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Conservation status of Primulaceae, a plant family with high endemism, in China

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ABSTRACT

Primroses, approximately 1000 species from the family Primulaceae, are mostly distributed in subalpine to alpine areas and attract attention due to their high ornamental value. However, they have been increasingly threatened by human activities and climate change in recent decades. China harbours 535 primrose species from 12 genera, most of which are endemic. In this study, we established a distribution database of the primroses in China, then explored the geographic pattern of the richness of primrose species in relation to environmental factors and evaluated their conservation status. The results showed that the primrose richness was highest in the mountainous areas from the eastern Himalayas to the Hengduan Mountains, with habitat heterogeneity (explaining 37.6% of the variance) and temperature seasonality (26.0% of the variance) together explaining this pattern. Furthermore, the richness of endemic and threatened primroses had been strongly affected by the long-term climate change since the Last Glacial Maximum. On average, national nature reserves (NNRs) covered 29.5% of the distribution areas of primroses. However, there were still 97 less-protected species, each of which had a distribution area < 2000 km^2 covered by NNRs. By analysing this group, we proposed that nature reserves need to be established in several conservation gaps mainly located in Southwest China to protect the primrose species in China.

1. Introduction

Primulaceae, the primrose family, is a large angiosperm family consisting of 22 genera and nearly 1000 species mainly distributed in the high mountains of the northern temperate zone (Hu and Kelso, 1996; Boucher et al., 2016). Known as one of the three most important horticultural plant taxa in the world (Richards, 2003), the primrose family offers many species that have been widely cultivated for hundreds of years owing to their high ornamental value. Harbouring 12 genera and > 500 primrose species, which account for more than half of all primrose species, China has the largest distribution of primroses globally (Hu, 1994; Hu and Kelso, 1996), partly because of the high diversification rate of this family and long geological history in this area (Yan et al., 2018). The Hengduan Mountains and the Himalayas in the southwestern China are the modern distribution, diversity and diversification centres of primrose species (Hu, 1994). More importantly, most of these primrose species are endemic to China (Huang et al., 2014), and this number continues to increase, as new species and varieties are continuously discovered (Li et al., 2017; Huang et al., 2019).

Recently, an increasing number of primrose species are facing threats, partly because of the increase in overexploitation and habitat destruction, the dispersal limitation induced by pollination distances as well as their dependence on specific microhabitats (Van Geert et al., 2008; Van Rossum, 2008; Yamamoto et al., 2017a, 2017b). At the same time, as a group typically distributed in alpine regions, primroses may encounter more severe survival challenges due to the rapid warming at high altitudes under global change (Güsewell et al., 2017; He et al., 2019; Yan and Tang, 2019). However, in China, most studies on primroses have focused on genetics, phylogenetic geography, and horticultural introduction (Zhang et al., 2008; Li et al., 2019), with little attention being paid to their distribution and conservation at large scales. Considering China's high levels of species richness and endemism in primrose species, this knowledge gap may cause great losses to global primrose resources.

Exploring the patterns and drivers of large-scale patterns of primrose richness is helpful for informing future conservation strategies for this group (Kreft and Jetz, 2007). Among the vast number of hypotheses for the large-scale patterns of species diversity, energy hypotheses consider that contemporary climate shape the current patterns of

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biodiversity (Jetz and Rahbek, 2002; Field et al., 2005; Wang et al., 2009), which may apply to primroses. Studies showed that the current climatic niche breadth of primrose species determined whether they could adapt to warmer and drier future conditions (Theodoridis et al., 2018). Meanwhile, evolutionary/historical hypotheses propose that evolutionary history may play a key role in the distributions of cold-adapted species and species with low dispersal abilities, which has been validated in many species groups (Liu et al., 2017; Theodoridis et al., 2017). In addition, habitat heterogeneity, which might be severely altered by future land-use changes, is thought to influence the richness patterns by providing microhabitats and changing species diversification rates (Qian and Ricklefs, 2000). Hence, current climate, historical climate change and habitat heterogeneity should all be covered for a comprehensive research of divers of the primrose distribution.

In situ conservation is considered to be the most effective method for biodiversity conservation (Richard et al., 2006; Primack, 2014), as it can best protect the original habitat and genetic diversity of the target species (Heywood and Dulloo, 2007). As a country with high biodiversity and richness of threatened species (Tang et al., 2006; Jenkins et al., 2013), China has made great efforts in constructing its nature reserve network (Zhao et al., 2013). Different researchers have identified conservation priorities for different species groups based on various algorithms (Huang et al., 2016b; Shrestha and Wang, 2018). However, there are still gaps between the current conservation status and the expected goals (Huang et al., 2016a; Zhang et al., 2015b; Chi et al., 2017).

In this study, we first developed distribution databases for the primrose species and national nature reserves (NNRs) in China. Using these databases and environmental data, we explored the richness patterns in relation to the contemporary climate, habitat heterogeneity and long-term climate change, and identified hotspots of primrose species. Then, we identified the conservation priority areas for primrose species. The scientific questions we asked included the following: (1) How are primroses in China distributed geographically, and where are their hotspots? (2) What environmental factors determine the richness patterns of primrose species in China? (3) What is the conservation status of the primroses in China, and how to further protect them?

2. Methods

2.1. Data collection

2.1.1. Distribution of primroses in China

According to the Flora of China (Hu and Kelso, 1996), there are 12 genera, i.e., Anagallis, Androsace, Bryocarpum, Cortusa, Glaux, Lysimachia, Omphalogramma, Pomatosace, Primula, Samolus, Stimpsonia, and Trientalis, and > 500 species in the family Primulaceae in China. Data on the distribution of primrose species in China were obtained from six sources: 1) national, provincial and local floras of China, 2) data on the occurrence of endemic species derived from the Diversity and Geographical Distribution of Endemic Seed Plants in China (Huang et al., 2014), 3) scientific articles related to field investigations of primrose species, 4) checklists from nature reserves, 5) specimen records available from the National Specimen Information Infrastructure (NSII, http://nsii.org.cn), and 6) records from the Global Biodiversity Information Facility (GBIF, 2020, https://www.gbif.org/). All species names were standardized using the Flora of China (Hu and Kelso, 1996) and the Catalogue of Life (http://www.catalogueoflife.org/).

Among all these sources, distribution records from the first four resources are county-level occurrences, which usually lead to overestimating the distribution range of species. Therefore, we also collected information on the occurrence elevations and habitat types of each species. By overlapping the county-level records with a digital elevation model (DEM) (with a resolution of 30 m from http://reverb.echo.nasa.gov/reverb/redirect/wist) and a vegetation map of China (1:1,000,000) (Editorial Committee of Vegetation Map of China, 2007), we used the grid-cells with suitable habitats for the corresponding species (e.g. swamp meadow for *Primula farinosa*) in its county of occurrence as the refined distribution areas. Then, these distribution data were uniformly converted into grid-cells with a resolution of 25 km. Finally, a total of 116,030 distribution records for 535 species were obtained.

We separated the species into two groups based on their distribution range size, i.e., widespread and small-ranged species. The halves of all species with the smallest and largest distribution ranges were considered small-ranged and widespread species (Araújo et al., 2008; Liu et al., 2017), respectively. We also analysed data for two additional groups of primrose species, namely, endemic and threatened species, as they are of high conservation value. The species that are only naturally distributed in China were identified as endemic according to Huang et al. (2014). The threatened species were identified according to the Ministry of Environmental Protection of China and the Chinese Academy of Sciences (2013) and Qin et al. (2017). In addition, the species in the following IUCN categories were also treated as threatened species in this study: extinct in the wild (EW), critically endangered (CR), endangered (EN), vulnerable (VU) and near threatened (NT). Our dataset contained 268 widespread, 267 small-ranged, 356 endemic and 217 threatened species.

2.1.2. Environmental factors

We explored the relationship between the primrose richness and the contemporary climate, habitat heterogeneity and long-term climate change in China. Contemporary climate data were obtained from the WorldClim website (Hijmans et al., 2005, http://www.worldclim.org/) with a spatial resolution of 30 arc-seconds, which were then transformed into a resolution of 25 km in ArcGIS 10.2 (ESRI, Redlands, US) by calculating average of all data points within each grid-cell. The climatic variables included the mean annual temperature (MAT, °C), mean temperature of warmest quarter (MTWQ, °C) and coldest quarter (MTCQ, °C), mean annual precipitation (MAP, mm), temperature (TSN, unitless) and precipitation seasonality (PSN, unitless). In addition, we calculated the potential evapotranspiration (PET, mm), actual evapotranspiration (AET, mm), moisture index (Im, unitless) and water deficit (WD, defined as the difference between PET and AET) using the mean monthly temperature and precipitation (Thornthwaite and Hare, 1955; Francis and Currie, 2003).

Four variables were used to represent the habitat heterogeneity within each 25 km grid-cell: range of altitude (RALT, m), number of vegetation types (VEG, unitless), range of MAT (RMAT, °C) and MAP (RMAP, mm). Range of altitude (RALT) is the difference between the highest and lowest elevations in each grid-cell based on the above-mentioned DEM. Number of vegetation types (VEG) was obtained by overlapping the vegetation map of China with the 25 km grid-cell system. While range of MAT (or range of MAP) represents climatic heterogeneity, reflected as the difference between the maximum and minimum MAT (or MAP) within each grid-cell.

Long-term anomalies in temperature (TANO) and precipitation (PANO) were represented by the absolute values of the difference in MAT (and MAP) between the Last Glacial Maximum (LGM) and the present. The climate data in the LGM were also derived from the WorldClim website (Watanabe et al., 2011).

2.1.3. Spatial database of nature reserves in China

By the end of the first half of 2016, China had established 2732 nature reserves, including 446 national nature reserves (NNRs), covering nearly 15% of its land area. We only included the NNRs in this study, since they usually have more specific geographical boundaries and are better managed than most provincial and lower-level nature reserves (Zhao et al., 2013). To evaluate the representativeness of primroses in these NNRs and select the priority areas for conservation, we used ArcGIS version 10.2 (ESRI, Redlands, US) to digitize all terrestrial NNRs.

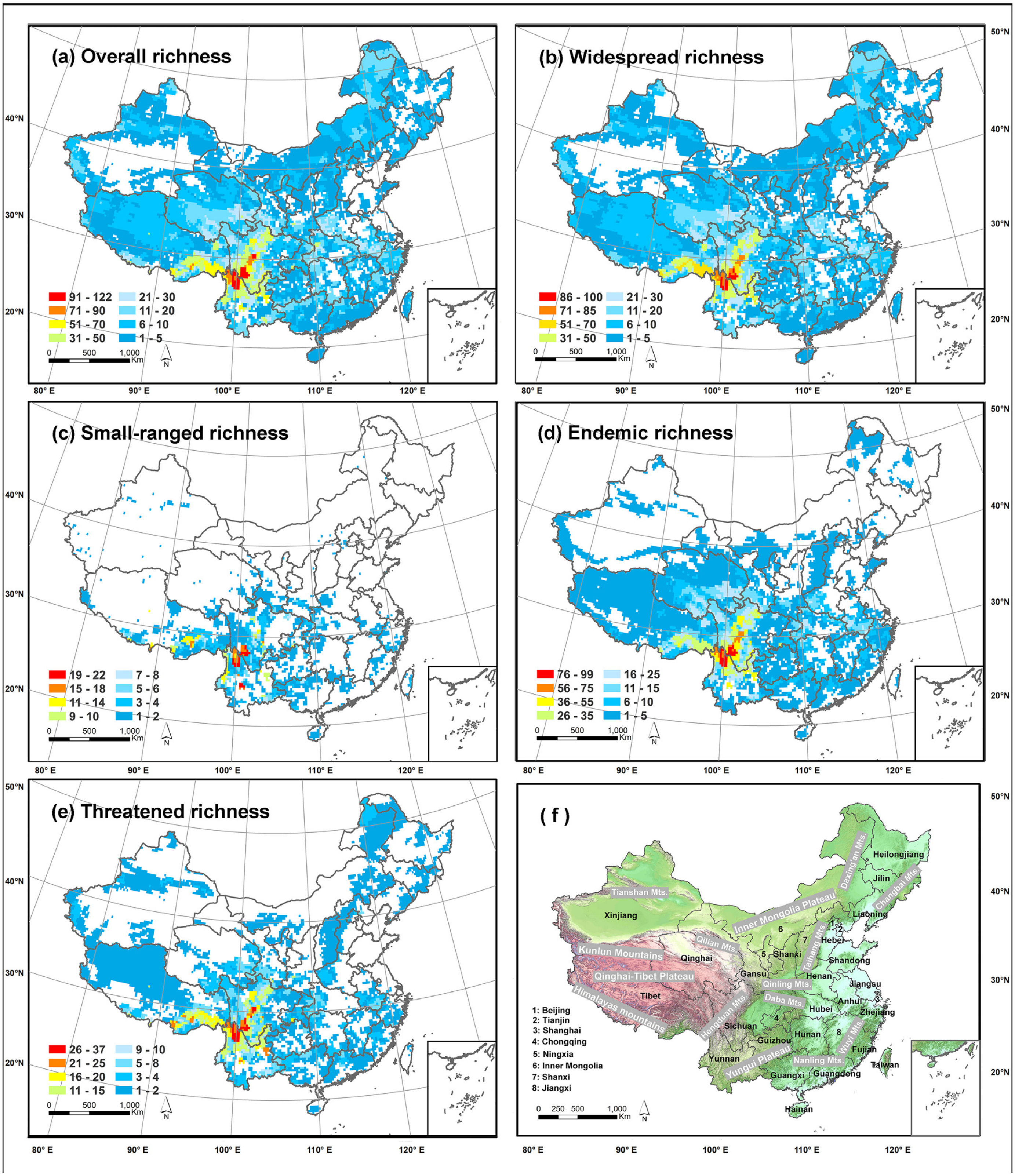

Fig. 1. Patterns of Primulaceae richness in China. (a) Overall species, (b) widespread species, (c) small-ranged species, (d) endemic species and (e) threatened species. Panel (f) illustrates the administrative areas and topography of China.

2.2. Data analysis

2.2.1. Hotspot identification

The species richness of primroses was represented by the total number of primrose species in each grid-cell. Then, we applied the complementary algorithm (Dobson et al., 1997) to identify the biodiversity hotspots of primroses in China. The rationale of this algorithm is recognizing the minimum number of grids that could cover all the species. Specifically, the complementary algorithm first selects the grid-cell that has the highest species richness. Then, it removes the distribution records of the species contained in that grid-cell and continues to select the grid-cell with the most species from the rest. This process is repeated until all species are included in the grid-cells selected previously. Compared with the species richness algorithm, the complementarity algorithm selects less grid cells to capture an equivalent number of species and is better at capturing the small-ranged species (Shrestha and Wang, 2018).

2.2.2. Relationship between species richness and environmental variables

When analysing the relationship between species richness and environmental variables, we first removed grid-cells with < 5 species, as richness in these grid-cells might be biased by the incomplete inventory. Since the frequency distribution of the species richness is Poissonian, we chose generalized linear models (GLMs) with Poissonian residuals to evaluate the explanatory power of each environmental factor in terms of the species richness patterns. This analysis was conducted for the richness of overall species as well as different species groups, i.e., widespread, small-ranged, endemic, and threatened species. The GLMs we used had quasi-Poissonian errors to eliminate the influence of overdispersion. The coefficients of determination (R^2) of the models were estimated as (Liu et al., 2017):

$$R^2 = 1 - (\text{residual deviance/model DF})/(\text{SR deviance/residual DF}) \quad (1)$$

where DF and SR represent the degree of freedom and species richness, respectively. As a complement to the GLMs, we used random forest models with all environmental factors to assess their relative importance in explaining the species richness patterns. Random forest analysis is also considered to be applicable to the analysis of nonlinear relationships (Breiman, 2001).

2.2.3. Identification of the conservation priority area

We first overlaid the distribution of each primrose species in China with the NNRs map to calculate the coverage of the distribution ranges by NNRs. Compared to some previous analyses, the average coverage was higher for primroses than for other plant groups (Chi et al., 2017; Zhang et al., 2015a, 2015b). In this case, the target groups used for analysis (i.e., endemic, small-ranged and threatened species as the three were considered of more conservation value) were not able to effectively represent the species that need further conservation. Furthermore, the species that were not protected by any NNRs were small in number and scattered in distribution, and the data were thus not sufficient for the analysis of conservation status. Therefore, other standards need to be applied to identify the species that need further conservation. According to the Criteria B of the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2012), species whose area of occupancy is smaller than 2000 km^2 will be listed in the threatened category. Considering that distribution of a species outside the conservation systems may be vulnerable to human disturbance, we listed the primroses with a distribution area covered by NNRs < 2000 km^2 as less-protected species. We then applied the complementary algorithm based on these species after eliminating the areas covered by NNRs. The grid-cells including all these species were selected as the conservation priority area of primroses in China. This approach takes existing conservation systems into account and directly uses species that have not been adequately protected to perform the analysis, which is more targeted than other approaches.

All statistical analyses were carried out using the basic (R Core Team, 2018) and *randomForest* packages in R version 3.5.2 (Liaw and Wiener, 2002).

3. Results

3.1. Geographical patterns of primrose richness in China

In general, the richness of primroses was highest in southwestern China, especially from the eastern Himalayas to the Hengduan Mountains, followed by Qinghai Province and the middle-lower reaches of the Yangtze River, but lowest in the northwest China, the North China Plain, and the northeast China (Fig. 1a). The widespread species showed a similar pattern to that of the overall species (Fig. 1b). The small-ranged primrose richness showed a fragmented pattern that further retreated to the southwest and was mostly concentrated in the southeastern part of the Hengduan Mountains (Fig. 1c). The endemic and threatened primrose species also showed similar patterns to the overall richness, but they had plenty of distribution gaps in the northeast, northwest, and central parts of China (Fig. 1d and e).

The complementary algorithm suggested that 82 grid-cells (a total area of approximately 5.13×10^4 km^2, accounting for 0.53% of China's landmass) included all primrose species in China, 21 grid-cells included all widespread species, 76 grid-cells included all small-ranged species, 63 grid-cells included all endemic species, and 52 grid-cells included all threatened species (Fig. 2). These grid-cells were identified as corresponding hotspots. They were mostly located in the topographically transitional zone (or the region with abrupt variation in elevation). Among them, the most important (the largest red dots in Fig. 2) were mainly distributed in the Hengduan Mountains of central and southern Sichuan Province as well as in southern Tibet, northern and central Yunnan Province (Jingdong Autonomous County). Others were scattered on the Yunnan-Guizhou Plateau and in the Qinling Mountains, the Daba Mountains, Guangxi Province, and Zhejiang Province (Fig. 2).

3.2. Relationship between primrose species richness and environmental variables

The GLMs indicated that variables related to habitat heterogeneity showed the strongest explanatory power in terms of the overall primrose richness in China, followed by climate seasonality, long-term climate change, and water availability, while the effects of energy-related variables were relatively lower. Specifically, the strongest predictor, RALT, explained 33.14% ($P < 0.001$) of the variance, followed by RMAT ($R^2 = 27.17\%, P < 0.001$), TSN ($R^2 = 25.95\%, P < 0.001$) and TANO ($R^2 = 23.77\%, P < 0.001$) (Table 1). The random forests identified TSN, RALT, MAP, and TANO as the four most important factors (Fig. 3a).

For the other groups, RALT and TSN were always among the top three factors with the highest explanatory power, while the importance of TANO was highlighted in the endemic and threatened species. In addition, the explanatory power of all environmental factors involved was relatively low for small-ranged species (the R^2 for the full model including all explanatory factors was $35.71\%, P < 0.001$), indicating that the key factors controlling the richness patterns were not included in the models. Specifically, the best predictors were RALT ($R^2 = 31.01\%, P < 0.001$), RMAT ($R^2 = 25.67\%, P < 0.001$), and TSN ($R^2 = 21.99\%, P < 0.001$) for the widespread species richness; TSN ($R^2 = 16.64\%, P < 0.001$), RMAT ($R^2 = 14.16\%, P < 0.001$), and RALT ($R^2 = 13.82\%, P < 0.001$) for the small-ranged species richness; TSN ($R^2 = 32.57\%, P < 0.001$), TANO ($R^2 = 31.01\%, P < 0.001$) and RALT ($R^2 = 23.77\%, P < 0.001$) for the endemic species richness; and TSN ($R^2 = 33.31\%, P < 0.001$), RALT ($R^2 = 32.92\%, P < 0.001$), and TANO ($R^2 = 29.40\%, P < 0.001$) for the threatened species richness (Table 1). Compared with the GLMs, the results based on random forests additionally emphasized the importance of MAP for all three groups (Fig. 3).

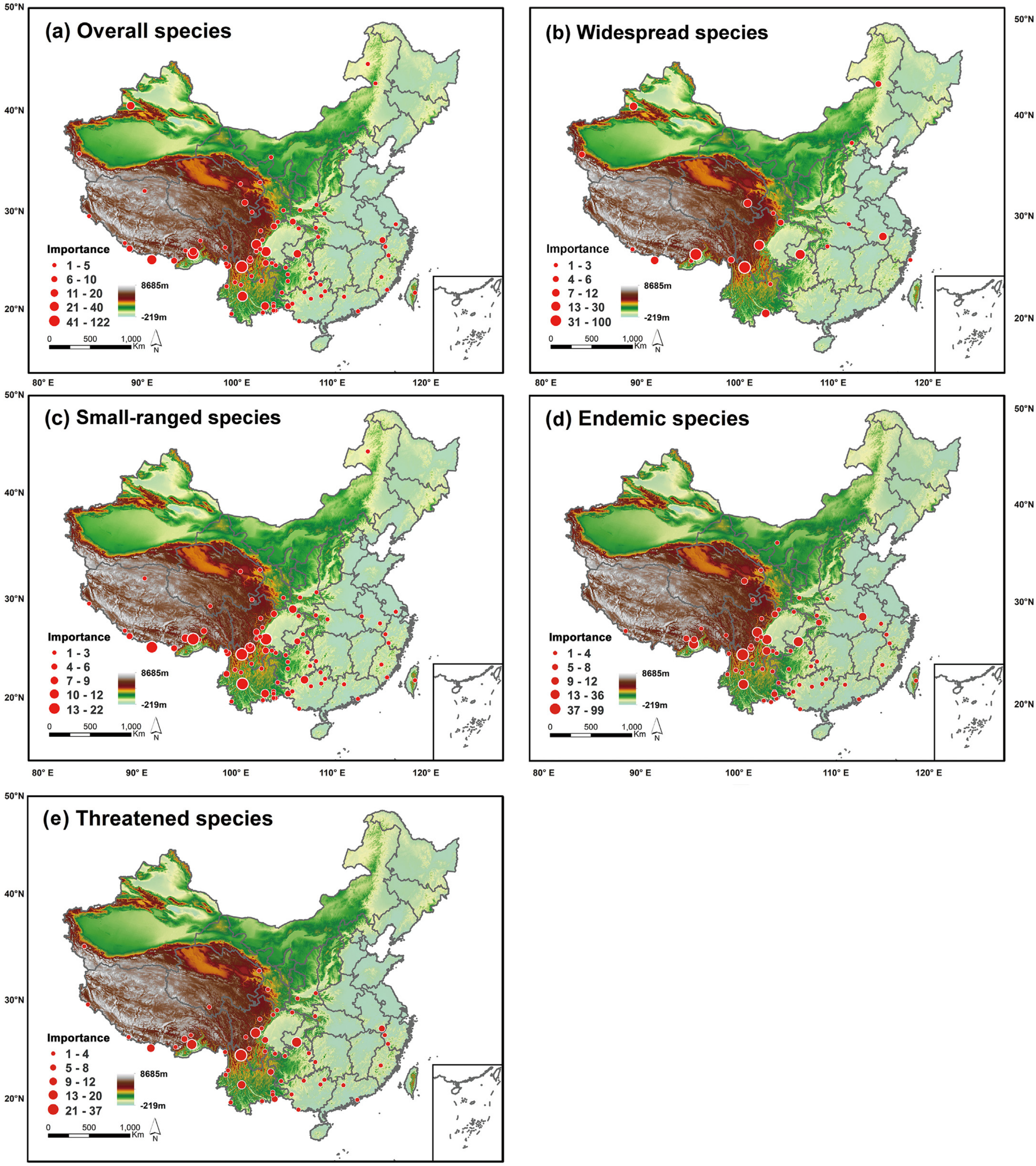

Fig. 2. Hotspots in China of (a) overall species, (b) widespread species, (c) small-ranged species, (d) endemic species and (e) threatened species of primroses based on the complementary algorithm. The importance value is equal to the number of new species included in the corresponding grid when it is selected. Large dots indicate more newly found species and are more important for the conservation of primroses.

3.3. Priority area for the conservation of primroses in China

On average, NNRs covered 29.5% (standard deviation = 19.4%) of the distribution areas of all primrose species in China. However, there were still 40 species (7.48% of the total) not covered by any NNRs (Fig. 4). A total of 97 species were identified as less-protected species, i.e., with an distribution area covered by NNRs < 2000 km^2. These less-protected species were concentrated at the junction of southern Sichuan

Table 1
Correlations (R^2, %) between species richness of Primulaceae and the selected environmental factors evaluated by generalized linear models (GLMs).

	Overall	Widespread	Small-ranged	Endemic	Threatened
No. of species	535	268	267	356	217
Environmental energy					
MAT (°C)	1.35***	0.72***	0.17	1.49***	2.71***
MTWQ (°C)	0.97***	1.35***	1.91***	0.24**	0.43***
MTCQ (°C)	7.20***	5.35***	0.30	6.23***	9.94***
PET (mm)	0.07	0.26**	1.33***	0.02	0.06
Water availability					
Im (unitless)	14.58***	14.12***	0.06	15.30***	14.47***
WD (mm)	12.88***	11.92***	0.76**	14.83***	14.17***
AET (mm)	1.86***	1.24***	0.87***	1.59***	2.47***
MAP (mm)	4.28***	3.30***	1.09***	3.52***	5.02***
Climatic seasonality					
TSN (unitless)	25.95***	21.99***	16.64***	32.57***	33.31***
PSN (unitless)	4.47***	3.65***	0.10	3.38***	3.82***
Habitat heterogeneity					
VEG (unitless)	18.43***	16.80***	4.97***	20.82***	17.71***
RALT (m)	33.14***	31.01***	13.82***	23.77***	32.92***
RMAT (°C)	27.17***	25.67***	14.16***	19.34***	26.85***
RMAP (mm)	5.80***	5.33***	0.39*	2.12***	7.18***
Long-term climate change					
TANO (°C)	23.77***	20.73***	5.20***	31.01***	29.40***
PANO (mm)	0.09	0.10	2.48***	0.02	0.14*

Abbreviations: MAT, mean annual temperature; MTWQ, mean temperature of the warmest quarter; MTCQ, mean temperature of the coldest quarter; PET, potential evapotranspiration; Im, moisture index; WD, water deficit; AET, actual evapotranspiration; MAP, mean annual precipitation; TSN, temperature seasonality; PSN, precipitation seasonality; VEG, number of vegetation types; RALT, range of altitude; RMAT, range of MAT; RMAP, range of MAP; TANO, MAT anomaly; PANO, MAP anomaly.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

and northern Yunnan as well as in southeastern Tibet (Fig. 5a). The complementary algorithm selected 46 grid-cells as the conservation priority area for primrose species in China. These grid-cells were distributed in the eastern Himalayas, the Hengduan Mountains, the Yunnan-Guizhou Plateau, south-western Yunnan and the Daba Mountains (Fig. 5b).

4. Discussion

4.1. Richness patterns of the primrose species in China

The distribution pattern of biodiversity is the foundation and traditional core of macroecology (Shade et al., 2018). Mountains are recognized as biodiversity hotspots worldwide (Rahbek et al., 2019). In this study, we explored the geographic patterns of primrose richness in China and identified the priority areas for conservation based on evaluating their current in situ conservation status. We found that southwestern China represented the most concentrated area of primrose species, while the richness of primroses in the North China, Northeast China, and Xinjiang was relatively low. The groups of the widespread, small-ranged, endemic and threatened primrose species also showed similar patterns (Fig. 1). Such richness patterns are very similar to those of other groups previously reported in China (López-Pujol et al., 2006; Wang et al., 2011; Zhang et al., 2015b). In addition, the hotspots of primroses were mainly located in mountainous areas, especially in areas with large elevation ranges (Fig. 2), possibly because the diverse elevation levels provide heterogeneous niches for different species (Tang et al., 2006). Based on the distribution pattern, we further clarified its relationship with contemporary climate, habitat heterogeneity and long-term climate change.

In the majority of the previous studies on the determinants of richness patterns, the most relevant factor was often contemporary water-temperature conditions, with coefficients of determination up to 70%–90% (Currie et al., 2004; Chu et al., 2019). However, in our study the explanatory power of environmental energy was very low, indicating that the primrose species in China were not sensitive to current temperature. On the contrary, water availability was positively correlated with the richness patterns (Fig. 3). In the context of climate change, precipitation in southwestern China may increase (Hu et al., 2012), which is expected to benefit the survival of primroses. Meanwhile, consistent with many previous studies of different taxonomic groups (Zhang et al., 2015b; Liu et al., 2017), TSN had an important influence on the richness pattern of primroses in China (Fig. 3, Table 1). Considering that TSN is one of the main indicators of climatic seasonality, this result confirms the climate stability hypothesis (Stevens, 1989) to some extent, which states that a stable climate tends to increase local species richness.

Habitat heterogeneity is thought to play a major role at small to medium scales, and as the geographic extent increases, the explanatory power of factors related to habitat heterogeneity decreases (Sarr et al., 2005; Stein et al., 2014). While the particular importance of RALT to primroses in our results may be caused by the general dependence of primroses on microhabitat conditions (such as forest edges, rock seams, etc. Hu and Kelso, 1996). This characteristic makes this family highly affected by microclimate, weakening the role of large-scale factors. In addition, being characterized by narrow niches and distributions makes it easy to be represented by local heterogeneity.

In addition, long-term climate change (especially TANO) was of high explanatory power in terms of the richness of the endemic and threatened primrose species in China (Table 1). Since the Quaternary, as the most significant climatic event, the glacial-interglacial cycle has played an important role as a strong environmental filtering mechanism in species survival on the 10–100 ka time scale (Mittelbach et al., 2007), and the temperature anomaly from the LGM to the present represents one of the strongest climatic changes in between. As a result, species with narrow climatic niches and an insufficient ability to track climate changes are most restricted in distribution range (Theodoridis et al., 2018). Furthermore, mountains are more conducive to the retention of species than plains, thus shaping the present patterns of plant diversity to some extent (Sandel et al., 2011). Our study showed that the TANO of the Hengduan Mountains in the past was relatively small, which created conditions for the survival of primroses in China.

The important contributions of climatic seasonality and long-term climate change to the richness patterns of primroses in China reflect the sensitivity of this family to climate fluctuations. Therefore, current climate change is likely to bring serious challenges to their survival. Although previous studies found that the seasonal anomaly in global temperatures has been decreasing since 1950 (IPCC, 2013), the warming trend that has been the fastest in the past 50 Ma (Solomon, 2007) can have strong negative impacts on the survival of primroses. In the meantime, the more rapid warming process and the decrease in space for migration on high mountains may make the situation even worse.

4.2. Conservation of the primroses in China

Establishing nature reserves is an important measure for biodiversity conservation. In addition, due to the restrictions caused by limited funds and local economic and social development, the identification of priority areas for conservation has become necessary (Myers et al., 2000). Selecting priority areas for conservation requires first clarifying the target groups and suitable methods. In most relevant studies, the target groups usually involve overall, small-ranged, endemic and threatened species, while the methods usually include traditional hotspot method, the complementary algorithm, and gap analysis (Brooks et al., 2006).

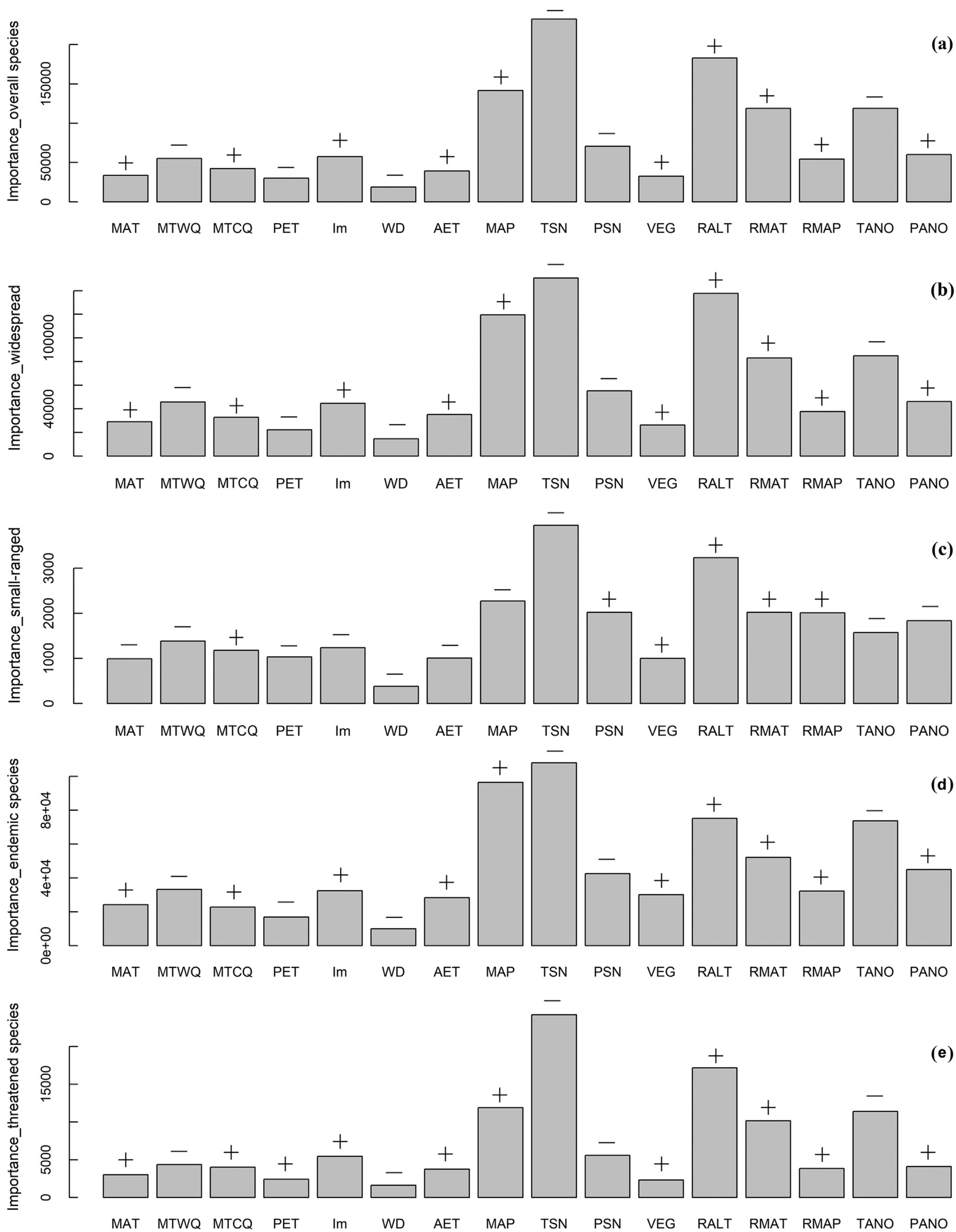

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Fig. 3. Results of the random forest models for the richness of (a) overall species, (b) widespread species, (c) small-ranged species, (d) endemic species and (e) threatened species. The relative importance of variables is represented by the increase in node purity. Plus (+) and minus (−) signs indicate positive and negative association respectively between the explanatory variable and species richness. Abbreviations: MAT, mean annual temperature; MTWQ, mean temperature of the warmest quarter; MTCQ, mean temperature of the coldest quarter; PET, potential evapotranspiration; Im, moisture index; WD, water deficit; AET, actual evapotranspiration; MAP, mean annual precipitation; TSN, temperature seasonality; PSN, precipitation seasonality; VEG, number of vegetation types; RALT, range of altitude; RMAT, range of MAT; RMAP, range of MAP; TANO, MAT anomaly; PANO, MAP anomaly.

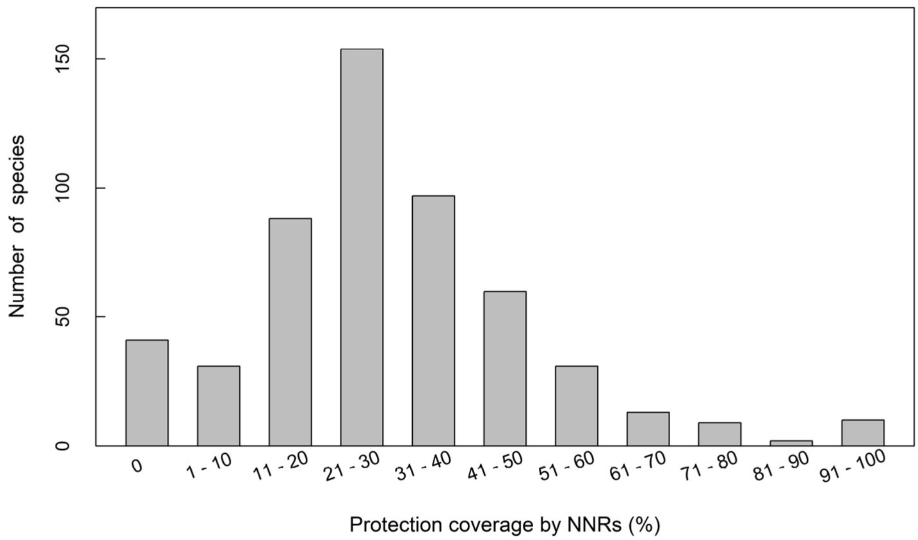

Fig. 4. Frequency distribution of coverage of primroses by national nature reserves (NNRs) in China.

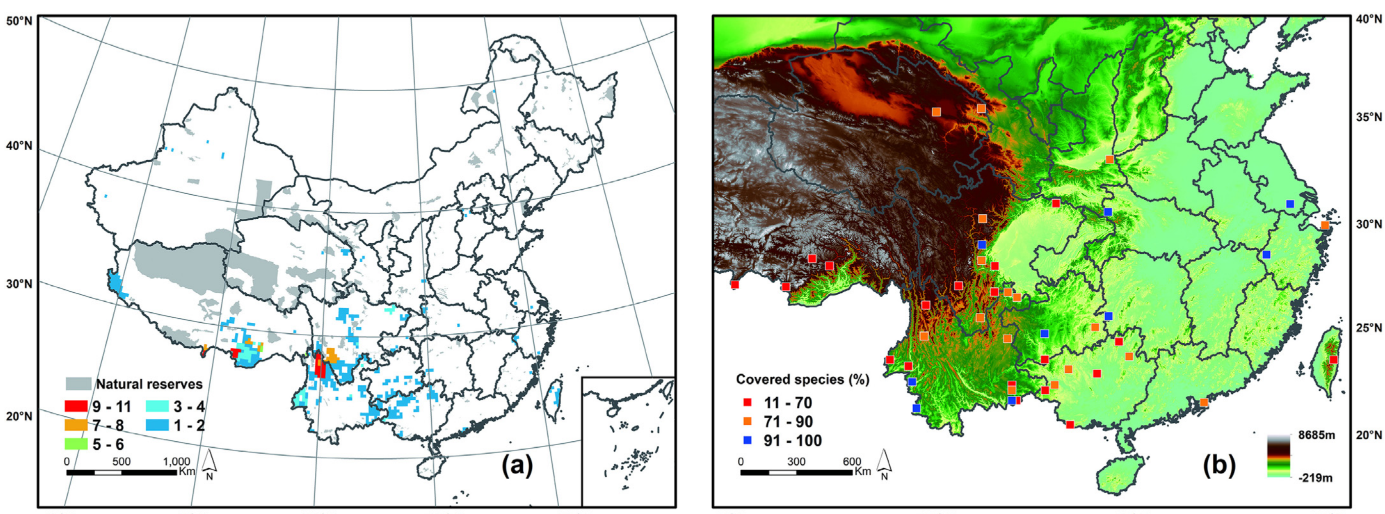

Fig. 5. Richness patterns (a) of the less-protected species and (b) conservation priority of the primroses in China based on the complementary algorithm. The different colours in (a) represent different levels of species richness. While the different colours in (b) indicate the proportion gradients of the species selected by the complementary algorithm. Specifically, red grid-cells are the areas first selected in order which contain 70% of all species together. Furthermore, orange and blue grid-cells cover the remaining 20% and 10% of the species, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Our study showed that the conservation priority areas were located in the eastern part of the Himalayas, the Hengduan Mountains, the Yungui Plateau, south-western Yunnan and the Daba Mountains. Among them, the junction area of northwestern Yunnan Province and southwestern Sichuan Province (Yulong County and Shangri-La city) was also identified as the most important conservation gap for orchids (Zhang et al., 2015b), threatened plants (Zhang et al., 2015a) and other species groups in China. Therefore, we propose that a new nature reserve should be established first in this area.

Comparing the less-protected species with other small-ranged, endemic and threatened species of primroses, although they showed similar richness patterns (average correlation coefficient (r) $>$ 0.69 for all pairs, P $<$ 0.001), their respective hotspots identified by the complementary algorithm were very different. The results suggest that the hotspots identified for all four species groups together accounted for only 13.8% of the total number of hotspots (15 of 109 grid-cells). The hotspots identified for only less-protected species accounted for 19.6% of all hotspots (9 of 46 grid-cells), which was highest among the four groups (Fig. 6), indicating that in the case of a high level of protection coverage, the conservation areas identified according to the commonly used small-ranged, endemic and threatened groups may not be sufficiently effective and representative.

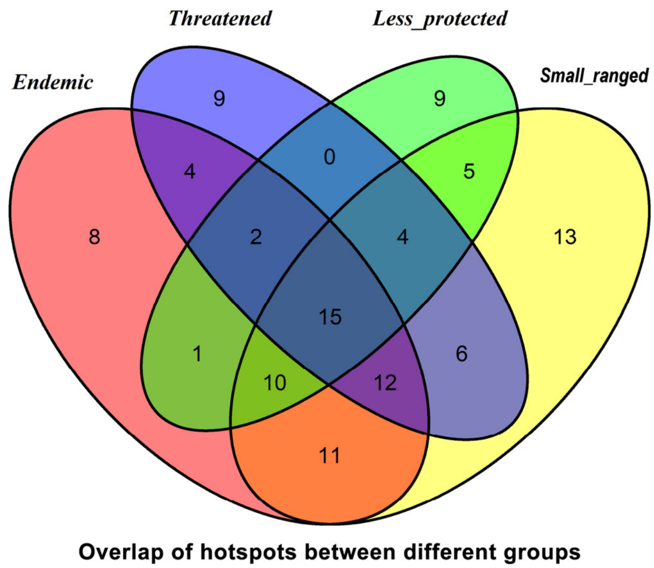

Fig. 6. Overlaps of and differences in hotspots based on different primrose species groups in China, as depicted by the complementary algorithm. A total of 118 grid-cells were identified as hotspots for all four groups.

Most of the previous studies on priority areas for conservation in China did not take existing biodiversity conservation systems into consideration, especially when selecting the target groups (Huang et al., 2012; Huang et al., 2016b; Xu et al., 2017; Yu et al., 2017), which is likely to make the results for future conservation less credible. Based on this situation and considering the current area as well as the continued growth of nature reserves in China (Cao et al., 2019), we suggest that subsequent studies should be based on existing conservation systems. It is feasible to select species that have not been adequately protected as the target group by setting a certain threshold of protection coverage and then carry out further conservation analysis. This proposal can also apply to other countries and regions that have a certain conservation base.

4.3. Uncertainty of the present study

In this study, we explored the patterns and drivers of the richness of primrose species in China, and identified their conservation priority, providing a scientific basis for the policy makers. However, some caveats should be noticed. First, the distribution data of our study was not based on field investigations, but from different existing databases. Although we have considered all possible data sources, the lack of investigations in some places will cause a certain degree of bias in data, which might distort species richness patterns (Dorazio, 2014). Since most of the nature reserves have detailed species checklists, the data bias may lead to overestimation of the conservation percentage. Meanwhile, most of the records are county-level occurrences, which may slightly overestimate the distribution range of species, though they have been refined with elevation range and habitat types. Second, we assumed that nature reserves and species range may coincide when both occurred in the same 25 km grid-cell, which might also overestimate the conservation percentage. Finally, the environmental variables selected are generally large-scale factors, and do not include soil properties or micro-topography, limiting the interpretation of the richness patterns of the primroses in China. These results further emphasized the necessity to setup more protected areas for the primrose species in China.

5. Conclusions

Species of Primulaceae in China are concentrated in the southwestern region, especially in the eastern Himalayas to the Hengduan Mountains. The richness and hotspots of widespread, small-ranged, endemic, and threatened groups also showed similar patterns to those of overall species. Habitat heterogeneity, temperature seasonality and long-term climate change are the most important determinants of the diversity patterns of primroses. Furthermore, long-term climate change (especially temperature changes since the LGM) has a particularly significant impact on the richness of endemic and threatened species. In the context of global climate change, the high sensitivity of primrose species to climate fluctuations on both short- and long-term scales can make them particularly vulnerable to extinction. The analysis of less-protected species indicates that there are many conservation gaps for primroses in southern Tibet, the Hengduan Mountains and the Yungui Plateau. More conservation efforts in these areas will benefit the survival of the primroses in China in the future.

Author statement

Yun-Hao Bai: Conceptualization, Methodology, Software, Data curation, Writing; Original draft preparation; Si-Yi Zhang: Data Curation; Methodology; Yanpei Guo: Reviewing and Editing; Zhiyao Tang: Supervision; Project administration; Funding acquisition; Writing; Reviewing and Editing.

Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data accessibility

Data are available from the Dryad Digital Repository: https://datadryad.org/stash/share/Mj_Qe39X-B-jM4lNGpmkIdIfw5yhvoNmCOXEVoq90t8.

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