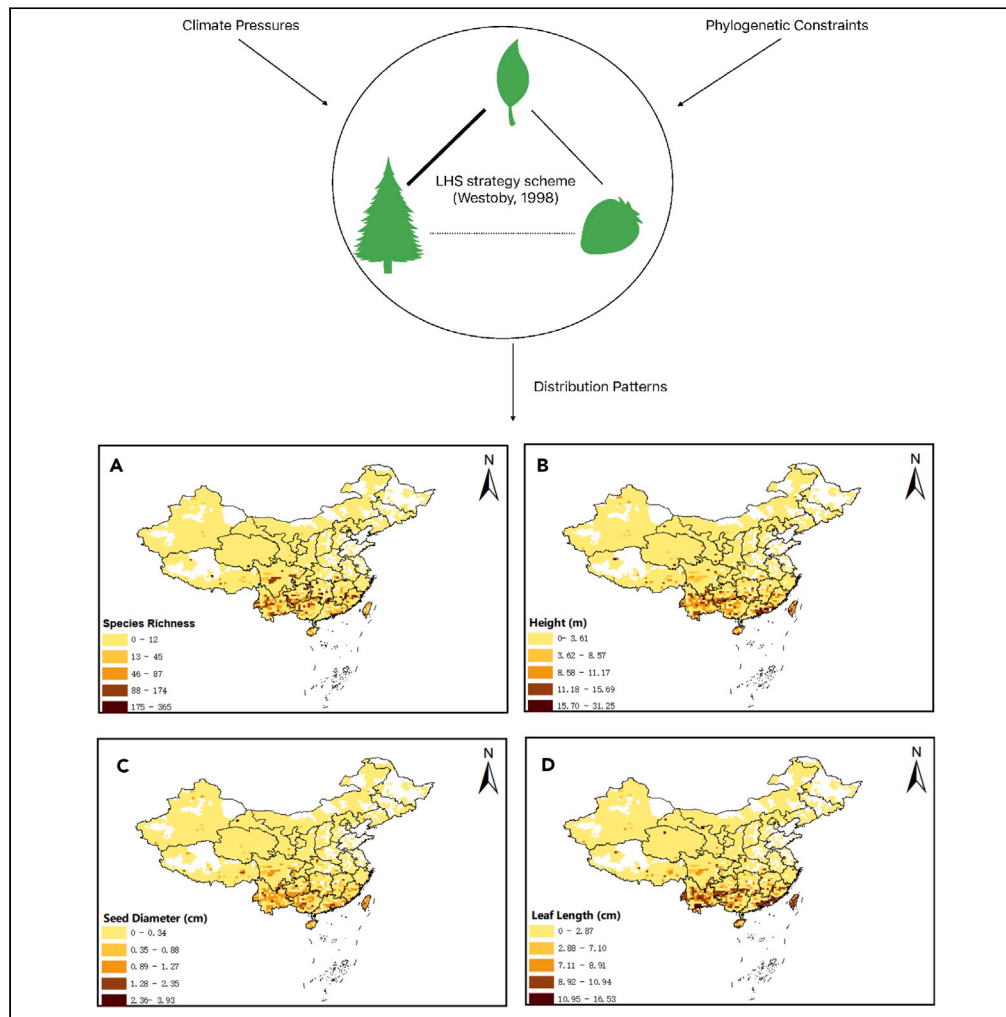


Article

Phylogenetic conservatism and coordination in traits of Chinese woody endemic flora



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Highlights

Leaf length, maximum height, and seed diameter show moderate-high phylogenetic signals

Leaf length and maximum height are phylogenetically conserved coordinated

This study highlights the phylogenetic ancestry's role in endemic distribution

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Article

Phylogenetic conservatism and coordination in traits of Chinese woody endemic flora

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SUMMARY

Range-limited endemic species, often labeled as endangered due to their low adaptability to climate change, exhibit unclear evolutionary mechanisms influencing their distribution. This study explores the relationship between leaf length, maximum height, and seed diameter and their linkage to phylogeny and climate in the macroecology of 1,370 woody endemics. Using Bayesian analytical method that allows partitioning phylogenetic and environmental variances and covariance, we revealed moderate to high phylogenetic signals in these traits, indicating evolutionary constraints potentially impacting climate change adaptability. The study uncovered a phylogenetically conserved coordination between height and leaf length which showed to be independent of macroecological patterns of temperature and precipitation. These findings emphasize the role of phylogenetic ancestry in shaping the distribution of woody endemics, highlighting the need for prioritized *in-situ* conservation and providing insights for *ex situ* conservation strategies.

INTRODUCTION

As an important component of global biodiversity, range-limited endemic species have higher extinction risk compared to widespread species according to the IUCN red list.¹ Endemics are used to characterize community uniqueness and delineate conservation priorities.^{2–4} Biological characteristics, such as genetic processes and dispersal modes, and environmental factors, such as high environmental heterogeneity and dramatic climate change, are the main components that mediate the number of endemics.^{5–7} High environmental heterogeneity and dramatic climate change most likely result in alterations of endemic taxa biology compared to widespread taxa or their ancestors, e.g., in lower heterozygosity, genetic drift, and a higher risk of inbreeding depression.^{8–10} Consequently, the ability of endemics to adapt to changing environments is reduced,^{11,12} raising the hypothesis that endemics are generally poor dispersers with strong dependencies on the different environments and phylogenetic contexts.¹³ The distribution of endemics is a central question in biogeography and evolutionary ecology,^{14,15} as they play a crucial role in shaping regional biodiversity.¹⁶ However, there is a significant gap in our understanding of the mechanisms and macroevolutionary processes driving endemics current distribution, which is important in providing background information for their conservation.

Traits response to environment and their trade-offs (trait evolutionary covariances) reveal patterns of adaptation influencing species distribution, which reflect interaction between genetics and environment.^{17,18} Functional traits are expected to evolve in response to natural selection, and their variation is often interpreted as being adaptive.^{19–21} Phylogenetic constraints and evolutionarily labile adaptation are two controversial theories,²² but they often occur simultaneously in the real world.^{23,24} Moreover, examination of large-scale trait-trait (and trait-environmental) relationships have been proven as a powerful tool to revealing global “trait spectra” or “trait strategy”.^{25–28} Different integration strategies for traits have independent functions to maintaining species fitness and can provide valuable information about species’ response to the environment.²⁹ For example, increase of seed and leaf size with height at maturity has been observed in woody plants across steep environmental gradients on large scale.^{30–33} As such, trait-trait relationships on large scale argued that the long-standing evolutionary history and environmental selective pressure should be considered and characterized when addressing macroevolutionary questions.^{28,34}

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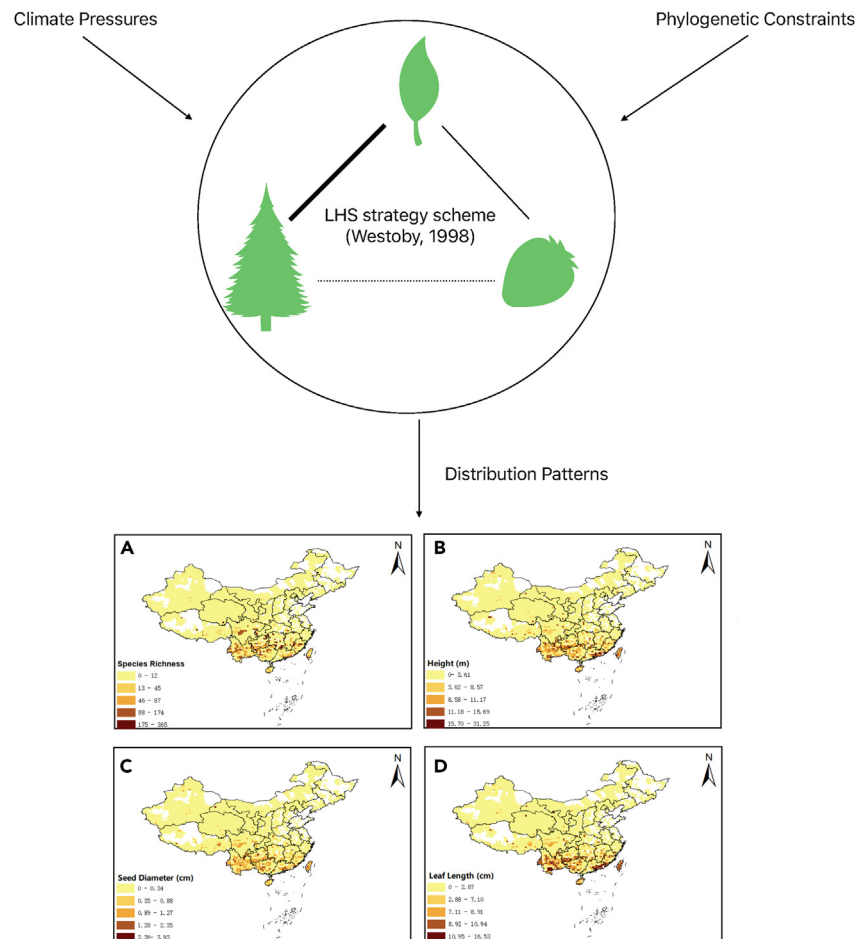


Figure 1. Schematic diagram of climate pressure and phylogenetic constrain together effect evolutionary of trait and traits trade-offs (evolutionary covariances)

And therefore, reveals the current distribution patterns of species richness, (A) community weighted mean (CWM) of maximum height, (B) seed diameter, (C) and leaf length (D) for woody endemics in China.

Recently, evolutionary comparative methods offer opportunities to partition the effect from these two parts (i.e., evolutionary history and environmental selective pressure).^{24,28,35} The leaf economic spectrum (LES) multivariate correlations characterization that restricts the global diversity of leaf functional traits onto a single axis of variation explains the tight integration of leaf traits across plant ecological strategies.^{25,34,36} Studies on *Helianthus* genus found that global-scale models of LES poorly explained regional scales when the effect of natural selection pressure and evolutionary constraint were disentangled.³⁷ The evolutionary relationship among global hydraulic traits (xylem conductivity, xylem resistance to embolism, sapwood allocation relative to leaf area, and drought exposure, essential adaptive variation attribute across species and biomes) revealed that most experience the same selective pressure, while not all pairs of hydraulic traits showed evolutionary integration.²⁸ However, previous studies focused on specific function rather than a whole-plant strategy, and the correlation of functional traits largely failed to partition the phylogenetic effect.

The three-dimensional strategy scheme (LHS: specific leaf area-height at maturity-seed mass) proposed by Westoby appears to represent one of the most important life history strategies for plants, affecting their abilities for light capture, competition, species dispersal, and establishment by mediating biotic and abiotic environmental interactions.^{30,38} LHS has been repeatedly examined in different habitats,^{39,40} however, there is scarce knowledge on the degree of LHS evolution under phylogenetic constraints and adaptation. To our knowledge, whether the LHS holds for endemic species and how it relates to phylogeny and climate have never been tested.

Understanding the conservative nature of traits evolution and their correlation will improve our knowledge on plant strategies,⁴¹ and may provide insight to explaining the current distribution of geographically limited endemics along environmental gradients.^{42,43} In this study, we compiled a database of 1,370 endemic species, including species occurrence, three functional traits (LHS), and a newly derived species-level phylogeny. Using state-of-the-art Bayesian analytical method,²⁴ we aim to disentangle the contributions of evolutionary history and climate to the macroecology patterns of LHS in woody endemic floras of China (Figure 1). Specifically, we ask the following questions: (1) what is the

Table 1. Covariance partition for the three functional traits studied considering annual precipitation (AP) and mean annual temperature (MAT) as environmental variables of interest

Trait 1	Trait 2	Environmental variables	N observations	Total correlation	Phylogenetic correlation	Non phylogenetic correlation	Non-attributed phylogenetic correlation	Environmental phylogenetic correlation	Labile environmental correlation	Residual correlation
Height	Seed diameter	AP, MAT	826	0.03 (ns)	0.02 (ns)	0.00(ns)	0.02 (ns)	0.01 (ns)	0.00 (ns)	0.00 (ns)
Height	Leaf length	AP, MAT	1175	0.26***	0.24***	0.02*	0.18***	0.05 (ns)	0.00 (ns)	0.02*
Leaf length	Seed diameter	AP, MAT	889	0.06***	0.05(ns)	0.01***	0.03 (ns)	0.02 (ns)	0.00 (ns)	0.01***

Number of observations in each case is shown. Statistical significance is shown in each case. Signif. codes: "****": $p < 0.001$; "***": $p < 0.01$; "**": $p < 0.05$ ".": $p < 0.1$ " ": $p > 0.1$.

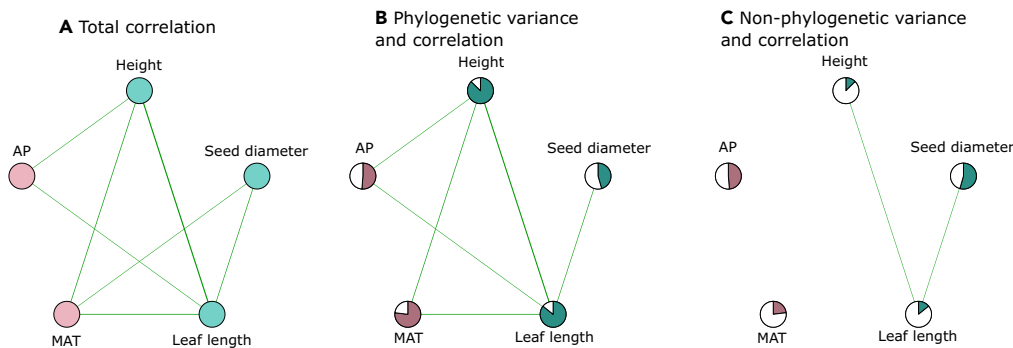


Figure 2. Correlation networks showing correlation between functional traits and annual precipitation (AP) and mean annual temperature (MAT) (A) represents the total correlation; (B) represents phylogenetic correlation coefficients and phylogenetic variance as pie charts in the nodes and (C) represents non-phylogenetic correlation coefficients and non-phylogenetic variance. Lines represent statistically significant correlation coefficients (all of them are positive). Line width is proportional to correlation coefficients. Light red nodes represent AP and MAT. Light green nodes represent functional traits.

relationship of LHS for endemic flora in China? (2) Is the observed variability and coordination among LHS traits phylogenetically conserved? and (3) How is variability in LHS traits and their coordination related to climate and the distribution of these endemics in China? We hypothesize that LHS traits and their relationship will show significant phylogenetic conservatism. This phylogenetic conservatism will be partly explained by environmental variables, which may be due to range-restricted endemics' biological attributes, such as lower heterozygosity and adaptability. If our hypothesis is true, woody endemic species of China may exhibit a phylogenetically conserved pattern of adaptation in LHS strategies in response to climate, potentially impacting their adaptive capability in response to rapid environmental changes. Disentangling evolutionary patterns will provide background information for improving the predictive accuracy of endemic species distribution and aiding in their conservation.

RESULTS

Correlation between LHS in endemic woody plants of China is related to climatic conditions

Height/leaf length and seed diameter/leaf length are positively correlated (Tables 1 and S1; Figure 2), however, these correlation coefficients are rather low, total correlation between height/leaf length, seed diameter/leaf length are 0.26, 0.06, respectively (Table 1, total correlation). When environmental variables are excluded, their correlation value was further decreased (Tables 1 and S1, phylogenetic correlation), indicating that relationships between LHS traits is related to climatic conditions.

Each of the three traits presents positively phylogenetic correlations with climatic variables annual precipitation (AP) and mean annual temperature (MAT). Then, lineages inhabiting warm (high MAT) and wet (high AP) climates present higher leaf length, height, and seed diameter and tend to be closely related. While other distant lineages may inhabit cold and dry sites presenting lower leaf lengths, height, and seed diameter also tend to be closely related. The relationship between height and seed diameter is not correlated in our dataset.

LHS traits show phylogenetic signal not explained by climatic conditions

Significant phylogenetic variance (reported as relative phylogenetic variance, i.e., equivalent to Pagel's lambda phylogenetic signal) in all variables, especially maximum height and leaf length (Tables 2 and S2; Figure 2). While seed diameter showed a moderate relative phylogenetic variance (phylogenetic variance = 0.46). Most of the phylogenetic variance is not related to AP and MAT (Figure 3). Similar results are shown by using principal components summarizing a more comprehensive list of climatic variables (Figure S2). So, phylogenetic conservatism in these traits of endemic woody flora may not be strongly related to the climatic niche at this scale (Tables 2 and S2; Figures 3 and S2).

Phylogenetic components are more related to LHS than environmental variables

Positive associations were observed between functional distance/phylogenetic distance, seed diameter distance/phylogenetic distance, height distance/phylogenetic distance, with correlation coefficients of 0.294, 0.296, and 0.071, respectively (as shown in Figures 4A, 4C, 4E, and 4G). However, the connections between functional distance/phylogenetic distance, seed diameter distance/phylogenetic distance, height distance/phylogenetic distance did not exhibit statistical significance (as shown in Figures 4B, 4D, 4F, and 4H). These findings are supported by spatially explicit analyses. Furthermore, significant positive correlations were identified between functional richness (FRic), and phylogenetic diversity (PD), functional richness of maximum height (FHmax) and PD, functional richness of seed diameter (Fseed) and PD, and functional richness of leaf length (Fleaf) and PD, with correlation coefficients of 0.81, 0.74, 0.68, and 0.72, respectively (Figure 5). The correlation coefficients between climatic variables (PC1) and FRic, FHmax, Fseed, and Fleaf were considerably lower, indicating a stronger relationship between phylogenetic components and the LHS than with environmental variables.

Table 2. Variance partition for the three functional traits studied considering annual precipitation (AP) and mean annual temperature (MAT) as environmental variables of interest

Trait	Environmental variables	N observations	Phylogenetic variance	Non-phylogenetic variance	Non-attributed phylogenetic variance	Environmental phylogenetic variance	Labile environmental variance	Residual variance
Height	AP, MAT	1205	0.87***	0.13***	0.87***	0.04 (ns)	0.00 (ns)	0.13***
Seed diameter	AP, MAT	913	0.46***	0.54***	0.45***	0.03 (ns)	0.00 (ns)	0.55***
Leaf length	AP, MAT	1321	0.86***	0.14***	0.85***	0.07 (ns)	0.00 (ns)	0.15***

Number of observations in each case is shown. Variances are represented as proportional variances over total variance, ranging from 0 to 1. Phylogenetic variance is equivalent to the phylogenetic signal as measured by Pagel's Lambda. Statistical significance is shown in each case. Signif. codes: "****": $p < 0.001$; "***": $p < 0.01$; "**": $p < 0.05$; ".": $p < 0.1$; " ": $p > 0.1$.

DISCUSSION

Coordination of LHS in shaping endemics distribution pattern

Using a comprehensive dataset including geographical occurrence, functional traits, climatic conditions, and a newly derived phylogeny, we have shown explicit relationship between LHS and how they relation to the climate variables in woody endemic floras in China. Our results indicated that LHS patterns of endemics reflect strong phylogenetic patterns. Furthermore, total correlations between traits and environmental variables indicate a key role of non-random evolutionary processes, supporting that LHS is constrained by environmental variables related to temperature and precipitation. However, the relationship between climate and LHS seems to be rather low, being phylogeny the main driver of variation and covariation in these traits. Our results are supported by the contemporary endemics' distribution where they are highly concentrated in Southern as compared to Northern China.^{3,4,44} Southern and Northern China are characterized by warm and wet, and cold and dry climates, respectively.⁴⁵ Globally, the tropics with high temperature and AP climates often correlate with highly concentrations of endemics.^{46,47} Global trait patterns have revealed universal rules indicating that species with larger leaf size, greater maximum height and larger seeds are more likely to occur in tropical regions.^{25,32,48–51} The observed coordination of traits may be associated with functional and developmental processes.²⁸ Hence, the coordination of LHS in woody endemic flora of China is expected to be related to their geographic distributions.

We contend that current distribution models, which overlook the role of phylogeny and trait correlations, may be inadequate for predicting species' distributions, particularly for those with conserved traits. Conserved traits and phylogeny may underlie constrained distributions, and species exhibiting such distributions are more likely to fail in tracking future climate change.

Phylogenetic constraint and adaptation of LHS

All three traits show phylogenetic conservatism (as measured by phylogenetic signal), suggesting that their values in endemic lineages are likely to be influenced by those of their evolutionary ancestors.²⁸ Phylogenetic conservatism was also confirmed by stronger correlations between phylogenetic distance and functional distance of each trait, comparing to correlations between climate distance and functional distance of each trait (Figures 4 and 5). Moreover, spatial specific analysis showed that FRic of each trait (Fleaf, FHmax, and Fseed) was significantly correlated to PD, but less explained by climate variable (Figure 5). In addition, environmental component explains small fraction of traits' variation when accounted for as fixed effects. Substantial variation of trait values across studied lineages indicates that adaptive process appears to leave ample opportunities for trait differentiation under these constraints during the long evolutionary history.^{19–21} Interestingly, seed diameter was less constrained by phylogeny compared to maximum height and leaf length, supporting the notion that the production of seed size and quality are depended on environmental conditions during a particular period of time.^{52,53}

Evolutionary correlations among LHS

Maximum height and leaf length are coordinated and phylogenetically conserved in endemic woody flora of China

The significant phylogenetic correlations between leaf length and maximum height are still apparent when considering the effects of temperature and precipitation, so a deeper hardwired integration due, for instance, to a genetic correlation between traits may be occurring in the current study context at this scale. Long-term hardwired traits correlations could be explained as being functionally, developmentally, physiologically, phylogenetically, and genetically integrated.²⁸ It appears that smaller woody plants are incapable of supporting heavy crowns as they are likely to have thinner trunks,⁵⁴ and have a built-in function that limits large leaves production.⁵⁵ Game-theoretic models predict taller plants to have larger leaf size, which could be attributed to resource utilization and support costs.⁵⁶ Taller plants are more likely to intercept more light, while photosynthesis is the basis of plant growth,⁵⁷ and is associated with leaf size and ability on radiation loading. On another hand, supporting cost and water utilization of leaf area increase with height.⁵⁸ Our results on woody endemic species of China confirmed that maximum height and leaf size are positively correlated. Additionally, the strong phylogenetic correlation between maximum height and leaf length persisted after considering climate factors, because of the strong taxonomic (phylogenetic) effects.^{59,60} Hence, this pair of traits is consistent with our hypothesis that they represent a deeper evolutionary integration.

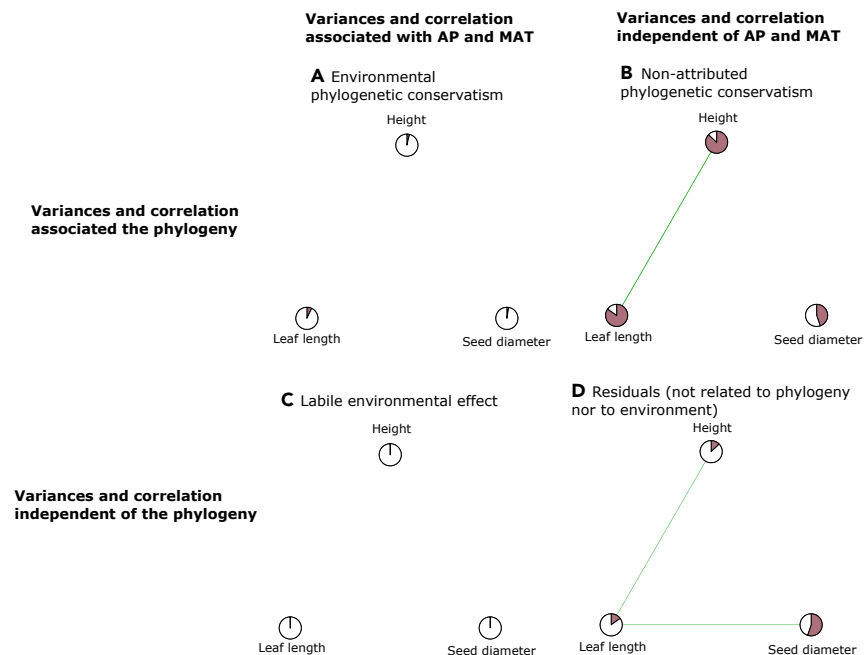


Figure 3. Correlation networks showing variances and correlations between functional traits and annual precipitation (AP) and mean annual temperature (MAT)

(A) represents both the phylogeny and the environmental variables considered, AP and MAT (i.e., environmental phylogenetic conservatism); (B) represents only the phylogeny (i.e., non-attributed phylogenetic conservatism); (C) represents only the environmental variables (i.e., labile environmental effect) and (D) represents not the phylogeny nor the environmental variables (i.e., residuals). Lines represent statistically significant correlation coefficients (all of them are positive). Line width is proportional to correlation coefficients.

Leaf length and seed diameter correlation is low and showed to be independent both of climate and phylogeny

The relationship between leaf size and seed size is not always apparent. A triangular relationship (or Corner's Rules) between leaf size and seed size was found in temperate woody species by Cornelissen,⁵⁵ that small leaves may prevent production of large seeds, hence species with small leaves only produce small seeds, while species with large leaves may have small, medium, and large seed size. Positive correlation between leaf size and seed size for sclerophyll species across Australian arid land was found by Westoby and Wright,⁶¹ but rejected triangular relationship. Another studies in Neotropical Forests found seed size and leaf size were independent.⁶² However, these previous studies failed to explain the underlying reason. Recently, Flores-Moreno proposed that neutral or selective process and phylogeny in plants might contribute to the observed correlations between traits.⁶³ Similarly to Westoby and Wright,⁶¹ we observed a positive correlation between leaf length and seed size and height, even though the correlation coefficient was rather low (Figure 3; Table 2). This correlation showed to be independent both of the phylogeny and the environmental variables considered. Therefore, there might be another ecological axis explaining this covariation.

Seed diameter and maximum height are independent

Relationship between seed diameter and maximum height is well documented,^{64,65} that taller plants tend to produce larger seeds.^{48,62} However, the relationship between plant height and seed diameter in our results does not present a significant correlation. We reject a direct evolutionary trade-off between this pair of traits based on data availability in our studied subspecies group, consistent with previous results.⁶²

Endemic species might be threatened under future climate change

Our results show a phylogenetic correlation between maximum height and leaf length and between leaf length and seed diameter, which showed to be independent of the macroclimate. Seed diameter and maximum height showed to be independent. Consequently, most endemics experienced niche shrinking,⁶⁶ are likely to inherit ancestral traits due to long-term selection,⁶⁷ and occur in places similar to their ancestors as they are involved in local adaptation to specific niches.⁶⁸ Whereas some endemics experienced "recent adaptive radiation" but showed phylogenetic niche conservatism, leading to low rates of divergence in traits that are associated with the climate niche.^{67,69} The distribution of endemics may track their ancestors' ecological niches, and occasionally, adapt to novel localities if there is a chance. Meanwhile, each trait responses independently to climate stress and is constrained by phylogeny, yet evolved in an apparently coordinated fashion. We highlight that the importance of *in-situ* conservation of phylogenetical conserved endemics under rapidly climate change, as endemics

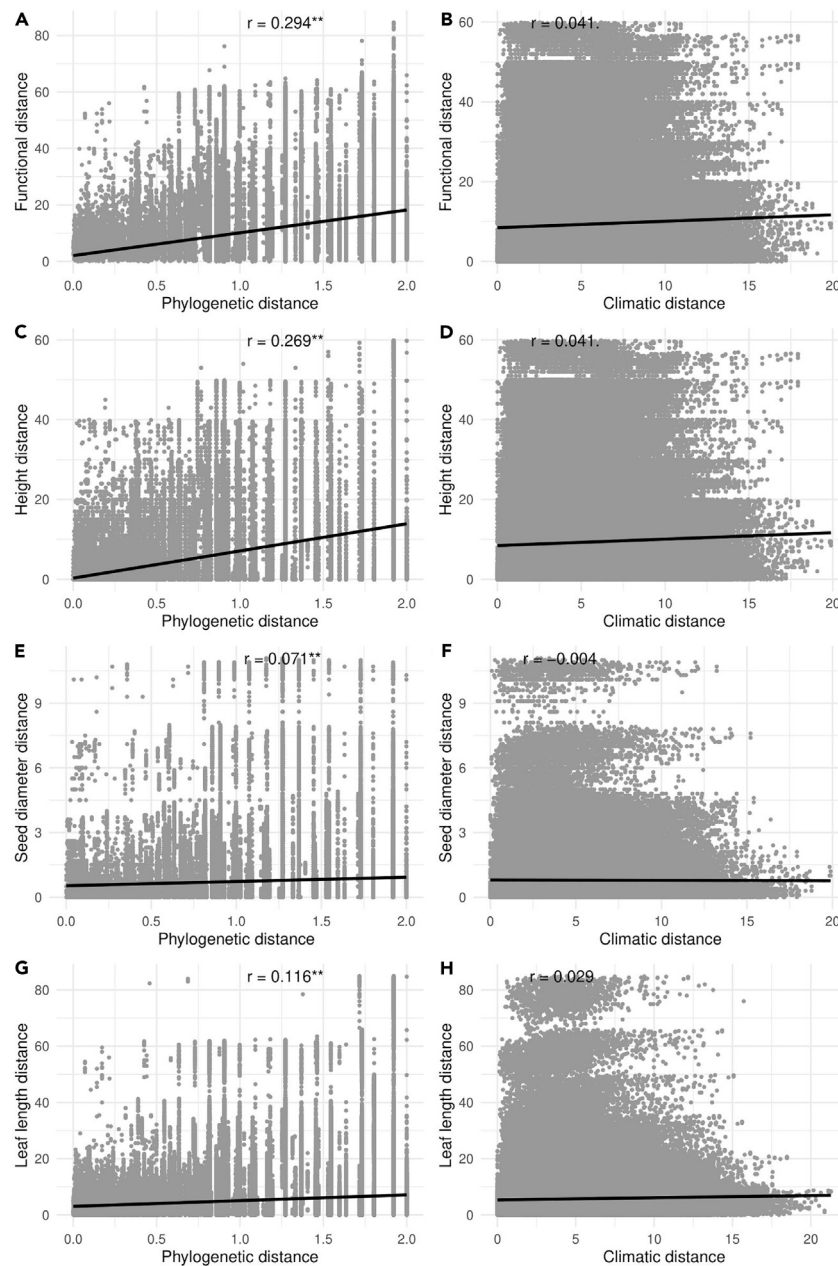


Figure 4. Relationship between phylogenetic and climatic distances and functional distances (involving maximum height, seed diameter, leaf length altogether, and separately) for all pairwise combinations of species

(A) relationship between functional distance and phylogenetic distance; (B) relationship between functional distance and climatic distance; (C) relationship between height distance and phylogenetic distance; (D) relationship between height distance and climatic distance; (E) Relationship between seed diameter distance and phylogenetic distance; (F) relationship between seed diameter distance and climatic distance; (G) relationship between leaf length distance and phylogenetic distance; (H) relationship between leaf length distance and climatic distance. In the “Y” axis, functional differences between pairwise combinations of species for LHS all together and individually, respectively. In the “X” axis, phylogenetic distances among pairwise combination of species calculated as the Euclidean distance between the three first climatic principal components for each pair species (second column). Pearson correlation coefficient calculated using a mantel test and its significance is also shown in each case (r). Signif. codes: “****”: $p < 0.001$; “***”: $p < 0.01$; “**”: $p < 0.05$; “.”: $p < 0.1$; “ ”: $p > 0.1$.

may fail to dispersal to their suitable niches.⁷⁰ On another hand, understanding coordination and local adaptation of LHS for endemic flora will improve the predictive accuracy of species distribution under different climate scenarios compared to single traits. Such information would be important for *ex situ* conservation planning.

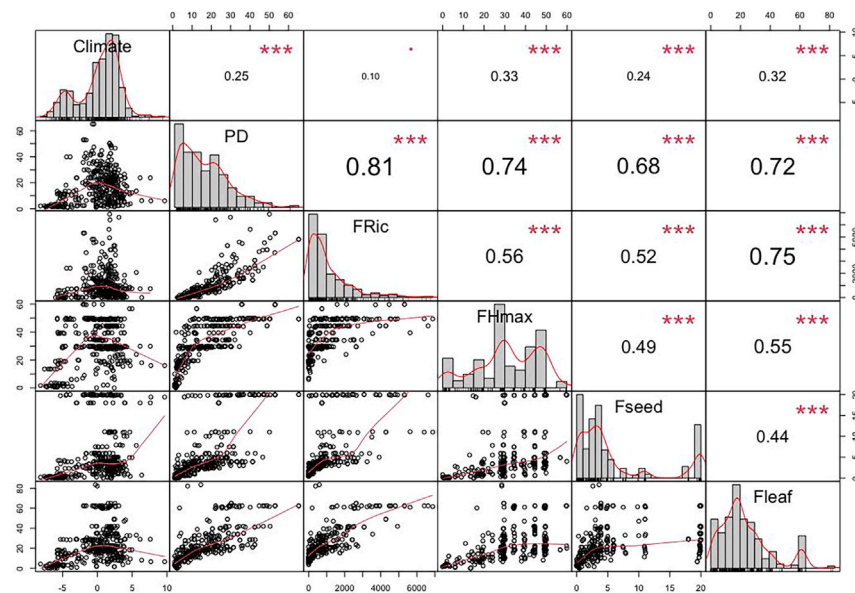


Figure 5. Relationship between phylogenetic diversity (PD), first component of climatic variables (PC1) and functional richness (involving maximum height (FHmax), seed diameter (Fseed), leaf length (Fleaf) separately and altogether (FRic) for all pairwise combinations on spatial patterns Pearson correlation coefficient and its significance is also shown in upper semi-matrix. Signif. codes: "****": $p < 0.001$; "***": $p < 0.01$; "**": $p < 0.05$; ".": $p < 0.1$.

Conclusion

We provided a biogeographically and phylogenetically explicit contextualization of the leaf-height-seed ecological strategies (LHS), use by geographical occurrence and a newly derived phylogeny for woody endemic species of China. We found phylogenetically conserved traits in endemic lineages, and the coordinated evolution of LHS traits is related to the phylogeny. Our results indicate that high proportions of range-limited endemic lineages may fail track future climate change. Uncovering the role of adaptation and coordinated evolution for endemic traits will yield informative insights into future biodiversity conservation strategies.

Limitations of the study

To elucidate the relationships between traits, phylogeny, and climate over extended evolutionary periods, conducting analyses with historical data, including species distributions and paleoclimate, is crucial. Accessing paleoclimate data, for instance, from the Last Glacial Maximum, is relatively straightforward through various climate models (e.g., the Paleoclimate Modeling Intercomparison Project hosted by the Paleoclimate Working Group at <https://www.cesm.ucar.edu/working-groups/paleo>). Nevertheless, obtaining historical distribution data for Chinese woody endemic species that align with paleoclimate data presents a significant challenge.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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 - Materials availability
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- METHOD DETAILS
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 - Phylogenetic tree construction
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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2024.109885>.

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AUTHOR CONTRIBUTIONS

R.Z., J.H., and Q.W. contributed to conceiving the research ideas. J.H. and Q.W. data collection and created the maps. Q.W., J.H., and Y.X. constructed the phylogenetic tree. Q.W., P.S.M., and Y.X. performed the data statistical analyses. Q.W., J.H., P.S.M., W.G., Q.J., and Y.A.E. led writing of the paper and all authors approved the final manuscript.

DECLARATION OF INTERESTS

The authors declare no conflict of interest.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Source code	This study	https://zenodo.org/records/11063028
Source data	This study	https://zenodo.org/records/11063208
Software and algorithms		
R software	R core Team	https://www.r-project.org/
Biopython	Cock et al. ⁷⁹	http://www.biopython.org

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Qing Wang (qing.wang@alumni.ubc.ca).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- The data accompanying this study were made available on zenodo at <https://zenodo.org/records/11063028>.
- The source code accompanying this study were made available on zenodo at <https://zenodo.org/records/11063208>.
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

METHOD DETAILS

Datasets

A dataset of Chinese endemic woody flora including their name, county-level distribution, mean leaf length, potential maximum height, and seed diameter were compiled from various literature sources (e.g., Flora of China, local flora, monographs, and research articles). The LHS according to Westoby defined a three-dimension scheme including specific leaf area, height of plant's canopy at maturity, and seed mass.³⁸ The positive relationships between leaf length and specific leaf area,^{71–73} and seed diameter and seed mass have been well documented.^{49,74} Due to the limitation of data availability, we used leaf length, maximum height, seed diameter to examine the evolutionary relationship of LHS. We then projected the county-level distribution data into equal-area (50*50 km² grid cells) using China Geodetic Coordinate System 2000.⁷⁵ Grid cells containing at least two endemic species and land area covering more than half of grid cells (1,250 km²) were delimited as operational geographic units (OGUs). A total of 1,370 woody endemics belong to 109 families and 360 genera (Extended data). Distribution patterns of species richness, community weighted mean (CWM) of leaf length, maximum height, and seed diameter for woody endemics in China were shown in [Figure 1](#).

All climate data were retrieved from the Climatologies at high resolution for the earth's land surface areas (CHELSA: <https://chelsa-climate.org/timeseries/>).^{76,77} A total of 19 bioclimatic variables (time period: 1979–2013) were downloaded, including mean annual air temperature, mean diurnal air temperature range, isothermality, temperature seasonality, mean daily maximum air temperature of the warmest month, mean daily minimum air temperature of the coldest month, annual range of air temperature, mean daily mean air temperatures of the wettest quarter, mean daily mean air temperatures of the driest quarter, mean daily mean air temperatures of the warmest quarter, mean daily mean air temperatures of the coldest quarter, annual precipitation amount, precipitation amount of the wettest month, precipitation amount of the driest month, precipitation seasonality, mean monthly precipitation amount of the wettest quarter, mean monthly precipitation amount of the driest quarter, mean monthly precipitation amount of the warmest quarter, and mean monthly precipitation amount of the warmest quarter. Climate data for each OGU were extracted by using the "raster::extract" function in the "terra" package.⁷⁸

Phylogenetic tree construction

To construct the species-level phylogeny for the 1,387 Chinese endemic woody seed plants, we followed five steps: (1) DNA sequences obtain. All target sequences of four plastid genes (atpB, matK, ndhF and rbcL) and one mitochondrial gene (matR) were obtained from Genbank (www.ncbi.nlm.nih.gov/genbank/) by Biopython;⁷⁹ (2) Sequence screening. When more than one for the same gene of a species were detected, only the longest sequence was selected; (3) Sequence concatenates and alignment. All five genes were concatenated and then

aligned using the MAFFT;⁸⁰ (4) Model selection. To select the best scheme and evolutionary model, the GTR+R10+F nucleotide substitution model was obtained by using ModelFinder;⁸¹ and (5) Phylogeny construction. A maximum likelihood phylogeny was inferred using IQ-TREE under the GTR+R10+F model for 5,000 ultrafast bootstraps,^{82,83} as well as the Shimodaira–Hasegawa–like approximate likelihood-ratio test.⁸⁴ Steps 3 to step 5 were compiled in PhyloSuite_v1.2.2 software.⁸⁵ To make the phylogeny ultrametric, we used the “chronos” function of the ape R package.⁸⁶ Additionally, sequences obtained from GenBank may have identification errors, especially for tropical species.⁸⁷ Thus, the final phylogeny has been evaluated by a taxonomist, while species occurrence in the wrong position of the phylogeny has been removed.

Statistical analysis

We implemented a principal components analysis (PCA) using the stats R package⁸⁸ to summarize climatic variables describing species’ climatic niches (Figure S1). The first three axes explained 86.6% of the climate data variance (Figure S1) and were used to characterize the climate niche for Total correlations (without considering phylogenetic component) and phylogenetic correlations (or evolutionary correlations, considering phylogenetic component). In addition, MAT and AP were the most important environmental variables in endemics.³ We also analysis total correlations and phylogenetic correlations by using MAT and AP.

Total correlations, phylogenetic correlations and variance-covariance partition

We performed a variance-covariance partition using the *TrEvol* (<https://github.com/pablosanchezmart/TrEvol>),²⁴ which uses Bayesian phylogenetic mixed models developed in the *MCMCglmm* R package to partition the amount of variance-covariance on pairwise variables related to the phylogeny and to environmental variables of interest.⁸⁹ We calculated the total correlation among traits, which then was decomposed into four components. The first component is the non-attributed phylogenetic conservatism, which is the amount of variances and covariances that are only related to the phylogeny, being independent of the environmental variables considered. The second component is the environmental phylogenetic conservatism, and is the amount of variance and covariance related both to the phylogeny and to the environmental variables considered. The third component is the evolutionarily labile environmental effect, being the amount of variance and covariance in the data that is independent of the phylogeny but it is related to the environmental variable considered. The final component is the residual variance and covariance, which are not related to the phylogeny nor to the environmental variables. Variances are reported relative to total variance, and covariances as correlations and we represent results as trait networks by using the *plotNetworks* function of the *TrEvol* package.

As the Bayesian framework operates with posterior distributions of estimates, we calculated the phylogenetic signal for the posterior distributions of the variance portions, obtaining a distribution for each component of the variance and covariance, from which mean and credible intervals were calculated. P-values related to the probability that the distribution contained zero were calculated in the *TrEvol* package, importing functions from the *BayesR* R package.⁹⁰

Phylogenetic distance, functional distance, phylogenetic diversity and functional diversity

The phylogenetic distance between two species is the time that each has evolved independently of the other.⁹¹ We employed the *phydist* function from the *Picante* R package to compute the pairwise phylogenetic distances.⁹² We computed the pairwise functional dissimilarities (distances) between species using the *daisy* function and the Gower’s distance, which allows for simultaneous use of nominal, categorical and continuous variables.⁹³ Phylogenetic diversity is characterized as the aggregate of the lengths of phylogenetic branches encompassed by a group of species that exist together. Functional richness was used to calculate functional diversity in our case as we only have the specie’s name and richness data in each OGU. Functional richness and phylogenetic diversity were calculated using the “dbFD” function in the ‘FD’ package.⁹⁴