Journal for Nature Conservation 68 (2022) 126197

Contents lists available at ScienceDirect

Journal for Nature Conservation

journal homepage: www.elsevier.com/locate/jnc

Historical plant records enlighten the conservation efforts of ferns and Lycophytes' diversity in tropical China

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A R T I C L E I N F O

Keywords:
Pteridophytes
Collecting history
Endemism
Protected areas

A B S T R A C T

Historical records, e.g., herbarium vouchers, contain information about species distribution since the early days of the scientific exploration of floras until today. These data provide crucial evidence to map the biodiversity of the area of interest and most importantly enable the evaluation of the conservation effectiveness for a given group of organisms. This study aimed to explore the ferns and lycophytes' diversity of Xishuangbanna Dai Autonomous Prefecture in tropical China with special emphasis on conservation efforts provided by the currently established protected areas (PAs). Instead of relying exclusively on current observation, the database was compiled from digitalized herbarium vouchers and publications being explored with special attention on the temporal and spatial dimensions of collecting efforts. Utilizing the indices including species richness, weighed endemism, corrected weighted endemism, and beta diversity, hotspots of ferns and lycophytes' diversity were identified. In turn, the proportion of hotspots located outside PAs was estimated as a measure of conservation gaps in Xishuangbanna. Our results revealed a long collecting history of ferns and lycophytes in Xishuangbanna and this prefecture accumulated a considerable number of historical records covering 20.2 % of Chinese and 3.6% of global fern diversity. The accumulation of historical records showed strong parallelism to the historical events shaping modern China. The spatial distribution of ferns and lycophytes in Xishuangbanna was characterized by a concentration of species richness in southern valleys and endemism in western and northern mountains. In terms of conservation, existing PAs showed higher effectiveness in the protection of species richness, whereas lower effectiveness was observed in the protection of endemism and beta diversity. Our research provided a key reference for understanding the diversity and conservation of ferns and lycophytes in Xishuangbanna, as well as highlighting the locality for future collecting and conservation efforts.

1. Introduction

The ongoing biodiversity crisis resulting in a rapid loss of species globally and regionally by extinction (Butchart et al., 2010; Johnson et al., 2017) threatens the integrity of the ecosystem underpinning human health and well-being (Cardinale et al., 2012; Humphreys et al.,2019; Turner et al., 2007). The establishment of protected areas (PAs) worldwide has been one of the proven and widely favored strategies for halting, easing, and having potential for reversing the trend of species loss that has arguably been caused by habitat loss and degradation (CBD, 2018; Pouzols et al., 2014; Saout et al., 2013; WWF, 2020). The global coverage of PAs is approaching Aichi Target 11 to conserve at least 17% of terrestrial and inland waters, and 10% of coastal and marine areas, which is likely to be surpassed in the near future (UNEP-WCMC & IUCN, 2021). To fully realize the benefits of PAs including their crucial role in Convention on Biological Diversity (CBD) vision of "Living in Harmony with Nature" by 2050 (CBD, 2021), the evaluation of the conservation effectiveness of PAs is an indispensable step (Coad et al., 2015; Stoll-Kleemann, 2010; Watson et al., 2016).

Gap analysis designed to assess the coverage of biodiversity by existing PAs is one of the crucial steps to obtain important insights into the degree of PAs' effectiveness (Brooks et al., 2004; Rodrigues et al., 2004; Tuvi et al., 2011). These analyses are crucial as a reference for the management of existing PAs and future expansion of PAs by identifying priority areas for biodiversity conservation (Brooks et al., 2004; Rodrigues et al., 2004; Venter et al., 2014). Besides recording the current distribution effected by landscape transformation, historical records, e. g., herbarium vouchers document the temporal and spatial distribution of species (Nualart et al., 2017), performing as vital data sources for gap analysis (Daru et al., 2019; Xu et al., 2021; Yu et al., 2017). Species

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https://doi.org/10.1016/j.jnc.2022.126197
Received 11 January 2022; Received in revised form 2 May 2022; Accepted 3 May 2022
Available online 10 May 2022
1617-1381/

richness has been frequently employed in such gap analysis (Brooks et al., 2004; Gary et al., 2019; Xu et al., 2021), whereas other biodiversity indices such as endemism assessing range-size rarity (Kessler et al., 2001) and beta diversity depicting variation in community composition (Whittaker, 1960) have been less frequently employed although they enhance our understanding of biodiversity by addressing different aspects of biodiversity being critical to conservation priority settings (Fleishman et al., 2006). Until now, some preferences have been given to access terrestrial vertebrates (Brooks et al., 2004; Rodrigues, Andelman, et al., 2004; Venter et al., 2014) and tree species (Cumming et al., 2015; Lipow et al., 2004; Thakur et al., 2018) excluding many lineages with a major contribution to ecosystem functioning. For instance, ferns and lycophytes are major contributors to terrestrial ecosystems by affecting several ecological processes such as water balance (Ambrose, 2004), nutrient cycling (Mehltreter et al., 2010), carbon storage (Lyu et al., 2019), and succession (Coomes et al., 2005). Additionally, they have proved to be an ideal group for gap analysis in recent studies (de Souza et al., 2021; Heringer et al., 2020).

The tropics have been widely considered to be key regions for global biodiversity conservation (Collen et al., 2008; Kessler et al., 2009; Meyer et al., 2015; Mittermeier et al., 1998) by accommodating a disproportionately large amount of biodiversity on earth (Gaston, 2000; Mutke & Barthlott, 2005). Southern Yunnan marks not only the northern border of the Indo-Burma Biodiversity Hotspot (Myers et al., 2000) but also contributes extensively to the tropical plant diversity occurring in China (Zhu, 2013). In particular, the Xishuangbanna Dai Autonomous Prefecture — for simplicity henceforth called "Xishuangbanna" — is highly renowned as the most biodiverse region in tropical China (Guo et al., 2002; Li et al., 2007) by accounting for nearly 16% of China's plants diversity (Li et al., 1984), 21.7% of mammals (Xu et al., 1987) and 36.2% of birds (Xu et al., 1987) despite covering only 0.2% of the country's land area. Besides, this prefecture accommodates the largest area of tropical rainforest in China (Guo et al., 2002). To conserve this extraordinary rich biodiversity, more than 20% of Xishuangbanna's land has been protected in PAs (Hammond et al., 2015). However, biodiversity loss in Xishuangbanna, even within PAs, is accelerating due to recent land-use upheaval caused by the continuous expansion of rubber plantations and rapid urbanization (Guo et al., 2002; Li et al., 2009; Sarathchandra et al., 2018), while the conservation effectiveness of PAs in this region still requires further investigation.

Previous studies conducted in Xishuangbanna highlighted the efficiency of PAs using endangered plant groups (Huang et al., 2020; Yang et al., 2021), hence including a limited number of ferns and lycophytes. In contrast, this study has been designed to explore the effectiveness of the PAs by focusing on a gap analysis covering all ferns and lycophytes recorded in Xishuangbanna. Specifically, we aimed to obtain: 1) the current knowledge of ferns and lycophytes' collections in Xishuangbanna by exploring the accumulation of historical records in Xishuangbanna; 2) spatial distribution and hotspots of ferns and lycophytes' diversity in Xishuangbanna; 3) effectiveness of PAs and conservation gaps considering the spatial and temporal distribution of ferns and lycophytes' diversity in Xishuangbanna.

2. Materials and methods

2.1. Study area

Xishuangbanna is located in the southwest of China sharing its border with Laos in the south and southeast, and Myanmar in the southwest (Fig. 1). The political structure of the prefecture consists of 1 city (Jinghong) and 2 counties (Menghai, Mengla) — that are further divided into 32 towns and similar administrative units respectively (Fig S1). The topography of Xishuangbanna is heterogenous with unevenly distributed high mountains and deep valleys ranging from 460 m to 2,431 m above sea level (Fig S1). Xishuangbanna is dominated by a tropical monsoon climate, with an annual mean temperature of 21 °C and annual precipitation of about 1,500 mm and a pronounced rainy season from May to October contributing about 90% of the annual rainfall (Hammond et al., 2015). Due to the complex topography, the local climate varies both horizontally and vertically, resulting in a strong differentiation of vegetation types and ecosystem functioning (Fang et al., 2020). Generally, the natural vegetation in Xishuangbanna is classified into four forest types (Fig S1): (1) tropical rain forest, (2) tropical seasonal moist forest, (3) tropical monsoon forest, and (4) tropical montane evergreen broad-leaved forest. The tropical montane evergreen broad-leaved forest is the dominant forest in Xishuangbanna, which is usually found above 900 m. The tropical seasonal moist forest is restricted to the limestone mountains mainly found in the vicinity of Menglun (Mengla County). The tropical monsoon forest occurs along the banks of major rivers, e.g., Lancang River, whereas tropical rain forests are mainly distributed in the humid valley below 1,000 m in the southeast of the prefecture (Zhang & Cao, 1995; Zhu et al., 2015).

2.2. Protected areas (PAs) in Xishuangbanna

In 1958, Xishuangbanna's first national nature reserve i.e., Xishuangbanna National Nature Reserve was established to protect the rich biodiversity and tropical forest ecosystem (Xu et al., 1987). The PA

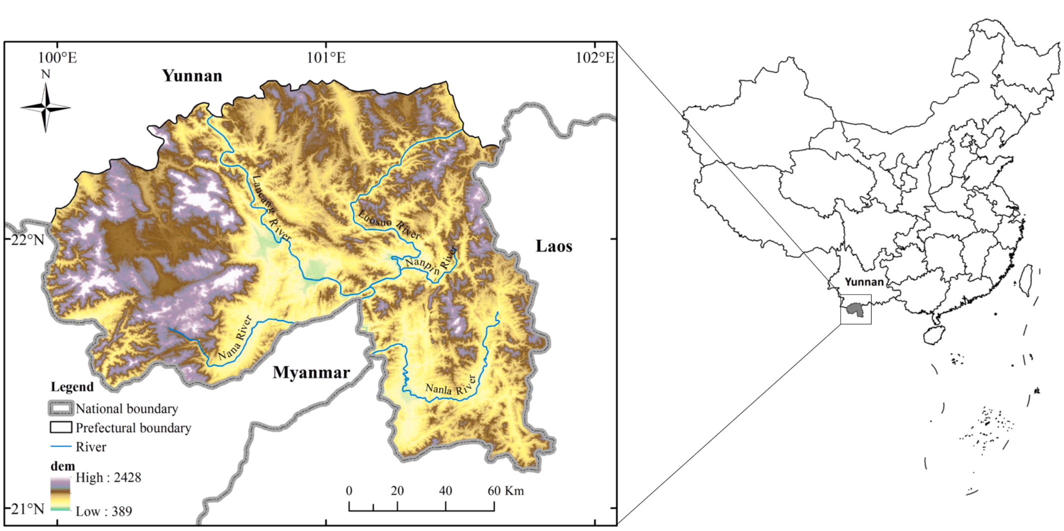

Fig. 1. The location of Xishuangbanna Dai Autonomous Prefecture (Yunnan, China).

consisted of four unconnected sub-reserves located in the town of Mengyang, Menglun, Mengla and Menglong (Xu et al., 1987) but the last reserve was canceled in 1980 due to the serious damage by human activities such as rubber planting (Xu et al., 1987). Two new sub-reserves i.e., Mangao and Shangyong sub-reserve were added subsequently (Wang, 2010). The Naban River Watershed National Nature Reserve established in 1991 (Wang, 2010), is the second national nature reserve in Xishuangbanna, which is located on the west side of Lancang River and close to the Mengyang sub-reserve on the east side (Fig S1). This reserve is the first nature reserve being managed with the concept of small watershed biosphere protection in China. The ownership of forests, administrative divisions, and residents remain unchanged to achieve the goal of sustainable utilization of natural resources and harmonious coexistence with nature (Wang, 2010). Besides these national nature reserves, there are several other types of PAs in Xishuangbanna, such as prefectural nature reserves, which are playing an increasingly important role in the protection of Xishuangbanna's biodiversity (Wang, 2010). Two new PAs, i.e., Bulong Prefectural Nature Reserve on the southwest border and Yiwu Prefectural Nature Reserve on the eastern border, were established in 2009 (Su & He, 2016) and 2014 (He & He, 2017), respectively. Both reserves were set up to protect a considerable area of tropical forests that are home to several rare animals and plants (He & He, 2017; Su & He, 2016).

2.3. Assembling of historical records

To compile historical records of ferns and lycophytes in Xishuangbanna, we integrated the data from the Chinese Virtual Herbarium (CVH, https://www.cvh.ac.cn/), National Specimen Information Infrastructure (NSII, https://www.nsii.org.cn/), Global Biodiversity Information Facility (GBIF, https://www.gbif.org/), and several studies published in the recent years (Cicuzza, 2021; Li & Zhu, 2005; Li & Zhu, 2009; Li et al., 2008; Phoutthavong et al., 2019; Zhao et al., 2015). The collecting time of historical records was proofread according to the digital photos of herbarium vouchers, whereas geographical references of historical records were manually checked by plotting these records on the Xishuangbanna's map using ArcMap 10.7 (https://www.esri.com/). Specifically, records with ambiguous or potentially erroneous geographical references, such as records plotted outside Xishuangbanna, were double-checked with the aim to correct the coordinates. Records without geographical references were assigned to closest coordinates of the locations, usually villages or geographic landmarks, named in the detailed description of collecting sites (Khine & Schneider, 2020). Species names of historical records were firstly resolved by the Taxonomic Name Resolution Service v 5.0 (TNRS, https://tnrs.biendata.org/). In case of errors in species identification, digital photos and geographical distribution of each species were verified according to the description in Flora of China (https://www.iplant.cn/foc), complemented by Flora Reipublicae Popularis Sinicae (https://www.iplant.cn/frps) and Flora Yunnanica (https://db.kib.ac.cn/YNFLORA/SearchEngine.aspx). Taxon identification followed the family and genera classification of the Pteridophyte Phylogeny Group (PPG I, 2016), and species determination according to Flora of China (https://www.iplant.cn/foc). The endemism status of each species derived from historical records was assessed by the description of species ranges as given in Flora of China, Flora Reipublicae Popularis Sinicae and Flora Yunnanica. The threat status of each species was referenced to Species Red List of Yunnan Province (https://bio360.kun.ac.cn/index/redlist), supplemented by the Information System of Chinese Rare and Endangered Plants (https://www.iplant.cn/rep/protlist).

2.4. Temporal and spatial distribution of historical records

To visualize the temporal accumulation of historical records in Xishuangbanna, the sum of records per year was firstly calculated and assigned to twenty years' intervals. e.g., before 1940, 1940–1959, 1960–1979, 1980–1999 and 2000–2020. To reveal the spatial distribution of historical records in Xishuangbanna, the number of historical records at different time intervals were visualized on the map of Xishuangbanna at a grid scale of $0.05^{\circ} \times 0.05^{\circ}$ ($\approx$ 5 km $\times$ 5 km). The relationship between collecting sites and altitude, as well as main roads in Xishuangbanna were mapped using the Digital Elevation Model (ASTER Science Team, 2019) and the main roads map of Xishuangbanna (https://www.webmap.cn/) in Arcmap v.10.7.

2.5. Spatial distribution, hotspots and conservation gaps

To explore the distribution of ferns and lycophytes' diversity in Xishuangbanna, a spatial analysis at a grid scale of $0.05^{\circ} \times 0.05^{\circ}$ was performed in Biodiverse v 3.1 (Laffan et al., 2010). Four diversity indices, namely species richness representing the sum of the number of distinct/unique species occurring in a grid cell, weighted endemism representing the sum of the inverse of the range size of each species in a grid cell, corrected weighted endemism representing the weighted endemism divided by the species richness in a grid cell, and beta diversity representing a measurement of the pairwise compositional differences without the influence of richness gradients (Simpson dissimilarity index) were calculated to depict the species diversity, endemism, and turnover for ferns and lycophytes in Xishuangbanna. The definition and formula for each index were explained in the supplementary. The correlation between indices were observed using Pearson correlation coefficient. Diversity hotspots for conservation priorities were defined by the grid cells with the highest 10% value of the four biodiversity indices (Lennon et al., 2001; Xu et al., 2021; Yu et al., 2017). Conservation gaps considering the proportion of hotspots located outside PAs were identified by overlaying the hotspots with the map of the exiting PAs in Xishuangbanna. Hotspots partially overlapping with PAs were considered protected by PAs.

3. Results

In total, 12,655 historical records of ferns and lycophytes in Xishuangbanna were assessed, of which 89% were derived from digital herbarium vouchers and 11% from published documents. After addressing species identity, 429 species belonging to 30 families and 89 genera were occurred in Xishuangbanna (Table S2). The five most species-rich families, e.g., Polypodiaceae (67 spp.), Pteridaceae (57 spp.), Dryopteridaceae (51 spp.), Thelypteridaceae (39 spp.), and Athyriaceae (33 spp.), contained 58% of recorded species. The five most species-rich genera were *Pteris* (26 spp.), *Asplenium* (24 spp.), *Selaginella* (24 spp.), *Tectaria* (20 spp.), and *Diplazium* (18 spp.), contributing 26% of the species diversity. Forty-six species recorded in Xishuangbanna are endemic to China, of which 10 species, namely *Arachniodes fengii*, *Arachniodes pseudoassamica*, *Bolbitis confertifolia*, *Cyrtomium latifalcatum*, *Leptochilus mengsongensis*, *Microlepia crassa*, *Polystichum paradeltodon*, *Pteris menglaensis*, *Pteris subquinata*, and *Pteris undulatipinna*, were only found in Xishuangbanna (Table S2). More than ten percent of the species, i.e., 49 spp., were assessed to be threatened (Table S2), of which 6, 12, and 31 were "Critically Endangered" (CR), "Endangered" (EN) and "Vulnerable" (VU), respectively. Among these threatened species, 5 species were endemic to Xishuangbanna: *A. fengii*, *P. paradeltodon*, *C. latifalcatum*, *P. undulatipinna*, and *L. mengsongensis* (Table S2). Notably, eleven percent of recorded species were assigned as "Data Deficient" (DD) due to insufficient data and changes in taxonomic status.

3.1. Accumulation of historical records of ferns and lycophytes in Xishuangbanna

Of the 12,655 records in Xishuangbanna, 11,838 provided sufficient information for collecting year and location to determine the spatial and temporal variation of the historical records (Fig. 2A, 2B, 2C). Three explicit troughs (before 1936, 1937–1952 and 1962–1974) and three

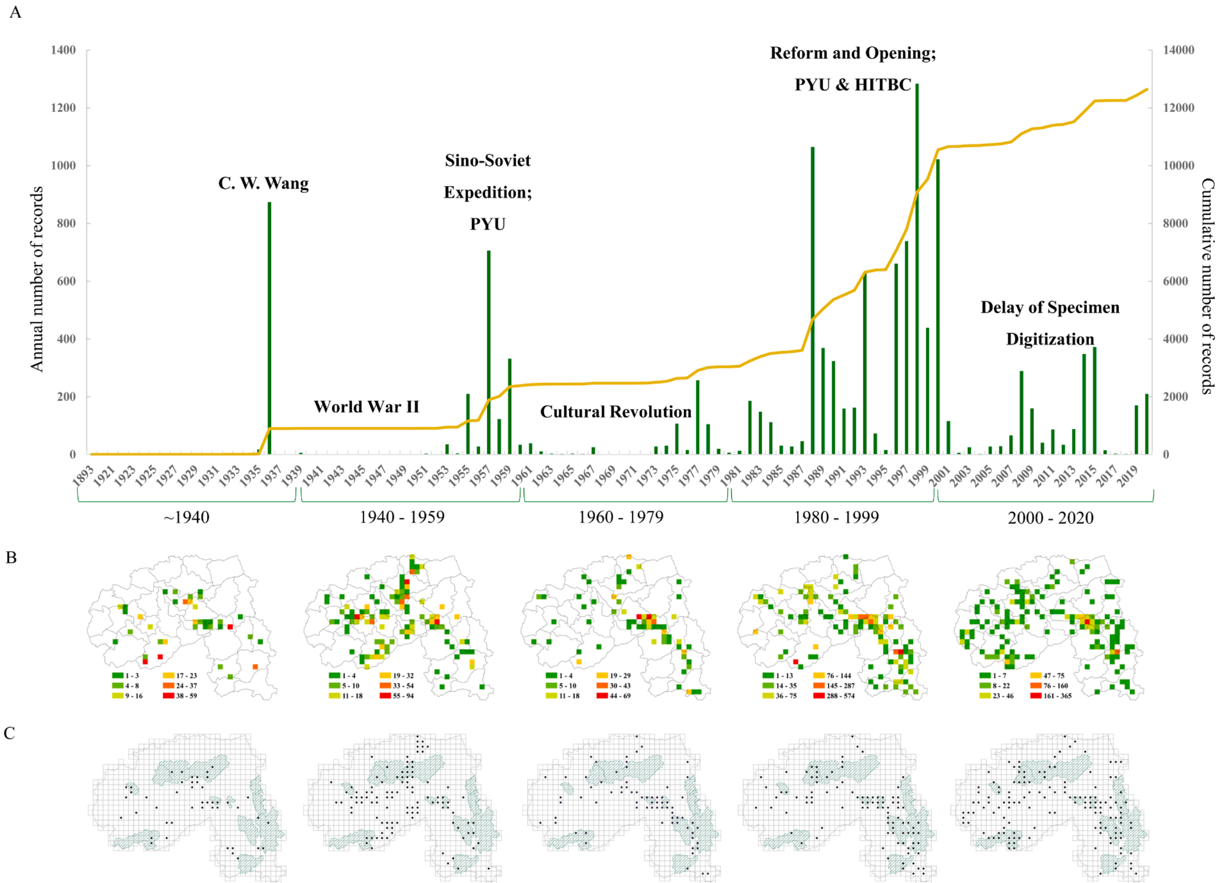

Fig. 2. Temporal Accumulation of Historical Records: (A) Accumulation of records plotted over a timeline from 1893 to 2020 which was divided into five time intervals to visualize the historical records obtained (1) before 1940, (2) from 1940 to 1959, (3) from 1960 to 1979, (4) from 1980 to 1999, and (5) from 2000 to 2020. The accumulative graph (yellow) exhibits the assembly of the total number of records over time using a scale from 0 to 14,000 (right scale) whereas the green columns illustrate the number of records per year using a scale from 0 to 1,400 (left scale). Periods with major and few collecting efforts are marked with their coincidence to major historical events; (B) Distribution of the records plotted using grid cells of 0.05° × 0.05° (≈ 5 km × 5 km) divided into the same time interval as Fig. 2A. The color gradient from low (green) to high (red) visualizes the contribution of the cells to the total amount of records during the interval. (C) Distribution of the collecting sites plotted using the grid cells and periods employed in Fig. 2A with the distribution of protected areas visualized (dark green). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

main peaks (1936, 1955–1960 and 1988–2000) of fern collecting were observed in Xishuangbanna (Fig. 2A). About 71.5% of the historical records were contributed by collections after 1988, especially as a consequence of a sharp increase in research activities between 1988 and 2000 (Fig. 2A). Entering the 21st century, an obvious decline in the accumulation of historical records was observed (Fig. 2A). In terms of the spatial distribution, a large number of historical records were obtained from collecting sites located at hot-humid valleys or basins in the south, whereas fewer records originated from the mountains in the west and north (Fig. 2B). Specifically, before the 1960 s, most collecting sites of the historical records were clustered in the lowlands or areas closer to main roads providing access, such as Mengyang town, Menglun town and Menglong town (Fig. 2B, S2). After the 1960 s, the collecting sites tended to occur in high mountains or more remote areas in the southwest and southeast (Fig. 2B, S2). Although the annual number of historical records declined after 2000, these collecting efforts covered more sites of Xishuangbanna compared to previous temporal periods (Fig. 2B, 2C).

3.2. *Spatial distribution of ferns and lycophytes' diversity in Xishuangbanna*

Grid cells with high species richness occurred mostly in the southwest and southeast of Xishuangbanna such as in the basin of Menglun town, Bubeng village and Mengsong village (Fig. 3A). The spatial distribution of weighted endemism highly correlated with that of species richness ($r = 0.90$) resulting in grid cells with a high number of both indices (Fig. 3A, 3B). Grid cells with a high value of corrected weighted endemism were scattered across the mountains, especially those located in the western and northern parts of Xishuangbanna, where the values of species richness and weighted endemism were relatively low (Fig. 3A, 3B, 3C). Thus, corrected weighted endemism had weaker relationship with species richness ($r = 0.25$). Spatial distribution of beta diversity showed an extent of similarity with that of corrected weighted endemism ($r = 0.35$) (Fig. 3C, 3D). The monotonic correlation between the threatened species and other indices such as number of endemic species, species richness, and weighted endemism richness is $r = 0.57$, 0.69, and 0.66, respectively, therefore this index is excluded from the assessment of PA's effectiveness and conservation gaps.

3.3. *Hotspots, conservation gaps and effectiveness of PAs for ferns and lycophytes*

Hotspots of species richness and weighted endemism were mainly located along river valleys and within mountain basins in the eastern part, namely Menglun town (at the intersection of Luosuo River and Nanpin River), Mengyang town and Mandian village (on the bank of Lancang River), and Bubeng village (on the bank of Nanla River). Furthermore, both hotspots were common in the limestone regions surrounding Menglun town, such as Mengxing village, Mengyuan village

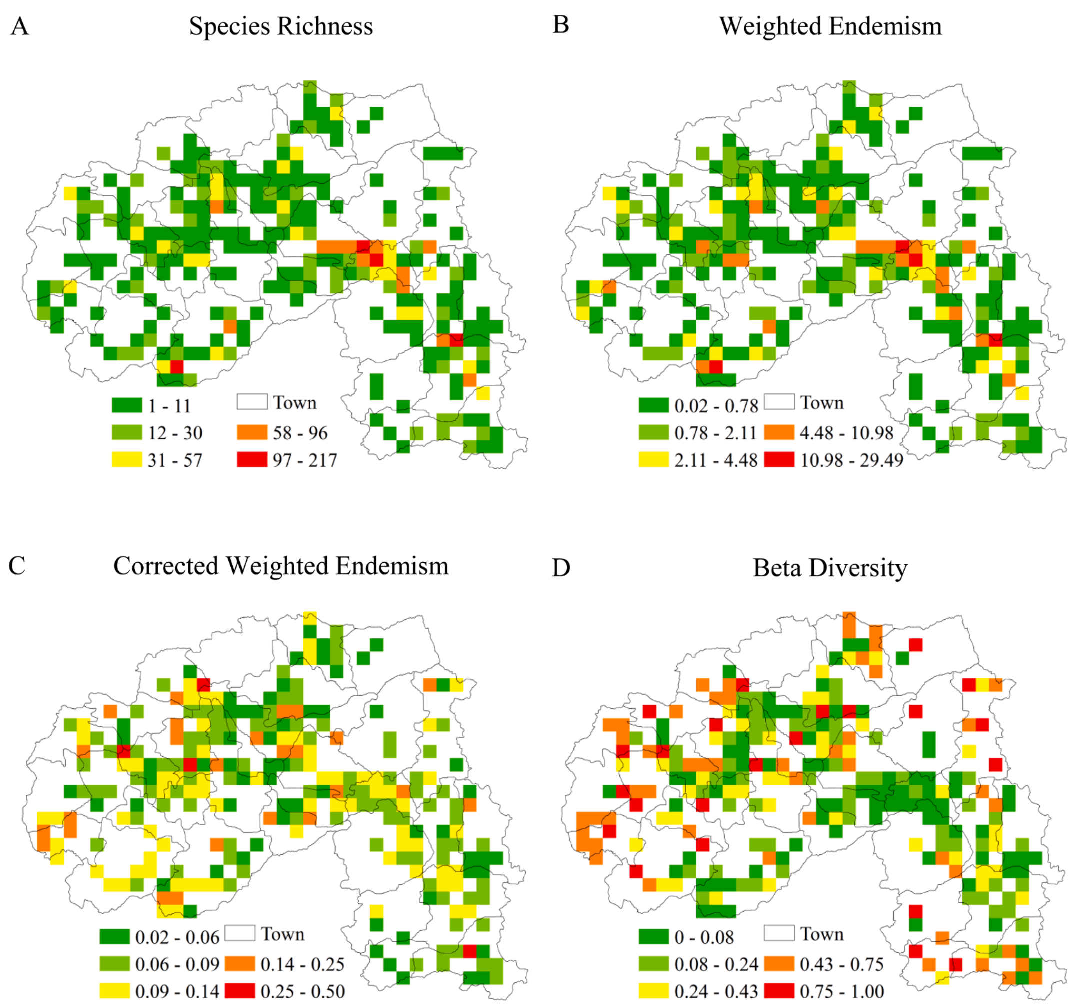

Fig. 3. Spatial Distribution of Ferns and Lycophytes' Diversity (FLD) in Xishuangbanna plotted against a grid cell resolution of 0.05° × 0.05° (≈ 5 km × 5 km). Four different indices were employed to characterize the FLD and visualized using a continuous color gradient ranging from green (lowest values) to red (highest value). (A) species richness (SR), (B) weighted endemism (WE), (C) corrected weighted endemism (CWE), (D) beta diversity (BD). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and Yiwu town (Fig. 4A, 4B, S1, S3). In contrast, hotspots of corrected weighted endemism and beta diversity were scattered on the western plateaus and mountains (Fig. 4C, 4D, S3). Notably, the western border of Xishuangbanna was defined as the diversity hotspot for all dimensions, especially in the Hesong village experiencing the overlap of all diversity indices. The conservation gaps were identified for each of the four diversity indices (Fig. 4A, 4B, 4C, 4D) and the consensus of all four indices (Fig. 4E). The existing PAs in Xishuangbanna covered 45% of all hotspots, 62% of species richness and weighted endemism hotspots (Fig. 5A). Hotspots defined by corrected weighed endemism and beta diversity were less covered by PAs, i.e., 42% and 35% respectively (Fig. 5A). In terms of species, 86% (367 spp.) of the total species, 78% (38 spp.) of the threatened species, and 65% (30 spp.) of the endemic species were allocated in PAs (Fig. 5B). Among all PAs, Bulong Prefectural Nature Reserve, Naban River Watershed National Nature Reserve, Menglun Sub-Reserve, and Mengla Sub-Reserve of Xishuangbanna National Nature Reserve played an important role in the conservation of ferns and lycophytes in Xishuangbanna regarding the highest number of historical records, total species, threatened species and endemic species (Table S2). Among these 367 species protected inside PAs, nearly 60% (216 spp.) of the species occurred only in one or two reserves, and only two species (i.e., *Pteris esquirioli* and *Cibotium barometz*) were found in seven reserves (Table S2). None of the species recorded were shared among all eight reserves (Table S2).

4. Discussion

Historical records, including herbaria records, are invaluable for the scientific community and society to have the better understanding of biodiversity and distribution patterns. Despite the in general positive impact of the digitization to natural history collections by empowering the global plant community (Hedrick et al., 2020), some authors argued for a decline of botany as a consequence of reduce attention to the expansion of natural history collections (Crisci et al., 2020). Therefore, our study has highlighted the importance of continuing efforts to maintain and expand natural history collections for the assessment of diversity hotspots and conservation gaps in Xishuangbanna.

4.1. Collecting efforts of ferns and lycophytes in Xishuangbanna

The accumulation of historical records over time shows the consistency with historical events, reflecting the influence of social history on fern collections in Xishuangbanna. In 1936, C.W. Wang, one of the pioneer plant collectors in Yunnan, contributed extensively to the major source of historical records in this period (Bao et al., 1998), including records of some rare species, such as *Pteris undulatipinna* Ching and *Mickelopteris cordata* (Hook. & Grev.) Fraser-Jenk. (=*Parahemionitis cordata* (Roxb. ex Hook. & Grev.) Fraser-Jenk.). After the establishment of the Tropical Crops Research Institute and the Tropical Plant Research

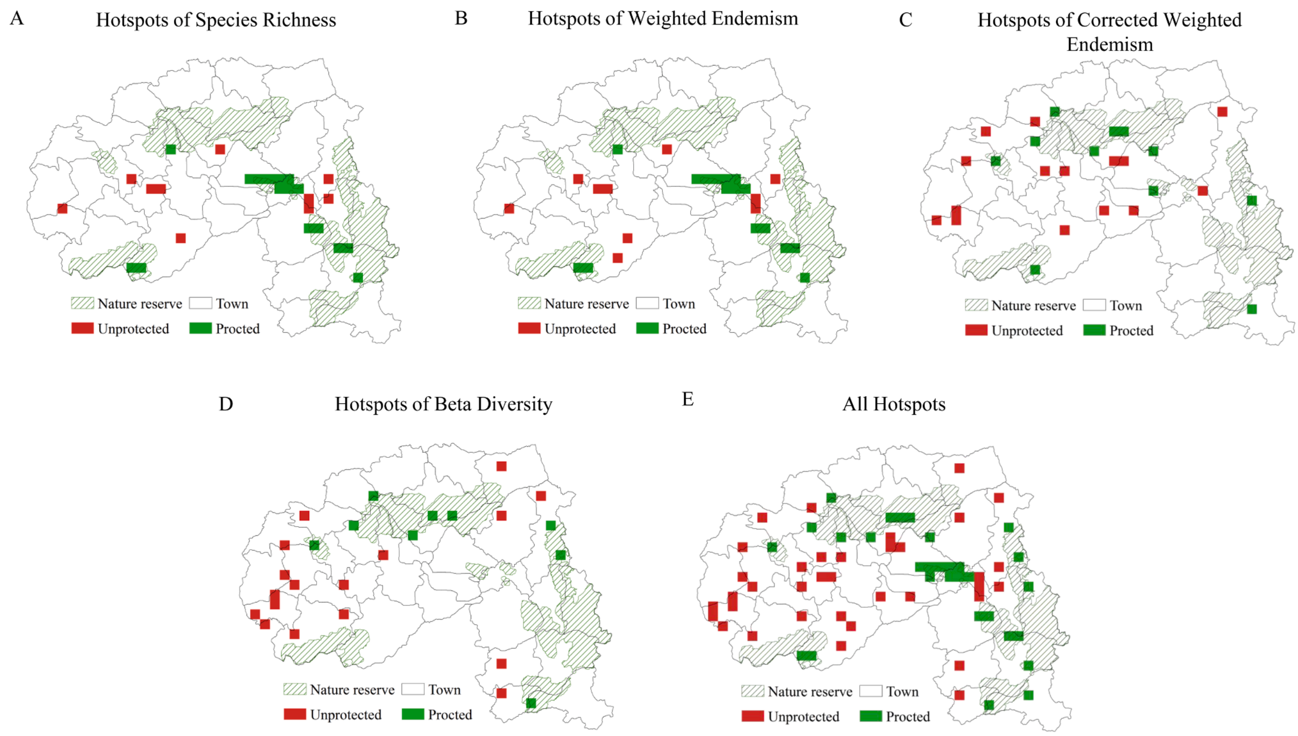

Fig. 4. Hotspots of Ferns and Lycophytes' Diversity in Xishuangbanna plotted against the protected areas—red grid cells are identified as hotspots outside the nature reserves (Unprotected), green grid cells as hotspots inside the nature reserves (Protected) for (A) species richness (SR), (B) weighted endemism (WE), (C) corrected weighted endemism (CWE), (D) beta diversity (BD), (E) combination of all hotspots for 4 diversity indices. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

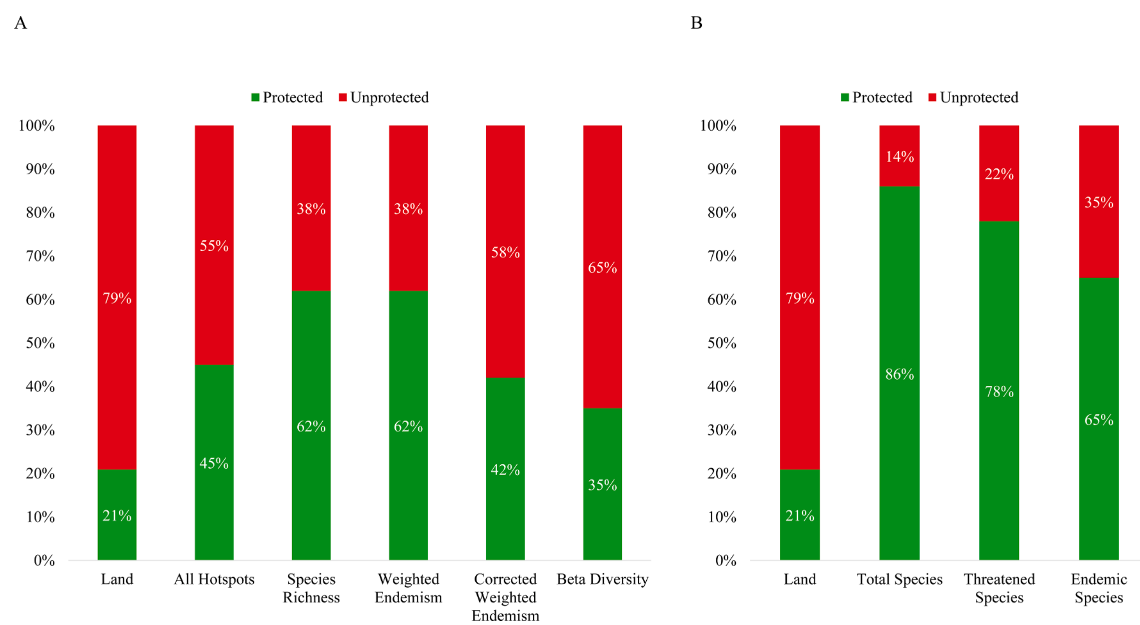

Fig. 5. Contrasting the proportion protected and unprotected by nature reserves for (A) total land, all hotspots, hotspots of species richness (SR), hotspots of weighted endemism (WE), hotspots of corrected weighted endemism (CWE), and hotspots of beta diversity (BD) by nature reserves; for (B) total species, threatened species and endemic species.

Institute in the 1950 s, survey activities gradually increased (Xu et al., 1987). In particular, the Sino-Soviet biological expedition enforced a rapid increase of historical records between 1955 and 1959. The most significant increase in historical records was attributed to the period of Reform and Opening since 1978, which enabled China's economy and science to experience rapid developments (National Science Foundation of China, 2012). In contrast, periods of social unrest had a negative impact by limiting economic, social and scientific undertakings (Giles et al., 2019; Hu, 2007; Kanbur & Zhang, 2005). Entering the 21st century, the accumulation of historical records in Xishuangbanna experienced an abrupt decrease following the delay of specimen digitization (Meyer et al., 2016; Paton et al., 2020), and the alteration of research interest (Zhang et al., 2019).

In terms of the spatial distribution of historical records, the central region, especially Jinghong city, has experienced the highest loss of collecting sites (red dots in Fig S2) in the past 100 years, while the western and eastern borders have experienced an increase (blue dots in Fig S2). This pattern is arguably related to the recent land-use change chiefly caused by rubber planting and urbanization (Cao et al., 2017; Xu et al., 2014). Rubber planting was first introduced in Xishuangbanna in 1956 and explosively expanded after 1978 (Li et al., 2007) and is mainly concentrated in southern lowlands (Yang et al., 2021), such as Menglong town, Menghan town and Gasa town of Jinghong city. Unfortunately, these areas also coincide with the main distribution range of tropical rain forests (Zhang & Cao, 1995). The vegetation transition from tropical rain forest to rubber forest has affected not only the local micro-environment and climate (Hammond et al., 2015; Singh et al., 2021), but also the biodiversity and ecosystem functioning (Li et al., 2007) and results in the loss of collecting sites that were observed in the central part of Xishuangbanna. In contrast, mountainous areas near the prefectural borders are less affected by land-use change, and vegetation there is better preserved as well (Fig S1). Although undergoing land-use changes affect the collecting priority, some sites have also retained (white dots in Fig S2) with a certain amount of collection to date due to the effectiveness and expansion of PAs, and cultural beliefs of the Dai people on sacred mountains (Liu et al., 2002). Additionally, high fragmentation of fern diversity has been recorded for forest remnants in this part (Cicuzza, 2021).

4.2. Spatial distribution of ferns and lycophytes' diversity in Xishuangbanna

Xishuangbanna is located at the northern border of the Indo-Burma Biodiversity Hotspot (Myers et al., 2000) and contributes significantly not only to China's biodiversity but also to global biodiversity. Previous studies have reported on the rich diversity of animals (Jiang et al., 1998), seed plants (Hou et al., 2018; Liu et al., 2015), and mosses (Quan et al., 2021). Here, we compiled the exiting information of ferns and lycophytes' diversity accounting for approximately 20.2% of species reported in China (Wang et al., 2015) and 3.6% of the world (PPG I, 2016). Moreover, the high proportion of threatened (11.4%) and endemic (10.7%) species highlights the regional importance for the conservation of China and global ferns and lycophytes' diversity.

Uneven distribution of ferns and lycophytes coincided with heterogenous geographic and climatic conditions in Xishuangbanna. The lowland valleys and basins in the eastern part are rich in fern species whereas a few hotspots are located in the low altitude of the western plateau (Fig. 3A, S3). The strong differentiation of the hydrothermal conditions between east and west (Xu et al., 1987) nurtures species richness hotspots with many fern species tending to occur in humid tropical valleys (Fig S3). In contrast, relatively few species show ecological preferences required to occur in dry and cold conditions (Kessler, 2010; Kessler et al., 2011). The climates in the east of Xishuangbanna are mainly shaped by the southwest monsoon and affected by the warm and humid airflow from the southeast (Xu et al., 1987). These conditions enable an increase in annual precipitation of about 300 mm in the eastern parts compared to the west (Xu et al., 1987). In addition, the average altitude of more than 1,300 m at the western plateau has a comparably lower temperature (Xu et al., 1987), thus the temperature of the lowland in the east is moderate for ferns. A further abiotic factor is the abundance of karst formation in Menglun town and its surrounding areas (Fig S1) including Jinuo village, Mengyuan village, Mengxing village and Yiwu village (Zhu, 2020) which is reflected by the occurrence of many limestone specialists with highly restricted distribution ranges (Li et al., 1996; Phoutthavong et al., 2019).

Endemism hotspots unfolded by the corrected weighted endemism are located in the higher mountain areas in the west (Fig. 3C, Fig S3). These findings are consistent with the previously published conclusions that the peak of fern endemism tends to occur at a higher altitude than that of species richness (Kessler, 2010; Kluge & Kessler, 2006; Vanderplank et al., 2014). Rare species in terms of regional frequency, especially epiphytic species, increase with the altitude in Xishuangbanna (Cicuzza, 2021), which implies that high mountains in the western and northern region provide suitable habitats for narrow ranged species. The lowland areas in the east where limestone outcrops are located maintain a certain degree of endemism in line with the substrate specialization of range-restricted species in these areas (Zhu, 2020).

Beta diversity based on Simpson dissimilarity index resembles the pattern of corrected weighted endemism. Hotspots are distributed in western and northern mountain ranges representing species replacement caused by habitat preferences (Qian et al., 2020). These hotspots highlight the aggregation of the rare species (Calatayud et al., 2020) and specialists (Denelle et al., 2020), whereas the distribution of widespread species dominating lowland habitats represents the regional flora composition under stable climate situations (Cicuzza, 2021; Given, 1993). Beta diversity reveals another dimension of biodiversity defining several hotspots, i.e., areas with distinct species composition which needs a longer period to recover than species richness in tropical forests once it was damaged (Poorter et al., 2021).

Inevitably, anthropogenic influences also play an important role in the distribution of species diversity and composition in Xishuangbanna. For instance, in Menglong town located in the southern basin of Jinghong, few species were recorded, mostly related to the transformation of vegetation from tropical rain forest to the rubber plantation in recent years (Yang et al., 2021).

4.3. Effectiveness of protection by PAs

Successful establishment and management of PAs are one of the key strategies for the conservation of global biodiversity (CBD, 2018; Saout et al., 2013; WWF, 2020). In our findings, the existing PAs in Xishuangbanna have demonstrated their effectiveness in the protection of ferns and lycophytes with nearly 90% of total species occurring in 21% of the prefecture's total land area (Fig. 5B). Species richness representing the diversity of a region is relevant for the evaluation of conservation effectiveness (Prendergast et al., 1999; Whittaker, 1972); however, the application of a single index reduces the accuracy by losing valuable information (Fleishman et al., 2006). Beta diversity which has a similar pattern with corrected weighted endemism generated several conservation gaps that locate outside of PAs (Fig. 4D), indicating the gap of exiting PAs to cover the variation in community composition.

The effectiveness between PAs is different in line with their targets, objectives and characteristics. The majority of ferns and lycophytes are protected by four reserves (Table S2). Other nature reserves are allocated in higher altitudes with a colder and drier climate (Xu et al., 1987) which in turn reduce the richness of fern floras but presented higher species endemism. For instance, the Mangao sub-reserve in the northwest mainly focuses on the conservation of montane evergreen broad-leaved forest and the pine forest where the diversity and abundance of terrestrial ferns are relatively low (Zhang et al., 2017). Mengyang and Shangyong sub-reserve set up to protect mainly the habitat of Asian elephants (Pan et al., 2009; Yang et al., 2018) are other examples for less effective for other organisms.

Although our study highlighted the effectiveness of the current protection system, other effective area-based conservation measure plays their role in this context (IUCN-WCPA Task Force on OECMs, 2019). Some region outside PAs in Xishuangbanna has established community-based conservation in line with their traditional and cultural belief (Liu et al., 2002; Zhang et al., 2020). For instance, Hesong village in the west of Menghai county providing habitats for many endemic species (Fig S3) benefits from the local protection of community forest (Wang, 2010). Thus, striking a balance between biodiversity conservation and the livelihood of people is expected to facilitate the management of biodiversity conservation both inside and outside the PAs as a certain number of villages are scattered (Guo et al., 2002).

Finally, we want to raise the issue that many grids located in PAs had little or no recent occurrence data (Table S1) that the current status of diversity is not able to be defined. Due to the hotspots inside PAs, the probability of no ferns and lycophytes occurrence in these grids is very low. Therefore, this pattern suggests the urgent need to enhance our efforts to document the biodiversity currently protected in these PAs by joint efforts involving the PAs management and taxon experts. Moreover, the conservation of the hotspots occurring outside PAs are arguably best incorporated with more conservation actions, such as forest restoration, effective land-use management, and enhancement of the community awareness to live in harmony with nature, and more conservation attention also needs to be paid to the unprotected species.

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.

Acknowledgements

We express our deepest gratitude to colleagues who recorded ferns and lycophytes occurring in Xishuangbanna during the last one hundred years. This research would have been impossible without the effort to maintain by the curators of various herbaria and digitization of this crucial information by the teams of the CVH, NSII, GBIF, and the herbaria holding the vouchers. We also thank the staff of nature reserves for their assistance in our investigation. This work was funded by the National Natural Science Foundation of China (NSFC, Grant 32050410300) and post-doctoral orientation training in Yunnan Province (Y7YN021B14) given to PKK, and the Yunnan Province Grants and National Funding provided to HS.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2022.126197.

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