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Spatio-temporal variation in potential habitats for rare and endangered plants and habitat conservation based on the maximum entropy model

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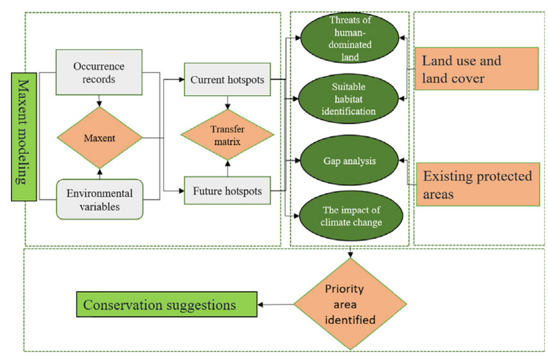
HIGHLIGHTS

- Current and future habitats of rare and endangered plants were modeled.
- The conservation efficiency of existing protected areas needs to be improved.
- Human activities drive habitat fragmentation and loss.
- Climate change drives habitat shift.
- Developing dynamic conservation strategies is critical.

GRAPHICAL ABSTRACT



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ABSTRACT

Rare and endangered plants (REPs) act as key indicators for species habitat priorities, and can thus be critical in global biodiversity protection work. Human activities and climate change pose great threats to REPs, so protection should be a top priority. In this study, we used the maximum entropy model (Maxent) to identify current and future (2050) potential habitats of REPs in the Xishuangbanna tropical area of China. We compared potential habitats with existing protected areas (PAs) in gap analysis, and used a transfer matrix to quantify changes in potential habitats. By comparing the potential distribution obtained with existing land use and land cover, we analyzed the impact of human-dominated land use changes on potential habitats of REPs and identified the main habitat patch types of REPs. The results showed that the current potential habitat area of hotspots is 2989.85 km^2, which will be reduced to 247.93 km^2 by 2050, accounting for 15.60% and 1.29% of the total research area, respectively. Analysis of land use and land cover showed that rubber plantation was the human-dominated land use posing the greatest threat to potential habitats of REPs, occupying 23.40% and 21.62% of current and future potential habitats, respectively. Monsoon evergreen broad-leaved forest was identified as the main habitat patch type for REPs in Xishuangbanna and occupied the highest proportion of potential habitat area. Gap analysis showed that only 35.85% of habitat hotspots are currently included in existing PAs and that this will decrease to 32.26% by 2050. This emphasizes the importance of protecting current and future potential habitats of REPs in a dynamic conservation approach that can adapt to changes in future climate and human activities.

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1. Introduction

Plants are the primary producer in the Earth's ecosystem, and are an important basis for biodiversity (Hong, 1990). Complex relationships between plants and other organisms are essential for many ecosystem services (Reddy, 2017). Rare and endangered plants (REPs) are a key component of biodiversity, and their existence indicates healthy ecosystem services (Pereira Leitão et al., 2016; Dee et al., 2019). REPs are species with narrow geographical distribution, highly specific habitat requirements, and/or confined to small populations with low genetic diversity and greater risk of extinction (Cuthbert, 1995; Khan et al., 2012). Protecting REPs is the premise and foundation for protecting biodiversity, which should be one of the most urgent tasks (Ye et al., 2020).

REPs are particularly vulnerable to environmental change because of their particular physiological characteristics (Fischer et al., 1997), such as high habitat adaptation requirements, narrow distribution range, low competitiveness, and weak production and diffusion ability (Markham, 2014). Moreover, human interference and climate change have increased the risk of extinction for REPs (Ren et al., 2014). Nowadays, around a quarter of the world's plant species are now at risk of extinction because of human activities and climate change (Gamal et al., 2020). The number of species threatened with extinction far exceeds existing conservation measures, and the situation will continue to worsen in future (Volis, 2019).

The influence of humans on REPs is mainly reflected in the decrease in potential habitats for REPs caused by various activities resulting in land use change (Gauthier et al., 2017). Without suitable habitats, species cannot survive, so habitat loss and deterioration are the main causes of the disappearance of threatened species (Pykälä, 2019). The destruction of natural habitats is leading to loss of biodiversity and ecosystem services, and will be exacerbated by the expansion of agriculture as a result of increased global population and per capita consumption (Gonçalves-Souza et al., 2020). Habitat loss has indirect effects on species richness through habitat fragmentation (Püttker et al., 2020). Human activities result in habitat loss and fragmentation (Schemske et al., 1994). The development of commercial plantations, such as rubber and tea plantations, has led to a decline in biodiversity (Yi et al., 2014; Zheng et al., 2015), but the impact of these land uses on REPs has not been quantified. In addition, unsustainable logging and overexploitation are occurring, increasing the rate of extinction of REPs in the wild (Reddy, 2017). At the same time, invasive alien species are threatening local native plant communities, causing instability (Padalia et al., 2014; Yan et al., 2020).

In addition to human activities, global climate change is having a significant impact on REPs. Climate change has been identified as the major threat to biodiversity in the 21st century (Dawson et al., 2011). Knowledge that climate change is a threat to biodiversity is well established, but the effects on REPs have been relatively poorly studied (Maschinski et al., 2006). Relevant studies have confirmed that long-term increases in CO_2 concentration and temperature lead to changes in physiological responses of REPs (Jeong et al., 2018). Endemic species with narrow ranges may be more vulnerable to climate change (Maschinski et al., 2006). Priority should be given to basic research to predict how species will react to future climate change (Jeong et al., 2018).

In order to slow the pace of extinction of REPs, conservation biologists, botanists, and other scholars have performed extensive research. Some of these studies have examined the phytochemistry and biology of REPs (Jiang et al., 2020). However, most studies have focused on just one or a few REPs, without considering protection of most REPs in an area (Baruah et al., 2020; Gamal et al., 2020; Li et al., 2020; Searle and Meyer, 2020). Native forests are the best habitat for protected and endangered species (Dong et al., 2010). To protect REPs, priority should be given to identifying special habitats where REPs are valued. Good habitat is the basis for growth, reproduction, and dispersal of these REPs, as well as their refuge in the face of environmental changes. Although potential habitats are important, assessments of habitat distribution and suitability of rare plant species are often not incorporated into the planning process (Wu and Smeins, 2000).

The establishment of nature reserves is now the main form of biodiversity conservation (Chape et al., 2005), the direct way to protect endangered species (Swart et al., 2018), and the most widely accepted and accessible measure world-wide (Kumar, 2010). However, due to lack of scientific data and comprehensive planning in the early stages of creation of nature reserves, there are still inevitably conservation gaps (Huang et al., 2020b; Ye et al., 2020). Xishuangbanna Nature Reserve in China was established in 1958. It consists of Shangyong, Mengyang, Mengla, Mangao, and Menglun sub-reserves, with a total area of 2474.39 km^2 (Liu et al., 2014). The Xishuangbanna region is part of the Indo-Myanmar tropical biodiversity hotspot and contains a significant number of REPs and animals (Myers et al., 2000). However, no previous study has assessed the effectiveness of these protected areas (PAs), especially for conservation of REPs.

In this study, we used the maximum entropy (Maxent) model to identify potential habitats of REPs in Xishuangbanna. By comparing modeled hotspots of REPs with existing PAs, we performed gap analysis to assess the effectiveness of existing PAs. In addition, using current land use and land cover data, we extracted land use and land cover corresponding to the hotspots of REPs. We used this to analyze the impacts of human-dominated land on the potential distribution of REPs and identify the main habitat patch types of REPs. Finally, we predicted the potential distribution of REPs under future (2050) climate change. In a novel approach, we used the ArcGIS tool to make a transfer matrix, which allowed us to calculate the future increase or decrease in the area of potential distributions. This provided an effective means for quantitative analysis of potential habitat changes of REPs under the impact of climate change. The following research questions were considered:

(1) Do the existing PAs in Xishuangbanna effectively protect the potential habitat of the local REPs?
(2) Which land use is most harmful to potential habitats of REPs and what is the main habitat type of REPs?
(3) How will the potential distribution of REPs change under future climate change (to 2050)?

2. Materials and methods

2.1. Study area

Our study area was the whole of Xishuangbanna (21°08′32″-22°35′52″N, 99°56′37″-101°50′35″E), a Dai autonomous prefecture in southern Yunnan province of China, bordering Laos and Myanmar, with an area of 19,161.53 km^2 (Fig. 1). It is located at the northern edge of the tropics and has a typical tropical monsoon rainforest climate, but there are obvious temporal and spatial differences in precipitation and temperature. In 2000, the maximum annual precipitation difference was 364.11 mm and mean annual temperature was 8.58 °C, which is projected to increase to 610 mm and 10 °C, respectively, by 2050. Thus during the 50-year period, mean annual precipitation will decrease by 25.76 mm, while mean annual temperature will increase by 0.69 °C. In addition, the spatial distribution of precipitation and temperature will differ significantly. By 2050, local climate variability will increase, reflecting high precipitation areas moving from the south of Xishuangbanna to the south-east and north-east, and the high temperature area shrinking in extent to the south (seeing Fig. S1). The region is rich in tropical biological resources due to its high rainfall, high temperature in winter, and foggy weather (Zhu, 1994; Zhu et al., 2006). REPs are particularly abundant (Zhang and Cao, 1995). Xishuangbanna is a national ecological demonstration zone, a national scenic spot, and a member of the United Nations biodiversity protection circle. It has 31

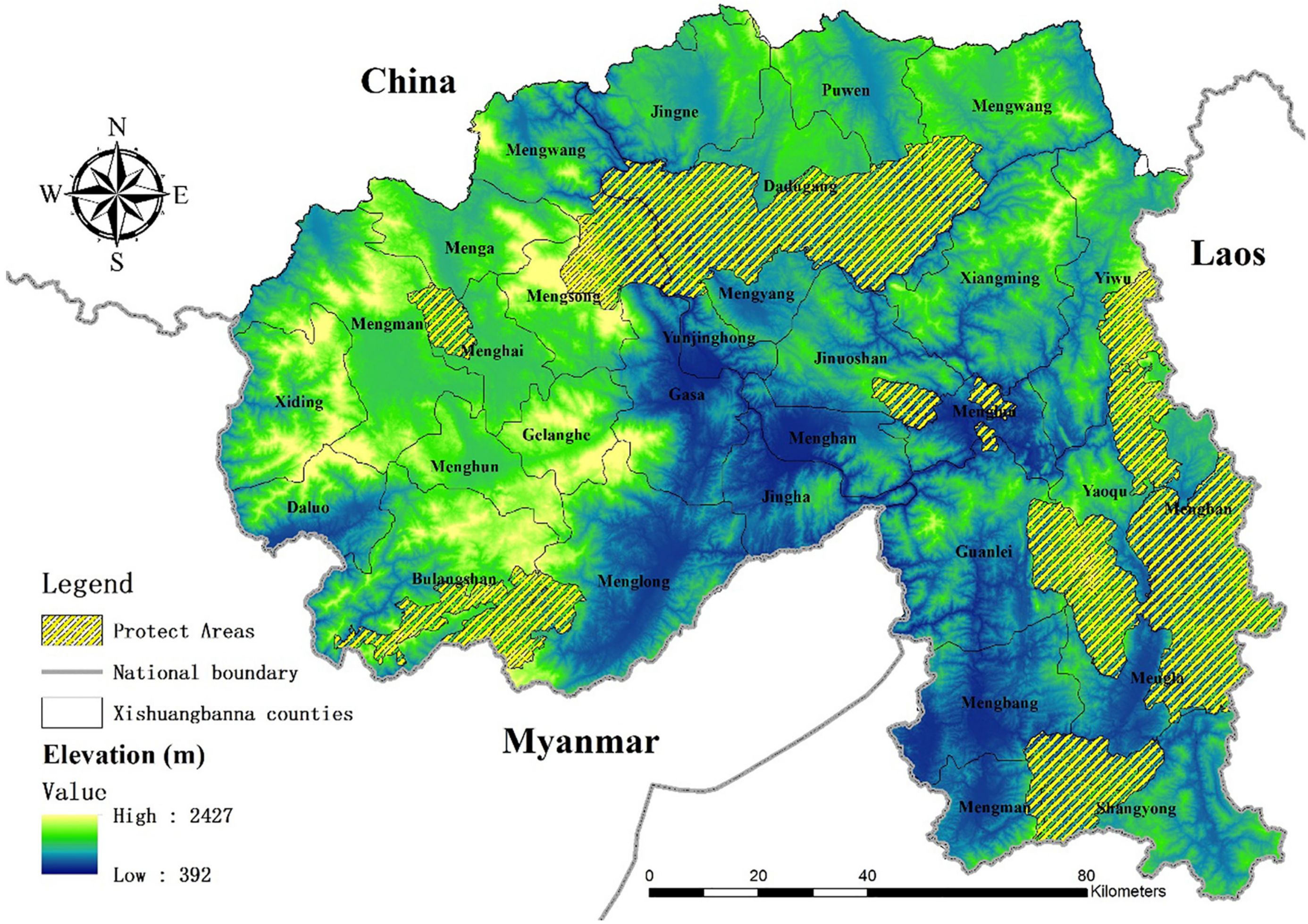

Fig. 1. Geographical location of Xishuangbanna in south-west China, distribution of counties, and land elevation.

townships, inhabited by 13 ethnic groups. Xishuangbanna has always been the area with the richest biodiversity in China (Mann, 2009), and is of great significance to the maintenance of regional biodiversity (Zhang and Cao, 1995). Our research area also included the Naban River Watershed National Nature Reserve (Ghorbani et al., 2011) and the Yiwu and Bulong State-level Nature Reserves.

2.2. Species occurrence data

The selected REPs in our study were derived from the list of National Key Protected Wild Plants (1999), including Class I and Class II protected plants, drawn up by China Forestry Bureau and Ministry of Agriculture (Wang and Xie, 2004). It is the most authoritative source with an endemic focus according to Chinese experts (Ren et al., 2012; Wang et al., 2015). In addition, we considered that the International Union for Conservation of Nature (IUCN) criterion is worldwide and relevant protection levels of REPs are listed (Huang et al., 2020b). Based on the above, we selected a total of 39 plant species (Table S1).

The coordinates for REP distributions used in this study were obtained through field investigation from April to June 2019. Our field survey plan included: (1) Survey route design, designed according to the vegetation coverage and terrain accessibility of Xishuangbanna; (2) coordinate point collection, using hand-held GPS (Garmin 64 s) to record the coordinates of REPs found in the field; (3) post-processing, where the collected coordinate points were imported into the computer and converted into .csv format table by ArcGIS for saving. In order to prevent double calculation by the model, we kept only one coordinate of any REPs occurring within 1 km of each other (Xiaoyu et al., 2018). We collected a total of 674 coordinates of REPs, which covered most of the Xishuangbanna area (Fig. S2). The Maxent model requires at least five different coordinates for each species to obtain more accurate and reliable results (Pearson et al., 2007), so 499 records on 24 eligible REPs were used for final model analysis (Table 1).

2.3. Environmental variables

The selected environmental variables comprised 19 bioclimate variables, three topo-graphical variables (plus slope, aspect, and elevation) (Abolmaali et al., 2018), and one soil variable (Padalia et al., 2014).

The bioclimate variables were derived from Worldclim version 2 (www.worldclim.org). The values used were the average for the periods 1970–2000 and 2041–2060 at 30 s (1 km^2) spatial resolution (Fick and Hijmans, 2017), and all associated layer data reflecting precipitation and temperature. In ArcGIS10.2 (©ESRI), elevation, slope, and aspect (compass direction) were extracted from the digital elevation model (DEM) downloaded from the Geospatial Data Cloud (www.gscloud.cn) with 30 m resolution. Aspect influences plant growth by regulating light, moisture, soil nutrients, and pH (Cao et al., 2020a; Jolokhava et al., 2020; Zang et al., 2020).

Data on soil type were downloaded from the Soil and Terrain database for China (SOTER China) (https://files.isric.org/public/soter/CN-SOTER.zip), compiled in the project 'Land Degradation Assessment in Drylands' (JA et al., 2008; Zang et al., 2020; Naudiyal et al., 2021). The soil type map of Xishuangbanna was extracted, and the corresponding area and proportion were calculated (Fig. S3, Table S2).

Table 1
The 24 rare and endangered plants (REPs) selected for modeling in this study, their endangered status class on the National Key Protected Wild Plants (NKPWP) list (China) and the IUCN Red List, endemism in Xishuangbanna, and the number of records collected.

Species	NKPWP	IUCN[a]	Endemism	Records
Alcimandra cathcartii	I	LC	–	9
Cycas pectinata	I	VU	–	17
Eleutharrhena macrocarpa	I	NE	–	13
Parashorea chinensis	I	EN	–	20
Alsophila costularis	II	LC	–	17
Alsophila gigantea	II	LC	–	14
Brainea insignis	II	VU	–	10
Caryota urens	II	LC	–	10
Cibotium barometz	II	NE	–	30
Dalbergia fusca	II	NT	–	40
Dracaena cochinchinensis	II	VU	–	6
Fagopyrum dibotrys	II	LC	–	8
Horsfieldia tetratepala	II	NE	Yes	15
Magnolia henryi	II	DD	–	36
Mangifera sylvatica	II	EN	–	12
Myristica yunnanensis	II	EN	–	18
Parakmeria yunnanensis	II	VU	–	5
Paramichelia baillonii	II	LC	–	75
Pterospermum menglunense	II	EN	Yes	16
Terminalia myriocarpa	II	NE	–	43
Tetrameles nudiflora	II	VU	–	26
Toona ciliata	II	LC	–	39
Trigonobalanus doichangensis	II	EN	–	13
Amoora dasyclada	II	VU	Yes	7

[a] Critically endangered (CR), endangered (EN), near threatened (NT), vulnerable (VU), not evaluated (NE), data deficient (DD), least concern (LC).

We converted the projection system for all variable layers to WGS_1984_UTM_Zone_48N, and we converted all variable layers to ASCII files for further analysis, using ArcGIS. In order to reduce the effect of highly correlated variables, we calculated Pearson's correlation coefficient by IBM SPSS 23.0 (Akomolafe and Rahmad, 2019) (Table S3). If two variables were highly correlated ($|r| > 0.8$), we removed one (Yang et al., 2013; Abolmaali et al., 2018). At the end, we selected 15 variables for modeling (Table S4).

2.4. Distribution modeling

We applied Maxent version 3.4.1 to model current and future (2050) potential habitats of Xishuangbanna REPs (Phillips, 2017). The default Maxent model may overfit and the results may then be less transferable (Wiltshire and Tanner, 2020). Therefore some of the selected parameters needed to be adjusted.

Model parameters were set as follows: (1) We used the regularization multiplier (RM) to avoid over-fitting, which affects the performance of the model (Naudiyal et al., 2021). The default RM value is 1, and it is generally considered that intermediate RM is better than a low or high value (Anderson and Gonzalez, 2011). In tests, we set RM to 0.9, 1, 1.1, and 1.2, and found that the average area under the receiver operating characteristic curve (AUC) value was 0.75, 0.83, 0.87, and 0.79 respectively. Hence, we set RM to 1.1 (Huang et al., 2020b); (2) we set cross-validation type to four replicates; and (3) for features, we selected feature type based on the number of samples. We had few occurrences, so we selected a generalized linear model (Elith et al., 2011); (4) we set random test percentage to 25%. The program then randomly sets aside 25% of the REPs coordinates for testing, using 75% of them as training, and transforms the model with random background values for multiple iterations (Phillips et al., 2017). Other parameters remained the default (Lu et al., 2021). The jackknife test was applied to assess the importance of those variables (Jiang et al., 2014). AUC was used to evaluate model performance (Phillips and Dudík, 2008), with $0.7 < \text{AUC} < 0.8$, $0.8 < \text{AUC} < 0.9$, and $\text{AUC} > 0.9$ considered to indicate acceptable, good, and highly accurate model performance, respectively (Swets, 1988).

The modeling process comprised four steps: Step 1: We modeled the potential habitats of each REP separately, and used ArcGIS to convert the output ASCII layers of Maxent models to float raster. Step 2: Using ArcGIS, we reclassified the potential habitat layer obtained from Maxent for each REP into 0 (under the presence thresholds) or 1 (above the presence thresholds) based on the 10 percentile training presence thresholds (i.e., the value outside the lowest 10 percentile localities of the predicted value was used as the threshold) (Nazeri et al., 2012; Huang et al., 2020b). Step 3: With the help of the ArcGIS raster calculator tool, we added the potential distribution of all REPs together to obtain the final hotspots map of REPs in Xishuangbanna. Step 4: By referring to previous research (Han et al., 2019) and combining with the actual number of REPs used, we divided the hotspots into four groups: i) Not suitable: no REPs present; ii) Low suitability, no. of REPs = 1–5; (iii) medium suitability, no. of REPs = 6–10; (4) high suitability, no. of REPs >10. The higher the REPs richness, the more suitable the habitats. The purpose with grouping hotspots in this way was to distinguish the adaptability of different habitats and to identify potential habitats most suitable for REPs.

2.5. Model accuracy and validation

Model accuracy in modeling the current and future (2050) distribution of REPs in Xishuangbanna was acceptable. The average AUC value for potential distribution modeling of all REPs was 0.919 (Table S5), indicating that the prediction accuracy of the model was high. In addition, we validated the model by comparing the outputs with data from field survey points (Evcin et al., 2019). The potential distributions predicted by the model were highly compatible with the occurrence data collected by GPS. This means that our model is successful and can be used for assessing the distribution of REPs in the study region.

2.6. Evaluating potential habitats of REPs

Human influence on REPs is mainly reflected in land use (Busch and Reisch, 2016). Natural forests that are far from human interference are obviously the best habitats for REPs, while construction land, farmland, and artificial forests are inevitably not suitable for the maintenance of REPs (Gang et al., 2004). In order to evaluate the suitability of potential habitats of REPs identified by the model, we extracted land use and land cover corresponding to the REPs hotspots (no. of REPs >5), and counted the area and proportion of each land use and land cover in the hotspots. We obtained land use and land cover data for Xishuangbanna, covering 19 land types in 2016, from the Yunnan Institute of Forest Inventory and Planning. We then identified the natural community types on which REPs depend and identified the human developments that posed the greatest threat to the potential habitats, based on area and proportion in the hotspots.

2.7. Gap analysis

Gap analysis is a popular method for evaluating the effectiveness of PAs (Fonseca and Venticinque, 2018; Yang et al., 2020a). In order to assess the effectiveness of existing PAs in protecting REPs in Xishuangbanna, we compared the modeled hotspots with existing PAs. We then extracted hotspots inside and outside the PAs and calculated their area and proportion, to evaluate the conservation efficiency of the existing PAs. Finally, we removed gaps occupied by agricultural land, artificial plantations (rubber plantations, tea plantations, orchard) and built area, and identified the remaining gaps as priority conservation areas for REPs.

2.8. Predicting potential habitat under future climate change

In order to assess the impact of future climate change on REPs, we used the Maxent model to predict potential habitats of REPs in Xishuangbanna in 2050. We plotted the results of the model in a binary map and compared it with the current hotspots layer, to analyze changes in terms of the area and spatial distribution of hotspots. We then compared modeled hotspots of REPs in 2050 with current PAs, and identified future conservation gaps under predicted climate change. Finally, we created a transfer matrix to quantify the changes in hotspots of REPs from the current to the future point. The advantage of a transition matrix table is that it can quantitatively analyze the transition relationship between different hotspots.

3. Results

3.1. Current and future potential habitats of REPs in Xishuangbanna

The mapping of potential habitat layers for the 24 selected REPs showed that the potential habitat of each REP differed in spatial distribution and area, but that most had some overlaps (Fig. 2). The hotspots of *Paramichelia baillonii, Cycas pectinata*, and *Brainea insignis* were found to be close to each other and they all had a large area of low probability of existence, almost covering the entire Xishuangbanna. The hotspots of *Mangifera sylvatica*, *Cibotium barometz*, *Dalbergia fusca*, and *Alsophila costularis* were mainly concentrated in the north-east. The hotspots of *Aglaia dasyclada*, *Eleutharrhena macrocarpa*, and *Toona ciliata* were scattered throughout Xishuangbanna, while the hotspots of *Fagopyrum dibotrys*, *Terminalia myriocarpa*, *Horsfieldia tetratepala*, *Magnolia henryi*, and *Alsophila gigantea* were mainly concentrated in the south-east. The main hotspots of *Pterospermum menglunense* and *Dracaena cochinchinensis* were distributed in the central part of Xishuangbanna. The hotspots of *Tetrameles nudiflora*, *Caryota urens*, *Myristica yunnanensis*, *Parashorea chinensis*, and *Parakmeria yunnanensis* were more similar, and were very small and distributed only in the east-central part of Xishuangbanna and at the periphery. Only *Trigonobalanus doichangensis* and *Alcimandra cathcartii* hotspots were concentrated in the west.

Superimposition of the binary maps showed the final hotspot of REPs in Xishuangbanna (Fig. 3). In terms of area, current hotspots with 1–5 REPs occupied 38.54% of Xishuangbanna's total area, while hotspots with 6–10 REPs covered 13.61%. Hotspots with more than 10 REPs made up the smallest area, just 1.99% of the total area. In terms of spatial distribution, the hotspots of REPs in Xishuangbanna were mainly concentrated in the east and south-east, while the distribution of REPs in the west was very small (Fig. 3A). The county with the largest area of hotspots with more than 10 REPs was Shangyong (178.48 km^2), followed by Mengla (115.43 km^2), Xiangming (17.39 km^2), Menglun (13.22 km^2), Yaoqu (11.20 km^2), Yiwu (10.58 km^2), and Mengyang (9.38 km^2).

According to the predictions, the potential habitats of REPs will be greatly reduced in future. The total area of hotspots with more than 5 REPs predicted for 2050 was 247.93 km^2 and the area of hotspots of more than 10 REPs in Xishuangbanna was only 2.78 km^2, 99.27% less than the current area. Hotspots with 6–10 REPs declined by 90.59%. The future hotspots were small and concentrated only in the south-east of Xishuangbanna. The county with most hotspots of >10 REPs in the future was found to be Shangyong, with these hotspots covering 2.49 km^2, accounting for 89.48% of all hotspots (>0 REPs) (Fig. 3B). In general terms, the hotspots of REPs in Xishuangbanna indicated a tendency to move to the south-east, and to become smaller in area and more scattered.

3.2. Potential habitat suitability assessment

The largest natural forest in Xishuangbanna is currently monsoon evergreen broad-leaved forest, with an area of 7015 km^2, accounting for 36.62% of the whole study area in 2016. There are also vast rubber plantations that occupy an area of 4847.49 km^2, accounting for 25.30% of the total area of Xishuangbanna in 2016. Cropland was the third largest land use in 2016, accounting for 11.61% of the total. The area of tea plantations was also large, much larger than that of many other natural forest types (Fig. S4). The land use and land cover extracted for the hotspots are shown in Fig. 4.

The main land cover in potential hotspot areas was monsoon evergreen broad-leaved forest, which accounted for 47.69% of total hotspot area, indicating that this type of forest is the main habitat of REPs in Xishuangbanna (Table S6). Among the artificial plantations, rubber plantation occupied the largest potential hotspot area, accounting for 23.40% of the total. Thus, rubber plantations were the greatest threat to potential habitats for REPs. Tea plantations were the second greatest threat, accounting for 2.48% of the total area of potential hotspots. Cropland covered 8.25% of potential hotspot habitat (Table S6).

3.3. Gap analysis and priority conservation identification

The area of current hotspots with more than 5 REPs covered by the existing PAs was 1071.03 km^2, while the area of these hotspots not protected by the PAs was 1918.82 km^2. The area of hotspots with more than 10 REPs in the PAs was 196.00 km^2, and the area outside the PAs was 185.78 km^2. In general, the area of protected hotspots only accounted for 35.85% of total hotspots, i.e., 64.15% of the total area of potential hotspots was unprotected. This means that existing PAs in Xishuangbanna are inadequate in protecting these REPs and there are still many conservation gaps (Fig. 5).

Among the current hotspots with more than 5 REPs, built area, water, cropland, rubber plantations, tea plantations, orchards, and other artificial forests occupied an area of 1107.56 km^2 (Table S6). On excluding these human-dominated land types, which are not suitable for the survival of REPs, a total of 1916.87 km^2 of hotspots were finally determined to be the highest priority for conservation. The priority conservation areas with the largest patch areas were mainly in south-central and east Shangyong National Nature Reserve and the north-east of Yiwu State-level Nature Reserve (Fig. 6A).

Under the impact of future climate change, by 2050 the total area of hotspots with more than 5 REPs will be reduced to 247.93 km^2, 91.70% less than the current hotspot area, of which 79.97 km^2 will be within the PAs and 167.96 km^2 are outside the PAs (Fig. S5). In the future, the most suitable patch habitat for REPs will still be monsoon evergreen broad-leaved forest (42.85%), while rubber forest (21.62%) will still be the greatest threat, followed by cropland (14.18%) (Fig. S6, Table S7). We removed artificial plantations (59.15 km^2), cropland (35.15 km^2), built area (4.93 km^2), and water (10.70 km^2) from hotspot area. A total of 138.01 km^2 of potential habitats were identified as priority conservation areas, located mainly in the south-east of Xishuangbanna, in the south-west and south-east of Shangyong National Nature Reserve (Fig. 6B).

In the future (2050), the potential habitats of REPs will change dramatically (Table 2). By 2050, only 19.48% of potential habitats with 1–5 REPs will remain, and about 80.01% will no longer be adapted to REPs. Only 4.23% of the potential habitats of 6–10 REPs will be retained, and 43.44% will become unadapted areas. In addition, the number of REPs in nearly half of the areas will be reduced to only 1–5. Of the potential habitats with more than 10 REPs, less than 0.50% of the area will remain, of which 25.28% will see the number of REPs reduced to 6–10, and more than half will see the number of REPs reduced to 1–5. In general, the adaptive habitat for REPs in Xishuangbanna will become increasingly less available under the influence of human disturbance and climate change. The specific transfer area is shown in Table S8.

4. Discussion

4.1. Conservation efficiency in existing PAs in Xishuangbanna needs to improve

Xishuangbanna Nature Reserve plays an important role in protecting tropical forests and local biodiversity, but does not fully consider the specific needs of REPs in the region. Our analysis showed that only 35.85% of REPs hotspots (with >5 REPs) are currently covered by the

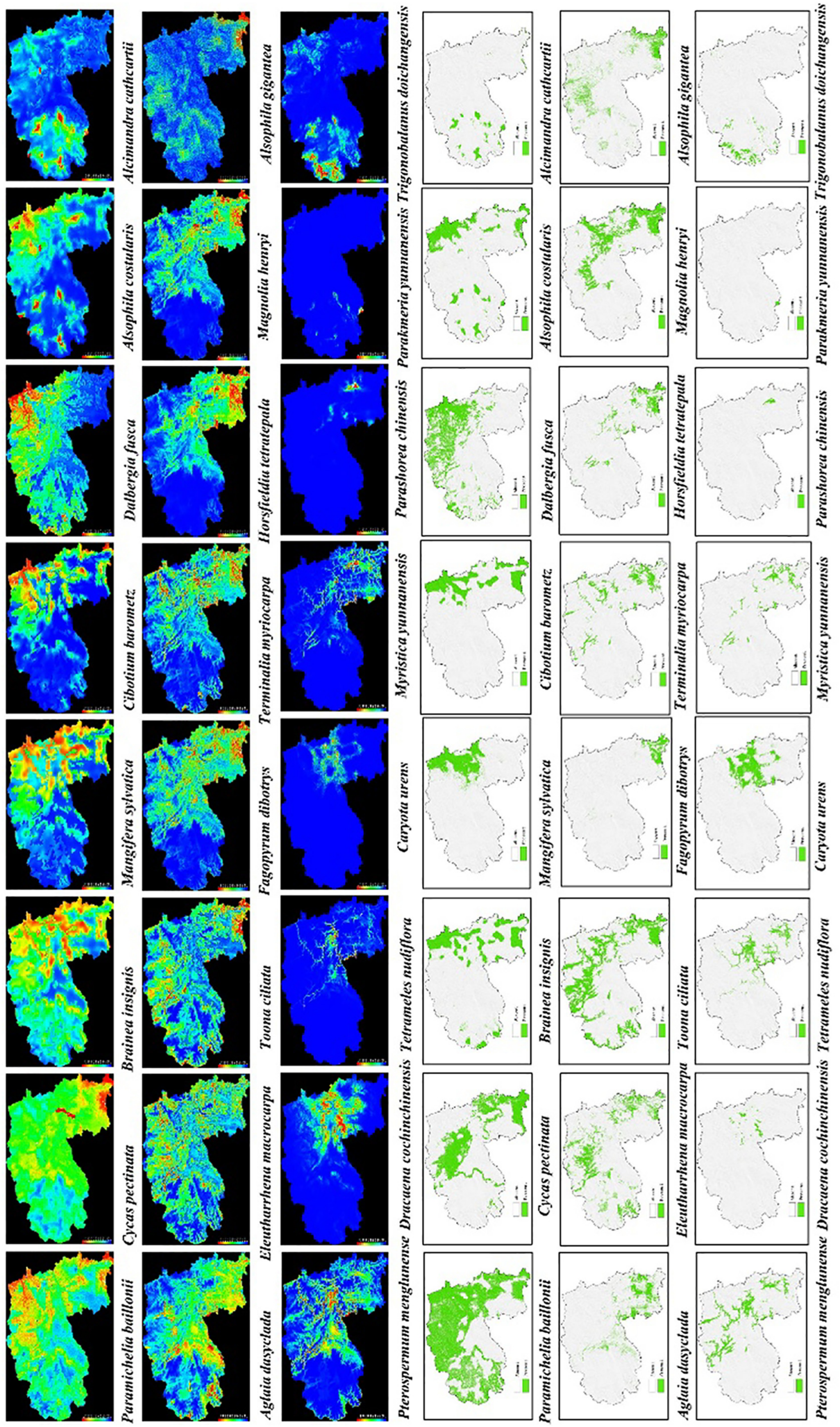

Fig. 2. Probability of presence (top) and binary maps (bottom) depicting current potential habitats of 24 selected rare and endangered plants (REPs) in Xishuangbanna, based on Maxent model output. Relative probability of REPs presence ranges from 0 to 1. Red areas have the highest predicted probability, followed by yellow and green areas, while blue areas have the lowest probability. In the binary maps, presence is indicated by green and absence by gray.

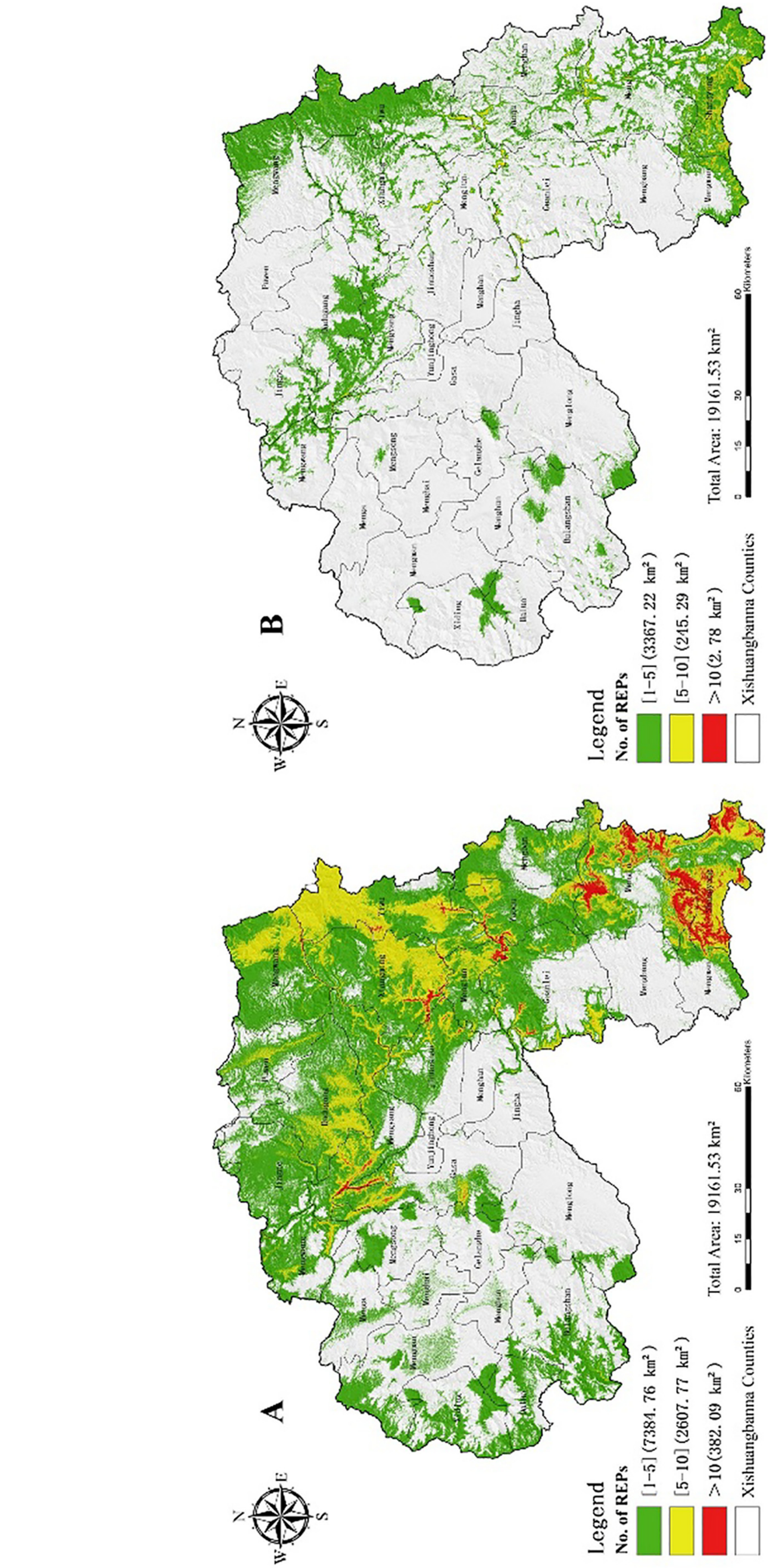

Fig. 3. Distribution of (A) current and (B) future potential hotspots of rare and endangered species (REPs) in Xishuangbanna, and the area of each hotspot. Green represents areas with 1–5 REPs, yellow areas with 6–10 REPs, and red areas with >10 REPs.

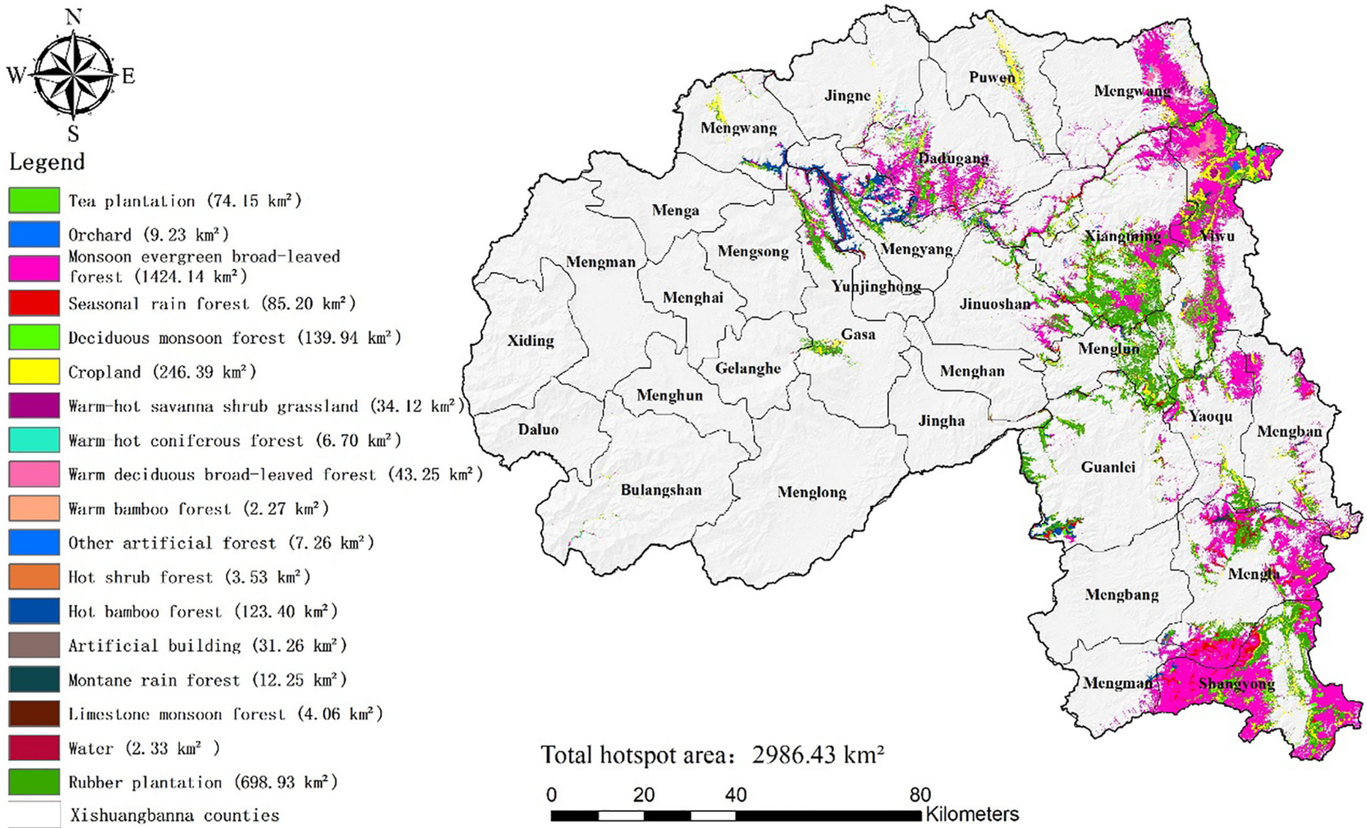

Fig. 4. Current land use/land cover in potential hotspots with >5 rare and endangered species (REPs) and the area occupied by these. Note: "Total hotspot area" is area of hotspots with >5 REPs.

eight existing PAs in Xishuangbanna, while the remaining 64.15% of the hotspots lie outside the PAs, without any conservation measures. Modeling showed that this conservation gap will increase to 67.74% by 2050, and it is likely to increase further over time.

Some existing PAs, such as Mangao National Nature Reserve and Bulong State-level Nature Reserve, do not contribute much to conservation of REPs and contain only small areas of potential habitats for REPs (Fig. 5). This means that conservation of REPs in existing PAs needs to be improved.

4.2. Human activities drive habitat fragmentation and loss

Human activities are the main cause of endangered species (López-Pujol et al., 2006). Human activities lead to changes in land use and land cover, and expansion of human land use is a serious threat to the natural habitat of endangered species (Olker et al., 2016; Dai et al., 2019). Xishuangbanna's forest cover has been reduced by deforestation, from more than 60% to less than 30% (Zhang and Cao, 1995). Due to the establishment of rubber plantations, a large area of natural forest in Xishuangbanna has been destroyed (Zhu, 1992; Li et al., 2007).

Our analysis showed that rubber forests currently occupy 23.40% (698.93 km^2) of the potential hotspot area for hotspots with more than 5 REPs. It is thus clear that rubber plantations are the greatest threat to the potential habitats of REPs in Xishuangbanna. Unfortunately, rubber plantation area in Xishuangbanna is predicted to expand to 75% by 2050, increasing the pressure on local biodiversity (Zomer et al., 2014). In addition, tea plantations, orchards, and other artificial forest types occupy 90.64 km^2 of potential hotspot area. The Xishuangbanna region is known for its many varieties of tea, and high prices have made tea an important resource for economic growth, leading to rapid replacement of wild habitats by tea plantations (Meng et al., 2019). In our field surveys, we found that tea plantations were even scattered in the primeval forest. The expansion of these artificial plantations has led to fragmentation of virgin forest, resulting in degradation or complete loss of suitable habitats for REPs.

Cropland currently accounts for 8.25% (246.39 km^2) of the potential hotspot area (hotspots with >5 REPs) in Xishuangbanna. It is clearly apparent that expansion of agriculture leads to fragmentation and loss of natural habitats. At the same time, ethnic minorities in the region have a long history of using wild plants, which has led to overexploitation of many plants with edible or medicinal properties (Cao et al., 2020b). These threats, together with the characteristics of REPs themselves, increase the risk of extinction of REPs in Xishuangbanna.

4.3. Climate change drives habitat shift

Most REPs are less resistant to change than common species, and may be strongly affected by climate change (Vincent et al., 2020). In addition, the habitats of REPs will be shifted under future climate change (Cao et al., 2020). From the potential habitat transfer matrix in Table 2, it can be seen that under future climate change (by 2050), there will be only 247.93 km^2 of hotspots with more than 5 REPs.

The conventional conservation approach is to protect habitats, but it does not take into account alterations in species habitats in response to environmental change. As can be seen from Table S8, 344.42 km^2 of the area currently free of REPs will have 1–5 REPs by 2050, and 3.44 km^2 will have 6–10 REPs. Out of an area that currently has 1–5 REPs, an area of 0.26 km^2 will have more than 10 REPs and a 34.91 km^2 area will have 6–10 REPs. In the current hotspots with 6–10 REPs, in an area of 1.73 km^2 the number of REPs will rise to more than 10. These changes show that hotspots of REPs are not static, but change in response to environment changes.

Areas with no or few REPs currently receiving no attention may become new hotspots in the future, while hotspots that are now suitable

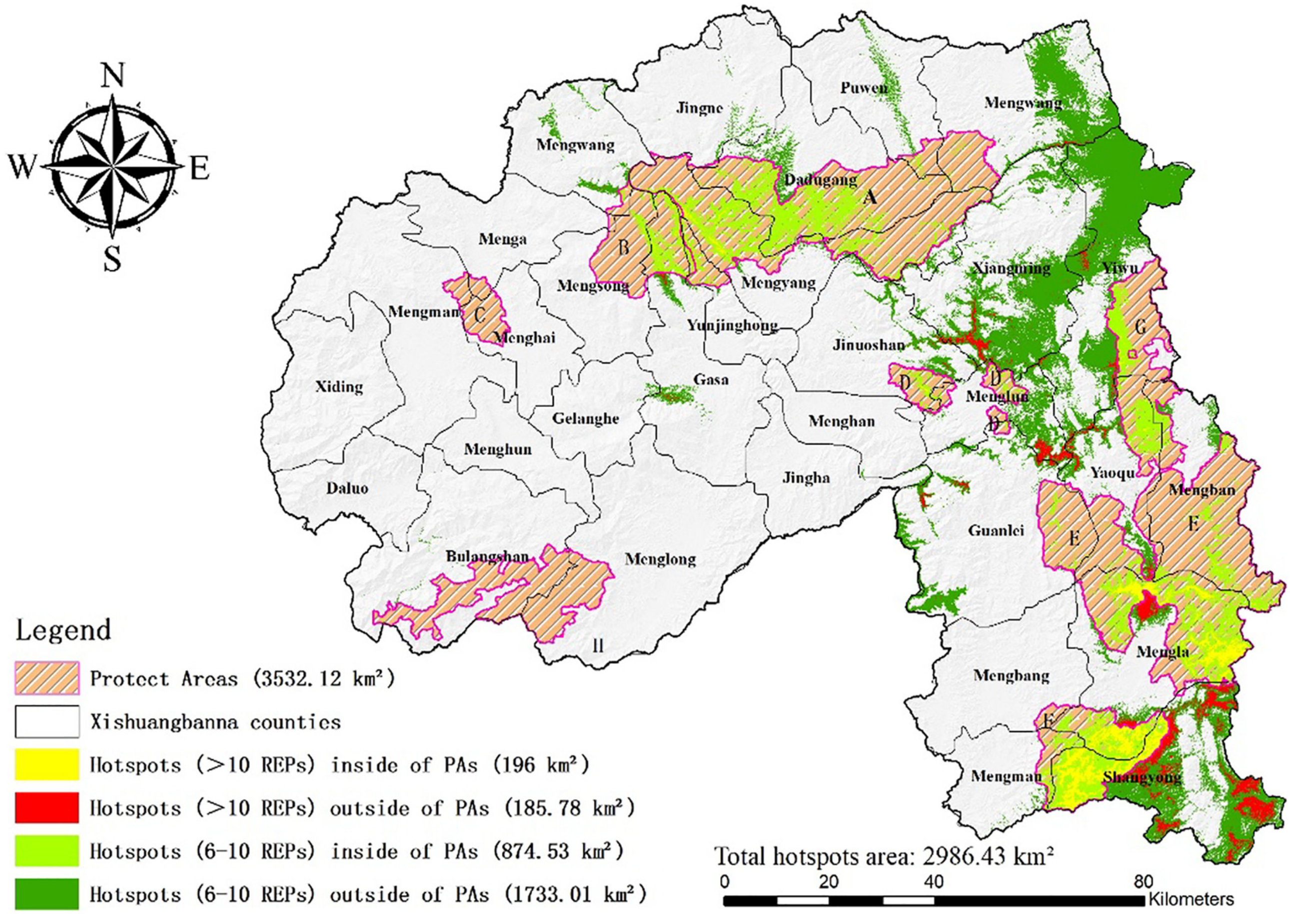

Fig. 5. Current conservation gaps for potential habitats of rare and endangered species (REPs) in Xishuangbanna. Area falling within and outside protected areas (PAs) is shown for two classes of hotspots, those with 6–10 REPs and those with >10 REPs. A) Mengyang National Nature Reserve, B) Nanban River National Nature Reserve, C) Mangao National Nature Reserve, D) Menglun National Nature Reserve, E) Mengla National Nature Reserve, F) Shangyong National Nature Reserve, G) Yiwu State-level Nature Reserve, H) Bulong State-level Nature Reserve.

for species may become inhospitable in the future. This requires establishers and managers of PAs to pay attention to protection of potential habitats of rare species during the planning phase. Instead of only considering the actual habitat of these species at present, they should seek to predict possible changes in the potential habitat of the species in the future, and to update the boundary of the PAs over time.

4.4. Conservation suggestions

For effective conservation of REPs in Xishuangbanna and beyond, we suggest the following six measures:

(1) Fill existing conservation gaps. This could be done by slightly expanding the existing PAs (Pollock et al., 2017) or setting up new PAs for large hotspots that are far from existing PAs.
(2) Protect and restore the integrity of monsoon evergreen broad-leaved forest. We identified this type of forest as the most important habitat patch for REPs in Xishuangbanna, so its management needs to be strengthened to protect the homeland of REPs.
(3) Replace the current pattern of land use by humans with diversified development, by preventing expansion of rubber and tea plantations into natural forests. We suggest use of Xishuangbanna's rich tropical flora and fauna resources and diversified minority cultures to develop ecological tourism. We also suggest making full use of Xishuangbanna's advantageous climate conditions, replacing low-yielding and low-price crops with tropical fruits of high economic value, and improving the income of local farmers.
(4) Establish protection actions at county level and strengthen conservation cooperation. In view of the narrow and scattered habitats of REPs, county-level conservation may be the best way to protect these plants. In addition, political borders often coincide with conservation gaps. Our results showed many hotspots of REPs at the boundaries of Xishuangbanna counties, so the focus should be on conservation cooperation at county level in order to better protect these cross-border hotspots.
(5) Strengthen legal constraints and market oversight. Relevant authorities need to strengthen the system of deterrents and e.g., severely punish those who reclaim virgin forests without permission or steal REPs and animals for market trade, so as to eliminate the excessive exploitation of REPs caused by economic interests.
(6) Strengthen monitoring and investigation of REPs in the wild, and determine the distribution trend of REPs over time.

4.5. Limitations of the research and future prospects

Use of accurate species distribution models is considered important in plant conservation (Gamal et al., 2020). The Maxent model only requires presence data, and not absence data (Elith et al., 2006). Even when the sample size is small, Maxent can obtain reliable prediction results (Hea-Jung et al., 2018). Many researchers have tested and confirmed that Maxent is reliable in modeling potential distribution of species (Phillips et al., 2006; Guisan et al., 2007). With the contribution of many users, the Maxent model is becoming one of the most powerful

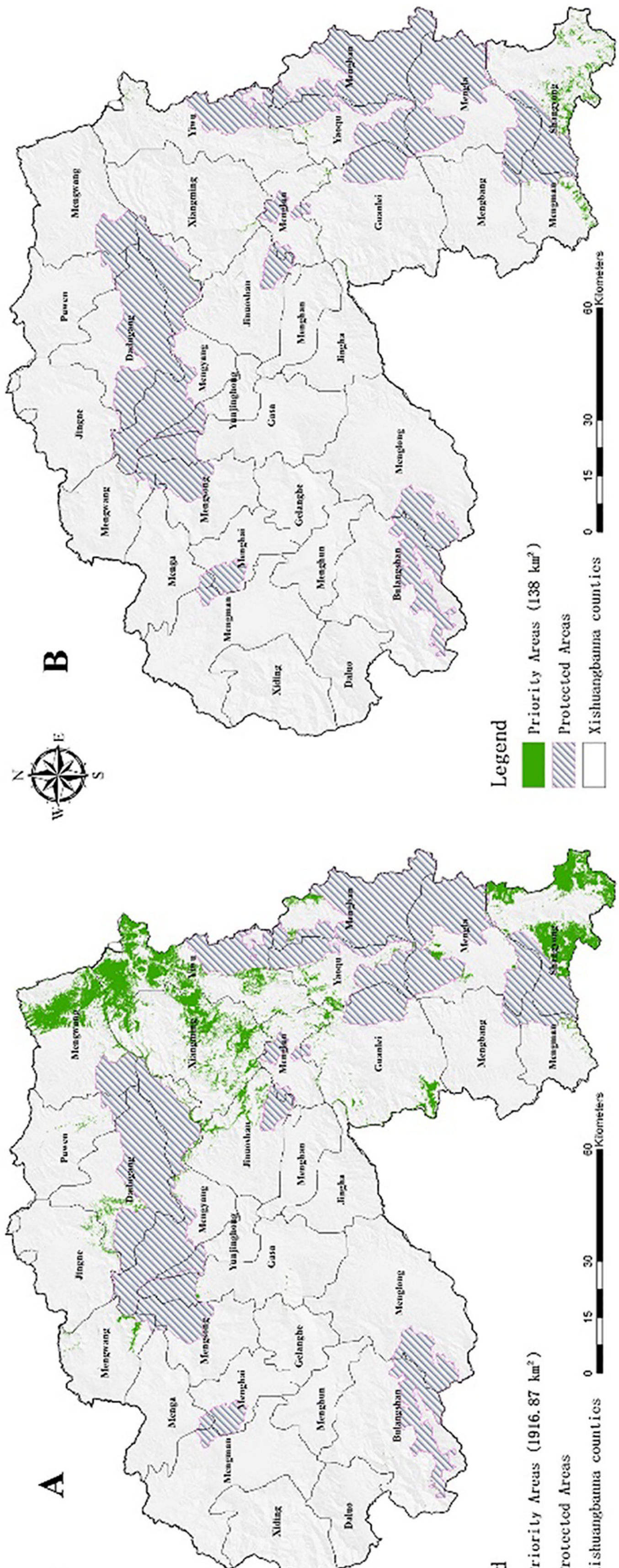

Fig. 6. Maps showing (A) current and (B) future priority conservation areas of potential habitats of rare and endangered species (REPs).

Table 2
Transfer matrix between potential habitats of rare and endangered plants (REPs) in Xishuangbanna from 2019 to 2050. Values in bold indicate proportion with no change.

		2050			
		No REPs	[1–5] REPs	[6–10] REPs	[>10] REPs
2019	No REPs	**96.04%**	3.92%	0.04%	0.00%
	[1–5] REPs	80.05%	**19.48%**	0.47%	0.00%
	[6–10] REPs	43.44%	52.30%	**4.23%**	0.03%
	[>10] REPs	16.50%	57.78%	25.28%	**0.45%**

tools for species habitat identification and future distribution prediction (Wan et al., 2020). However, the model also has an inherent flaw in that its predictions are based on the theoretical niche, rather than the actual niche (Kumar and Stohlgren, 2009; Pearson, 2010). In reality, a species may fail to disperse due to geographical barriers, human interference, or related competing species (Yang et al., 2013).

Some researchers have combined the Maxent model with ecological niche factor analysis (ENFA) and generalized linear models (GLM) (Rupprecht et al., 2011), resulting in higher accuracy of the simulation results. We only used the Maxent model, but the accuracy and verification results were good, indicating that our prediction results were reliable. However, it is undeniable that there will be some deviation in our results. In the process of our field investigation we encountered some geographical inaccessibility, which is bound to result in some areas with more coordinates and some areas with fewer coordinates, or even no records.

In addition, our field survey ran from April to June, and the phenological periods of plants differ. Some plants may be easily identified during this period, while others may not. Therefore, the number of coordinates collected for different plants will vary greatly, which will lead to deviations in the results. The only environmental variables we used were bioclimatic variables, topographic variables, and soil type, but the growth of plants is also determined by soil nutrients (Gao et al., 2019), microorganisms (Xu et al., 2020), etc. Data on other variables were difficult to obtain, which meant the variables we used do not meet the actual needs of REPs.

Competition is a common interaction for plant species (Farji-Brener and Lescano, 2017). There may be competition in the overlapping portions of each REP's potential habitat, and our habitat hotspots are no exception to this inherent influence. However, the Maxent model focuses on the spatial adaptability of REPs, so it is difficult to reflect the competitive relationship among REPs (Liu et al., 2019). Future studies should explore the effects of competition among REPs on their spatial distribution, in order to improve the performance of the model. For anthropogenic disturbance, we only analyzed the impacts of land use on potential habitats, while other studies have also considered the threats posed by grazing, population, and road development to potential habitats of REPs (Han et al., 2019).

In addition, our analysis focused only on REPs as a group, but some REPs rely on insects for pollination (Ma et al., 2009; Liu et al., 2020), some require special mycorrhizal fungi to facilitate germination of their seeds (Yang et al., 2020b), and some need animals as important seed dispersers (Tang et al., 2008; CAO et al., 2011). Mammals in Xishuangbanna also face many threats (Huang et al., 2020a), but our study did not cover protection of animals. Future research should focus simultaneously on key insect pollinators, fungi, and endangered animals, with the aim of protecting multiple target species. This may be more effective in protecting these rare and endangered species, and all local biodiversity.

5. Conclusions

We used the Maxent model to identify potential habitats for REPs in Xishuangbanna, China. The results indicated that existing PAs in Xishuangbanna only cover 35.85% of the current potential habitat hotspots for REPs, with more than half of hotspots remaining unprotected. By 2050, the area of hotspots with >5 REPs will be reduced to 247.93 km^2, with 79.97 km^2 within PAs and 167.96 km^2 outside PAs. The existing PAs are thus not effective in protecting REPs, and immediate measures are needed. Xishuangbanna's REPs have been seriously affected by human land use, with expansion of artificial plantations and agricultural land being the main reasons for loss of habitat. Based on existing conservation gaps and land use and cover data, the area of current priority conservation was identified as 1916.87 km^2 and the area of future (2050) priority conservation as 138.00 km^2. Climate change is another driving force of REPs habitat changes. Using a transfer matrix, we showed that there will be a future shift between different potential habitats. Developing dynamic conservation strategies is critical in the face of climate change, and of great significance to conservation of REPs habitats in Xishuangbanna and other regions.

CRediT authorship contribution statement

Zongbao Yang: Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Yang Bai:** Conceptualization, Funding acquisition, Supervision, Validation, Writing – original draft, Writing – review & editing. **Juha M. Alatalo:** Writing – original draft, Writing – review & editing. **Zhongde Huang:** Writing – review & editing. **Fen Yang:** Writing – review & editing. **Xiaoyan Pu:** Writing – review & editing. **Ruibo Wang:** Writing – review & editing. **Wei Yang:** Writing – review & editing. **Xueyan Guo:** Writing – review & editing.

Declaration of competing interest

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.

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Appendix A. Supplementary data

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