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Policy analysis

Anthropogenic climate change increases vulnerability of *Magnolia* species more in Asia than in the Americas

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ABSTRACT

Quantifying anthropogenic climate change vulnerability is essential for estimating the risk of species extinction and developing conservation strategies. The *Magnolia* genus is widespread in the Americas and Asia, with nearly half of species currently threatened. Here, we used climate-niche factor analysis to study the vulnerability of *Magnolia* species to future climate change. We found that the vulnerability of *Magnolia* species to future climate change is negatively related to range size. We further identified that narrow-ranged *Magnolia* species distributed in Asia are more vulnerable than those distributed in the Americas, with protected area coverage also lower in Asia than the Americas. Moreover, the conservation status ranking of *Magnolia* species classified by the IUCN Red List will likely be changed under climate change, as some Near Threatened and Least Concern species were estimated to be more vulnerable to climate change than species currently classified as Endangered. Our results highlight that conservation assessments, policies and actions need to consider spatial vulnerabilities of species to climate change.

1. Introduction

Anthropogenic climate change is recognized as a major threat to global biodiversity (Bellard et al., 2012; Dawson et al., 2011; Thuiller et al., 2005), and has already led to the climate-related local extinction of hundreds of species (Wiens, 2016). Extinction risk is expected to increase under future climate change, with up to one-sixth of species threatened under prevailing conservation policies (Urban, 2015). Generally, dispersal or local adaptation is a common response of species to climate change (Aitken et al., 2008; Christmas et al., 2016; Huntley et al., 1995). However, for tree species, dispersal to suitable regions through propagule might not be fast enough to cope with the rate of climate change (Dyer, 1994, 1995; Iverson et al., 2004; Liang et al., 2018; Malanson and Cairns, 1997; Peters, 1990). In addition, tree species often have a limited adaptive capacity to changing climate (Du et al., 2020; Lindner et al., 2010; Petit and Hampe, 2006). Therefore, many tree species are highly sensitive to climatic changes as illustrated by massive extinctions among tree taxa during past climatic fluctuations (e.g., Eiserhardt et al., 2015).

Previous research suggested that regional characteristics caused by ecological and historical characteristics of flora (e.g., mountain flora have narrow tolerances of habitat, with marginal habitat for many species) and/or specific environmental conditions may result in substantial differences in the response of species to climate change (Thuiller et al., 2005). Specifically for trees, regional studies have highlighted high risks from climate change with fast decreasing climate suitability in British Columbia (Hamann and Wang, 2006), Mediterranean regions (Serra-Diaz et al., 2014), Europe (Dyderski et al., 2018; Meier et al., 2012) and North America (McKenney et al., 2007), while assessments for Asian trees are still largely lacking (but see, e.g., Deb et al., 2017).

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Species diversity in disjunct genera of the contemporary floras in eastern regions of Asia greatly exceeds that in North America, even though Eastern Asia and North America have similar latitudes and climates (Guo, 1999; Latham and Ricklefs, 1993). Therefore, we expect that the threats of some species distributed in the Americas and Asia under future climate change will differ. Moreover, the niche breadth of species increases with latitude (Chu et al., 2019), with narrower niches at low latitudes (Brown, 2014). We hypothesize that species distributed in high-latitude regions will tolerate greater levels of climate change than those distributed at low latitudes. In addition, research has shown plant species with smaller range sizes are generally more vulnerable to climate change than widespread species (Schwartz et al., 2006; Vincent et al., 2020).

The *Magnolia* genus belongs to the ancient family Magnoliaceae, consisting of 330 species of trees and shrubs (Sánchez-Velásquez et al., 2016). Due to historical geological and climate-linked extinctions from western Eurasia and western North America (e.g., Eiserhardt et al., 2015), the *Magnolia* genus now has a complex biogeographic pattern, with intercontinental disjunctions in the Northern Hemisphere. This genus also has a wide altitudinal distribution range from northern latitudes to tropical ecosystems (Sánchez-Velásquez et al., 2016). In addition, Magnoliaceae is one of the earliest extant lineages of flowering plants (Nie et al., 2008a). Therefore, the *Magnolia* genus has been a model system in the study of intercontinental disjunctions and the origin and diversification of angiosperms, attracting research attention from biogeographers and molecular botanists (Hebda and Irving, 2004; Nie et al., 2008b; Veltjen et al., 2019; Wang et al., 2020; Ye et al., 2019). Moreover, the *Magnolia* genus is culturally important, with some taxa of high importance in horticulture (Jiang et al., 2005; Seaton et al., 2014; Watkins et al., 2020) or with potential applications in medicine and agriculture (Bai et al., 2003; Koo et al., 2001; Martínez et al., 2006; Ramírez-Reyes et al., 2015; Schühly et al., 2001). At the same time, nearly half of *Magnolia* species are classified as globally threatened with extinction (Sánchez-Velásquez et al., 2016), with the Botanic Gardens Conservation International advocating for conservation assessments of *Magnolia* to be a global priority (Rivers et al., 2016). The International Union for Conservation of Nature (IUCN) Red List has conservation assessments for 304 *Magnolia* species, of which 48% are considered threatened (Critically Endangered, Endangered, and Vulnerable), 32% are considered not threatened (Least Concern and Near Threatened), and the remaining species are Data Deficient (Rivers et al., 2016).

However, the large number of species and the disjunct distribution of the genus poses challenges to research the risks of climate change from both ecological and conservation perspectives. Although several studies have focused on the impact of climate change on the distribution of individual *Magnolia* species (Shalisko et al., 2018; Vásquez-Morales et al., 2014), research on the response of the *Magnolia* genus to climate change has not yet been explored. Moreover, existing conservation assessments mainly focuses on current drivers of species decline without identifying potential future risks, such as the threat posed by climate change (Akcakaya et al., 2014; Wheatley et al., 2017). Some recent studies have shown that climate change could affect the ranking of Red Listed Species (Rinnan and Lawler, 2019; Wang et al., 2021).

Moreover, in order to mitigate the loss of biodiversity, in-situ conservation, i.e., protecting species in their natural habitat, is generally favored (Grenyer et al., 2006; Heywood and Dulloo, 2005). Protected areas (PAs) have expanded in recent decades (Geldmann et al., 2018; Ren et al., 2015; Schleicher et al., 2019), with 209,000 PAs worldwide by 2014 (Juffe-Bignoli et al., 2014). However, half (50.2%) of tree species' ranges are on average not located in current PAs (Guo et al., 2020). Additionally, the potential protection provided by PAs needs to be examined while considering near-future climate change (Halpin, 1997; Hannah et al., 2007; Lawler, 2009). More generally, climate change needs better integration into conservation strategies. This is true generally, but also for *Magnolia* sp. specifically.

In ecology and conservation planning, the vulnerability of species to climate change has been used to quantify climate-related threats on species extinction (Füssel and Klein, 2006; Serra-Diaz et al., 2014; Stanton et al., 2015; Summers et al., 2012). Since the Fourth Assessment Report of the United Nations Intergovernmental Panel on Climate Change (IPCC), species' vulnerability is generally thought of as a function of both intrinsic (sensitivity and adaptability) and extrinsic (exposure) traits (Pacifici et al., 2015). Indeed, the impact of climate change on species is not only related to the magnitude of climate change within the species' habitat (exposure), but also related to the species' ability to tolerate climate change (sensitivity) and adjust to those changes (adaptability) (Turner et al., 2003; Williams et al., 2008). In recent decades, several methods have been developed to assess species' vulnerability to climate change, including correlative, mechanistic and trait-based approaches (Pacifici et al., 2015). Commonly used correlative approaches based on species distribution models (also known as ecological niche models) often emphasize exposure to predict the distribution changes of species (Butt et al., 2016; Leclerc et al., 2020). Mechanistic and trait-based approaches, on the other hand, can be limited by a lack of data on species' physiology and traits and cannot therefore be used extensively for vulnerability assessment of species (Pacifici et al., 2015). Recently, Rinnan and Lawler (2019) developed a new approach named the climate-niche factor analysis (CNFA), which based on occurrence data and bioclimatic variables infers species sensitivity and exposure to climate change. This approach can provide both species vulnerability assessments and spatially explicit insights into geographic patterns of climate change vulnerability. In this study, we first assessed the vulnerability of the *Magnolia* genus to future climate change. We then examined whether there are differences in vulnerability of *Magnolia* species in the Americas and Asia to climate change. Finally, we determined the priority protected species and protected areas of the *Magnolia* genus.

2. Materials and methods

2.1. Occurrence data and species ranges

In this study, we used occurrence data for *Magnolia* from the TreeChange dataset compiled and cleaned by Serra-Diaz et al. (2018). This dataset contains occurrence records for 232 *Magnolia* species, with the original species occurrence data being collated from five widely used and publicly available databases: the Global Biodiversity Information Facility (GBIF; http://www.gbif.org), the public domain Botanical Information and Ecological Network v.3 (BIEN; http://bien.nceas.ucsb.edu/bien/), Latin American Seasonally Dry Tropical Forest Floristic Network (DRYFLOR; http://www.dryflor.info/; Banda-R et al., 2016), RAINBIO database (http://rainbio.cesab.org/; Dauby et al., 2016) and the Atlas of Living Australia (ALA; http://www.ala.org.au/). The cleaning process for the TreeChange dataset relies on a series of tests ranging from typical coordinate errors that appear in public databases, cross-checks with country citations, spatial outliers, and environmental outliers (Serra-Diaz et al., 2018). In the dataset, the average number of occurrence records across *Magnolia* species is 130, with the maximum number being 9023. There are 162 *Magnolia* species with more than 20 records.

Among the 232 *Magnolia* species, 127 species are distributed in Asia and 105 species distributed in the Americas. To examine the climatic conditions of *Magnolia* species between Asia and the Americas, we projected current climatic space for occurrence data of *Magnolia* species distributed in Asia and the Americas onto axes of annual mean temperature and precipitation (Fig. S1). Fig. S1 shows that the *Magnolia* species share relatively similar climatic conditions between the two continents, suggesting high similarity in climatic requirements at the regional level of *Magnolia* species.

We then estimated the ranges of *Magnolia* species with ≥20 occurrence records by constructing alpha hulls based on the computational geometry method by Edelsbrunner et al. (1983), as implemented using the "ashape" function of the alphahull package (Pateiro-López and Rodríguez-Casal, 2010) in R (ver. 3.5.1; R Core Team, 2018). We applied the most commonly used alpha level (6 degrees) to estimate the range of each species (García-Roselló et al., 2015; Mauri et al., 2017). For those disjunct records not included in the alpha-hull range, we calculated a 10 km buffer around each point record and then merged with the alpha hull range. To avoid overestimating range size for species with less than 20 occurrences, we only made a 10 km buffer around each point record. This method has recently been used in a study investigating global tree distributions, where it was found estimates of range size were consistent with estimates from other external databases (Guo et al., 2020).

2.2. Bioclimatic variables

We downloaded four bioclimatic variables for current (representative of 1979–2013) and future climate for 2070 (average of 2061–2080) from the CHELSA dataset at a 30 arc-*sec* spatial resolution (Karger et al., 2017, 2018) and resampled to a 5 arc-min spatial resolution. For the future climate scenario, we used three global climate models (GCMs; i.e., CESM1-BGC, IPSL-CM5A-LR, and MPI-ESM-MR) that widely varied in their projections (Sanderson et al., 2015) to account for uncertainty with projected climates (Baker et al., 2016). We also used two representative concentration pathways (RCPs) for prescribed greenhouse gas emissions: (1) RCP 4.5, which represents a medium CO_2 emissions, where global temperatures rise 1.8 ± 0.7 °C by the late-21st century; and (2) RCP 8.5, which represents high CO_2 emissions, with a global temperature increase of 3.7 ± 1.1 °C by the late-21st century (IPPC, 2013). We used four important bioclimatic variables for tree species distributions in our study, namely annual mean temperature (AMT), minimum temperature of the coldest month ($Temp_{min}$), annual precipitation (AP), and precipitation of the driest quarter ($Prec_{dr}$). AMT and AP are the two commonly used bioclimatic variables in plant species distribution modeling and plant physiology studies (Andivia et al., 2018; Gardner et al., 2019; Song et al., 2021). Moreover, extreme climate events play a key role in determining biodiversity patterns, which is often different from the effects of stable climate change (Walther, 2010). $Temp_{min}$ and $Prec_{dr}$ capture extreme climate conditions, and likely reflect the bioclimatic variables limiting species distribution (Araújo and Peterson, 2012; Zimmermann et al., 2009).

2.3. Climate change vulnerability assessments

For assessing climate change vulnerability of *Magnolia* species, we first calculated sensitivity and exposure through CNFA (Rinnan and Lawler, 2019). Sensitivity was quantified by the marginality, which reflects the niche centroid distance between the species' habitat and the global range, and the specialization, which is the ratio of size of the global niche to that of the species' niche (Hirzel et al., 2002). The habitat for each species is defined by the climatic conditions of the range where the species occur, while the global range corresponds to the set of terrestrial climatic conditions on earth. To quantify marginality and specialization for each species, we used species' range and the current climate within the global range before calculating sensitivity. We calculated marginality, specialization and sensitivity using the "cnfa" function in the CENFA package (Rinnan, 2018), Exposure was quantified through a dissimilarity measure of current and future climate within the species' range (Rinnan and Lawler, 2019). We calculated exposure using the "departure" function in the CENFA package (Rinnan, 2018) for the six future climate scenarios (i.e., the three GCMs × two RCPs) for each species. Considering the long life-span of trees does not allow for rapid adaptation to climatic variation (Lindner et al., 2010; Petit and Hampe, 2006), vulnerability to climate change for each species was obtained as the geometric mean of sensitivity and exposure, implemented using the "vulnerability" function in the CENFA package (Rinnan, 2018). Similar to exposure, we calculated for each species vulnerability for the six future climate scenarios. To calculate spatial sensitivity, exposure and vulnerability to climate change, we used the "predict" function in the CENFA package (Rinnan, 2018).

We then tested the agreement of the estimated vulnerability under the three GCMs (i.e., CESM1-BGC, IPSL-CM5A-LR, and MPI-ESM-MR). Vulnerability across *Magnolia* species were highly correlated among the three GCMs ($R^2 > 0.99$, p-value < 0.001; Table S1), and the mean spatial vulnerabilities of all *Magnolia* species were also highly correlated ($r > 0.8$; Table S2). Therefore, we averaged the exposure and vulnerability of species across GCMs and used it for subsequent analysis.

2.4. Vulnerability analysis across species

We expected vulnerability to change according to species range size. We therefore identified and analyzed vulnerability for narrow- and wide- ranged species in Asia and the Americas. We identified these groups based on the relationship between species range and vulnerability scores using segmented regression in the segmented package (Muggeo, 2020). This approach fits regression models with segmented relationships between response (i.e., vulnerability) and explanatory variables (i.e., species range area), and identifies breakpoints (i.e., species range area thresholds) where linear relations change (Muggeo, 2020). Because the explanatory variables (i.e., species range area) showed different relationships to the response variable (i.e., vulnerability) above and below range area breakpoints, we classified species' as narrow-ranged or widespread species when they were below or above the breakpoint, respectively. We additionally performed a *t*-test on the significance of the difference on vulnerability of the grouped species.

To study whether *Magnolia* species in the Americas and Asia have different vulnerability to climate change, we examined the sensitivity, exposure, and vulnerability of the grouped narrow-ranged species using multivariate analysis of variance (MANOVA). At the same time, we estimated 95% confidence intervals using t-test for the difference of the mean marginality and specialization between American and Asian narrow-ranged species, respectively. We performed the same analysis as above for widespread species.

2.5. Spatial vulnerability analysis

To investigate the spatial vulnerability of *Magnolia* species, we summarized the spatial sensitivity, exposure and vulnerability of species in ~10 × 10-km grid cells using an assemblage-based approach (Xu et al., 2019), calculating the mean sensitivity, exposure and vulnerability across the species in each grid cell for all, narrow-ranged and widespread species, respectively. To explore the impact of different potential future CO_2 emission pathways on the vulnerability of the *Magnolia* species, we calculated the difference between the mean spatial vulnerability under RCP 8.5 and 4.5 for all, narrow-ranged and widespread species, respectively. We used linear regression models to examine the relationship between latitude and mean spatial vulnerability under RCP 4.5 of narrow-ranged and widespread species, respectively. We also used linear regression models to check the variation of the increment of vulnerability (i.e., the difference between the mean spatial vulnerability under RCP 8.5 and 4.5) with latitude for narrow-ranged and widespread species, respectively.

2.6. Identification of priority protected species and protected areas

In order to detect whether climate change is likely to affect threat levels of *Magnolia* species in the IUCN Red List, we started by using the conservation status of both narrow-ranged and widespread species in the Americas and Asia according to the IUCN Red List, i.e., Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC) or Data Deficient (DD), and then assessed how vulnerable each group was to climate change vulnerability. Furthermore, we divided the mean spatial vulnerability of all species into the three levels of high, medium and low, to represent the priority for conservation protection. We classified mean spatial vulnerability of all species into three levels using three quantiles. That is, mean spatial vulnerability greater than the 2/3 quantile was considered High, mean spatial vulnerability between the 2/3 and 1/3 quantile was Medium, and mean spatial vulnerability less than the 1/3 quantiles was Low. In order to unify the classification standards, we used the same values to divide mean spatial vulnerability of narrow-ranged and widespread species into the three levels.

To investigate conservation protection of *Magnolia* species in the different vulnerability classes, we used terrestrial PAs from the World Database on Protected Areas (downloaded July 2020; UNEP-WCMC, 2017), resampled to 5 arc-min spatial resolution. For each of the three vulnerability levels, we further calculated percentages of PAs for all, narrow-ranged and widespread species, respectively. For example, the percentage of PAs on High level for narrow-ranged species = the area of PAs on the High level for narrow-ranged species/ the area of the High level for narrow-ranged species. By 2019, China has over 11,800 PAs, covering 18% of its total land territory (http://www.xinhuanet.com/english/2019-10/31/c_138518505.htm, accessed on 18-10-2021). We assumed these PAs have a uniform distribution, and then 18% of the Low, Medium and High level areas of *Magnolia* species in China would fall into PAs. And then we recalculated the percentages of PAs for all, narrow-ranged and widespread species in Asia. Due to the incomplete data of PAs in China in the World Database, we consider this estimate for the percentages of PAs in Asia to be optimistic.

3. Results

3.1. Vulnerability across species

Magnolia species exhibited a negative relationship between range size and vulnerability to climate change (RCP 4.5: p-value < 0.001, $R^2 = 0.45$; RCP 8.5: p-value < 0.001, $R^2 = 0.45$; Figs.1a, S2a). The identified breakpoint from the segmented regression analyses was 2477.4 km^2 (Figs. 1a, S2a). Vulnerability decreased much more strongly when increasing area for range sizes less than 2477.4 km^2 than for larger range sizes (Figs. 1a, S2a). There was a significant difference in the vulnerability of narrow-ranged and widespread species divided by the identified breakpoint, with the vulnerability of narrow-ranged species being higher than that of widespread species (Figs. 1b, S2b).

Magnolia species distributed in the Americas and Asia had different vulnerabilities to climate change, especially for narrow-ranged species (widespread species: p-value < 0.01; narrow-ranged species: p-value < 0.001), which has much greater vulnerability in Asia (Fig. 1c). The overall marginality of *Magnolia* species in the Americas was slightly higher than those in Asia (Fig. S3a), with the difference in mean marginality between the Americas and Asia not exceeding 1.9 (Table S3). The overall specialization of narrow-ranged species in the Americas was much lower than in Asia (Fig. S3b), with the 95% confidence interval of the difference in mean specialization between the Americas and Asia being between −22.8 and − 1.9 (Table S3). In other words, the overall niche size of narrow-ranged species in Asia was smaller than in the Americas. Hence, narrow-ranged species in Asia are likely to be more sensitive to climate change than narrow-ranged species in the Americas (Fig. S4a). Consequently, despite lower future climate exposure in Asia (Fig. S4b), Asian narrow-ranged species are more vulnerable to climate change (Fig. 1c). For widespread species, sensitivity of Asian species is slightly lower (Fig. S4a), and the exposure of the Asian species is also lower (Fig. S4b); hence, the vulnerability of the Asian species to climate change becomes lower than that of American species, although the difference is small (Fig. 1c). In addition, the exposure of species under a high CO_2 emission scenario (RCP 8.5) is generally higher than for species under a low CO_2 emission scenario (RCP 4.5) (Fig. S4b). Therefore, the vulnerability of species to the climate change under high CO_2 emissions is also higher (Fig. 1c).

3.2. Spatial patterns of vulnerability

Under RCP 4.5, the mean value of spatial vulnerability for *Magnolia* species was relatively high at low latitudes, i.e., between 10°N and 10°S, while the *Magnolia* species distributed in highland mountains (such as Southwest China and Central Mexico) showed low vulnerability (Fig. 2a). In particular, vulnerability of *Magnolia* species in Asia exhibited a decreasing trend with increasing latitude (widespread: $R^2 = 0.2$, p-value < 0.001, Fig. 3a; narrow-ranged: $R^2 = 0.1$, p-value < 0.001, Fig. 3b), while the relationship between latitude and spatial vulnerability in the Americas was much weaker (Fig. 3). Under RCP 8.5, the vulnerability of *Magnolia* was higher than that for RCP 4.5, except for small areas in Central Mexico and Southern Brazil (Fig. 2b). Analyzing the difference in mean spatial vulnerability between RCPs 8.5 and 4.5, the increase in the mean spatial vulnerability of narrow-ranged species and widespread species in Asia decreased with the increase of latitude (widespread: $R^2 = 0.3$, p-value < 0.001, Fig. 4a; narrow-ranged: $R^2 = 0.1$, p-value < 0.001, Fig. 4b). However, in the Americas, only the narrow-ranged species showed a decreasing trend in the mean spatial vulnerability increase from RCP4.5 to RCP8.5 with latitude ($R^2 = 0.07$,

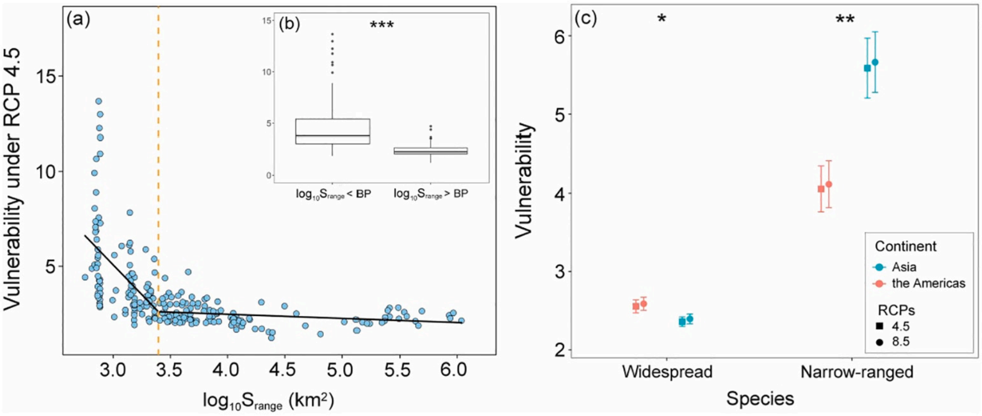

Fig. 1. The vulnerability of *Magnolia* species under future climate projections for the year 2070. (a) Relationship between vulnerability and range size. The vulnerability of each species was the mean of the vulnerability cross three global circulation models (GCMs; i.e., CESM1-BGC, IPSL-CM5A-LR, and MPI-ESM-MR) under the representative concentration pathway (RCP) 4.5. The broken line is estimated with segmented regression and the dashed vertical line shows the breakpoint (BP; $x = 3.395$). S_{range} is the species range area. (b) Comparison of vulnerability between narrow-ranged and widespread species as identified by the segmented regression shown by the dashed line in (a). The asterisks represent significant different in climate change vulnerability between narrow-ranged and widespread species: *** is p-value < 0.001. (c) The average value of vulnerability of widespread and narrow-ranged species distributed in the Americas and Asia, respectively. The vulnerability was the mean of vulnerability made from three GCMs under RCPs 4.5 and 8.5, respectively. Error bars represent standard errors. The asterisks represent significant different in climate change vulnerability of *Magnolia* species distributed in the Americas and Asia: * is p-value < 0.05 and ** is p-value < 0.01.

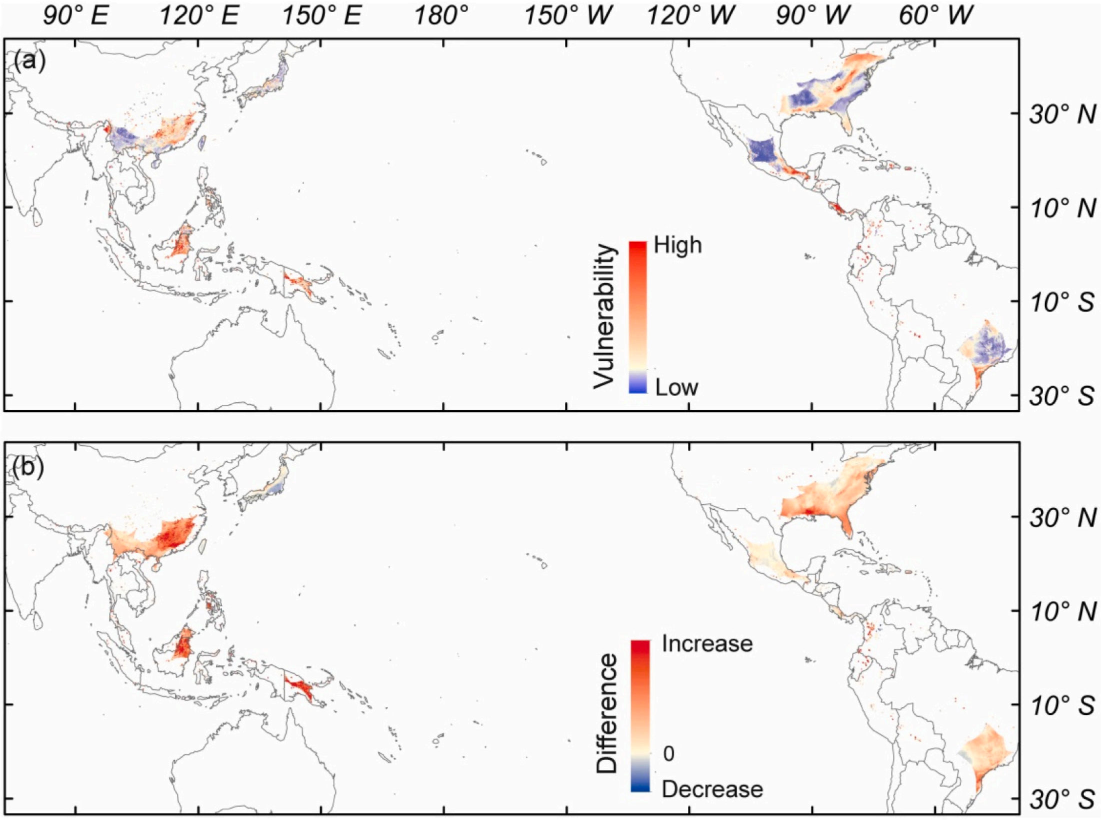

Fig. 2. (a) Mean spatial vulnerability of *Magnolia* species under future climate projections for the year 2070 under the representative concentration pathway (RCP) 4.5. The spatial vulnerability of each species was the mean of the spatial vulnerability for three global circulation models (GCMs; i.e., CESM1-BGC, IPSL-CM5A-LR, and MPI-ESM-MR); (b) The increase in mean spatial vulnerability of *Magnolia* species from RCP 4.5 to RCP 8.5.

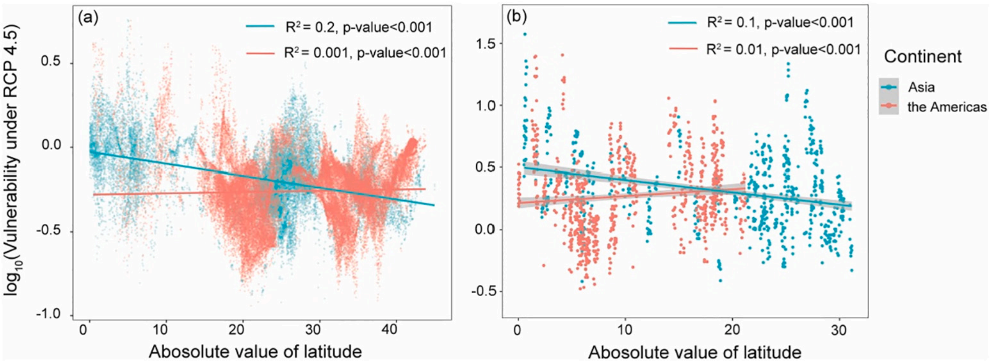

Fig. 3. Relationship between mean spatial vulnerability and latitude under future climate projections for the year 2070 under the representative concentration pathway (RCP) 4.5. (a) Mean spatial vulnerability for widespread species; (b) Mean spatial vulnerability for narrow-ranged species. The spatial vulnerability of each species was the mean of the vulnerability across three global circulation models (GCMs; i.e., CESM1-BGC, IPSL-CM5A-LR, and MPI-ESM-MR). The vertical axis is the logarithm of mean spatial vulnerability, and the horizontal axis is the absolute value of latitude.

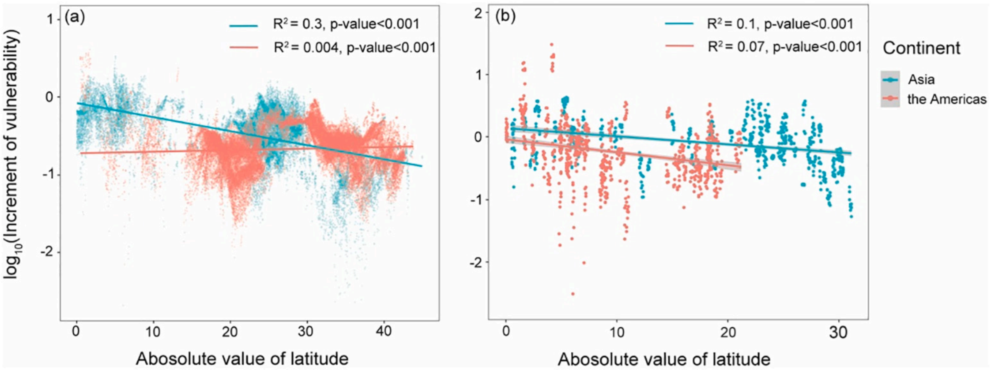

Fig. 4. Relationship between increase in mean spatial vulnerability and absolute value of latitude under future climate for the year 2070. (a) The increment of mean spatial vulnerability for widespread species; (b) The increase in mean spatial vulnerability for narrow-ranged species. The increase in mean spatial vulnerability is the difference of spatial vulnerability predicted under the representative concentration pathway (RCPs) 4.5 and 8.5. The spatial vulnerability of each species was the mean of the vulnerability cross three global circulation models (GCMs; i.e., CESM1-BGC, IPSL-CM5A-LR, and MPI-ESM-MR).

p-value < 0.001, Fig. 4b). By 2070, *Magnolia* species distributed in low latitudes will experience greater climate change, i.e., higher climate exposure (Fig. S5b). Further, under high carbon emissions (RCP 8.5), climate exposure of *Magnolia* species will be strongly increased, especially at lower latitudes (Fig. S5c).

3.3. *Priority protected species and protected areas*

The vulnerability of *Magnolia* species to future climate change does not closely match their current conservation status in the IUCN Red List, although CR and EN exhibited relatively high vulnerability, especially for widespread species. Among the widespread species distributed in the Americas, the projected vulnerability of LC species is higher than that of EN and NT species (Figs. 5a, S6a), while in Asia, NT species are the most vulnerable to climate change among all the conservation status of the IUCN Red List (Figs. 5b, S6b). For narrow-ranged species, DD species are more vulnerable to climate change, and their vulnerability exceeds that of EN species in the Americas (Figs. 5a, S6a). In addition, LC species are more vulnerable to climate change than NT species among the narrow-ranged species distributed in Asia (Figs. 5b, S6b).

Under future climate change, the areas where *Magnolia* species are most in need of protection occur mainly at low latitudes (between 15°N and 15°S), and in southeastern China and coastal areas in the southern United States (Figs. 6, S7). Among these areas, some small areas for *Magnolia* species (e.g., in northern South America) are already located in PAs, while large parts (e.g., Kalimantan and New Guinea) are mostly unprotected (Figs. 6, S7). The proportion of protected habitats of Asian *Magnolia* species is lower than that for species found in the Americas (Table 1). For example, the proportion of PAs in the areas where narrow-ranged species are the most in need of protection (high vulnerability) is ca. 32% in the Americas and is ca. 23% in Asia (Table 1). Even under optimistic estimates, the proportion of PAs in the areas where narrow-ranged *Magnolia* species are the most in need of protection in Asia (ca. 30%) does not exceed that in the Americas.

4. Discussion

Our results show that vulnerability to climate change increases steeply with declining range size for *Magnolia* species with a range size below 2477.4 km^2. In other words, narrow-ranged species of *Magnolia* are more sensitive to climate change than widespread species. Our finding supports Schwartz et al. (2006) who showed extinction vulnerability of tree species of the eastern United States increases with decreasing range size. Species with a narrow distribution may be locally limited by climate (Collen et al., 2006), even if they are dispersal-limited at larger scales (Seliger et al., 2021; Svenning and Skov, 2004), and more likely to be negatively affected by localized stochastic events (Purvis et al., 2000). Further, across all land plants, narrow-ranged species tend to be concentrated in areas relatively more exposed to future climate change and land use intensification (Enquist et al., 2019). Therefore, narrow-ranged species have a higher risk of extinction caused by climate change, and our findings show that this is also the case for *Magnolia*.

On a global scale, *Magnolia* species distributed in Asia and the Americas show significant differences in their vulnerability to climate change, especially for narrow-ranged species. A cross-taxa meta-analysis (including plants, birds, fish, mammals, invertebrates, reptiles, and amphibians) showed that extinction risks under climate change vary among regions, with the highest extinction risk in South America, Australia, and New Zealand (Urban, 2015). Although these findings indicated extinction risk in Asia to be lower than in South America, the author speculates that Asia may face a higher risk of species extinction from climate change than estimated, due to limited studies. Indeed, the floras of eastern Asia have been estimated to exhibit higher extinction risk than eastern North America under future changes in climate and land cover (Song et al., 2021). For narrow-ranged species of the *Magnolia* genus found in the Americas and Asia, our results support this suggestion, i.e., our estimated climate vulnerability for the narrow-ranged *Magnolia* species in Asia were higher than that in the Americas. Despite *Magnolia* species in the Americas and Asia having similar climatic requirements (Fig. S1) and experiencing only small differences in climate exposure, the relatively narrow niche of most narrow-ranged *Magnolia* species in Asia results in greater estimates of climate change sensitivity for Asian species.

Magnolia species in low latitudes may face greater climate change and therefore have greater climate-related vulnerability. In particular, vulnerability of *Magnolia* species distributed in Asia shows a significant negative correlation with latitude (Fig. 3). Although dispersal poleward and upward could be a common response of species to climate change to avoid extinction (Parmesan and Yohe, 2003), for *Magnolia* species found on islands the climate-related extinct risk will increase due to dispersal constraints, with this particularly pronounced in Southeast Asia (e.g., Kalimantan and New Guinea). Our findings also show that *Magnolia* species are less vulnerable to climate change in mountainous regions, such as in southwestern China, the tropical montane cloud forest of Mexico, and the Paraná Plateau in Brazil. For example, in southwestern China, the large elevation gradient coupled with the influence of the

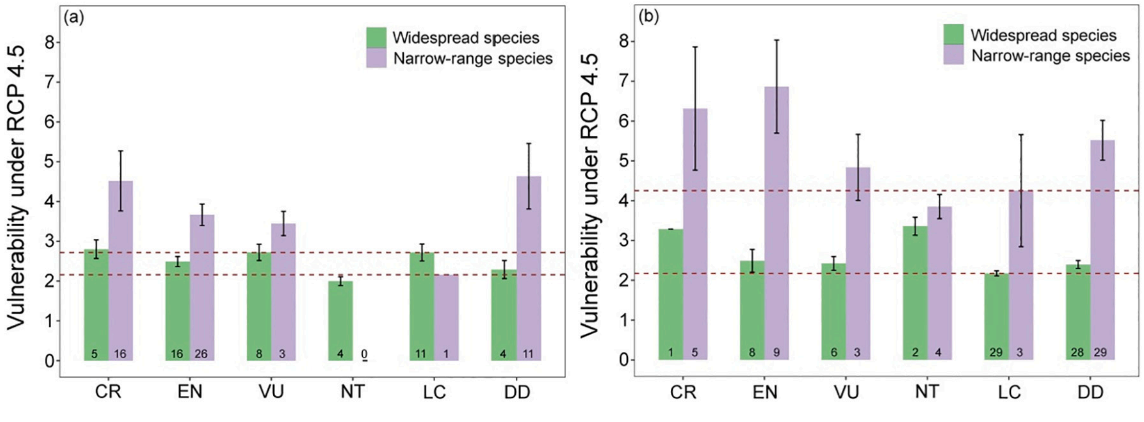

Fig. 5. Comparison of vulnerability of *Magnolia* species grouped by IUCN red list categories under future climate projections for the year 2070 under the representative concentration pathway (RCP) 4.5. (a) *Magnolia* species distributed in the Americas; (b) *Magnolia* species distributed in Asia. The vulnerability of each species was the mean of the vulnerability across three global circulation models (GCMs; i.e., CESM1-BGC, IPSL-CM5A-LR, and MPI-ESM-MR). Horizontal axis is the abbreviations for the IUCN red list categories, CR: Critically Endangered, EN: Endangered, VU: Vulnerable, NT: Near Threatened, LC: Least Concern, and DD: Data Deficient. The red dashed lines are the horizontal lines passing through the vulnerability of Least Concern species (widespread and narrow-ranged spread). Error bars represent standard errors. The numbers at the bottom of the bars represents the total number of *Magnolia* species belonging to each group. For RCP 8.5, see Fig. S6. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

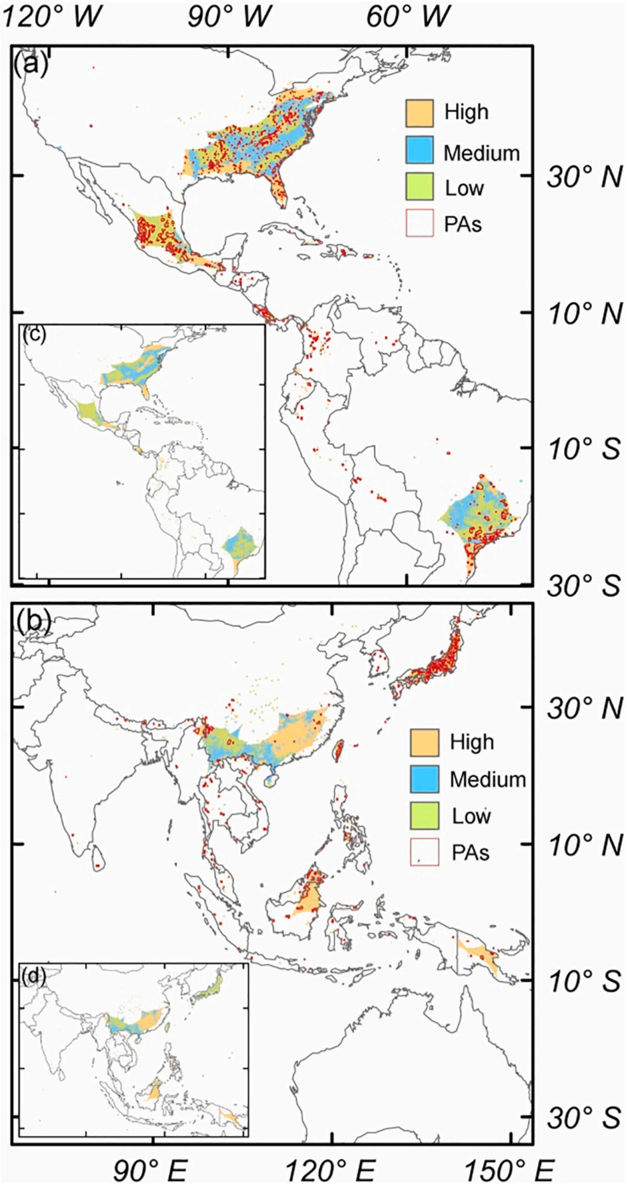

Fig. 6. Protected areas (PAs) with three levels of vulnerability for *Magnolia* species distributed in the Americas (a) and Asia (b) under future climate for the year 2070 under the representative concentration pathway (RCP) 8.5, respectively. (c) and (d) are the three levels of vulnerability areas without PAs. The spatial vulnerability of each species was the mean of the vulnerability across three global circulation models (GCMs; i.e., CESM1-BGC, IPSL-CM5A-LR, and MPI-ESM-MR). High, Medium and Low represent high, medium and low vulnerability areas, and also represent the conservation prioritization order. The PAs are outlined by red lines. For RCP 4.5, see Fig. S7. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Percentage of protected areas (PAs) with three levels of vulnerability of *Magnolia* species distributed in the Americas and Asia under future climate projections for the year 2070 under the representative concentration pathways (RCPs) 4.5 and 8.5. The vulnerability of each species was the mean of the vulnerability cross three global circulation models (GCMs; i.e., CESM1-BGC, IPSL-CM5A-LR, and MPI-ESM-MR). High, Medium and Low represent high, medium and low vulnerability areas, and also represent the priority protection order. The value in brackets is a virtual optimistic estimate of the percentage of PAs in Asia.

	The Americas			Asia		
	High	Medium	Low	High	Medium	Low
RCP 4.5						
All species	15.1%	6.5%	9.4%	11.6% (18.9%)	9.1% (20%)	9.5% (21%)
Widespread species	14.8%	6.5%	9.4%	11.4% (18.8%)	9.0% (19.9%)	9.5% (21%)
Narrow-ranged species	30.7%	32.1%	25%	22.5% (29.2%)	0% (15.4%)	0% (14.4%)
RCP 8.5						
All species	16.0%	6.6%	9.4%	8.7% (16.9%)	8.7% (20.2%)	15.0% (22.8%)
Widespread species	15.5%	6.7%	9.4%	8.3% (16.6%)	8.6% (20.2%)	15.0% (22.8%)
Narrow-ranged species	32.0%	17.5%	21.7%	23.2% (30%)	0% (17.1%)	0% (10%)

East Asian monsoon climate provides complex habitats for tree species with suitable macroclimatic and topoclimatic conditions (Tang et al., 2018). Our results also support Tang et al. (2018) that southwestern China is a long-term climate refuge for relict species, reflecting its complex habitat that allows for buffering against impacts of future climate change (cf. Sandel et al., 2011). These results do not suggest that mountain *Magnolia* species are safe from future climate change. Some studies have even suggested that plant species in mountain regions may be relatively more sensitive to climate change (Beniston et al., 1997; Messerli and Ives, 1997; Ohmura, 2012), in contrast to our findings. In any case, future climate change may drive high extirpation rates for mountain plants, notably endemic species (Dullinger et al., 2012). A recent study comparing the regional disparity in extinction risk of disjunct plant genera between eastern Asia and eastern North America pointed out that species in the mountain regions of southern and southwestern China risk high extinction rates (Song et al., 2021).

Previous studies have shown threat status assessments in the IUCN Red List of species do not adequately account for threats posed by potential (or future) climate change (Thomas et al., 2004; Thuiller et al., 2005). We found that the vulnerability of some LC *Magnolia* species to future climate change was higher than that of VU *Magnolia* species, consistent with the results of Rinnan and Lawler (2019) and Wang et al. (2021). For example, the widespread species *M. equatorialis*, distributed in western Amazonia, is currently considered relatively abundant, with only minor threats mainly coming from oil extraction and associated deforestation (Vázquez-García et al., 2012, 2013). However, we found that the LC species *M. equatorialis* is more vulnerable to future climate change than all the VU *Magnolia* species distributed in the Americas. Another LC species *M. oblonga* distributed in high-elevation broadleaved forest of India and Bangladesh is also highly vulnerable to climate change. Moreover, its narrow habitat is being destroyed by deforestation for small-scale agriculture and tea production (IUCN, 2015), with no conservation actions currently being implemented (Behera et al., 2002; Rana et al., 2012). The goal of the Red List criteria is to measure the relative extinction risk of species under prevailing circumstances, but it does not represent a priority mechanism for species conservation (Collen et al., 2016). In this case, future climate change may further increase the extinction risk of LC species of *Magnolia* species, highlighting the need to continuously monitor and update the Red List as human-driven climate change continues to strengthen. In addition, although some *Magnolia* species are classified as DD species (e.g., *M. pterocarpa*), they clearly have relatively small populations and at least some occur where the habitat has suffered high rates of deforestation (Kundu, 2009). It is worth noting that DD represents the inability to distinguish whether the species is threatened because of limited information about processes affecting the species, but not a category of threat (Mace et al., 2008). Our results show five out of the eleven DD species in the Americas and eight out of the twenty-nine DD species in Asia are more vulnerable to climate change than currently recognized VU species. Therefore, our findings support the conservation proposal by Mace et al. (2008) that DD species should be protected to the same degree as threatened species, at least until more information is obtained. In addition, our results provide important information on which DD species may need most conservation actions to counteract future pressure from climate change.

Although PAs are important for biodiversity conservation, their effectiveness is also key to reducing future biodiversity loss (Banjac et al., 2019; Ervin, 2003; Feng et al., 2021; Hockings and Phillips, 1999). Our results show that *Magnolia* species distributed in low-latitude regions will be relatively more threatened by climate change. However, the corresponding high vulnerability areas located in PAs in low-latitude regions are scattered across large areas. The high vulnerability areas of some of the larger islands in Southeast Asia, for example Kalimantan and New Guinea, have a low percentage of PAs. In general, the distribution area of narrow-ranged species of *Magnolia* is better covered by PAs than that of widespread species for both continents, and the high-vulnerability areas for narrow-ranged species are protected to a much higher degree than that of widespread species. However, even the high-vulnerability areas of narrow-ranged species are less than 32% covered by PAs. Therefore, the effectiveness of PAs for safeguarding the diversity of *Magnolia* species towards future climate pressures should be further improved. Moreover, our results also show that the vulnerability of narrow-ranged *Magnolia* species to climate change is higher in Asia than in the Americas. Since the data on PAs in China in World Database on Protected Areas (WDPA) we used is incomplete, we also calculated another proportion of Asian *Magnolia* species that are protected under a more optimistic scenario (i.e., where 18% of *Magnolia* species habitats in China fall into PAs). We still observed the same result as using only WDPA, where the proportion of high-vulnerability narrow-ranged *Magnolia* species protected in PAs in Asia is lower than that in the Americas. Although PAs in China covers 18% of the total land territory, the distribution of PAs is not uniform and the PAs in southeastern China still account for less than 18% of this region's area (Bai et al., 2020). In other words, less than 18% of high-vulnerability narrow-ranged *Magnolia* species are protected in China, and the proportion of high-vulnerability areas for narrow-ranged *Magnolia* species in PAs in Asia is still much lower than that in the Americas. The main reasons for this difference are that there are few PAs in high-vulnerability areas in Southeast Asia and the coverage of national-level nature reserves in China are biased towards non-forest areas (Ren et al., 2015; Wu et al., 2011), e.g., with poor coverage of natural forests in southeastern China (Wu et al., 2011).

In general, the vulnerability of *Magnolia* species under the high CO_2 emission pathway (RCP 8.5) was higher than that under the low CO_2 emission pathway (RCP 4.5), with parts of Mexico and Brazil the main exception. In order to overcome the low statistical power caused by limited of sampling of narrow-ranged species, we quantified the niche using the estimated species range instead of occurrence points, i.e., to limit sampling bias. Despite using this approach, there could still have been some underestimation of climate change vulnerability for rarer *Magnolia* species. Conversely, we note that all niche estimates reflect a species' realized niche, and especially for small-range species may be affected by niche truncation (Nüchel et al., 2018), i.e., the species' climate niche is not fully expressed due to, e.g., dispersal constraints or anthropogenic habitat loss. This could potentially lead to over-estimates of the climate sensitivity of small-range species (Faurby and Araújo, 2018). This limitation can only be effectively addressed through experimental studies, which are not generally practical for long-lived species such as *Magnolia* species. Nevertheless, there is evidence that small-range species are indeed more sensitive to climate change (Vincent et al., 2020). In addition, our research mainly focuses on the vulnerability of *Magnolia* species under climate change. Although land use changes have a great impact as well (e.g., deforestation), it is not within the scope of this study.

In conclusion, *Magnolia* species with narrow ranges are estimated to be much more vulnerable to climate change than widespread species in the genus. For widespread *Magnolia* species, the differences in vulnerability of *Magnolia* species distributed in Asia and the Americas are relatively small. At the same time, the two continents have relatively small differences in the extent of protected areas for widespread *Magnolia* species. For narrow-ranged species, climate change vulnerability is higher and protected area coverage lower for Asian *Magnolia* species than American species. Moreover, the conservation status ranking of *Magnolia* species classified by the IUCN Red List is likely to change under future climate change, as some NT and LC species were estimated to become more vulnerable to climate change than EN species. *Magnolia* species classified as DD should be protected to the same degree as threatened species before obtaining more risk assessment information. Our results highlight that conservation assessments, policies and actions for *Magnolia* species need to take future climate change into account. Climate change vulnerability could provide important information for conservation prioritization strategies to balance other factors that influence decisions, such as cost, and chance of success.

Declaration of competing interest

We declare no conflicts of interest.

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CRediT authorship contribution statement

Wen-Ting Wang: Conceptualization (equal); formal analysis (lead); writing – original draft preparation (lead); writing – review and editing (lead); funding acquisition (equal). **Wen-Yong Guo**: Conceptualization (equal); formal analysis (supporting); writing – review and editing (equal). **Scott Jarvie**: writing – review and editing (equal). **Josep M. Serra-Diaz**: Data curation (lead); writing – review and editing (equal). **Jens-Christian Svenning**: Conceptualization (equal); formal analysis (supporting); writing – review and editing (equal); funding acquisition (equal).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109425.

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