




Extinction risk of Chinese angiosperms varies between woody and herbaceous species

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Abstract

Aim: Understanding how species' traits and environmental contexts relate to extinction risk is a critical priority for ecology and conservation biology. This study aims to identify and explore factors related to extinction risk between herbaceous and woody angiosperms to facilitate more effective conservation and management strategies and understand the interactions between environmental threats and species' traits.

Location: China.

Taxon: Angiosperms.

Methods: We obtained a large dataset including five traits, six extrinsic variables, and 796,118 occurrence records for 14,888 Chinese angiosperms. We assessed the phylogenetic signal and used phylogenetic generalized least squares regressions to explore relationships between extinction risk, plant traits, and extrinsic variables in woody and herbaceous angiosperms. We also used phylogenetic path analysis to evaluate causal relationships among traits, climate variables, and extinction risk of different growth forms.

Results: The phylogenetic signal of extinction risk differed among woody and herbaceous species. Angiosperm extinction risk was mainly affected by growth form, altitude, mean annual temperature, normalized difference vegetation index, and precipitation change from 1901 to 2020. Woody species' extinction risk was strongly affected by height and precipitation, whereas extinction risk for herbaceous species was mainly affected by mean annual temperature rather than plant traits.

Main conclusions: Woody species were more likely to have higher extinction risks than herbaceous species under climate change and extinction threat levels varied with both plant traits and extrinsic variables. The relationships we uncovered may help identify and protect threatened plant species and the ecosystems that rely on them.

KEYWORDS

climate change, extinction risk, growth form, IUCN Red List, phylogeny, plant traits

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1 | INTRODUCTION

The extinction of plants across global terrestrial ecosystems is leading to biodiversity loss and altering ecosystem function and services (Cardinale et al., 2012). The extinction of rare plants will reduce community functional diversity and productivity (Rabelo et al., 2022). At the same time, the extinction of plants accelerates the homogenization of habitats and reduces regional phylogenetic diversity (Daru et al., 2021). Hence, high plant diversity is needed to maintain ecosystem services. However, global plant diversity is facing seriously threatened. The latest research shows that 39% of vascular plant species are threatened with extinction and nearly 600 species have become extinct since 1900 (Humphreys et al., 2019; Lughadha et al., 2020). However, despite increasing rates of plant species extinctions and endangerment, we still lack an understanding of the various intrinsic and extrinsic variables that lead to plant species extinctions.

Species' traits are commonly thought to be predictors of extinction risk, especially when species' traits are closely adapted to local environmental conditions (Fréville et al., 2007). Moreover, as sedentary organisms, plants are particularly sensitive to climate change and other human activities associated with global environmental change (Willis et al., 2008). Therefore, both extrinsic and intrinsic variables potentially associated with plant extinction risk should be analysed concurrently to disentangle the complex mechanisms underlying plant extinctions (Cornelissen et al., 2003; Fréville et al., 2007).

Extrinsic variables, including climate change and other human activities, have dramatically increased plant extinction risk worldwide (Chen et al., 2011). For example, highly productive species at low altitudes with high temperatures and precipitation generally have low extinction probabilities (Mittelbach et al., 2007), but extinction risk is often high for species at high altitudes where local environments are considered more fragile (Chu et al., 2021). Relatively stable climates, such as in the tropics, have also been hypothesized to maintain lineages in so-called "species museums" (Furness et al., 2021; Lu et al., 2018). However, warm and humid areas may have overall more threatened species because areas with higher biodiversity inevitably harbour higher numbers of rare species (Howard et al., 2020; Vamosi et al., 2018). Moreover, human activities such as logging, agriculture, and other forms of land use change have led to a sharp decline in the distribution and abundance of many plant species in recent decades (Marco & Santini, 2015) and have further reduced the distribution of many threatened species (Xu et al., 2019).

Niche conservatism—the tendency for ecological niches to be more similar due to shared ancestry—may increase extinction rates throughout clades under climate change (An et al., 2021; Lanfear et al., 2013). In this regard, intrinsic variables (shared evolutionary history) may contribute to plant extinction risk and therefore extinction threat levels should have a strong phylogenetic signal. A phylogenetic signal is defined as indices that measure the similarity of traits (including extinction levels) of different angiosperms in the evolutionary tree. Hence, uncovering potential phylogenetic signals

of species extinction risk could limit the need for individual species assessments and therefore be highly beneficial for conservation purposes (Shuai et al., 2021). As such, specifically examining potential phylogenetic signals of extinction risk will help us better understand the intrinsic, trait-based variables affecting plant extinction risk.

Traits reflect a combination of phylogeny and environmental adaptation (Fréville et al., 2007). Leaf traits and plant height are thought to have significant impacts on plant adaptability (Royer et al., 2005; Yang et al., 2019) and ultimately influence extinction risk (Moles et al., 2009; Royer et al., 2005). For example, larger leaves are more prone to frost damage (Dong et al., 2020), whereas long, narrow leaves are susceptible to seasonal drought (Baird et al., 2021). Plant maximum height is associated with patterns of precipitation and temperature (Mao et al., 2020; Moles et al., 2009) and studies of grassland ecosystems suggest that tall species face greater extinction risks in areas with low biomass and harsh environments (Fréville et al., 2007). Climbers, either epiphytes or vines, may have elevated extinction risks because they often depend on other species for mechanical support (Ellis, 2020; Zettlemoyer et al., 2019). Studies such as these suggest that plant trait may therefore mediate relationships between the extrinsic variables and extinction risk.

Growth form—especially herbaceous or woody—is one of the most studied plant traits affecting extinction risk (Humphreys et al., 2019). Woody plants tend to have a greater extinction risk than herbaceous plants (Figure 1), but the causes remain unclear (Humphreys et al., 2019). These differences may be related to underlying traits and evolvability. Woody plants (mostly perennial) are often K-selected species with long generation times but slow evolutionary rates, whereas herbaceous plants (mostly annual) are often r-selected species with short life spans but fast diversification (Lanfear et al., 2013; Smith & Donoghue, 2008). These differences suggest that woody lineages have stronger phylogenetic conservatism (Klimeš et al., 2022). Woody and herbaceous plants also typically differ in height and leaf traits (An et al., 2021; Mao et al., 2020). For example, herbaceous plants tend to be more resistant to frost and shade, whereas woody plants are more resistant to drought (Klimeš et al., 2022). Taken together, there is evidence that intrinsic variables such as plant traits and associated phylogenetic history may interact with extrinsic variables (e.g., climate change) to determine extinction risk (Davis et al., 2010). Hence, we hypothesized that a combination of plant traits, phylogeny, and environmental conditions may be responsible for differences in extinction risk across plant species.

China, with its vast area and heterogeneous ecosystems, has remarkable angiosperm diversity that has been the focus of many studies of plant diversity and distributions (e.g., Lu et al., 2018). China recently completed a national plant extinction risk assessment (Qin, Yang, et al., 2017), which presents a unique opportunity to assess variables associated with the extinction risk of Chinese angiosperms. We integrated data on plant species distributions and traits in a phylogenetic context to examine how both extrinsic (i.e., environmental) variables and intrinsic species traits (see details in Table 1) relate to extinction risk in Chinese angiosperms. We addressed the following three questions: Firstly, to what extent is there a phylogenetic signal

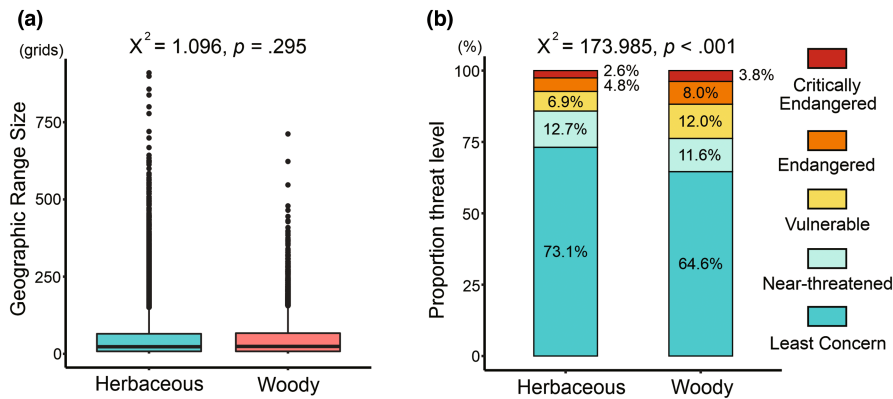


FIGURE 1 Geographic range size of herbaceous and woody species (a) and proportion of species in each threat level (b). Results of Kruskal–Wallis tests found no significant difference in the geographic ranges of woody and herbaceous species (a), but significant differences in the proportions of woody and herbaceous species across different threat levels

TABLE 1 Potential intrinsic and extrinsic predictors of extinction risk of Chinese angiosperms and hypothesized mechanisms

Predictor variables		Hypotheses
Intrinsic	Growth form	Woody species may be more vulnerable to climate change than herbaceous species (Humphreys et al., 2019)
	Climbing ability	Epiphytic and climbing species may have greater extinction risks because they rely on other taxa for mechanical support (Zettlemyer et al., 2019)
	Plant height	Taller species will face greater extinction threats in areas with harsh environments (Fréville et al., 2007)
	Leaf ratio	Species with greater leaf ratios may be better adapted to climate change and thus have lower extinction risk (Baird et al., 2021)
	Leaf size	Species with larger leaves may be less plastic and therefore face a higher extinction risk (Li, Huang, et al., 2020; Li, Zou, et al., 2020)
Extrinsic	Mean annual temperature	Climate affects growth and development and may limit the spatial distribution of many endemic species (Fréville et al., 2007)
	Annual precipitation	
	Temperature change	Changes in temperature and precipitation will significantly shrink the geographic range of many plants and make them more vulnerable to extinction (Chen et al., 2011)
	Precipitation change	
	Altitude	Species endemic to high altitudes have higher extinction risks (Ahmad et al., 2021)
	Normalized difference vegetation index (NDVI)	NDVI is a proxy for habitat productivity which influences energy and resources and therefore affects extinction risk (Evans et al., 2006)
	Human Footprint index	Higher human footprint is a proxy for local development intensity, which increases the extinction risk of local species (Feng et al., 2017)

in the extinction risk of Chinese angiosperms? Secondly, how is extinction risk related to extrinsic variables and plant traits? Thirdly, to what extent are these relationships consistent across woody and herbaceous species?

2 | METHODS

2.1 | Species checklists

Extinction risk status of Chinese angiosperms was obtained from the Red List of China Higher Plants (RLCHP) (Qin, Zhao, et al., 2017), which is a revised version based on the China

Biodiversity Red List in 2013. We used the RLCHP rather than the IUCN Red List (Wang & Xie, 2004) because the RLCHP has more up-to-date taxonomy and the IUCN Red List only has evaluations for 4182 Chinese angiosperms compared to 30,068 angiosperms in the RLCHP. The species in the RLCHP were mostly collected from specimen data, primary literature, and expert knowledge. Species described since 2017 were not included in this analysis due to a lack of comprehensive and standardized data on distributions or traits for such species. Furthermore, the newly described species from 2017 to 2022 are not expected to exceed 5% of the whole RLCHP in our study, based on the recent estimation (Du et al., 2020). Thus, the lack of inclusion will not impact on overall findings of the study.

Extinction risk evaluations are based on the same criteria as the IUCN Red List Categories and Criteria (Version 3.1) (IUCN, 2001) and Guidelines for Application of IUCN Red List Criteria at Regional and National Levels (Version 3.0) (IUCN, 2003). Of the 30,068 assessed angiosperm species (Qin, Zhao, et al., 2017): 40 species were considered extinct or on the verge of extinction (extinct, extinct in the wild, or regionally extinct), 3363 species were considered threatened (critically endangered, endangered, or vulnerable), and 2538 were considered near-threatened (Qin, Yang, et al., 2017). Next, we classified threat status as an ordinal response: 0, least concern (LC); 1, near-threatened (NT); 2, vulnerable (VU); 3, endangered (EN); and 4, critically endangered (CR). In this study, we did not include species that are already extinct (Qin, Yang, et al., 2017). We further excluded aquatic angiosperms, subspecies, hybrids, varieties, and species without trait data, resulting in 1830 near-threatened and 2624 threatened species. We also identified 10,434 least concern species that have complete trait records in the iPlant (<http://www.iplant.cn/>). Together, these species represent 98.4% of angiosperm families in China.

2.2 | Traits and extrinsic data

We focused on five trait variables for each species based on their morphological descriptions in the iPlant and Chinese Virtual Herbarium (CVH: <https://www.cvh.ac.cn/>): climbing ability (CL), growth form (GF), maximum height (H), leaf shape (represented by leaf ratio: LR), and leaf size (LS) (Table 1). Climbing ability represents species' adhering capacity and associated biomass allocation strategy (Medina-Vega et al., 2021) and was divided into non-climbing species (0), climbers (including lianas and vines; 1), and epiphytes (2). Growth form reflects different ecological strategies (Klimeš et al., 2022) and was divided into woody (trees, shrubs, and woody lianas; 0) and herbaceous (herbs and subshrubs; 1). Maximum height is a major determinant of a species' ability to compete for light (Moles et al., 2009) and was obtained for all non-climbing species (Moles et al., 2009). Finally, we used two leaf traits that reflect precipitation and temperature tolerances (Baird et al., 2021). Leaf shape is calculated as leaf length divided by leaf width, which reflects the specific leaf area of plants (Lin et al., 2020). Leaf size is calculated as leaf length \times leaf width, which reflects the ability of plants to capture light (Niinemets et al., 2006).

We obtained six extrinsic variables to examine the effects of climate, productivity, altitude, and human activities on species extinction risk (Table 1). We used mean values of extrinsic variables for each species across its geographical range. Geographic range data were obtained by converting species county-level distribution data of each species into a resolution of 100 km² grid cells (Lu et al., 2018). We then approximated the geographic range by the number of grid cells occupied by each species to minimize the potential bias of unequal sampling effort and to simplify the relationship between

geographic distribution and extinction risk (Xu et al., 2019). We downloaded a raster of normalized difference vegetation index (NDVI; representation of vegetation cover) and altitude at a 1 km² resolution from the Resource and the Environmental Science Data Cloud Platform (RESDC, <https://www.resdc.cn/Default.aspx>). We used the WorldClim database (Fick & Hijmans, 2017) at a 5-min resolution to extract recent (average for the years 1970–2000) data on mean annual temperature (MAT) and annual precipitation (AP). As a measurement of climate change, we calculated the differences between 1901 and 2020 based on long-term averages for MAT (temperature change: TC) and AP (precipitation change: PC) using data from the United Kingdom's National Centre for Atmospheric Science at 0.5° \times 0.5° resolution (Harris et al., 2020). Finally, we used Human Footprint indices (HFP) from Venter et al. (2016), which consolidated data on infrastructure, land cover, and human access to natural areas at a resolution of 1 km² as a broad indicator of human presence. We resampled these variables in ArcGIS (Version 10.2, ESRI, 2016) and calculated mean values for 100 \times 100 km grids across China.

2.3 | Phylogenetic tree construction and analysis

We used the V.PhyloMaker package (Jin & Qian, 2019) within R 4.0.5 (R Core Team, 2021) to build a phylogenetic tree for all threatened species in China. We chose Smith and Brown (2018) phylogeny for seed plants (GenBank taxa with a backbone provided by Open Tree of Life; GBOTB) to construct the phylogeny. We extracted the genus- or family-level largest cluster's root and basal node information from the mega-tree. Species not in the GBOTB were included as polytomies within their parental clade using the "phylo.maker" function. This function randomly inserts species that are not in the GBOTB tree into their relevant genera or families. To assess the impact of random species insertions on the model, we iteratively generated and analysed 10 trees for each random insertion. Finally, we used the "ggtree" package (Yu et al., 2018) in R to construct a phylogenetic tree representing plant extinction risk.

We used Pagel's λ (Pagel, 1999) to assess phylogenetic signal and phylogenetic generalized least squares (PGLS) regression to evaluate the relative influence of traits and extrinsic variables on species' extinction risk (Purvis et al., 2000; Shuai et al., 2021). We performed these analyses using the "phylolm" function in the "phylolm" package in R 4.0.5 (Ho & Ané, 2014; R Core Team, 2021). The evolutionary model of PGLS was assessed using a Brownian motion (BM) with 1000 bootstrap replicates. This approach simply predicts that traits of closely related species are more similar than those of distantly related species (Cooper et al., 2016). We also calculated pairwise correlation coefficients between all variables after using phylogenetic independent contrasts (PIC) to reduce multicollinearity and autocorrelation in phylogenetic regression (Carvalho et al., 2006). We found that no variables exhibited high levels of correlation ($r > 0.8$) (Figure S1).

2.4 | Threatened factors of angiosperms

We used an under-sampling bias correction method to reduce biases associated with uneven numbers of Chinese angiosperms across different extinction threat levels. The disproportionate number of least concern species (10,434 species) would inundate the analysis of threatened species (2624 species) and potentially lead to underestimated results in regression analyses (Salas-Eljatib et al., 2018). We corrected species unevenness across threat levels by randomly selecting an equal number of species across each threat level (sampling without replacement). The number of species at each threat level in the subset was based on the number of critically endangered species. This resulted in 396 total species at each threat level for the all-species analysis (179 herbaceous species and 217 woody species at each threat level). We repeated the under-sampling bias correction procedure 10 times and plotted rarefaction curves based on all iterations. We found that 10 iterations covered 98.78% of threatened species (98.97% of herbaceous and 98.90% of woody species) (Figure S2), which confirmed that under-sampling bias correction was an appropriate method for ensuring the representation of plant species across all threat levels.

We first conducted univariate PGLS analyses to test the effect of each predictor on extinction risk prior to under-sampling bias correction. We excluded CL because it was not significant in univariate PGLS for all growth forms in multivariate PGLS (Table S2). We then applied the under-sampling bias corrected subset to run multiple PGLS and model selection analyses and reported their mean values of variable coefficients. To evaluate patterns across threatened woody and herbaceous angiosperms, we performed model selection based on all possible variable combinations (4095 models for all species and 2047 models for herbaceous and woody species) for PGLS models for the relevant variables for each growth forms (Table S3). We used the second-order Akaike Information Criterion (AIC_c) to compare model fit and rank candidate models. We selected the top candidate models by assessing Akaike weights (w) and by comparing differences in AIC_c values (ΔAIC_c) between models (Burnham & Anderson, 2002). As our analyses frequently recovered multiple adequate models ($\Delta AIC_c \leq 2$), we used model-averaging to account for model selection uncertainty using the 'dredge' function in the MuMIn package (Bartoń, 2013; Burnham & Anderson, 2002). We also calculated Z-scores and standardized regression coefficients (B) for each variable to compare the relative effect of each covariate on extinction risk (Ashcroft et al., 2012). We reported the number of times each variable appeared in resulting models as a proxy of variable importance. Finally, we then calculated the contribution of each variable to extinction risk in the models using variance decomposition (Gross et al., 2017).

2.5 | Phylogenetic path analysis

Phylogenetic path analysis (PPA) facilitates the inference of causal relationships between variables in phylogenetic analyses, such as PGLS (Von Hardenberg & Gonzalez-Voyer, 2013). We conducted

PPA by using the "phylopath" package (Van der Bijl, 2018), which uses PGLS to evaluate the direct and indirect causal relationships between variables. We selected leaf size, leaf ratio, and maximum height as trait variables, and MAT, mean annual precipitation (MAP), and TC and PC as climate variables. We designed the following 4 models to examine the effects of traits and climate on extinction risk (see details in Figure S3): (1) null model (no causal relationship between variables); (2) only climate variables influence extinction risk; (3) only traits directly influence extinction risk (but climate may indirectly affect extinction risk by affecting traits); and (4) traits and climate jointly affect extinction risk. We also created a shared path in the above 4 models to represent correlations between climate and traits; that is, climate variables can affect traits.

3 | RESULTS

3.1 | Phylogenetic signal of extinction risk

We found a substantial and significant phylogenetic signal in the extinction risk of angiosperms in China when analysing all species together (Pagel's $\lambda = 0.796$, $p < .001$), and when woody ($\lambda = 0.599$, $p < .001$) and herbaceous ($\lambda = 0.694$, $p < .001$) species were analysed separately. Orchidaceae (479 species), Ericaceae (125 species), and Fabaceae (112 species) had the largest absolute number of threatened species. Species from 19 families were considered threatened and the proportion of threatened species in 46 families exceeded 50% (Figure 2 and Table S1).

3.2 | Effects of traits on extinction risk

The extinction risk of woody plants was significantly higher than that of herbaceous species. The model averages of the all-species analyses showed that both plant traits and extrinsic variables accounted for 37.36% of the variation in extinction risk, of which plant traits accounted for 45.72% of the estimates (Figure 3 and Table S3). Growth form was the most important trait in predicting extinction risk, accounting for 25.98% of the total parameter estimates across all species (Table S2). We also found that extinction risk increased with maximum plant height and decreased with leaf size, which together explained 17.02% of all the estimates.

The correlation between the extinction risk of herbaceous species was weaker than that of extrinsic variables, whereas the extinction risk of woody species was most strongly related to maximum height. Univariate PGLS regressions showed that extinction risk was related to maximum height, leaf size, and leaf ratio, regardless of growth form and consistent with the results in the all-species model (Table S2). However, the contribution of each trait differed substantially between growth forms. In herbaceous species, all traits accounted for 33.57% of the variation in extinction risk, of which plant traits accounted for only 7.5% and maximum plant height just 3.09% (Table S3). Similar to herbaceous plants, all traits accounted

FIGURE 2 Family level phylogeny and extinction risk of 192 angiosperm families in China based on Smith and Brown (2018). Bar plots at each tip show the relative proportions (see details in Table S1) of threatened (vulnerable, endangered, and critically endangered) and least concerned species in each family included in our study

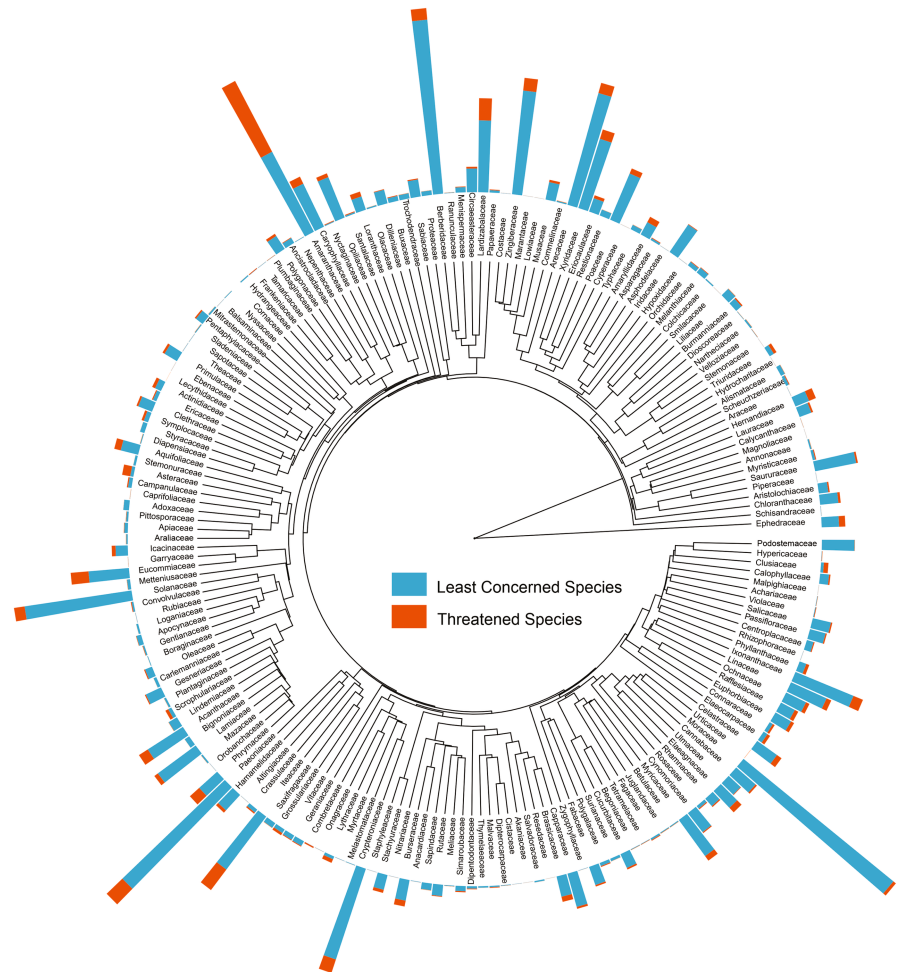
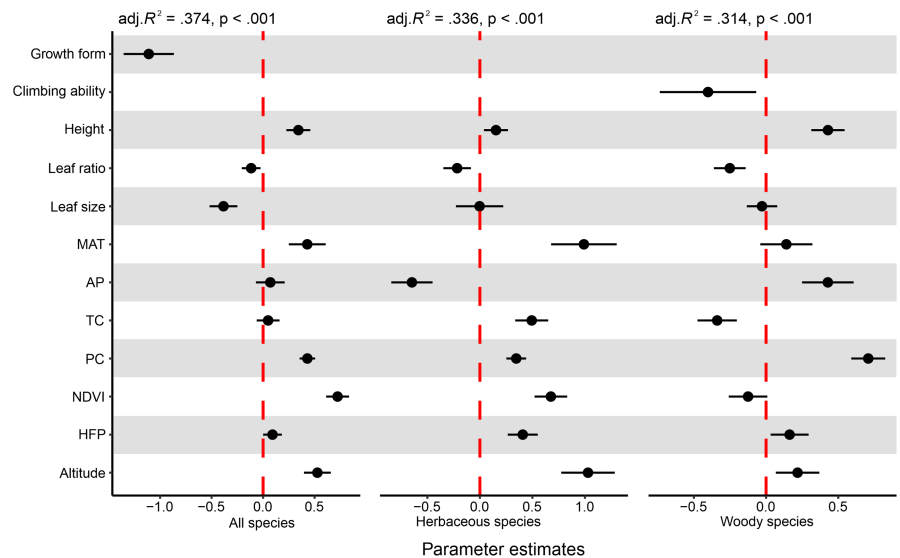


FIGURE 3 Average parameter estimates (standardized regression coefficients) of model predictors, associated 95% confidence intervals, and adjusted R^2 of averaged models for analyses of extinction risk for all species, herbaceous species, and woody species. Other data on model averages and model selections are shown in Table S3



for 31.45% of the variation in woody plant extinction risk. However, woody plant traits accounted for 25.04% of the estimates and maximum plant height accounted for 15.15% of the total estimates. Overall, the contributions of woody plant traits to predicted extinction risk were greater than those of herbaceous plants, accounting for 25.04% of the total estimates. Moreover, extinction risk increased with woody species' height, accounting for 15.15% of the total estimates.

3.3 | Effects of extrinsic variables on extinction risk

The effects of extrinsic variables on extinction risk were greater than those of traits (Table S2). The model-averaged results showed that extrinsic variables accounted for 54.27% of the variation in the all-species model (Figure 3 and Table S3). Altitude, MAT, PC, and NDVI were the most important extrinsic predictors of extinction

risk, accounting for 49.36% of the variation in the all-species analysis. The extinction risk of species increased with the altitude, MAT, MAP, and NDVI. In contrast, MAP, TC, and HFP only accounted for 4.91% of the total estimates.

The extinction risk of herbaceous species was mainly related to recent climate and human activities, whereas the extinction risk of woody species was significantly correlated with climate change. Univariate PGLS showed that the extinction risk of herbaceous species was positively correlated with MAT, HFP, altitude, and NDVI, but not with PC. Therefore, extrinsic variables played a decisive role in predicting the extinction risk of herbaceous species, accounting for 92.49% of the variation in the model. Among them, altitude and MAT were the most important predictors of herbaceous plant extinction risk, accounting for 20.74% and 19.95% of the variation, respectively. For woody species, extinction risk was mainly affected by PC and extrinsic variables overall accounted for 74.96% of the variation. Climate change including PC and TC were the most important extrinsic predictors of woody species' extinction risk, accounting for 25.00% and 12.00% of the variation, respectively. Interestingly, the extinction risk of woody species increased with PC and decreased with TC.

3.4 | Effects of traits and climate on extinction risk in PPA

The results of PPA showed that traits and climate jointly affect extinction risk (Figure S3). At the same time, climate mainly affected extinction risk through direct effects and traits were still strongly correlated with extinction risk when excluding climate variables (Table S4 and Figure 4). In herbaceous species, recent climate (MAT and AP) explained over half (61.6%) of the variation in extinction risk. The direct effects of climate variables on the extinction risk of herbaceous species were less than those of plant traits. Among them, climate change variables affected the extinction risk of herbaceous species mostly through indirect effects, whereas recent climate variables mainly affected extinction risk through direct effects. At the same time, 63.3% of the variation of trait effects on extinction risk can be explained by indirect effects of climate on extinction risk in herbaceous species. In woody species, precipitation (PC and AP) explained nearly half (47.0%) of the effects on extinction risk. Among them, only AP affected the extinction risk of woody species more through indirect effects on traits, and climate change explained 29.4% of the effects of traits on the extinction risk of woody species.

4 | DISCUSSION

The extinction risk of Chinese angiosperms showed significant phylogenetic signals. Not only did we find that the extinction risk of woody species was higher than that of herbaceous species but also that there were significant differences in the intrinsic and

extrinsic predictors of extinction risk for woody and herbaceous species. Specifically, traits had little effect on the extinction risk of herbaceous species, whereas plant height significantly affected extinction risk of woody species. Recent climate, altitude, and productivity (represented by NDVI) patterns significantly affected the extinction risk of herbaceous species, whereas the extinction risk of woody species was related to precipitation (both recent past and precipitation changes since 1901). However, after considering the influence of climate on traits, we found that taller woody and shorter herbaceous plants have a higher extinction risk, respectively.

4.1 | Phylogenetic signal of extinction risk in angiosperms

We found that extinction risks of extant Chinese angiosperms were affected by variables with a substantial phylogenetic signal. Earlier studies have found strong phylogenetic signals in angiosperm traits, such as leaf shape, leaf size, and plant height (An et al., 2021; Lanfear et al., 2013). In our analyses, although woody species had a higher extinction risk, the phylogenetic signal of their extinction risk was weaker than that of herbaceous species. One explanation for this pattern is that woody species are more affected by human factors. Woody species are larger and require more extensive ranges to maintain populations (Xu et al., 2018), and therefore are potentially more vulnerable to habitat fragmentation, logging, and other human activities than herbaceous species (Pouteau et al., 2022). Moreover, the legacy of long-term, high-intensity human activities in ancient China has pushed many woody plants to endangered status (Feng et al., 2017). In general, repeated, prolonged, and extreme human disturbance or natural disasters can increase extinction risk and consequently obscure the detection of phylogenetic patterns in extinction risk (Daru et al., 2013).

4.2 | Differences in extinction risk between woody and herbaceous species

Patterns of extinction risk varied greatly between woody and herbaceous species. Consistent with past studies, we found that woody species had a higher extinction risk than herbaceous species (Humphreys et al., 2019). This may be related to their traits and environments (Fréville et al., 2007), their relationships with humans (logging, in particular; Tabarelli et al., 2004)—as well as their generally lower genetic diversity, which may limit their ability to adapt over short time scales (Chung et al., 2020). Indeed, we found that plant traits had greater effects on woody plant extinction risk than that on herbaceous plants. Woody species also have higher rates of monoecious and dioecious sexual systems than herbaceous species, which may reduce their fecundity relative to herbaceous species that are capable of selfing (Gamba & Muchhala, 2020).

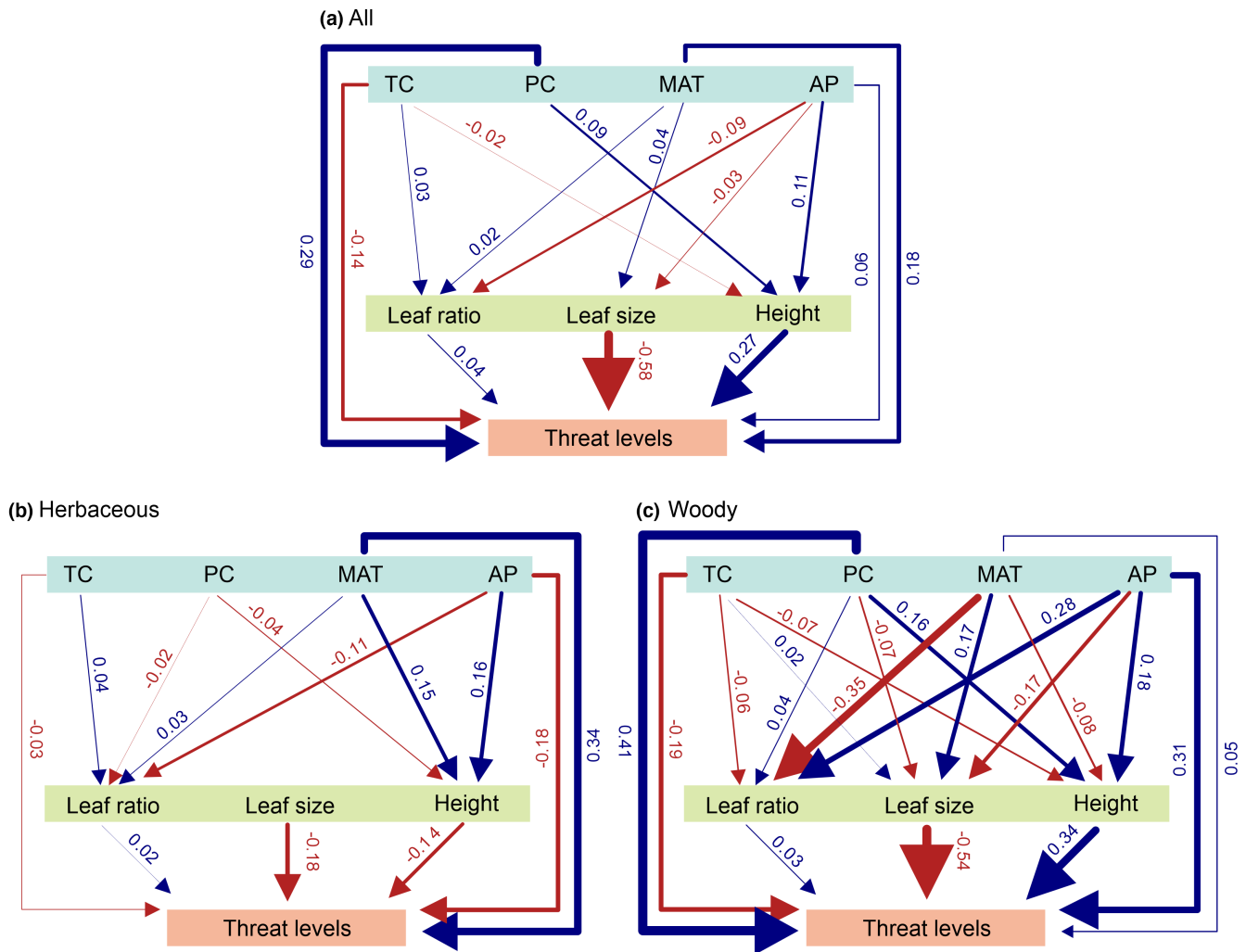


FIGURE 4 Phylogenetic path analyses (PPA) of plant traits, climate variables, and extinction risk for all (a), herbaceous (b), and woody (c) plant species. Blue and red arrows indicate significant positive and negative effects, respectively, and arrow thickness is proportional to the size of the correlation coefficient. Arrows with correlation coefficients $< .001$ are not shown. AP, annual precipitation; MAT, mean annual temperature; TC, temperature change; PC, precipitation change

We found that NDVI had little correlation with woody species extinction risk but was positively correlated with that of herbaceous species. This may be because locally productive areas support more regionally threatened herbaceous species and more threatened woody species in barren areas. Another possible explanation is that areas with higher NDVI tend to have higher forest coverage and therefore more companion or understorey herbaceous species (Spicer et al., 2022), which are often more vulnerable to climate and land use change (De Lombaerde et al., 2022). At the same time, herbaceous species face more severe competition in areas with milder climatic conditions and higher productivity, which may increase their extinction risk in these areas (Furness et al., 2021).

4.3 | Interactive effects of plant traits and environment on extinction risk

Anthropogenic climate change is among the most potent drivers of species extinction (Chen et al., 2011). The relatively weaker

correlation between climate change and extinction risk in herbaceous species compared to that for woody species further explains differences in extinction risk between growth forms. The increase in precipitation and temperature over the past century has significantly increased the extinction risk of woody species. Compared to herbaceous species, woody species have different life history strategies (e.g., longer lifespans and slower reproduction) and slower molecular evolution rates, which may increase their vulnerability to anthropogenic climate change (Klimeš et al., 2022; Smith & Donoghue, 2008). Woody species also have narrower hydraulic safety margins than herbaceous species, and thus may be more vulnerable to altered precipitation regimes (Choat et al., 2012). At the same time, the increase in evaporation and drought caused by the rise in temperature will also threaten the survival of these woody plants (Moles et al., 2009). The extinction risk of woody and herbaceous species was positively and negatively correlated with MAP, respectively. At the same time, herbaceous communities in dry grassland ecosystems are particularly vulnerable to climate change, which can reduce competition for invasive species (Baird et al., 2021), and further

negatively affect populations of native, threatened herbaceous species (Jin et al., 2019). For woody plants experiencing the effects of climate warming, boreal forests are example ecosystems that may be particularly sensitive to rising temperatures (Babst et al., 2019). This may explain why woody trees in colder areas are at greater risk of extinction overall (Eiserhardt et al., 2015).

We hypothesized that different relationships between plant traits and extrinsic variables may contribute to divergent extinction risks across herbaceous and woody species. We found that traits of woody species were more affected by climate change, which in turn led to an increased risk of extinction. We also found that extinction risks of woody and herbaceous species were related to leaf size and leaf ratio. Woody plant leaf size is positively correlated with mean annual temperature and MAP (Li, Huang, et al., 2020), and smaller leaf sizes are associated with cold, dry climates. In herbaceous species, shorter and narrower leaves are often found in cold and dry climates as well (Baird et al., 2021). Hence, these traits have strong environmental plasticity (Cristian & John, 2020). We found that maximum plant height was significantly correlated with various extrinsic variables: herbaceous species height was affected by both temperature and precipitation, whereas woody plant height was mainly affected by precipitation. These findings support the hypothesis that plant height is dependent on water availability (Koch et al., 2004). Our path analysis also showed that taller woody species and shorter herbaceous species had greater extinction risks. This contrasts with De Jonge et al. (2018), who found that shorter plants were more vulnerable to environmental change and, as a result, face a greater risk of extinction. At the same time, another possible explanation is that taller trees are frequently prioritized by logging operations (Tabarelli et al., 2004), whereas smaller herbaceous species may be more affected by microhabitats (Emma & Charles, 2007).

4.4 | Critical factors and conservation implications

We found that climbing and epiphytic species did not have elevated extinction risks, which is contrary to our hypothesis and previous research in other regions (Zettlemoyer et al., 2019). On the one hand, most climbers and epiphytes in China are concentrated in forest reserves with high biodiversity and strong protection (Figure S4) (Zhang et al., 2020). On the other hand, many threatened epiphytes, especially orchid species, may lack adequate conservation evaluation. Therefore, we suggest that more effort should be allocated to evaluating the threats to epiphytes and climbing plants.

Whereas we recovered the expected positive correlations between angiosperm extinction risk and both altitude and temperature, we also found a positive correlation with precipitation. Threatened angiosperms in China are most concentrated in two regions: the rain forests of Southwest China (Lu et al., 2018) and a narrow geographic area along the mountains of the Tibetan Plateau (Zu et al., 2021). Although high-altitude areas are often cold and dry with little human activity (Ma et al., 2020), we found only a weak

relationship between human footprint and extinction risk. This may be somewhat explained by our large spatial extents and the associated coarse-resolution grid. Highly anthropized areas likely contain a very small number of species and the area within the 100 km² grid may include both high and low levels of human activities. Moreover, China's protected area system covers 15.1% of China's land area, but only contains 13.1% of threatened plant species (Xu et al., 2017). Notably, existing reserves do not cover the mountainous areas of southwest China and the Tibetan Plateau where plant biodiversity is particularly high. We therefore suggest that future establishment of protected areas should prioritize the narrow area where the tropical rain forest in Southwest China transitions to the mountains of the plateau to increase the representation of threatened plant species.

Rare and threatened species play critical roles in forest ecosystems. Extirpations lead to loss of genetic diversity and sharp increases in extinction risk. As these plants become rarer and go extinct—locally or globally—there will be many cascading effects, including the possible extinction of herbivores that depend on these species (McIntyre & Whitham, 2003). Our results confirm that patterns of extinction risk differ among plant growth forms in Chinese angiosperms. Hence, it is particularly important to take different management and protection measures for herbaceous and woody species. We should also pay special attention to the protection of tall woody plants and herbaceous plants in high-altitude areas. Current sanctuaries tend to focus on flagship species, which may neglect the protection of more inconspicuous threatened plants (Chua et al., 2021). Considering that many geographic ranges of herbaceous and woody threatened species also overlap (Figure S4), forest protection should also consider herbaceous understorey species that are often neglected (Spicer et al., 2022). At the same time, because herbaceous and woody species have different relationships between extinction risk and environmental conditions, it is critically important to expand the scope of existing nature reserves to encompass diverse ecological niches and altitudinal gradients. Such expansion would greatly enhance species abilities to cope with future climate change.

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DATA AVAILABILITY STATEMENT

The dataset used in the analyses has been uploaded to an open-source online database (<https://doi.org/10.5281/zenodo.6527087>).

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REFERENCES

- Ahmad, M., Sharma, P., Rathee, S., Singh, H. P., Batish, D. R., Lone, G. R., Kaur, S., Jaryan, V., & Kohli, R. K. (2021). Niche width analyses facilitate identification of high-risk endemic species at high altitudes in western Himalayas. *Ecological Indicators*, 126, 107653. <https://doi.org/10.1016/j.ecolind.2021.107653>
- An, N., Lu, N., Fu, B., Wang, M., & He, N. (2021). Distinct Responses of Leaf Traits to Environment and Phylogeny Between Herbaceous and Woody Angiosperm Species in China. *Frontiers in Plant Science*, 12, 799401. <https://doi.org/10.3389/fpls.2021.799401>
- Ashcroft, M. B., Gollan, J. R., Warton, D. I., & Ramp, D. (2012). A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. *Global Change Biology*, 18(6), 1866–1879. <https://doi.org/10.1111/j.1365-2486.2012.02661.x>
- Babst, F., Bouriaud, O., Poulter, B., Trouet, V., Girardin, M. P., & Frank, D. C. (2019). Twentieth century redistribution in climatic drivers of global tree growth. *Science Advances*, 5, aat 4313. <https://doi.org/10.1126/sciadv.aat4313>
- Baird, A. S., Taylor, S. H., Pasquet-Kok, J., Vuong, C., Zhang, Y., Watcharamongkol, T., Scoffoni, C., Edwards, E. J., Christin, P. A., Osborne, C. P., & Sack, L. (2021). Developmental and biophysical determinants of grass leaf size worldwide. *Nature*, 592, 242–247. <https://doi.org/10.1038/s41586-021-03370-0>
- Bartoń, K. (2013). MuMIn: multi-model inference. R package version 1.5.
- Burnham, K. P., & Anderson, D. (2002). *Model selection and multi-model inference. A practical information-theoretic approach*. Springer-Verlag.
- Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, 486(7401), 59–67. <https://doi.org/10.1038/nature11148>
- Carvalho, P., Diniz-Filho, J. A. F., & Bini, L. M. (2006). Factors influencing changes in trait correlations across species after using phylogenetic independent contrasts. *Evolutionary Ecology*, 20, 591–602. <https://doi.org/10.1007/s10682-006-9119-7>
- Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333, 1024–1026. <https://doi.org/10.1126/science.1206432>
- Choat, B., Jansen, S., Brodribb, T. J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S. J., Feild, T. S., Gleason, S. M., Hacke, U. G., Jacobsen, A. L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P. J., Nardini, A., Pittermann, J., Zanne, A. E. (2012). Global convergence in the vulnerability of forests to drought. *Nature*, 491(7426), 752–755. <https://doi.org/10.1038/nature11688>
- Chu, X., Gugger, P. F., Li, L., Zhao, J., & Li, Q. (2021). Responses of an endemic species (*Roscoea humeana*) in the Hengduan Mountains to climate change. *Diversity and Distributions*, 27(11), 2231–2244. <https://doi.org/10.1111/ddi.13397>
- Chua, M. A., Tan, A., & Carrasco, L. R. (2021). Species awareness days: Do people care or are we preaching to the choir? *Biological Conservation*, 255, 109002. <https://doi.org/10.1016/j.biocon.2021.109002>
- Chung, M. Y., Son, S., Herrando-Moraira, S., Tang, C. Q., Maki, M., Kim, Y. D., López-Pujol, J., Hamrick, J. L., & Chung, M. G. (2020). Incorporating differences between genetic diversity of trees and herbaceous plants in conservation strategies. *Conservation Biology*, 34(5), 1142–1151. <https://doi.org/10.1111/cobi.13467>
- Cooper, N., Thomas, G. H., Venditti, C., Meade, A., & Freckleton, R. P. (2016). A cautionary note on the use of Ornstein Uhlenbeck models in macroevolutionary studies. *Biological Journal of the Linnean Society*, 118(1), 64–77. <https://doi.org/10.1111/bij.12701>
- Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., ter Steege, H., Morgan, H. D., van der Heijden, M. G. A., Pausas, J. G., & Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 51(4), 335. <https://doi.org/10.1071/bt02124>
- Cristian, R., & John, J. W. (2020). Recent responses to climate change reveal the drivers of species extinction and survival. *Proceedings of the National Academy of Sciences*, 117(8), 4211–4217. <https://doi.org/10.1073/pnas.1913007117>
- Daru, B. H., Davies, T. J., Willis, C. G., Meineke, E. K., Ronk, A., Zobel, M., Pärtel, M., Antonelli, A., & Davis, C. C. (2021). Widespread homogenization of plant communities in the Anthropocene. *Nature Communications*, 12, 6983. <https://doi.org/10.1038/s41467-021-27186-8>
- Daru, B. H., Yessoufou, K., Mankga, L. T., & Davies, T. J. (2013). A global trend towards the loss of evolutionarily unique species in mangrove ecosystems. *PLoS One*, 8(6), e66686. <https://doi.org/10.1371/journal.pone.0066686>
- Davis, C. C., Willis, C. G., Primack, R. B., & Miller-Rushing, A. J. (2010). The importance of phylogeny to the study of phenological response to global climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1555), 3201–3213. <https://doi.org/10.1098/rstb.2010.0130>
- De Jonge, M. M., Hilbers, J. P., Jongejans, E., Ozinga, W. A., Hendriks, A. J., & Huijbregts, M. A. (2018). Relating plant height to demographic rates and extinction vulnerability. *Biological Conservation*, 220, 104–111. <https://doi.org/10.1016/j.biocon.2018.02.008>
- De Lombaerde, E., Vangansbeke, P., Lenoir, J., Van Meerbeek, K., Lembrechts, J., Rodríguez-Sánchez, F., Luoto, M., Scheffers, B., Haesen, S., Aalto, J., Christiansen, D. M., De Pauw, K., Depauw, L., Govaert, S., Greiser, C., Hampe, A., Hylander, K., Klings, D., Koelemeijer, I., ... De Frenne, P. (2022). Maintaining forest cover to enhance temperature buffering under future climate change. *Science of The Total Environment*, 810, 151338. <https://doi.org/10.1016/j.scitotenv.2021.151338>
- Dong, N., Prentice, I. C., Wright, I. J., Evans, B. J., Togashi, H. F., Caddy-Retalic, S., McInerney, F., Sparrow, B., Leitch, E., & Lowe, A. J. (2020). Components of leaf-trait variation along environmental gradients. *New Phytologist*, 228(1), 82–94. <https://doi.org/10.1111/nph.16558>
- Du, C., Liao, S., Boufford, D. E., & Ma, J. S. (2020). Twenty years of Chinese vascular plant novelties, 2000 through 2019. *Plant Diversity*, 42(5), 393–398. <https://doi.org/10.1016/j.pld.2020.08.004>
- Eiserhardt, W. L., Borchsenius, F., Plum, C. M., Ordonez, A., & Svenning, J. C. (2015). Climate-driven extinctions shape the phylogenetic structure of temperate tree floras. *Ecology Letters*, 18(3), 263–272. <https://doi.org/10.1111/ele.12409>
- Ellis, C. J. (2020). Microclimatic refugia in riparian woodland: A climate change adaptation strategy. *Forest Ecology and Management*, 462, 118006. <https://doi.org/10.1016/j.foreco.2020.118006>
- Emma, J. P., & Charles, E. Z. (2007). Bryophytes in a changing landscape: The hierarchical effects of habitat fragmentation on ecological and evolutionary processes. *Biological Conservation*, 135(3), 315–325. <https://doi.org/10.1016/j.biocon.2006.10.016>
- ESRI (Environmental Systems Research Institute). (2016). *ArcGIS desktop 10.2*. Environmental Systems Research Institute.
- Evans, K. L., James, N. A., & Gaston, K. J. (2006). Abundance, species richness and energy availability in the North American avifauna. *Global Ecology and Biogeography*, 15(4), 372–385. <https://doi.org/10.1111/j.1466-822X.2006.00228.x>

- Feng, G., Mao, L. F., Benito, B. M., Swenson, N. G., & Svenning, J. C. (2017). Historical anthropogenic footprints in the distribution of threatened plants in China. *Biological Conservation*, 210, 3–8. <https://doi.org/10.1016/j.biocon.2016.05.038>
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(12), 4302–4315. <https://doi.org/10.1002/joc.5086>
- Fréville, H., McConway, K., Dodd, M., & Silvertown, J. (2007). Prediction of extinction in plants: interaction of extrinsic threats and life history traits. *Ecology*, 88(10), 2662–2672. <https://doi.org/10.1890/06-1453.1>
- Furness, E. N., Garwood, R. J., Mannion, P. D., & Sutton, M. D. (2021). Productivity, niche availability, species richness, and extinction risk: Untangling relationships using individual-based simulations. *Ecology and Evolution*, 11(13), 8923–8940. <https://doi.org/10.1002/ece3.7730>
- Gamba, D., & Muchhala, N. (2020). Global patterns of population genetic differentiation in seed plants. *Molecular Ecology*, 29(18), 3413–3428. <https://doi.org/10.1111/mec.15575>
- Gross, N., Bagousse-Pinguet, Y. L., Liancourt, P., Berdugo, M., Gotelli, N. J., & Maestre, F. T. (2017). Functional trait diversity maximizes ecosystem multifunctionality. *Nature Ecology and Evolution*, 1, 0132. <https://doi.org/10.1038/s41559-017-0132>
- Harris, I., Osborn, T. J., Jones, P., & Lister, D. (2020). Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Scientific Data*, 7, 109. <https://doi.org/10.1038/s41597-020-0453-3>
- Ho, L. T., & Ané, C. (2014). A linear-time algorithm for gaussian and non-gaussian trait evolution models. *Systematic Biology*, 63(3), 397–408. <https://doi.org/10.1093/sysbio/syu005>
- Howard, C., Flather, C. H., & Stephens, P. A. (2020). A global assessment of the drivers of threatened terrestrial species richness. *Mature Communications*, 11, 993. <https://doi.org/10.1038/s41467-020-14771-6>
- Humphreys, A. M., Govaerts, R., Ficinski, S. Z., Lughadha, E. N., & Vorontsova, M. S. (2019). Global dataset shows geography and life form predict modern plant extinction and rediscovery. *Nature Ecology and Evolution*, 3, 1043–1047. <https://doi.org/10.1038/s41559-019-0906-2>
- IUCN. (2001). *IUCN red list categories and criteria – version 3.1*. IUCN.
- IUCN. (2003). *Application of the IUCN red list criteria at regional levels – version 3.0*. IUCN.
- Jin, Y., & Qian, H. (2019). V. PhyloMaker: an R package that can generate very large phylogenies for vascular plants. *Ecography*, 42(8), 1353–1359. <https://doi.org/10.1111/ecog.04434>
- Jin, Y., Li, J., Liu, C., Liu, Y., Zhang, Y., Song, Q., Sha, L., Balasubramanian, D., Chen, A., Yang, D., & Li, P. (2019). Precipitation reduction alters herbaceous community structure and composition in a savanna. *Journal of Vegetation Science*, 30(5), 821–831. <https://doi.org/10.1111/jvs.12766>
- Klímeš, A., Šimová, I., Zizka, A., Antonelli, A., & Herben, T. (2022). The ecological drivers of growth form evolution in flowering plants. *Journal of Ecology*, early view., 110, 1525–1536. <https://doi.org/10.1111/1365-2745.13888>
- Koch, G. W., Sillett, S. C., Jennings, G. M., & Davis, S. D. (2004). The limits to tree height. *Nature*, 428, 851–854. <https://doi.org/10.1038/nature02417>
- Lanfear, R., Ho, S. Y., Jonathan Davies, T., Moles, A. T., Aarssen, L., Swenson, N. G., Warman, L., Zanne, A. E., & Allen, A. P. (2013). Taller plants have lower rates of molecular evolution. *Nature Communications*, 4, 1879. <https://doi.org/10.1038/ncomms2836>
- Li, G. Q., Huang, J. H., Guo, H., & Du, S. (2020). Projecting species loss and turnover under climate change for 111 Chinese tree species. *Forest Ecology and Management*, 477, 118488. <https://doi.org/10.1016/j.foreco.2020.118488>
- Li, Y. Q., Zou, D. T., Shrestha, N., Xu, X. T., Wang, Q. G., Jia, W., & Wang, Z. H. (2020). Spatiotemporal variation in leaf size and shape in response to climate. *Journal of Plant Ecology*, 13(1), 87–96. <https://doi.org/10.1093/jpe/rtz053>
- Lin, S., Niklas, K. J., Wan, Y., Hölscher, D., Hui, C., Ding, Y., & Shi, P. (2020). Leaf shape influences the scaling of leaf dry mass vs. area: a test case using bamboos. *Annals of Forest Science*, 77, 11. <https://doi.org/10.1007/s13595-019-0911-2>
- Lu, L. M., Mao, L. F., Yang, T., Ye, J. F., Liu, B., Li, H. L., Sun, M., Miller, J. T., Mathews, S., Hu, H. H., Niu, Y. T., Peng, D. X., Chen, Y. H., Smith, S. A., Chen, M., Xiang, K. L., Le, C. T., Dang, V. C., Lu, A. M., ... Chen, Z. D. (2018). Evolutionary history of the angiosperm flora of China. *Nature*, 554, 234–238. <https://doi.org/10.1038/nature25485>
- Lughadha, E. N., Bachman, S. P., Leão, T. C., Forest, F., Halley, J. M., Moat, J., ... Walker, B. E. (2020). Extinction risk and threats to plants and fungi. *Plants People Planet*, 2(5), 389–408. <https://doi.org/10.1002/ppp3.10146>
- Ma, M., Collins, S. L., & Du, G. (2020). Direct and indirect effects of temperature and precipitation on alpine seed banks in the Tibetan Plateau. *Ecological Applications*, 30(5), e02096. <https://doi.org/10.1002/eap.2096>
- Mao, L. F., Swenson, N. G., Sui, X. H., Zhang, J. L., Chen, S. B., Li, J. J., Peng, P., Zhou, G., & Zhang, X. S. (2020). The geographic and climatic distribution of plant height diversity for 19,000 angiosperms in China. *Biodiversity and Conservation*, 29, 487–502. <https://doi.org/10.1007/s10531-019-01895-5>
- Marco, M. D., & Santini, L. (2015). Human pressures predict species' geographic range size better than biological traits. *Global Change Biology*, 21(6), 2169–2178. <https://doi.org/10.1111/gcb.12834>
- McIntyre, P. J., & Whitham, T. G. (2003). Plant genotype affects long-term herbivore population dynamics and extinction: conservation implications. *Ecology*, 84(2), 311–322. [https://doi.org/10.1890/0012-9658\(2003\)084\[0311:PGALTH\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0311:PGALTH]2.0.CO;2)
- Medina-Vega, J. A., Bongers, F., Schnitzer, S. A., & Sterck, F. J. (2021). Lianas explore the forest canopy more effectively than trees under drier conditions. *Functional Ecology*, 35(2), 318–329. <https://doi.org/10.1111/1365-2435.13717>
- Mittelbach, G. G., Schemske, D. W., Cornell, H. V., Allen, A. P., Brown, J. M., Bush, M. B., Harrison, S. P., Hurlbert, A. H., Knowlton, N., Lessios, H. A., McCain, C., McCune, A., McDade, L., McPeck, M., Near, T. J., Price, T. D., Ricklefs, R. E., Roy, K., Sax, D. F., ... Turelli, M. (2007). Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, 10(4), 315–331. <https://doi.org/10.1111/j.1461-0248.2007.01020.x>
- Moles, A. T., Warton, D. I., Warman, L., Swenson, N. G., Laffan, S. W., Zanne, A. E., Pitman, A., Hemmings, F. A., & Leishman, M. R. (2009). Global patterns in plant height. *Journal of Ecology*, 97(5), 923–932. <https://doi.org/10.1111/j.1365-2745.2009.01526.x>
- Niinemets, Ü., Portsmuth, A., & Tobias, M. (2006). Leaf size modifies support biomass distribution among stems, petioles and mid-ribs in temperate plants. *New Phytologist*, 171(1), 91–104. <https://doi.org/10.1111/j.1469-8137.2006.01741.x>
- Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401, 877–884. <https://doi.org/10.1038/44766>
- Pouteau, R., Brunel, C., Dawson, W., Essl, F., Kreft, H., Lenzner, B., Meyer, C., Pergl, J., Pyšek, P., Seebens, H., Weigelt, P., Winter, M., & Kleunen, M. (2022). Environmental and socioeconomic correlates of extinction risk in endemic species. *Diversity and Distributions*, 28(1), 53–64. <https://doi.org/10.1111/ddi.13438>
- Purvis, A., Gittleman, J. L., Cowlshaw, G., & Mace, G. M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society B*, 267(1456), 1947–1952. <https://doi.org/10.1098/rspb.2000.1234>
- Qin, H., Yang, Y., Dong, S., He, Q., Jia, Y., Zhao, L., Yu, S., Liu, H., Liu, B., Yan, Y., Xiang, J., Xia, N., Peng, H., Li, Z., Zhang, Z., He, X., Yin, L., Lin, Y., Liu, Q., ... Xue, N. (2017). Threatened species list of China's

- higher plants. *Biodiversity Science*, 25(7), 696–744. <https://doi.org/10.17520/biods.2017144>
- Qin, H., Zhao, L., Yu, S., Liu, H., Liu, B., Xia, N., Peng, H., Li, Z., Zhang, Z., He, X., Yin, L., Lin, Y., Liu, Q., Hou, Y., Liu, Y., Liu, Q., Cao, W., Li, J., Chen, S., ... Xue, N. (2017). Evaluating the endangerment status of China's angiosperms through the red list assessment. *Biodiversity Science*, 25(7), 745–757. <https://doi.org/10.17520/biods.2017156>
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Rabelo, R. S., Tonin, A. M., Boyero, L., Miranda, F. G. G., Gomes, P. P., Bambi, P., Sena, G., & Gonçalves Júnior, J. F. (2022). Plant litter from rare species increases functional diversity and decomposition of species mixtures. *Ecosystems*, <https://doi.org/10.1007/s10021-022-00740-1>
- Royer, D. L., Wilf, P., Janesko, D. A., Kowalski, E. A., & Dilcher, D. L. (2005). Correlations of climate and plant ecology to leaf size and shape: potential proxies for the fossil record. *American Journal of Botany*, 92(7), 1141–1151. <https://doi.org/10.3732/ajb.92.7.1141>
- Salas-Eljatib, C., Fuentes-Ramirez, A., Gregoire, T. G., Altamirano, A., & Yaitul, V. (2018). A study on the effects of unbalanced data when fitting logistic regression models in ecology. *Ecological Indicators*, 85, 502–508. <https://doi.org/10.1016/j.ecolind.2017.10.030>
- Shuai, L., Chen, C., Liu, W., Xu, W., Wang, Y., Zeng, Z., Zhang, Z., Zhao, L., & Wang, Y. (2021). Ecological correlates of extinction risk in Chinese terrestrial mammals. *Diversity and Distributions*, 27(7), 1294–1307. <https://doi.org/10.1111/ddi.13279>
- Smith, S. A., & Brown, J. W. (2018). Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany*, 105(3), 302–314. <https://doi.org/10.1002/ajb2.1019>
- Smith, S. A., & Donoghue, M. J. (2008). Rates of molecular evolution are linked to life history in flowering plants. *Science*, 322(5898), 86–89. <https://doi.org/10.1126/science.1163197>
- Spicer, A. E., Radhamoni, H. V. N., Duguid, M. C., Queenborough, S. A., & Comita, L. S. (2022). Herbaceous plant diversity in forest ecosystems: patterns, mechanisms, and threats. *Plant Ecology*, 223, 117–129. <https://doi.org/10.1007/s11258-021-01202-9>
- Tabarelli, M., Cardoso, S., & Gascon, C. (2004). Forest fragmentation, synergisms and the impoverishment of neotropical forests. *Biodiversity and Conservation*, 13, 1419–1425. <https://doi.org/10.1023/B:BIOC.0000019398.36045.1b>
- Vamosi, J. C., Magallón, S., Mayrose, I., Otto, S. P., & Sauquet, H. (2018). Macroevolutionary patterns of flowering plant speciation and extinction. *Annual Review of Plant Biology*, 69, 685–706. <https://doi.org/10.1146/annurev-arplant-042817-040348>
- Van der Bijl, W. (2018). phylopath: Easy phylogenetic path analysis in R. *PeerJ*, 6, e4718. <https://doi.org/10.7717/peerj.4718>
- Venter, O., Sanderson, E. W., Magrath, A., Allan, J. R., Behr, J., Jones, K. R., Possingham, H. P., Laurance, W. F., Wood, P., Fekete, B. M., Levy, M. A., & Watson, J. E. M. (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications*, 7, 12558. <https://doi.org/10.1038/ncomms12558>
- Von Hardenberg, A., & Gonzalez-Voyer, A. (2013). Disentangling evolutionary cause-effect relationships with phylogenetic confirmatory path analysis. *Evolution*, 67(2), 378–387. <https://doi.org/10.1111/j.1558-5646.2012.01790.x>
- Wang, S., & Xie, Y. (2004). *China Species Red List, Vol. 1: Red List (in Chinese with English abstract)*. Higher Education Press.
- Willis, C. G., Ruhfel, B., Primack, R. B., Miller-Rushing, A. J., & Davis, C. C. (2008). Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proceedings of the National Academy of Sciences*, 105(44), 17029–17033. <https://doi.org/10.1073/pnas.0806446105>
- Xu, W. B., Svenning, J. C., Chen, G. K., Chen, B., Huang, J. H., & Ma, K. P. (2018). Plant geographical range size and climate stability in China: Growth form matters. *Global Ecology and Biogeography*, 27(5), 506–517. <https://doi.org/10.1111/geb.12710>
- Xu, W. B., Svenning, J. C., Chen, G. K., Zhang, M. G., Huang, J. H., Chen, B., Ordonez, A., & Ma, K. P. (2019). Human activities have opposing effects on distributions of narrow-ranged and widespread plant species in China. *Proceedings of the National Academy of Sciences*, 116(52), 26674–26681. <https://doi.org/10.1073/pnas.1911851116>
- Xu, W., Xiao, Y., Zhang, J., Yang, W., Zhang, L., Hull, V., Wang, Z., Zheng, H., Liu, J., Polasky, S., Jiang, L., Xiao, Y., Shi, X., Rao, E., Lu, F., Wang, X., Daily, G. C., & Ouyang, Z. (2017). Strengthening protected areas for biodiversity and ecosystem services in China. *Proceedings of the National Academy of Sciences*, 114(7), 1601–1606. <https://doi.org/10.1073/pnas.1620503114>
- Yang, Y. Z., Wang, H., Harrison, S. P., Prentice, I. C., Wright, I. J., Peng, C. H., & Lin, G. H. (2019). Quantifying leaf-trait covariation and its controls across climates and biomes. *New Phytologist*, 221(1), 155–168. <https://doi.org/10.1111/nph.15422>
- Yu, G. C., Lam, T. Y., Zhu, H. C., & Guan, Y. (2018). Two methods for mapping and visualizing associated data on phylogeny using ggtree. *Molecular Biology and Evolution*, 35(12), 3041–3043. <https://doi.org/10.1093/molbev/msy194>
- Zettlemoyer, M. A., McKenna, D. D., & Lau, J. A. (2019). Species characteristics affect local extinctions. *American Journal of Botany*, 106(4), 547–559. <https://doi.org/10.1002/ajb2.1266>
- Zhang, Y. B., Wu, H. D., Yang, J., Song, X. Y., Yang, D., He, F., & Zhang, J. L. (2020). Environmental filtering and spatial processes shape the beta diversity of liana communities in a valley savanna in southwest China. *Applied Vegetation Science*, 23(4), 482–494. <https://doi.org/10.1111/avsc.12514>
- Zu, K., Wang, Z., Zhu, X., Lenoir, J., Shrestha, N., Lyu, T., Luo, A., Li, Y., Ji, C., Peng, S., Meng, J., & Zhou, J. (2021). Upward shift and elevational range contractions of subtropical mountain plants in response to climate change. *Science of the Total Environment*, 783, 146896. <https://doi.org/10.1016/j.scitotenv.2021.146896>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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