**Original Article**

Phylogenetic conservatism in threatened species responses to climate change differs between functional types in the Gongga Mountains of China

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Abstract: Climate change has become one of the most critical threats to global biodiversity. However, whether phylogenetically related species respond to climate change in similar ways remains controversial. The answer to this question is crucial for understanding the impacts of climate change and the conservation on the tree of life. By integrating species distribution models with a molecular phylogeny of 50 threatened plant species from one of the global biodiversity hotspots, Gongga Mountains (Mt. Gongga) in southwest China, we evaluated the responses of threatened plant species to future climate change, and estimated whether species responses are phylogenetically conserved. Phylogenetic reconstruction was used to calculate the phylogenetic distance and null model to verify the reliability of the results. We found that correlations between responses of different species to future climate change decreased with the increase in their phylogenetic distance in the monocotyledonous or herbaceous species, but not in the dicotyledonous and woody species. Our results suggested that the responses of herbaceous and monocotyledonous threatened species in Mt. Gongga to future climate change tend to be phylogenetically

conserved, while the responses of woody and dicotyledonous threatened species are not. Our study provides evidence for the existence of phylogenetically non-random extinction in the monocotyledonous herbs in Mt. Gongga and highlights the importance of integrating phylogenetic information and evolutionary history into conservation planning. We also provide theoretical basis and technical support for designing effective conservation schemes for the protection of biodiversity under anthropogenic climate change.

1   Introduction

There is now abundant evidence showing the effect of ongoing climate change on the distributions and diversity of plants (Solomon 2007; Daniel and Zoe 2012; Storlie et al. 2014; Zu et al. 2021; Zu et al. 2023). The question of whether closely related species share similar adaptive response to climate change has attracted increasing attention because of its importance in understanding non-random extinctions on the tree of life (Russell et al. 1998; Mace et al. 2003). Therefore, studies exploring the impacts of climate change on the tree of life are urgently needed in management, the development of measures to guide the conservation of the species, etc. Recently, progresses in community ecology and macroecology provide useful data and tools to integrate climate suitability of endangered plants in response to climate change with the tree of life to better identify conservation priorities for threatened plants (Tamara 2012).

Previous studies indicated that climatic niche similarity for species tend to be negatively correlated with their phylogenetic distance between two species (Faith and Richards 2012; Serra-Varela et al. 2015). In other words, climatic niche of species tends to be phylogenetically conserved across lineages. These findings suggest that species extinctions due to climate change tend to be phylogenetically non-random across the tree of life (Sjostrom and Gross 2006; Vamosi and Wilson 2008). In general, phylogenetic non-random extinction will lead to disproportionate loss of unique evolutionary lineages (Williams 2000; New 2002; Faith et al. 2009; Eiserhardt et al. 2015) compared to a phylogenetically random extinction process (Thuiller 2011; Zhang et al. 2017). However, some other studies found no significant phylogenetic signals in the extinction risk of some animal and plant species under future climate change (Thuiller 2011; Pio et al. 2014). This might be because different lineages exhibit varying degrees of phylogenetic niche conservatism and hence have different adaptations to climate change. Species with different life forms, traits and evolutionary history may have different responses to climate change, while monocotyledons and dicotyledons have different traits and reflect different evolutionary history (Losos 2008; Dullinger et al. 2012). Therefore, in order to understand the nature of climate-driven extinction, it is necessary to analyze the phylogenetic signals of species responses to climate change across the tree of life for different groups (woody plants vs. monocotyledons vs. dicotyledons), separately.

Threatened species, i.e. the vulnerable (VU), endangered (EN) and critically endangered (CR) species according to the IUCN Red List, are of a global concern in biodiversity conservation (Wang et al. 2015). Recent studies suggest that threatened plant species are highly vulnerable to habitat loss and have increased pressure from invasive species and climate change (Xu et al. 2019). As threatened species have high extinction risks, how these species respond to climate change should be considered during the spatial prioritization for their conservation (Secretariat of the Convention on Biological Diversity 2010). For example, Zhang et al. (2014) evaluated the extinction risk of woody plant species in China and found that the distribution ranges of many species are likely to decline under future climate change. However, few studies have explored the existence of phylogenetic signal in the responses of threatened plant species to climate change. Recently, the increase in the availability of herbarium specimens, climatic data and DNA sequences are providing new opportunities to explore the phylogenetic signals in the responses of threatened plants to climate changes.

In order to assess the potential impacts of future climate change on threatened plant distributions, a useful and widely employed method is the species distribution models (SDM) (Pearson and Dawson 2003; Guisan and Thuiller 2005; Franklin 2010). SDMs use species occurrence data and environmental variables to predict the geographic range of a species and to identify the effects of climate change on species distributions, thereby supporting decision making in biodiversity conservation (Margules and Pressey 2000; Thorn et al. 2009). MaxEnt (Maximum Entropy) software is a powerful and an extensively used species

distribution model to simulate the potential distribution of threatened species with limited occurrence data (Phillips 2004; Ray et al. 2011; Wang et al. 2015).

Many threatened plant species are mainly distributed in the mountains, and these species are severely threatened because of the increasing intensity of climate change (Tang et al. 2006; Wang et al. 2015). Mt. Gongga (Sichuan province in China) located in the northern Hengduan Mountains (the highest peak of Hengduan Mountains) represents one of the diversity centers of threatened plant species in China (Zu et al. 2019). According to the Threatened Species List of China's Higher Plants (Qin et al. 2017), Mt. Gongga harbors approximately 101 threatened plant species. A recent study has demonstrated that numerous montane plants in this region are predicted to change their range sizes and shift upslope in response to future climate change (Liang et al. 2018). However, few studies have attempted to understand the phylogenetic signals in the responses of threatened plants to climate change in this biodiversity hotspot. Here, we used the MaxEnt to evaluate the impacts of future climate change on the suitably distributional habitats of threatened plant species in Mt. Gongga, and then explored whether responses of these plant species to climate change are phylogenetically conserved. We expect that 1) future climate change will lead to loss in the suitable habitats of the threatened species; 2) closely-related species respond similarly to future climate changes; and 3) the phylogenetic signal of 50 threatened plant species responses to climate change varies across different life forms (woody plants vs. herbs) and important taxonomic groups of flowering plants (monocotyledons vs. dicotyledons). To test these hypotheses, we explored the relationship between the similarities in species responses to climate change among the threatened plant species in Mt. Gongga and their phylogenetic distances and compared the differences in phylogenetic signals across different life forms. Our study provides useful insights for the effective protection of threatened plant species in southwest China.

2 Materials and Methods

2.1 Species distributions and climatic variables

The distributions of threatened plant species in Mt. Gongga were compiled from field surveys and herbarium specimens. We conducted comprehensive field work in Mt. Gongga during May-July 2018. During field work, we collected the occurrence records of all angiosperms. We selected the endangered plant species based on the recent threatened species list of China's higher plants (Qin et al. 2017). We also obtained the occurrence records from other online databases, such as Global Biodiversity Information Facility (GBIF, https://www.gbif.org/occurrence/search?continent=ASIA&country=CN), Chinese Virtual Herbarium (CVH, http://www.cvh.org.cn/cms/), Biodiversity of the Hengduan Mountains and adjacent areas of south-central China database (http://hengduan.uh.harvard.edu/fieldnotes), as well as National Specimen Information Infrastructure (NSII, http://www.nsii.org.cn). We cleaned the species' occurrence records including the collecting data and collecting site, and verifying the accuracy of plant geographic coordinates. We excluded duplicate species' occurrence records and that lacking information on their exact geographical locations, and only included records with correct information. For the species' occurrence records with precise location but no geographical coordinates, we used the description of the locality and assigned coordinates as precisely as possible to this location. We georeferenced their locations using GeoNames in Google Earth and ArcGIS 10.2 (Esri; Redlands, CA, USA), and this georeferencing process followed is that used by Hijmans et al. (1999). Finally, a total of 2,346 occurrence records for the 50 threatened plant species were collected both in the filed surveys and the online database. To reduce the potential influences of spatial biases in species distribution data on the performance of species distribution models, the occurrence records of each species were thinned to a spatial resolution of 5 arc minutes using the 'thin' function in the "spThin" R package (Zhang et al. 2014, Aiello-Lammens et al. 2015). The life forms and habitat data of each species were extracted from Flora of China (http://www.efloras.org) and the herbarium specimens deposited in the collection of the Chinese National Herbarium (PE) (http://pe.ibcas.ac.cn/).

To reduce the uncertainty in modeled species distributions due to small sample size, we included species with at least 10 occurrence records across China (Yu et al. 2014). We also ensured that the distributions of the studied threatened plant species are mainly in China. Finally, a total of 50 species of

threatened plant species distributed in Mt. Gongga were selected (Appendix 1). We obtained the information on the endemism from Huang et al. (2016) and the threatened species from Qin et al. (2017) (see Table 1), among which 70% of the species are endemic to China, and the remaining 30% have more than 70% of their distributions within China. The percentage is determined based on the distribution of these

Table 1 List of selected threatened plants species in Mt. Gongga, southwestern China. "Proportion" means the proportion of the distribution area in China to the total distribution area for each species. The "Record" column indicates the number that was available for model building after the data cleaning and thinning. The endangered plant species based on the recent threatened species list of China's higher plants (Qin et al. 2017).

Species	Family	Record	Proportion	Type
Acer pentaphyllum	Aceraceae	16	1.00	woody
Aconitum spiripetalum	Ranunculaceae	15	1.00	herbs
Aconitum tatsienense	Ranunculaceae	10	1.00	herbs
Aconitum tongolense	Ranunculaceae	14	1.00	herbs
Allium henryi	Liliaceae	61	1.00	herbs
Aralia continentalis	Araliaceae	14	0.72	herbs
Aralia cordata	Araliaceae	11	0.73	herbs
Arenaria brevipetala	Caryophyllaceae	11	1.00	herbs
Asarum himalaicum	Orchidaceae	50	0.93	herbs
Bletilla ochracea	Orchidaceae	72	1.00	herbs
Bletilla striata	Orchidaceae	255	0.70	herbs
Calathodes oxycarpa	Ranunculaceae	16	1.00	herbs
Cotoneaster schantungensis	Rosaceae	14	1.00	woody
Cotoneaster soongoricus	Rosaceae	45	1.00	woody
Cypripedium fasciolatum	Orchidaceae	11	1.00	herbs
Cypripedium flavum	Orchidaceae	70	1.00	herbs
Cypripedium franchetii	Orchidaceae	32	1.00	herbs
Delphinium chrysotrichum	Ranunculaceae	14	1.00	herbs
Dendrobium hancockii	Orchidaceae	14	1.00	herbs
Dendrobium nobile	Orchidaceae	87	0.72	herbs
Dioscorea althaeoides	Melanthiaceae	34	1.00	herbs
Dioscorea panthaica	Melanthiaceae	48	1.00	herbs
Dipelta yunnanensis	Caprifoliaceae	92	1.00	woody
Epilobium fangii	Onagraceae	16	1.00	herbs
Eucommia ulmoides	Eucommiaceae	146	1.00	woody
Euonymus szechuanensis	Celastraceae	19	1.00	woody
Gaultheria praticola	Ericaceae	10	1.00	woody
Gentiana yunnanensis	Gentianaceae	50	1.00	herbs
Gymnadenia conopsea	Orchidaceae	83	0.84	herbs
Gymnadenia orchidis	Orchidaceae	102	0.87	herbs
Gynostemma cardiospermum	Cucurbitaceae	26	1.00	herbs
Juglans regia	Juglandaceae	149	0.91	woody
Kingdonia uniflora	Ranunculaceae	16	1.00	herbs
Magnolia wilsonii	Magnoliaceae	45	1.00	woody
Nouelia insignis	Compositae	22	1.00	woody
Onosma paniculatum	Boraginaceae	34	0.97	herbs
Oxygraphis tenuifolia	Ranunculaceae	11	1.00	herbs
Paris delavayi	Melanthiaceae	16	0.89	herbs
Phoebe zhennan	Lauraceae	18	1.00	woody
Pleione yunnanensis	Orchidaceae	31	1.00	herbs
Primula davidii	Primulaceae	147	1.00	herbs
Rhodiola crenulata	Crassulaceae	88	0.81	herbs
Rhododendron dendrocharis	Ericaceae	21	1.00	woody
Rhododendron moupinense	Ericaceae	20	1.00	woody
Rhododendron souliei	Ericaceae	15	1.00	woody
Rhododendron trichanthum	Ericaceae	26	1.00	woody
Rhododendron yungningense	Ericaceae	18	1.00	woody
Satyrium yunnanense	Orchidaceae	12	1.00	herbs
Viburnum foetidum	Caprifoliaceae	122	0.99	woody
Viburnum kansuense	Caprifoliaceae	77	1.00	woody

endangered plants in the world and China.

The current bioclimatic data of 19 variables (Annual Mean Temperature, Mean Diurnal Range, Isothermality, Temperature Seasonality, Max Temperature of Warmest Month, Min Temperature of Coldest Month, Temperature Annual Range, Mean Temperature of Wettest Quarter, Mean Temperature of Driest Quarter, Mean Temperature of Warmest Quarter, Mean Temperature of Coldest Quarter, Annual Precipitation, Precipitation of Wettest Month, Precipitation of Driest Month, Precipitation Seasonality, Precipitation of Wettest Quarter, Precipitation of Driest Quarter, Precipitation of Warmest Quarter, Precipitation of Coldest Quarter) were obtained from WorldClim (Version 2.0; http://www.worldclim.org) at the spatial resolution of 5 arc minutes. For the future projections, the climate variables of the 2040s (mean of 2030 - 2049) and 2080s (mean of 2080 - 2099) were obtained from the CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS) (http://www.ccafs-climate.org/). The future climate data from CCAFS-Climate was produced by bias-correcting the original GCM outputs using spatial interpolation of the anomalies or deltas based on a total of 35 GCMs and all RCPs (Navarro-Racines et al. 2020). Three greenhouse gas concentration scenarios (i.e. RCP2.6, RCP4.5, and RCP8.5) were used to estimate the future climate suitability for the threatened plants. Pearson correlation coefficient (r) was used to examine the extent of cross correlation between variables (Liang et al. 2018). In order to avoid multicollinearity issue, eight bioclimatic variables with correlation coefficients < 0.75 were selected (Graham 2003).

2.2 Species distribution modeling

MaxEnt, a machine-learning approach to species distribution modelling, was used to obtain a least-biased statistical inference when sufficient information is not available (Kumar and Stohlgren 2009). This model is useful for building models of the relationship between each species' distributions and the climatic conditions (Chandra et al. 2020; Yan and Tang 2019), and is capable of producing distribution maps of comparable accuracy to ensemble methods (Emad et al. 2020). MaxEnt has been shown to outperform other modelling algorithms when the sample size of species distributions is small (Wisz et al. 2008; Elith et al. 2011;

Schwallier et al. 2016). Therefore, we used MaxEnt (version 3.4.1) to build the distribution models of the relationship between each species' occurrences and climatic variables. There are more than 1000 published applications of MaxEnt since 2006 (Merow et al. 2013, Fourcade et al. 2014). In our analyses, 75% of occurrence records of each species were randomly selected for model training and 25% for model testing (Liang et al. 2018). Following previous studies, the maximum iterations was set to 5,000 and the maximum number of background points was set to 10,000 (Yang et al. 2013; Tingley et al. 2014). In order to evaluate whether the selection of the number of background points may influence model predictions, we also repeated our model simulation using two levels of background points (i.e., 5000 and 10000) for the same species (*Acer pentaphyllum*), and the simulated distributions are similar (Appendix 2). This result is consistent with the finding in previous studies that the selection of the number of background points has no strong influence on model simulations (Bloom et al. 2018; Liang et al. 2018). The area under the curve (AUC) of receiver operating characteristics (ROC) was used to evaluate the model performance. The model was considered useful when the AUC values were above 0.7, with values closer to 1.0 indicated better model performance (Elith et al. 2011; Merow et al. 2013). To transform the predicted habitat suitability values of a species into binary distribution, a threshold value maximizing the sum of sensitivity and specificity (max SSS) was chosen. This method produces higher sensitivity and skill statistic in most cases than the other methods (Liu et al. 2013). The predicted values range from 0 to 1, where values close to '1' denote the most potential distribution of a species and values close to '0' represent the least suitable climatic habitat (Phillips et al. 2006). In order to further evaluate the quality of the species distribution maps simulated by SDMs, we also invited a botanical expert to check these maps. Based on his evaluation, the simulation results largely reflect species' actual ranges (S. Liao from Chinese Academic of Science, personal communication), suggesting that the model performance is relatively good.

2.3 Phylogenetic reconstruction and divergence time estimation

The phylogeny was reconstructed using DNA sequences from two chloroplast (*rbc*L, *mat*K) regions

and one nuclear (ITS) region. Specifically, *rbc*L, *mat*K and ITS account for 76%, 68% and 100% of species, respectively. The species without sequence data were replaced by closely related species in the same genera (in total 14 species, 28%). One gymnosperm *Gingko biloba* L. was set as the outgroup. The GenBank sequences (https://www.ncbi.nlm.nih.gov/genbank/) used in the analysis are listed in Appendix 3. Sequences were aligned with MAFFT v7.304b (Katoh and Standley 2013). MrModeltest 2.3 (Nylander, 2008) and Paup* v.4.0b10 (Wilgenbusch and Swofford 2003) were used to select the best-fitting substitution model for each DNA region using the Akaike Information Criterion (AIC). Bayesian Inference (BI) analysis was performed using MrBayes 3.2.6 on XSEDE (Huelsenbeck and Ronquist 2001). The Markov Chain Monte Carlo (MCMC) algorithm was run for 3,000,000 generations with four independent chains, and sampling one out of every 1000 generations. The first 25% of runs were discarded as burn-in. A Bayesian method implemented in BEAST v2.1.3 was used to estimate divergence times on the built phylogenetic tree. Divergence times were estimated under an uncorrelated lognormal relaxed molecular clock (GTR+Γ) model and a Yule tree prior (Drummond et al. 2012). Five fossils were used as the calibration points to date the phylogeny (Appendix 4). The Markov chain was run for 80 million generations and sampled every 8,000 generations. Tracer v1.7.1 was used to read the log file and check for convergence of the model likelihood, and the results were considered reliable once the effective sampling size (ESS) for all parameters exceeded 200. The first 25% of unstable runs from the collected data were discarded as burn-in. TreeAnnonator v2.1.2 was used to produce the final tree based on Maximum Clade Credibility (MCC). FigTree 1.4.2 was used to view and edit the mean node ages and 95% highest posterior density interval (HPD) of divergence time (Rambaut et al. 2009).

2.4 Climate suitability and phylogenetic distance

To assess the responses of species distributions to future climate change, two indicators were used: 1) the changes in the sums of the predicted suitability values of a species under current climate and each future climate change scenario based on the model prediction results, and 2) the changes in the predicted distribution areas between the current climate and each future climate change scenarios (Nenzén and Araújo 2011). The changes in both the sums of predicted suitability values of a species under current climate and each future climate change scenario and species distribution areas (*C*) between the current and future climate were both calculated using the following equation: $C = (A\text{-}B)/B$, where *A* and *B* denote the future and current sum of suitability values or geographical distribution area, respectively (Yu et al. 2014). The correlation coefficient (*r*) between the responses of each two species to future climate change was used to represent the similarities in species responses to future climate change and was calculated by "cor" function in R version 3.5.3.

The phylogenetic distance between each species pair was evaluated using the following three methods: (1) The divergence time between each species pair, which was obtained from the phylogeny using the R package "picante" in R 3.5.3. (2) The number of nodes between each species pair. (3) The sum of standardized (1) and (2), which was calculated as $N = (x\text{-mean } (x))/\text{sd } (x)$. The standardized values *N* (age) and *N* (time) were obtained respectively. $N \text{ (age)} + N \text{ (time)}$ was used as the standardized species phylogenetic distance between each species pair. The relationship between the correlation coefficient of each two species and their phylogenetic distances were examined using simple ordinary least squares (OLS) regressions to determine whether there was a phylogenetic signal in species' response to climate change. In addition, a null model was built to test the phylogenetic signal in a randomly generated phylogeny. The slope was calculated with 999 repetitions in R 3.3.3. In order to test the result, Z-test was performed. The Z value was calculated using the formula: $Z = (X - u_0)/(\sigma/\sqrt{n})$, where σ, u_o, x and *n* represent the standard deviation, the mean value, the slope and the number of samples, respectively. $|Z| \geq 1.96$ means that the differences between the two groups are significant.

3 Results

3.1 Effects of climatic factors on species distributions

The AUC values of all models for the selected species were greater than 0.80, which indicated that the model performed well for all species (Appendix 5). Among the bioclimatic variables used, temperature

seasonality had the highest average contribution (32.58%), followed by annual precipitation (23.09%) for all species. The most important climatic variables influencing the distributions of woody species and dicotyledons were temperature seasonality, with an average contribution of 45.15% and 43.72%, respectively. The best predictors of herbaceous species and monocotyledons were annual precipitation, with an average contribution of 29.38% and 49.91%, respectively (Table 2).

The suitable habitats of all the threatened species studied were largely concentrated in the Hengduan Mountains, Xishuangbanna, Daba Mountains and Wuling Mountains (Fig. 1a). The suitable habitats of herbaceous species were mainly in the Hengduan Mountains, Xishuangbanna and Daba Mountains, and the mean area of the suitable distribution ranges of herbaceous species was 23226.03 km² (Fig. 1b). Similarly, the suitable habitats of woody species were mainly in the Hengduan Mountains and Xishuangbanna, and the mean area of the suitable distribution ranges was 13932.06 km² (Fig. 1c). The suitable total habitat of these studied threatened species were found to decrease under future climatic conditions (RCP 2.6, RCP 4.5 and RCP 8.5 scenario), and the suitable distribution ranges of most species was predicted to shift to northern China (Appendix 6).

3.2 Response of dicotyledonous and monocotyledonous species to climate change

The molecular phylogeny with divergence times estimated using BEAST is shown in Fig. 2. For monocotyledons, the correlation coefficients between their responses to future climate change gradually decreased with the increase in their phylogenetic distance ($R^2 = 0.005$, $P < 0.05$). Similarly, with the increase in the standardized phylogenetic distance, the correlation coefficients between species responses to future climate change also decreased ($R^2 = 0.01$, $P < $
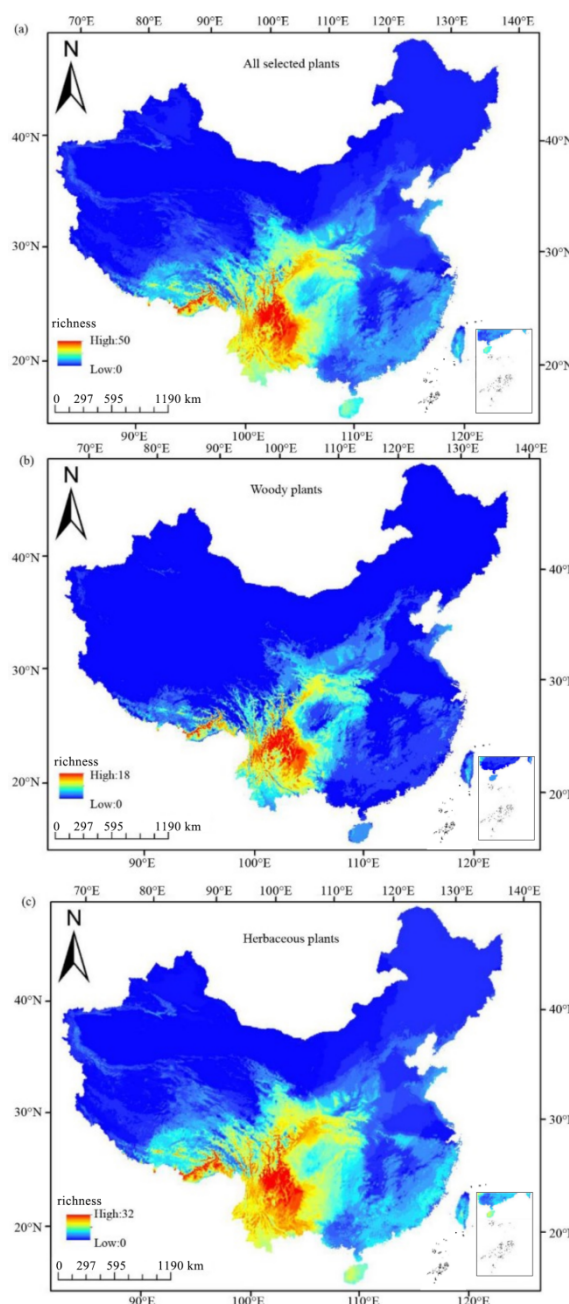

Fig. 1 Geographical patterns in the total suitability of (a) all selected plants, (b) woody plants and (c) herbaceous plants under current climatic condition.

Table 2 Climate variables used in species distribution models and their mean contributions in determining species distributions evaluated by the leave-one-out method. AMT: Annual Mean Temperature, TS: Temperature seasonality, MTWQ: Mean Temperature of Warmest Quarter, MTCQ: Mean Temperature of Coldest Quarter, AP: Annual Precipitation, PDQ: Precipitation of Driest Quarter, PWQ: Precipitation of Warmest Quarter, PCQ: Precipitation of Coldest Quarter. The bold text means the bioclimatic variables with higher average contribution for each group.

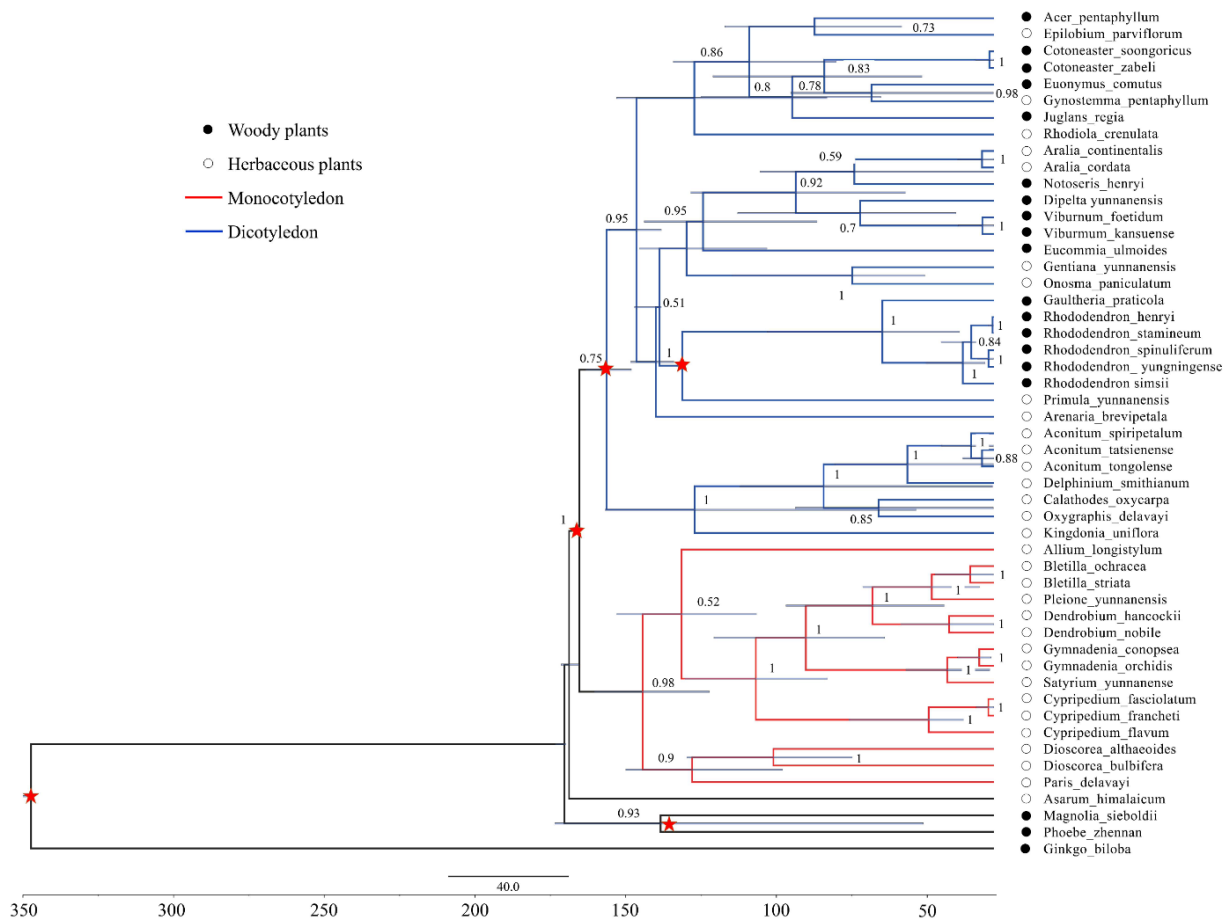|	AMT	TS	MTWQ	MTCQ	AP	PDQ	PWQ	PCQ
All Plants	1.63	**32.58**	10.43	19.67	**23.09**	1.54	5.21	6.47
Woody	2.28	**45.15**	7.64	23.03	11.46	1.25	2.65	6.53
Herbs	1.13	25.72	12.36	16.89	**29.38**	1.64	6.24	7.56
Monocots	0.55	11.05	11.29	27.34	**49.91**	1.77	1.56	2.49
Dicotyledon	1.97	**43.72**	10.39	15.57	11.36	1.39	6.40	9.20

Fig. 2 Phylogenetic tree of the threatened plant species and one outgroup taxa constructed with two chloroplast genes (*rbc*L, *mat*K) and one nuclear gene (ITS). The bars at each node indicate the 95% confidence interval of the estimated ages of the corresponding nodes. The numbers near each branch represent the support rate of the tree. The five red stars show the positions of the fossil calibration points used for dating. The red branches represent the dicotyledons, and the blue branches represent monocotyledons. The solid circles beside the tip labels represent woody plants, and the empty circles represent herbaceous plants.

0.05). However, for dicotyledons, the correlation coefficients between species responses to future climate change were not a significant function of the phylogenetic distances between species (Fig. 3). The |Z| values of the slopes for these relationships between correlation coefficients of species responses and phylogenetic distance / the standardized phylogenetic distance estimated by the null models for monocotyledons were 19.15 and 10.34 respectively, indicating the reliability of the observed results for dicotyledonous plants (Appendix 6).

3.3 Response of species with different life forms to climate change

The relationship between the similarities of species responses to future climate change and phylogenetic distance differed between the two life forms. For herbaceous species, the correlation coefficient between species responses to future climate change declined with the increase in phylogenetic distance evaluated by the divergence time between species ($R^2 = 0.05$, $P < 0.05$), the number of nodes between species ($R^2 = 0.03$, $P < 0.05$), and the standardized phylogenetic distance ($R^2 = 0.01$, $P < 0.05$). In other words, there was a weak phylogenetic signal in the response of these herbaceous threatened species to future climate change. In contrast, for the woody threatened species, with the increase in the number of nodes ($R^2 = 0.001$, $P < 0.05$) and the standardized phylogenetic distance between species ($R^2 = 0.002$, $P < 0.05$), the correlation coefficients between species responses to future climate changes increased (Fig. 4). The |Z| values of the slopes for these relationships between correlation coefficients of species responses and phylogenetic distance for herbs

estimated by the null models were all greater than 1.96, indicating the reliability of the observed results for herbaceous plants (Appendix 7).

4 Discussions

4.1 Phylogenetic signals in the responses of threatened species to climate change

Our findings suggest that the suitable distribution areas of both threatened herbaceous and woody species in Mt. Gongga would decrease under future climate change scenarios, and compared to woody species, herbaceous species are more severely threatened by future climate change in Mt. Gongga. Previous studies also found a decrease trends in the distribution ranges of European understory herbaceous plant species under future climate change (Hanewinkel et al. 2012). *Nepenthes* species in highland species lose a greater amount of potentially

suitable habitat compared to lower altitude species to future climate scenario (Schwallier et al. 2016). Moreover, a recent study indicated that *Meconopsis punicea* (representative endemic herbs in the alpine meadow) predicted to experience a contraction of suitable climate space across all the model under future climate change (He et al. 2019).

Exploring how extinctions are distributed across the tree of life helps us to understand the loss in evolutionary histories under anthropogenic climate change and their ultimate effects on ecosystem functioning (Pio et al. 2014). Recent studies suggest that non-random species loss may lead to different extinction rates of species in different clades, which may significantly influence forest functions (Davies and Yessoufou 2013; García-Valdés et al. 2018). This indicates that loss of phylogenetic distinctiveness due to climate change is much higher in some clades than in others. Narrow-ranged species have been found to be more sensitive to climate change than wide-ranged
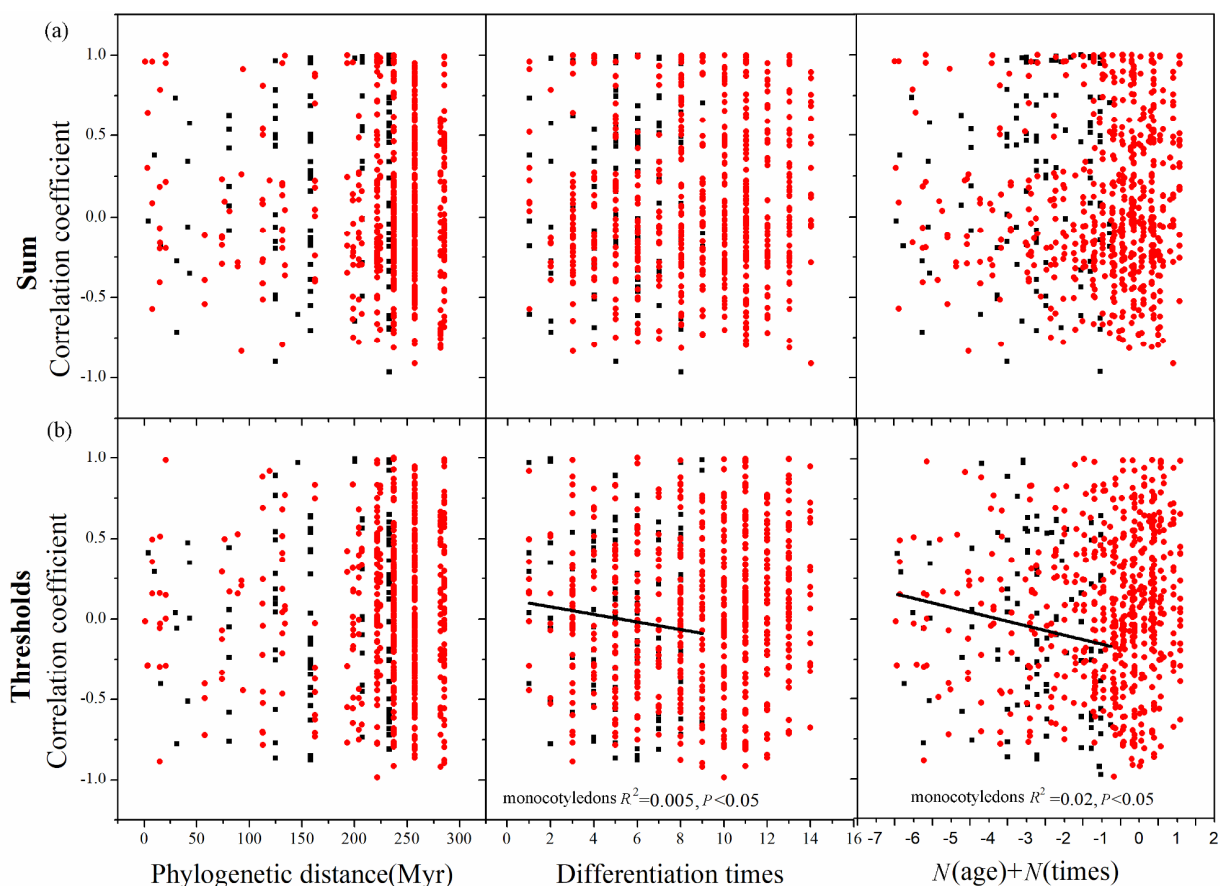

Fig. 3 Relationships between the similarities in species responses to future climate change and their phylogenetic distances for monocotyledons (black) and dicotyledons (red). The similarities in species responses to future climate change were evaluated by (a) the changes in the sums of the predicted suitability values of a species under current climate and each future climate change scenario (top row), and (b) the changes in the predicted distributions areas between the current climate and future climate change scenarios (second row).

species, which may lead to a disproportionate loss of evolutionary history (Zhang et al. 2017). Similarly, we found significant phylogenetic signals in the impacts of climate change on the threatened herbaceous plant species in Mt. Gongga. In other words, the more phylogenetically related the species are, the more consistent they are in their responses to future climate change. Our finding is consistent with the evidence that supports the existence of phylogenetically non-random extinction in birds, non-volant mammals and angiosperms found in previous studies (Webb and Pitman 2002; Sjostrom and Gross 2006; Kolanowska et al. 2017). Together these findings suggest that closely-related species tend to have similar responses to climate change, which leads to the phylogenetic selectivity of extinction risk (Willis et al. 2008). However, all the selected species are not at risk of the non-random extinction across the tree of life, indicating that non-random extinction may exist in some specific groups. This is similar with the previous research on the plant and animal groups in southern

Africa, and the result found that expected losses in phylogenetic diversity from climate change were similar with the random expectation (Pio et al. 2014). Future studies should be conducted on a global scale for the different groups.

4.2 Differences in the phylogenetically non-random extinction between life forms

The threatened herbaceous plant species in Mt. Gongga showed slightly phylogenetic signals in their responses to future climate change than the threatened woody plant species, which means that these herbaceous plants are more likely to be seriously threatened than the woody plants in Mt. Gongga due to future climate change. These results suggest that the similarity of responses of these threatened species to future climate changes decreased with the increase in phylogenetic distances between species. Two reasons may lead to this difference between the two life forms. First, herbaceous plant species shifted upward faster
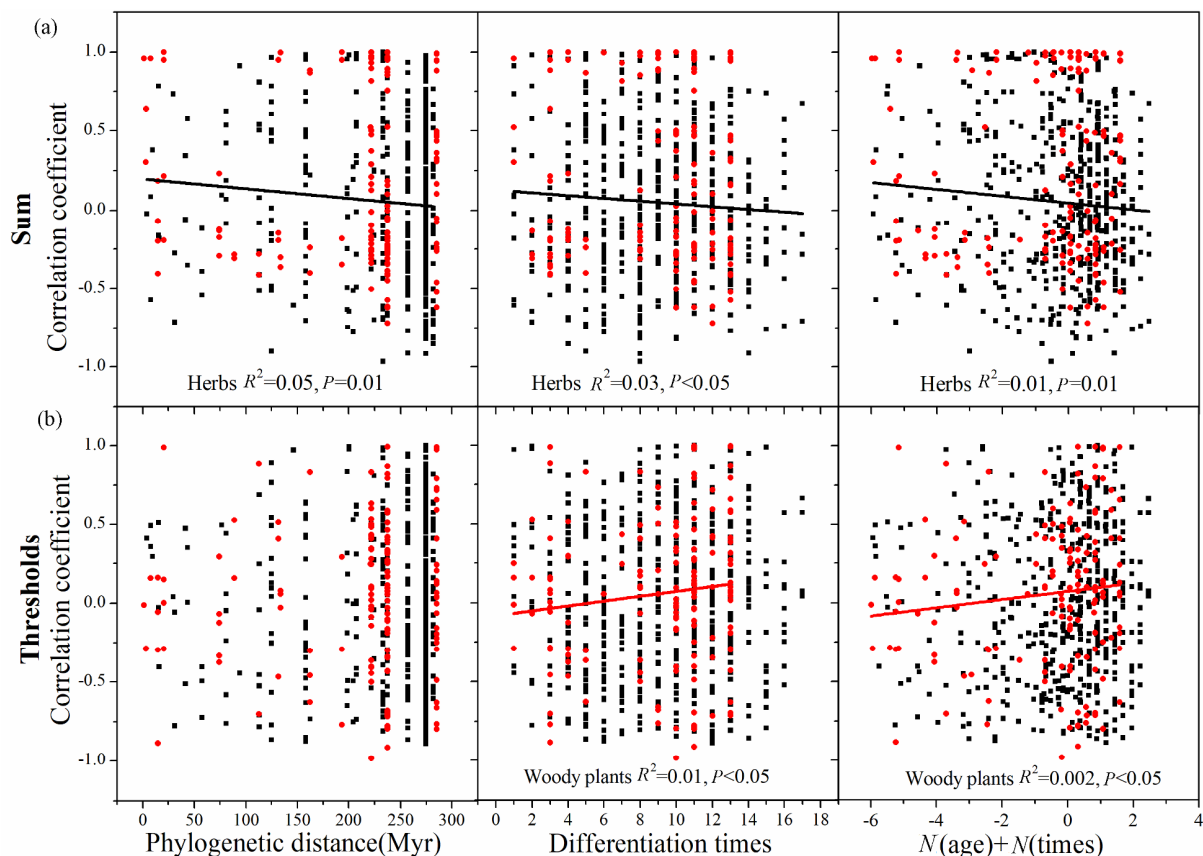

Fig. 4 Relationships between the similarities in species responses to future climate change and their phylogenetic distances for herbs (black) and woody plants (red). The similarities in species responses to future climate change were evaluated by (a) the changes in the sums of the predicted suitability values of a species under current climate and each future climate change scenario (top row), and (b) the changes in the predicted distributions areas between the current climate and future climate change scenarios (second row).

than woody plants in French mountain forests under the past climate changes (Lenoir et al. 2008), and which is consistent with the present study that herbaceous plant species shifted their centroid elevation further upward by +16 m on average than woody plants during the past times (Zu et al. 2021). The above research suggested that herbaceous species tend to be more sensitive to climate change than woody plants. On the contrary, woody species exhibit higher levels of persistence and seem to be under less threat than the herbaceous plants (Sjostrom and Gross 2006). Second, the dominant climatic factors of species distributions are different between herbaceous and woody species. The results show that the threatened woody species in Mt. Gongga are mainly driven by temperature, while the herbaceous plants are mainly affected by precipitation (Table 2). Previous studies have shown that woody species diversity in eastern Asia is most strongly affected by temperature (Wang et al. 2011), and that the less cold-tolerant woody species have difficulties to colonize temperate areas (Shiono et al. 2017). However, in tropical or subtropics areas, woody plants might be less influenced by climate change because many mountains in southwestern China act as long-term refugia (Tang et al. 2018). Besides, the woody plants generally are long-living species and have higher habitat suitability. Due to standing vegetation and local conditions, woody plants have less phylogenetic signals in their responses to future climate change. Besides, plant functional traits might play an important role in species responses to climatic change. Evaluating the effects of functional traits may have implications and need to be carried out on a larger taxonomic scale.

4.3 Implications for conservation planning

Assessment of potential climate change impacts on biodiversity is crucial for spatial planning of biodiversity conservation, including the expansion of protected areas network and management of the land areas outside protected areas for conserving inadequate species' habitats (Hannah 2002). Our study demonstrated weak phylogenetic signal in the impact of climate change on the threatened herbaceous and monocotyledonous plant species in Mt. Gongga, and suggests that climate-driven extinction may not be phylogenetically random in herbaceous and monocotyledonous species in subtropical forest under future climate change. These findings improve our

understanding on the climate change threat on the tree of life of plants and hence shed new light on biodiversity conservation and management in the future. These findings suggest that the phylogenetic uniqueness should be clearly considered in the spatial prioritization when expanding the network of protected areas to better conserve the evolutionary history of species.

In China, conserving the threatened wild species is urgently needed due to the rapid economic growth, environmental pollution, anthropogenic climate change and habitat occupancy (Lopez-Pujol et al. 2006; Jiang and Ma 2009). However, most current conservation efforts on both threatened plant species and plant species with extremely small populations in the wild (Ren et al. 2012) are mainly based on current distribution ranges of species. In order to better protect the diversity and phylogenetic distinctiveness of threatened plant species in China under future climate change, phylogenetic information of species should be incorporated into spatial prioritization (Redding and Arne 2007; Eiserhardt et al. 2015; Winter et al. 2013). Moreover, we found the possibility of non-random extinction in threatened herbaceous plant species, and the threatened monocotyledons, suggesting that threatened monocots and herbs should be of high conservation concern. The nature reserves in Mt. Gongga and other mountains in southwestern China could prioritize the conservation of these threatened monocots and herbs and their closely related species by establishing priority zones.

5 Conclusions

In conclusion, our study provides theoretical basis and technical support for designing effective conservation schemes for the protection of the tree of life in the mountainous area in southwestern China under anthropogenic climate change. In this work, we tried new ways to detect phylogenetic signals by building pairs comparisons representing the relationship between species, and replacing the traditional methods of phylogenetic signal analyses (such as lambda or Blomberg's K). While the modelling approaches and the phylogenetic analyses have many benefits, are not without limitations. In order to realize the real history of diversification, we also compared the major nodes and their ages in our phylogeny with those of the mega angiosperm phylogeny (Smith and Brown

2018). We found that the ages of the major nodes in our phylogeny were similar with mega phylogeny, and the species' phylogenetic distances in the tree we built were strongly positive correlation with the species' phylogenetic distances in the mega-tree (Appendix 8a). There are still slightly negative correlations between the similarities in species responses to future climate change and their phylogenetic distances in the mega-tree for herbaceous plant species (Appendix 8b). It is noteworthy that this study is based only on the threatened plants in Mt. Gongga, and caution is needed when transferring our conclusions to all plants. Further research is needed to test the phylogenetic non-random extinction in the tree of life of plants in different regions and groups, and the main thing is that it can be verified on a large scale for the threatened plants. In addition to climate change, human pressures may also have strong impacts on plant species' distribution (Zu et al. 2019), and further studies combining effects of both climate and human pressures are urgently needed.

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Author Contributions

ZU Kui-ling, WANG Zhi-heng and ZHU Xiang-yun conceived this research project. ZU Kui-ling analyzed the data and wrote the manuscript. JIANG Yong, JIA Guo-qing check the result and critically revised the text. PENG Shi-jia, Nawal SHRESTHA gave scientific suggestions on data analysis. All authors reviewed and commented on this manuscript.

Ethics Declaration

Availability of Data/Materials: Data supporting this paper are available from the corresponding author on request.

Conflict of Interest: No conflict of interest exits in the submission of this manuscript.

Electronic Supplementary Material

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