



Diversity and conservation of higher plants in Northwest Yunnan-Southeast Tibet

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ABSTRACT

Located on the southern margin of the Qinghai-Tibet Plateau, the Northwest Yunnan-Southeast Tibet (NYST) is a biodiversity hotspot. However, plant diversity in the region faces enormous threats, including forest fragmentation and overexploitation of natural resources. Here, we updated the catalogue of higher plants in NYST by integrating various data sources and referring to the newest results of molecular systematics and taxonomy. Combining phylogenetic approaches and a spatial analysis of forest landscape fragmentation, we assessed spatial variations in taxonomic richness and phylogenetic diversity, and identified potential geographic units for conservation gaps. NYST harbours nearly one-third of China's higher plant species, of which ~60% of the species listed as threatened are endemic. Among the genera, the highest number of endemic and threatened species belong to *Rhododendron*. The largest increase in the number of threatened species was observed in the Orchidaceae over the last 15 years. Seed plant taxonomic richness and phylogenetic diversity were significantly positively correlated at both the species and genus levels. Counties with large mountains are hotspots of phylogenetic diversity as well as total, endemic, and threatened species richness. The pattern of diversity of higher plants in the study area is likely related to the Himalayan-Tibetan Plateau uplift. The western part of Yulong County and the central to southern parts of Shangri-La County are conservation gaps in this area. In-depth local field surveys of plant diversity are needed, especially in those counties where there is large disparity between the number of species present and collected specimens (e.g., Yulong County). This study provides data and a theoretical basis for the study and conservation of NYST plant diversity.

1. Introduction

The largest and highest plateau on Earth, the Qinghai-Tibet Plateau harbours a rich diversity of unique plants (Zhang et al., 2016), with species diversity gradually increasing from the northwest to the southeast, peaking at the southeastern edge (Yu et al., 2020). Northwest Yunnan-Southeast Tibet (NYST) is located midway along the southeastern edge of the Qinghai-Tibet Plateau and is one of the main areas for biodiversity conservation (Ma et al., 2007; Qian et al., 2020; Su et al., 2019; Yang et al., 2016). With the rapid

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socioeconomic development in the region and pronounced global environmental changes, the region's biodiversity is undergoing profound changes that are of great concern to scientists, governments and the public (Qiu et al., 2018; Yang et al., 2016; Zhang et al., 2014b).

Flora of Yunnan and *Flora of Tibet* reflect the achievements of scholars in understanding higher plants in Yunnan and Tibet, including NYST (Cheng et al., 2020; Ma, 2015). As biodiversity surveys have increased in frequency in recent years, a large number of new taxa (including families) have been discovered and published (Bachman et al., 2018). In 2013–2019, ~23 angiosperm species were found or described in Yunnan each year (Cheng et al., 2020; Enroth et al., 2018; Qian et al., 2020). Furthermore, in-depth taxonomic and systematic studies have led to changes in the scope of delimitation and systematic positions of large numbers of families, genera and species (Bremer et al., 2009, 2003; Byng et al., 2016; Christenhusz et al., 2011). We still do not know exactly which plants are distributed in NYST and the spatial locations of distribution are especially uncertain. The threatened and endemic plants that are distributed in the NYST have not been fully elucidated (Chen et al., 2018; Li et al., 2020b; Ma, 2015; Mi et al., 2021). This lack of knowledge is very detrimental to the conservation and utilization of plants in the region. Therefore, updating of the list of higher plants in the NYST by integrating various data sources and referencing the newest results of molecular systematics and taxonomy and analyses of the spatial distribution of plant diversity are urgently needed (Ma, 2014, 2017; Mi et al., 2021; Qian et al., 2018). These efforts are necessary not only for the development of taxonomic disciplines but also to expand the foundation for further research in ecology, biodiversity and conservation, and biogeography.

An understanding of the spatial pattern of diversity is the foundation for biodiversity conservation. Phylogenetic diversity is an important measure of diversity based on evolutionary relationships between species (Cadotte and Davies, 2010; Pio et al., 2011). However, most recent studies have focused at the taxonomic level, regarding species as independent and equivalent units (Frankham et al., 2012; Tilman et al., 2001). This approach ignores the complicated relationship between species and phylogenetic history (Lu et al., 2018; Qian et al., 2017). Incorporating phylogenetic information into conservation analyses can provide insights into the contribution of evolutionary processes to diversity patterns and thus aid the preservation of evolutionary potential (Cai et al., 2021; Yan et al., 2013; Yu et al., 2019; Zhu et al., 2021). In the last 30 years, with the rapid accumulation of DNA sequence data through the global DNA barcoding project and the development of phylogenetic methods, a series of indices have been derived to describe phylogenetic diversity (Favre et al., 2015; Lu et al., 2018). Faith (1992) proposed a phylogenetic diversity (PD) indicator: the sum of branches on a phylogenetic tree conforming to a minimum spanning path. This indicator is not affected by changes in the taxonomic status of species and is beneficial when identifying taxa that have a long evolutionary history. Unfortunately, until recently, the science of maximizing biodiversity conservation was conducted separately from the science of understanding how it has diversified and dispersed over time (Costion et al., 2015; Thornhill et al., 2016). To allow more informed decisions on biodiversity conservation to be made, the two disciplines must be integrated more closely (Li and Yue, 2020).

Plant diversity on the planet is decreasing due to climate change and anthropogenic activities, such as land use changes, habitat fragmentation and resource overexploitation (Brummitt et al., 2015; Newbold et al., 2016; Urban, 2015). Previous studies have shown that the extinction of each species causes more species to fall into crisis, thus threatening the stability of the entire biosphere (Hooper et al., 2012).

The global conservation network has been strengthened to protect biodiversity around the world. However, the coverage of the network is considered inadequate, and it is unclear where new nature reserves should be located (Li and Pimm, 2020; Li et al., 2021; Yang et al., 2020). To date, 28 nature reserves have been established in NYST and are divided into four levels: national (6), provincial (9), municipal (9) and county (4). Southwest China is one of the areas of China with the most serious forest fragmentation over the past 300 years (Liu et al., 2019a; Liu and Tian, 2010). In particular, in recent decades, population growth and socioeconomic development (road construction, urbanization expansion and cash crop cultivation) have led to severe fragmentation of the region's thermal-subtropical-temperate forests (Li et al., 2008; Liu et al., 2019a; Miettinen et al., 2014). There are now more numerous but smaller forested patches, most of which are less than 10 ha in size and with decreased connectivity. Forest landscape fragmentation has led to the loss of biodiversity in Southwest China (Hua et al., 2016; Liu et al., 2019a; Wang et al., 2019). Chen et al. (2020) found that Yunnan and southeastern Tibet are the key areas of threatened forests in China. In 2018, *Regulations of Yunnan Province on Biodiversity Protection*, the first local law to protect biodiversity in China, was issued. In 2020, *Regulations on the Construction of National Ecological Civilization Highlands in the Tibet Autonomous Region* were adopted. Allocating limited conservation resources to the most deserving areas at the lowest cost is the best and most effective way to achieve regional biodiversity conservation (Yang et al., 2020). Therefore, following the identification of priority conservation units via the distribution of taxonomic richness (TR) and PD (Hu et al., 2021; Zhang et al., 2021b), the spatial patterns of forest landscapes in priority areas should be analysed, and forest patches with large areas and high connectivity could be selected as potential protected areas (Liu et al., 2019b; Matos et al., 2019; Zhang et al., 2017).

The objectives of this study are (1) to update the checklist of higher plants in NYST and analyse the total, endemic, and threatened species diversity in each county; (2) to assess the spatial variation in TR and PD; and (3) to identify conservation gaps in priority counties through forest landscape pattern analysis. This study provides data support and a theoretical basis for the study and conservation of plant diversity in NYST.

2. Methods

2.1. Study area

NYST (24°40'–30°20'N, 96°–101°20'E) is located in the hinterland of the "Three Parallel Rivers of Yunnan Protected Areas" which is located at the junction of Yunnan, Sichuan and Tibet and comprises 19 counties (Fig. 1) where different ethnic groups and cultures

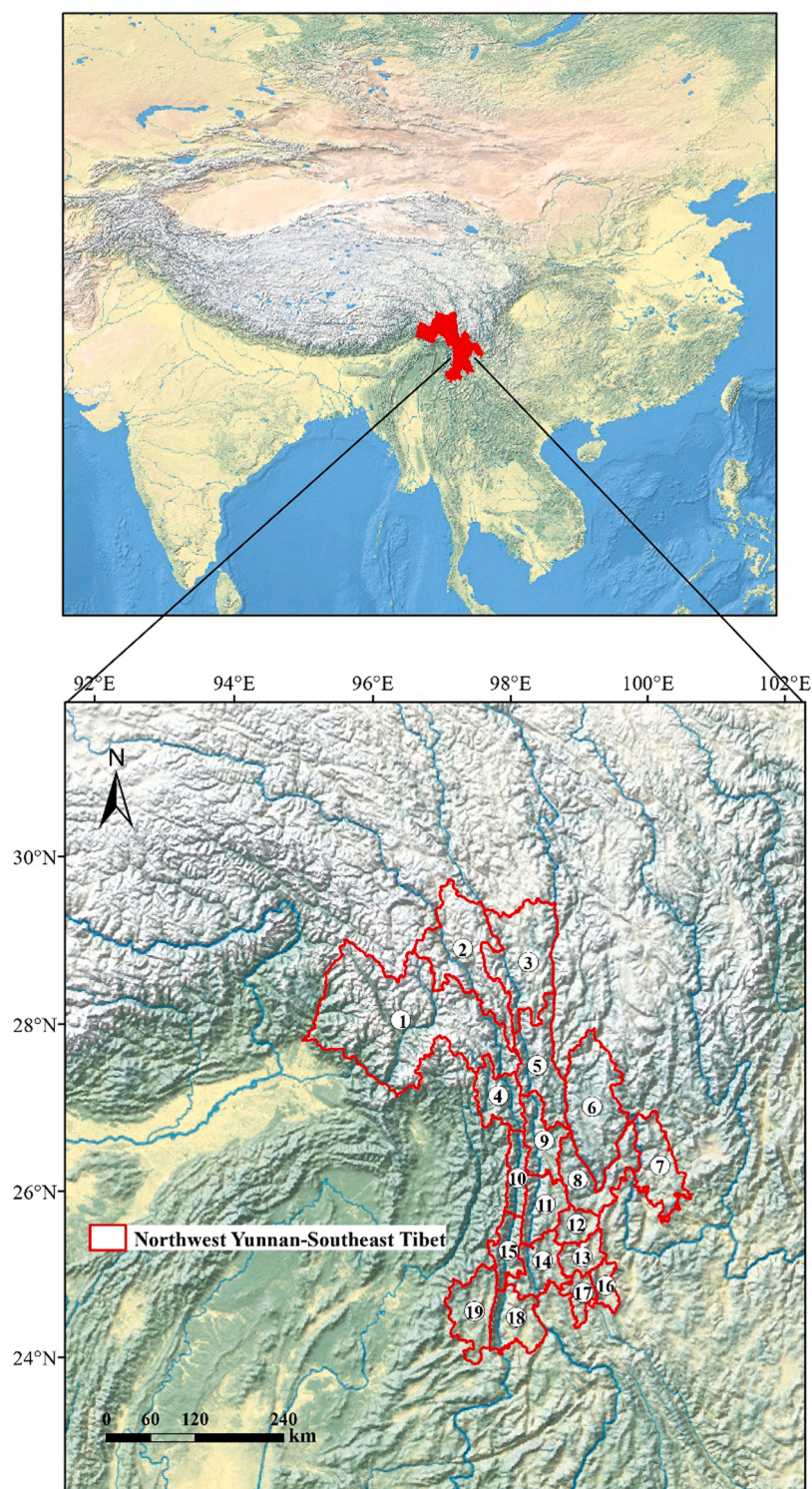


Fig. 1. Location of the study area. ①Zayü County, ②Zuogong County, ③Markham County, ④Gongshan County, ⑤Deqin County, ⑥Shangri-la County, ⑦Ninglang County, ⑧Yulong County, ⑨Weixi County, ⑩Fugong County, ⑪Lanping County, ⑫Jianchuan County, ⑬Eryuan County, ⑭Yunlong County, ⑮Lushui County, ⑯Dali County, ⑰Yangbi County, ⑱Longyang district, ⑲Tengchong County.

interact. This region features rugged terrain formed by ridges and rivers, with an elevation that spans more than 3000 m. The vegetation in the region shows vertical zonation. NYST belongs to the China-Himalayan forest subregion of the East Asian botanical region, which includes the Southeast Tibetan subregion, Dulong River-North Myanmar subregion, Three-River Gorge subregion, Central Yunnan Plateau subregion, and South Hengduan Mountain subregion. Northwestern Yunnan and southeastern Tibet share a highly similar composition of important families and genera of higher plants, which implies that they may have similar floral geographic backgrounds. In addition, both regions were part of the Gondwana paleocontinent, and both have been affected by the collision of the Indian and Eurasian plates since the Cenozoic (Ding et al., 2020; Rahbek et al., 2019). The above observations indicate that it is appropriate to combine northwest Yunnan and southeast Tibet into a single geographical unit for analyses of higher plant diversity (Yu et al., 2020). The total area of NYST is $12.80 \times 10^4 \text{ km}^2$, accounting for 1% of China's land area, but it harbours approximately one-third of the country's higher plants (Ma et al., 2007; Qian et al., 2020; You and Feng, 2013).

2.2. Data collection and processing

2.2.1. Data sources

- (1) The following books and biodiversity monographs on regional flora were consulted: *Flora of Yunnan* (Chinese Academy of Sciences, 1997-2006), *Flora of Tibet* (Wu, 1983-1978), *Flora of China* (Flora of China Editorial Committee, 2013), *China Species Red List* (Wang and Xie, 2004), *The Checklist of Biological Species from Yunnan* (2016) (Gao and Sun, 2016), *Species Red List of Yunnan Province* (2017) (Gao and Sun, 2017), *Bryophyte flora of Tibet* (Qinghai-Tibet Plateau Comprehensive Scientific Expedition Team, 1985), *The Vascular Plants and their Eco-geographic Distribution of the Qinghai-Tibet Plateau* (Wu, 2008), and *Vascular Plants in the Hengduan Mountains* (Qinghai-Tibet Plateau Comprehensive Scientific Expedition Team, 1994).
- (2) The literature consulted included taxonomic revisions published in domestic and foreign taxonomic journals involving NYST and reports of new taxa and new records in the region.
- (3) The following herbarium and public databases were consulted: Global Biodiversity Information Facility (GBIF, <https://www.gbif.org/>), National Specimen Information Infrastructure (NSII, <http://www.nsii.org.cn/>), Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (KUN), Herbarium of Institute of Botany, Chinese Academy of Sciences (PE), Chengdu Institute of Biology, Chinese Academy of Sciences (CDBI), Northwest Plateau Institute of Biology, Chinese Academy of Sciences (QTPMB), Herbarium of Sichuan University (SZ), Herbarium of Yunnan University (PYU), and Chinese Virtual Herbarium (CVH, <http://www.cvh.org.cn>). Specimen information of higher plants in NYST was collected from these databases to supplement the county distribution data.
- (4) Recent field investigation results and expert suggestions were supplemented and updated.

2.2.2. Data processing

(1) Synonymous processing

The family classifications and scientific names in the catalogue of higher plants were checked by Tropicos (<http://www.tropicos.org/>), Species 2000 (<http://www.sp2000.cn/joan/index.php>) and Flora of China (http://www.efloras.org/flora_page.aspx?flora_id=2). The taxonomic systems of gymnosperms and angiosperms were based on the Kirschner system and Angiosperm Phylogeny Group IV system (Byng et al., 2016), respectively. The processing protocol and taxonomic system used to compile the catalogue have been described by Chen et al. (2018).

(2) Intraspecies processing

To show the plant diversity in a more refined way, the concept of variety or subspecies was adopted. If there were more than two subspecies or varieties of a species, only the variety/subspecies (including original variety/subspecies) distributed in NYST was included. However, when based on statistics, if there was only one variety/subspecies distributed in NYST, we counted it as a species.

(3) Extraction of geographic distribution information

A species checklist of higher plants in the 19 counties was extracted according to the geographical distribution information. Much historical collection information has the issues of nonstandard location description and missing key data. In addition, due to the continual changes in administrative divisions (such as the change from Zhongdian to Shangri-La, etc.), many place names have changed, so we manually reviewed and revised the geographic distribution for each taxon.

We integrated the distribution data of higher plants in NYST into a county-level distribution database, including all species, all threatened species and all endemic species of higher plant. Based on the *IUCN Red List Categories and Criteria (Version 3.1)* and *Application of the IUCN Red List Criteria at Regional Levels (Version 3.0)* and with reference to *China Species Red List - Higher Plants (2015)* and *Species Red List of Yunnan Province (2017)* for the assessment of species IUCN categories, the following categories were included: extinct (EX), extinct in the wild (EW), regionally extinct (RE), critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), least concern (LC), and data deficient (DD). EX, EW and RE were collectively referred to as the extinction category, and CR, EN and VU were collectively referred to as the threatened category. Endemism information was divided into 3 categories: endemic to China, endemic at the provincial level (Yunnan/Tibet), and endemic at the county level.

2.3. Biodiversity analyses

To quantify the taxonomic and phylogenetic compositions of higher plants in NYST, we calculated genera/ species richness (TR) and Faith's phylogenetic diversity (PD) index at the species and genus levels for each county.

- (1) TR refers to the number of genera (genus richness) or species (species richness) of higher plants in a defined region (Cadotte et al., 2010; Huang et al., 2016). The numbers of families, genera and species of higher plants (angiosperms, gymnosperms, pteridophytes, and bryophytes), threatened higher plants and endemic higher plants in each county were counted according to the above-described updated list.
- (2) Faith's PD index is the sum of the lengths of all phylogenetic branches connecting taxonomic units in a defined region (Faith, 1992). We used the V.PhyloMaker package (Jin and Qian, 2019) in R software to graft the species present in the study area onto the backbone phylogenetic hypothesis and construct phylogenetic trees at the species and genus levels. The megatree implemented in V.PhyloMaker (i.e., GBOTB.extended.tre) is the largest and most up-to-date phylogeny of vascular plants (Jin and Qian, 2019) and is derived from the phylogeny of two megatrees recently published by Smith and Brown (2018) and Zanne et al. (2014). It includes 74,533 species and all families of extant vascular plants and generates phylogenies much faster than other software packages. Using GBOTB.extended.tre as a backbone, the divergence times of plants were determined according to the phylogenetic relationships inferred by Zanne et al. (2014), who used seven genetic regions for divergence time calibration in addition to fossil data. Given the scarcity of comprehensive time-calibrated phylogenies within families and genera, we followed previous studies and treated unresolved genera as polyphyletic within families and unresolved species as polyphyletic within genera (Kerkhoff et al., 2014; Qian and Jin, 2016). Our study focuses on the PD patterns of seed plants because of the incomplete phylogenetic relationships among pteridophytes and bryophytes.

2.4. Analyses on coverage of protected area

- (1) The methods for identifying priority counties for protection were as follows: We mapped the spatial distributions of TR and PD in ArcGIS 10.2. Hotspot analysis (Getis-Ord Gi*; Getis and Ord, 1992) was selected to identify hotspot counties with statistical significance in plant richness and PD patterns. This method is based on the local spatial autocorrelation metric of the distance weight matrix and is able to detect high-value and low-value clusters (Ord and Getis, 1995). Finally, hotspot counties were merged as priority counties for protection in the study area (Zhang et al., 2021b).
- (2) The methods for identifying potential protected areas were as follows: Habitat fragmentation is one of the important factors contributing to biodiversity loss (Chase et al., 2020; Haddad et al., 2015; Hargreaves, 2019). Forests are the dominant habitat type in the study area. Hence, forests were set as the focus in our study. To identify the locations of potential protected areas, the moving window method in Fragstats 4.2 was applied to analyse the landscape pattern of forests in the priority counties. Forest landscapes with large patch sizes, high connectivity and low patch density were selected as potential protected areas (Zhang et al., 2017). Features indicative of forest fragmentation or its effects on biodiversity as well as the correlations among indicators were considered (Cushman et al., 2012; Semper-Pascual et al., 2021; Yesuf et al., 2021). Three indicators, namely, mean patch area, patch density, and aggregation cohesion index, were selected to characterize forest fragmentation. Data on forest distribution were obtained from the Global Land Cover with Fine Classification System at 30 m in 2020 (GLC_FCS30-2020, <http://data.casearth.cn/sdo/detail/5fbc7904819aec1ea2dd7061>). The dataset can be used to analyse the spatial pattern changes in regional landscapes, and the accuracy of producers is 94.0% and the accuracy of users is 90.4% for global forest land-cover type (Liu et al., 2021b; Zhang et al., 2021a). We used the spatial data of the "forest" category in this dataset to map the distribution of forests in the study area, with evergreen broad-leaved forest, deciduous broad-leaved forest and evergreen coniferous forest as the main types. We retained only forest areas out of the 30 land cover types; these forest areas cover ~58% of NYST. The forest distribution map included either no forest (0) or forest (1). The maps of forest fragmentation indicators were classified into 3 classes, namely, low, medium and high, using the natural breaks (Jenks) algorithm. Then, areas with the following intersection of features were selected as potential protected areas: high average patch area, high aggregation and low patch density.
- (3) The Geographic Approach to Protect Biodiversity (GAP) was adopted as follows: Data on the distribution of nature reserves in NYST were overlaid with potential protected areas for analysis, and areas distributed outside protected areas were defined as conservation gaps (Maxted et al., 2008; Ramirez-Villegas et al., 2020). Data from the list of nature reserves were obtained from the Ministry of Ecology and Environment of the People's Republic of China (<https://www.mee.gov.cn/>), and the spatial distribution of nature reserves was obtained from Ye et al. (2015).

3. Results

3.1. Composition of higher plant diversity

NYST was found to harbour ~9786 species of higher plants, including 8232 angiosperms species, 73 gymnosperms species, 609 pteridophytes species and 872 bryophytes species.

The largest family of angiosperms in the study area was Asteraceae, with 669 species representing 103 genera. There were 34 single-species families in the region, including ancient relict plants (e.g., Eupteleaceae) and newly classified families (e.g.,

Escalloniaceae). The largest genus was *Rhododendron* (with 277 species), and genera with species numbers between 100 and 200 exhibited the following order: *Pedicularis* > *Saxifraga* > *Primula* > *Salix* > *Carex* > *Gentiana*, all of which were typical north-temperate elements. The species diversity of *Juniperus* (Cupressaceae) and *Abies* (Pinaceae) was high, with 14 and 15 species, respectively (Fig. 2 B).

Dryopteridaceae, Polypodiaceae, Athyriaceae, Pteridaceae and Thelypteridaceae were the top 5 families of pteridophytes in the study area, with a total of 439 species (~72% of all species; Fig. 2 C). *Dryopteris*, *Polystichum*, *Athyrium*, *Asplenium* and *Diplazium* were the top 5 genera of pteridophytes, with 216 species (~35% of all species). Pottiaceae, Frullaniaceae, Brachytheciaceae, Lejeuneaceae, Mniaceae, Meteoriaceae, Porellaceae, Bryaceae, Hypnaceae and Bartramiaceae were the top 10 families of bryophytes, with 400 species (~46% of all species), showing multifamily codominance (Fig. 2 D). *Frullania*, *Porella*, *Brachythecium*, *Scapania*, *Entodon*, *Bryum*, *Bazzania*, *Herbertus*, *Fissidens*, and *Didymodon* were the top 10 genera of bryophytes, with 230 species (~26% of all species).

3.2. Centres of TR and PD

NYST harbours 8305 species of seed plants representing 1372 genera from 194 families. The TR and PD values showed significant positive correlations in the study area (Pearson correlation coefficient $r = 0.990$, $P < 0.01$ at the genus level; $r = 0.987$, $P < 0.01$ at the

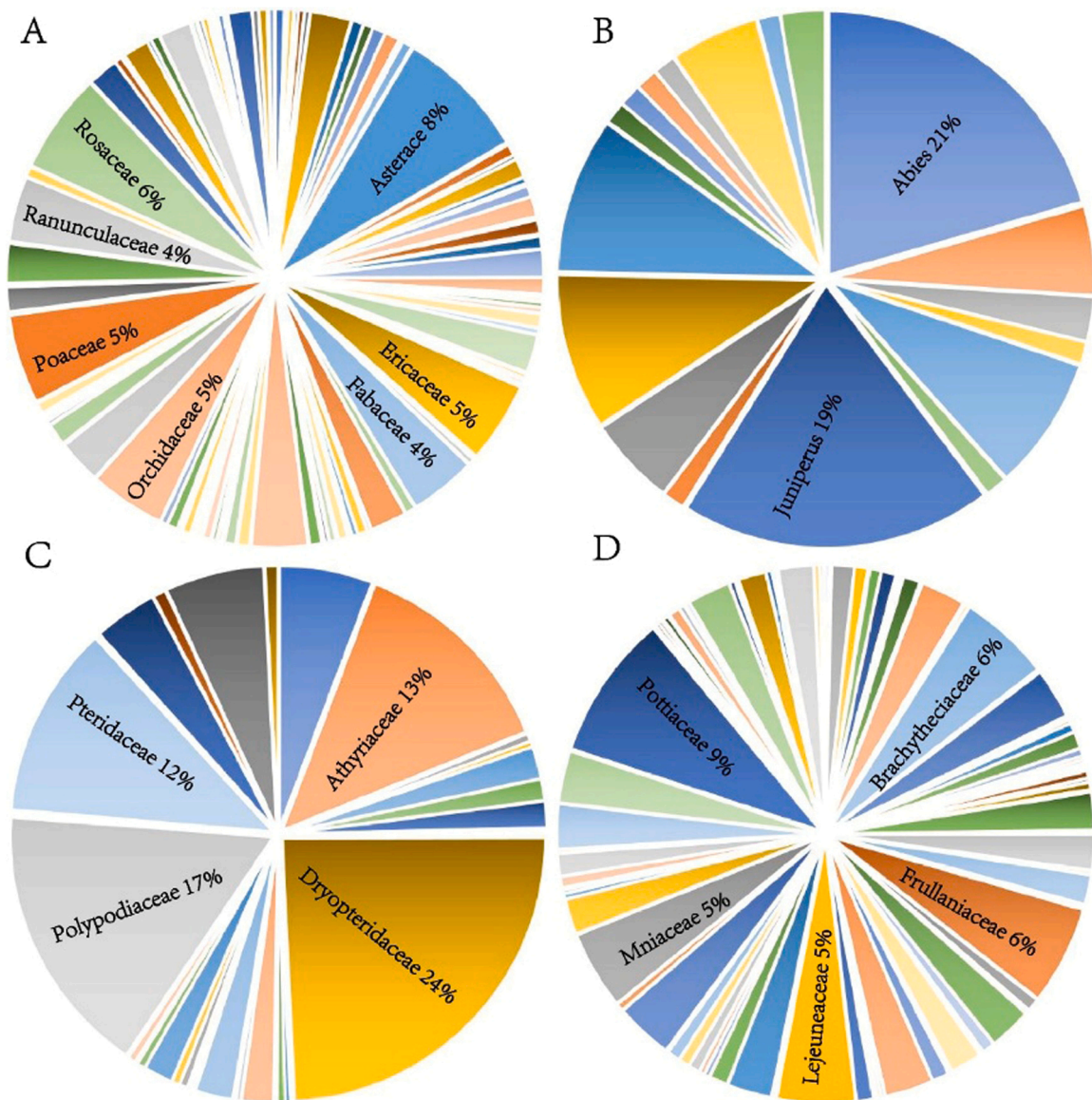


Fig. 2. Composition of higher plant diversity in NYST. A: Composition of angiosperm families; B: Composition of gymnosperm genera; C: Composition of pteridophyte families; D: Composition of bryophyte families.

species level). The strong correlation between PD and TR was also indicated by the spatial consistency of the phylogenetic and taxonomic composition of seed plants at the county level (Fig. 3). The centres of diversity at the species level were found in Shangri-La (TR=3183, PD=61198.0), Yulong (TR=3061, PD=62177.9), Deqin (TR=3002, PD=58811.9) and Gongshan (TR=2813, PD=61497.4) (Fig. 3 A, B). The centres of diversity at the genus level were Yulong (TR=854, PD=34291.9), Gongshan (TR=803, PD=34056.9) and Shangri-La (TR=784, PD=31905.6) (Fig. 3 C, D). However, Yulong County is the only county where the number of higher plant species is much greater than that of specimens, showing that the collection of specimens is severely incomplete (Supplement material). In addition, the disparity between the proportion of higher plants and the proportion of specimens is approximately

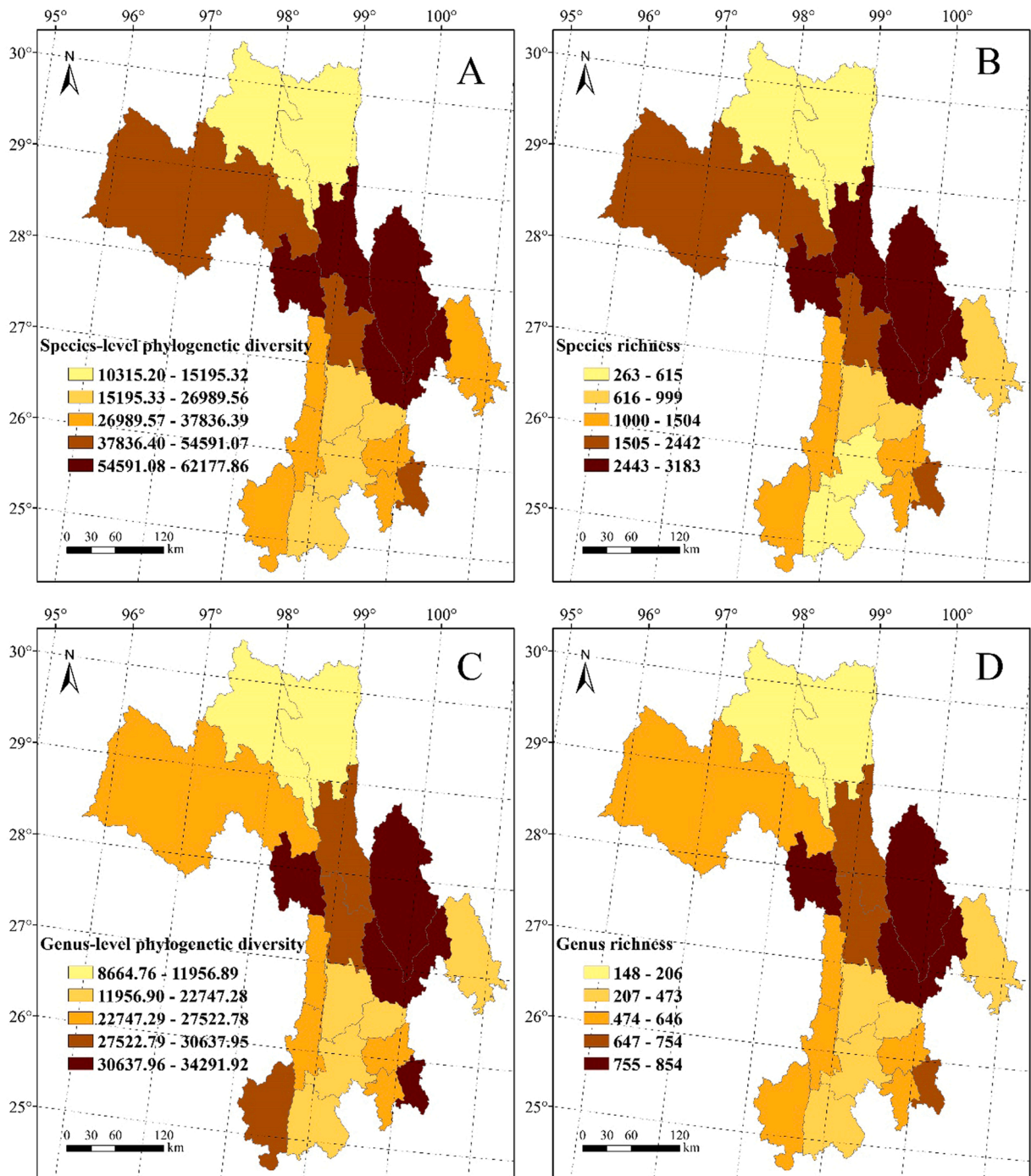


Fig. 3. Patterns of species richness and phylogenetic diversity for the seed plants of NYST, China. A: Species-level phylogenetic diversity; B: Species richness; C: Genus-level phylogenetic diversity; D: Genus richness.

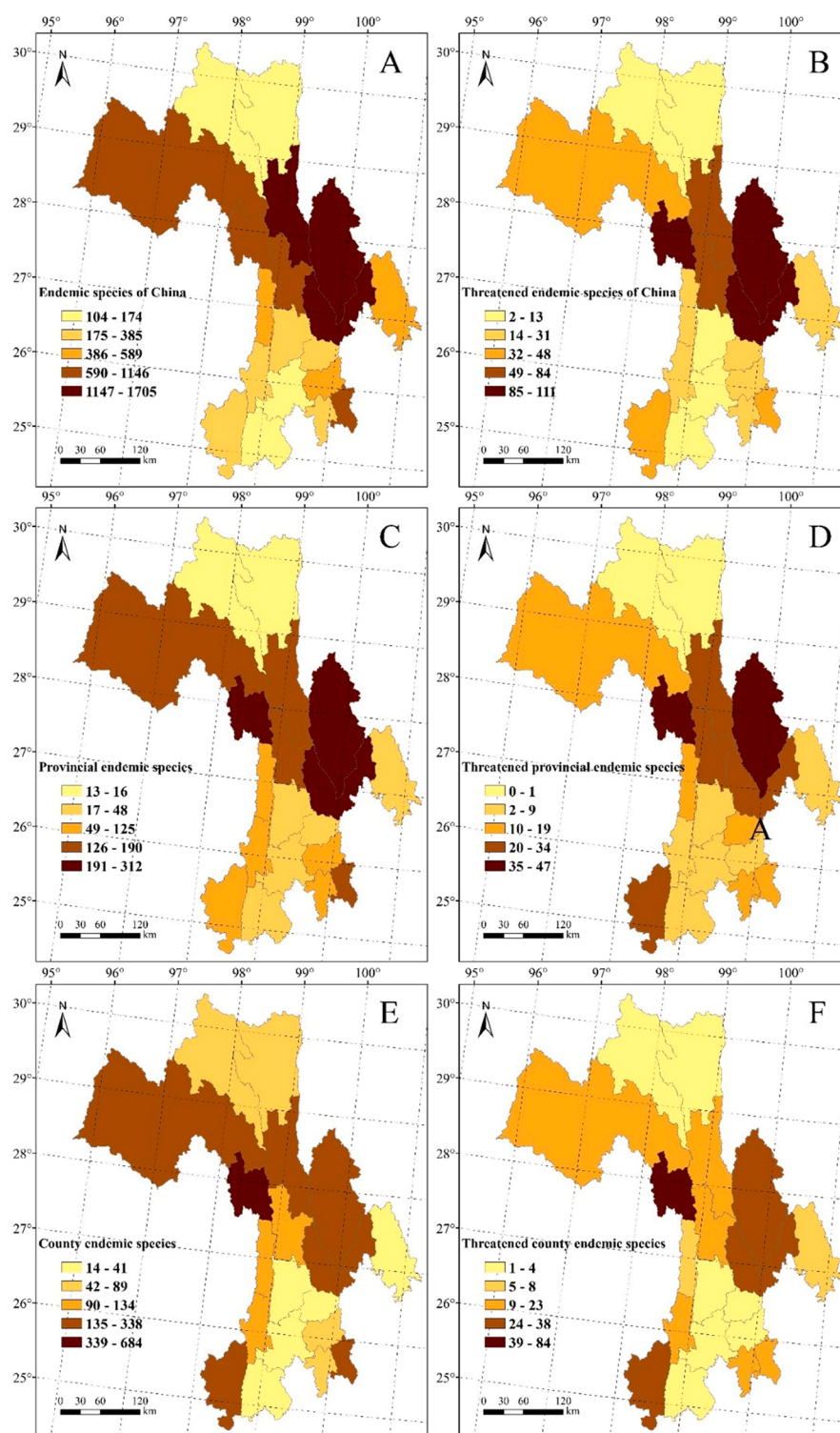


Fig. 4. Species richness patterns of threatened and endemic higher plants in NYST. A: Endemic species of China; B: Province-level (Yunnan/Tibet) endemic species; C: County-level endemic species; D: Threatened endemic species of China; E: Threatened province-level endemic species; F: Threatened county-level endemic species.

20% in Deqin, Zayü, Gongshan, Weixi, Shangri-La and Dali Counties ([Supplement material](#)).

3.3. Spatial patterns of threatened and endemic higher plants

There were 4337 Chinese endemic species (~44% of the total species), 1222 provincial endemic species (~12% of the total species), and 3115 county endemic species (~32% of the total species) in NYST. More than 80% of these endemic plants were

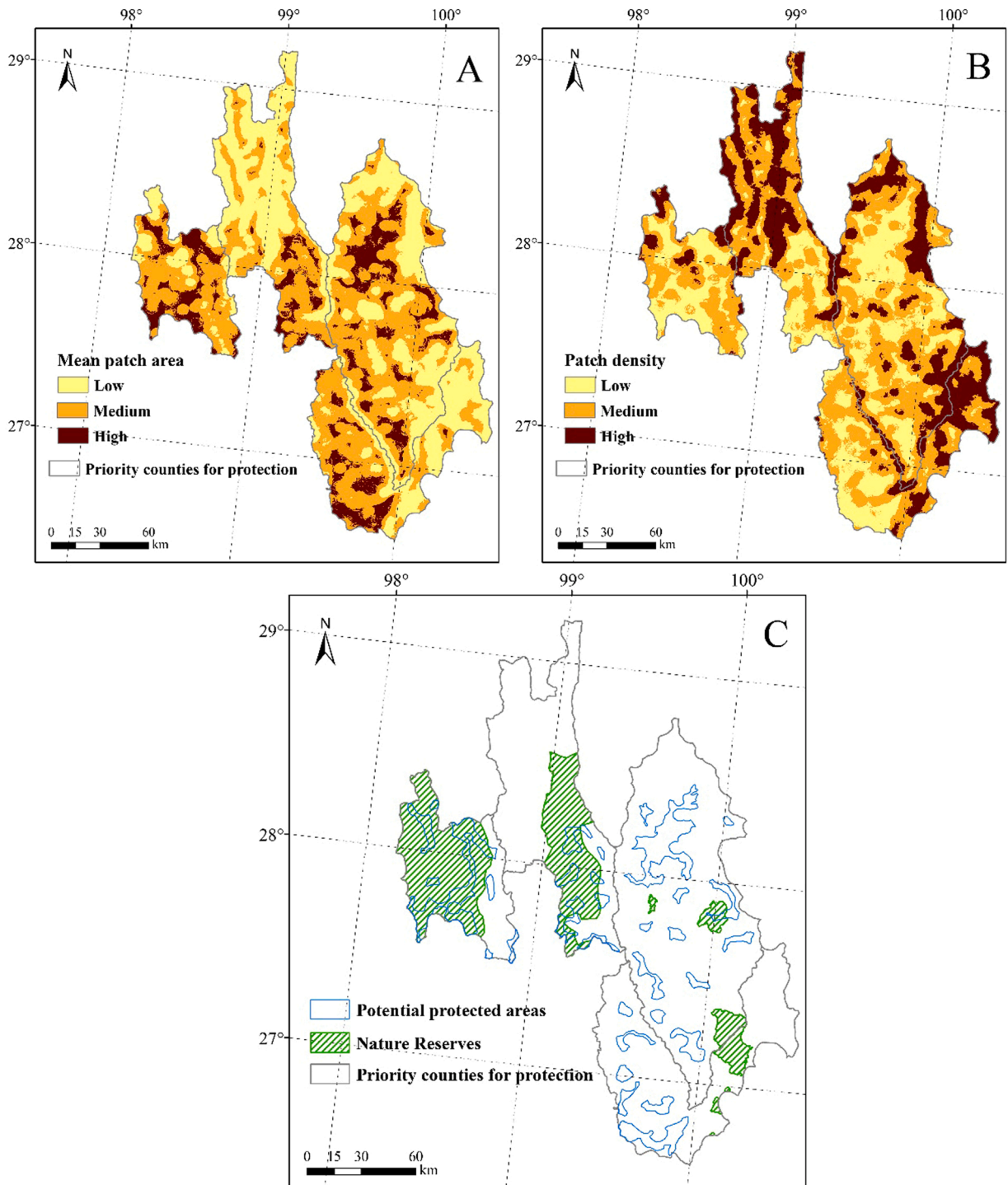


Fig. 5. Forest landscape pattern and GAP analysis in the priority conservation counties. A: Mean patch area; B: Patch density; C: GAP analysis.

angiosperms. The number of Chinese endemic species belonging to each of *Pedicularis*, *Rhododendron*, *Saxifraga*, *Salix*, and *Primula* exceeded 80. The proportion of Chinese endemic species in each county exceeded ~20% and peaked at ~50%. Shangri-La (1705), Yulong (1687), Deqin (1480), Gongshan (1146) and Weixi (1130) had more than 1000 Chinese endemic species (Fig. 4 A). Gongshan (312), Yulong (255) and Shangri-La (236) had more than 200 Yunnan-endemic species (Fig. 4 C). Gongshan (684) and Yulong (338) Counties had more than 300 county-endemic species (Fig. 4 E).

Five species in the region were listed in the extinction category: *Chelonopsis rosea* var. *siccanea* (endemic species of China, EX), *Premna mekongensis* var. *meiophylla* (endemic species of Yulong, EX), *Pedicularis humilis* (endemic species of Yunnan Province, EX), *Eucommia ulmoides* (endemic species of China, EW) and *Michelia velutina* (RE). A total of 661 species (~7% of the total species) were listed in the threatened category, including ~7% of the total angiosperm species, ~3% of the total bryophyte species, ~21% of the total gymnosperm species, and ~2% of the total pteridophyte species. The family with the most threatened species was Orchidaceae (24.36% of the total threatened species), and the genus with the most threatened species was *Rhododendron* (7.56% of the total threatened species). *Dendrobium*, *Aconitum*, *Cymbidium*, *Saussurea*, *Cypripedium*, *Dioscorea*, *Pedicularis*, and *Acer* all had more than 10 threatened species. Three counties, Gongshan (245, more than 1/3 of the threatened species), Yulong (153) and Shangri-La (152), had the most threatened species. Of the species listed in the threatened category, 211 were endemic to China, 173 were endemic to Yunnan, and 9 were endemic to Tibet; these endemic taxa represented ~59% of all threatened species in the region (Table 8, Fig. 4). Threatened Chinese endemic species were clustered in Shangri-La (111), Yulong (103) and Gongshan (100) (Fig. 4 B). Threatened provincial endemics were clustered in Shangri-La (47) and Gongshan (45) (Fig. 4 D). Threatened county-level endemics were clustered in Gongshan (84), Tengchong (38), Shangri-La (35) and Yulong (31) (Fig. 4 F).

3.4. Spatial analysis of conservation gaps

The counties identified as priority counties for conservation in NYST were Gongshan, Shangri-La, Deqin and Yulong (Figs. 4,5). Forests were the dominant landscape in these priority counties, accounting for ~72% of the total landscape. Among these counties, Gongshan had the lowest amount of forest landscape fragmentation and Gaoligong Mountain National Nature Reserve covered ~75% of the county (Fig. 5 A, B and supplementary material). Deqin had the highest level of forest landscape fragmentation and Baima Snow Mountain National Nature Reserve covered ~30% of the county. The potential protected areas in Gongshan and Deqin were largely covered by existing nature reserves (Fig. 5 C). The three provincial nature reserves of Bitahai, Haba Xueshan, and Napahai are located in Shangri-La, accounting for ~4% of the county, and the two provincial nature reserves of Lashihai Plateau Wetland and Yulong Snow Mountain are located in Yulong, accounting for ~5% of the county. Almost none of the potential protected areas in Shangri-La and Yulong were covered by existing nature reserves. The western part of Yulong and the central to southern parts of Shangri-La were conservation gaps in this area (Fig. 5 C).

4. Discussion

4.1. Higher plant diversity

Although NYST is an overall hotspot for biodiversity conservation, plant diversity in the region exhibits spatial heterogeneity (Wambulwa et al., 2021; Yu et al., 2020). The centres of PD and TR were in agreement and were mainly clustered in high-elevation counties (>3200 m) with massive mountains. Yulong (Yulong Snow Mountain), Shangri-La (Haba and Balagezong Snow Mountains), Gongshan (Gaoligong Mountain) and Deqin (Meili and Baima Snow Mountains) all show higher species richness and PD than other counties. However, adjacent counties without large mountains may show a decrease in plant diversity. Ninglang, which is adjacent to Yulong, has significantly lower plant diversity. This pattern may be related to the topographic complexity created by the enormous mountains, the geological history of stratigraphic uplift and climatic fluctuations (Ding et al., 2020; Li et al., 2020a; Rahbek et al., 2019). During the late Tertiary and early Quaternary periods, the Himalayas and Tibetan Plateau were uplifted as a result of the collision between the Indian and Eurasian tectonic plates. A large number of new habitats formed across a wide range of elevations in NYST, and the landforms were more heterogeneous than elsewhere (Su et al., 2019; Xing and Ree, 2017; Yu et al., 2019). The Nujiang, Lancang and Jinsha Rivers are also distributed across the region. Great topographic dynamics not only lead to significant habitat differentiation, favouring the coexistence of species, but also create dispersal barriers that may promote species diversification and radiation through allopatric and interspecific diploid hybridization (Chen et al., 2019; Muellner-Riehl et al., 2019). Additionally, plants are likely to undergo intraspecific population differentiation by natural selection in adapting to complex habitats (Yu et al., 2019; Zhu, 2015). However, orogenesis occurring in northwestern Yunnan was unevenly distributed, showing a decreasing trend from north to south (Feng and Zhu, 2009). Thus, north-south differences in the magnitude of stratigraphic uplift during orogenesis may have contributed to the higher plant diversity in the northern areas, and the relatively low plant diversity in the southern areas (Ma et al., 2007; Zhang et al., 2016). Hence, the Dulong River Basin, Yulong Snow Mountain, Haba Snow Mountain, Baima Snow Mountain, Meili Snow Mountain, Cang Mountain, Gaoligong Mountain and Biluo Snow Mountain are key protection areas in NYST.

The PD in NYST is lower than expected based on the TR, and temperate species are abundant, indicating that NYST is a region of rapid species evolution (Liu et al., 2017). It may be an important centre of typical north-temperate distribution components in the Yunnan-Xizang region (Li and Feng, 2013; Wu, 1991). With the retreat of the ancient Mediterranean Sea and uplift of the Himalayas, the dominant warm and humid climate was gradually replaced by a cool and temperate climate. The north-temperate flora components penetrated from north to south, thus creating the present-day temperate flora dominated by north-temperate components (Li et al., 2007; Yue and Li, 2021; Zhu, 2012). Many large north-temperate genera underwent high differentiation in northwestern Yunnan

(e.g., the northern part of the Gaoligong Mountains). *Rhododendron*, *Pedicularis*, *Primula*, *Salix* and *Corydalis* all include multiple divergent taxa adapted to the cold conditions of the plateau (Chen et al., 2019; Ding et al., 2020). In parallel, cold-tolerant gymnosperms (Pinaceae, Taxaceae and Cupressaceae species) also diverged and diversified in this region (Feng and Zhu, 2010; Li et al., 2012). Phylogenetic studies have shown that many plant lineages (e.g., *Gentiana*, *Saxifraga* and *Rhodiola*) diversified and radiated rapidly during the uplift of the Himalayan-Tibetan Plateau (Ebersbach et al., 2017; Favre et al., 2016; Zhang et al., 2014a). Recent rapid diversification may have also contributed to the origin of many new taxa (e.g., *Eriophyton* and *Formania*) in the region (Liu et al., 2014; Luo et al., 2016), which promotes anomalously high species richness with lower PD than predicted (Li et al., 2015; Liu et al., 2017).

The high TR and lower PD than expected in NYST confirm the importance of diversification processes for contemporary floristic assemblages. Similar patterns of floristic assemblages have been observed in South America, and recent phases of uplift in the northern Andes were associated with many population events (Richardson et al., 2001). In this study of such assemblages, different evolutionary processes (dispersal and in situ diversification) leading to contemporary species assemblages have been identified. Rapid speciation is considered important to ensure maximum levels of biodiversity in the present and future, as it allows rapid recovery of biodiversity after an extinction event (Li and Yue, 2020).

4.2. Threatened and endemic higher plants

Endemic plants are abundant in NYST. More than one-third of NYST species are endemic to China/Yunnan, and nearly 60% of the species listed in the threatened category are endemic. The relative percentage (20%–50%) of Chinese endemic species at the county level of this region is consistent with the survey by Wu et al. (2016) (Fig. 5). Through rapid speciation in the last few million years, a large number of endemic and narrow-range species have emerged (Feng and Zhu, 2009; Liu et al., 2017). *Diplazoptilon*, *Dipoma*, *Smithorchis*, and *Skapanthus* are new endemic genera that are strongly associated with climatic changes and uplift of the Tibetan Plateau (Chen et al., 2019; Ding et al., 2020). *Metanemone*, *Anemoclema* and *Forsstroemia* are paleoendemic genera that are mostly Arctic-Tertiary (or northern component) remnants or have a paleo-Mediterranean floristic origin (Zhang et al., 2009).

Among the counties, Gongshan has the highest numbers of narrow-area species (684 species) and threatened species (245 species; Fig. 5); these results are consistent with Chen et al. (2013). The diversity of endangered species is closely related to the diversity of endemic species in small habitats (Tang et al., 2006; Zhang and Ma, 2008). Thus, the protection of narrow habitats of endangered plants may be an important measure for protecting endangered plants in NYST. Subtropical evergreen broad-leaved forests and alpine meadows are the two habitat types that require special protection in the study area, and they are rich in endangered and endemic species (Urban, 2015). Previous studies showed that most endangered species in a region can be protected by preserving the few habitats in which they survive (Tang et al., 2006). Therefore, the conservation of endangered plants in NYST should be focused on Gongshan, Lijiang and Shangri-La, as these counties require the least possible investment to protect most of the endangered plants (Diao et al., 2021).

Traditional agriculture and animal husbandry still play important roles in the livelihoods of residents in the study area, and households are highly dependent on plant resources (Ma et al., 2007). The utilization value (i.e., medicinal or ornamental) of a species is significantly correlated with its threat category (Liu et al., 2015), and overharvesting may be the primary threat in NYST. According to the results of Ma et al. (2007), 78 endangered plants represented by 84 genera in 58 families were recorded in northwestern Yunnan, with Liliaceae having the greatest number of endangered species (10), Magnoliaceae and Ranunculaceae each having 7 endangered species, and Orchidaceae, Solanaceae, Theaceae and Pinaceae each having endangered 3 species. Our results showed that 243 endangered plants represented by 135 genera in 73 families occurred in northwestern Yunnan, with Orchidaceae having the greatest number of endangered species, i.e., 82, and Ericaceae, Ranunculaceae, Liliaceae, Orobanchaceae and Crassulaceae having 15, 10, 9, 7 and 7 endangered species, respectively. In summary, compared to the historical numbers, the numbers of threatened higher plant species in the study area has increased. Families with more threatened species tend to have higher utilization value, such as Orchidaceae, Ericaceae and Liliaceae, which have high ornamental and medicinal value.

Table 1
Analysis of red lists of higher plants in NYST.

IUCN Categories	NYST List	Proportion (%)	China Species Red List	Proportion (%)
EX	3	0.03	27	0.08
EW	1	0.01	10	0.03
RE	1	0.01	15	0.04
CR	59	0.60	583	1.69
EN	184	1.88	1297	3.76
VU	418	4.27	1887	5.48
NT	839	8.57	2723	7.90
LC	7452	76.15	24,296	70.53
DD	825	8.43	3612	10.48

4.3. Conservation implications

The nature reserve system in NYST plays an important role in the conservation of threatened plants, although many of the reserves were not established specifically for the conservation of plant diversity (Ma et al., 2007). We found that the proportions of higher plants in both the extinction and threatened categories in this area were lower than those in the national list, i.e., the *China Species Red List* (Table 1). This finding indicates that coverage and effectiveness of plant diversity conservation in NYST are probably higher than the national levels. However, nature reserves located in priority conservation counties may play a limited role in preventing forest landscape fragmentation (Fig. 5). Baima Snow Mountain, located in Deqin County, is the core area of the “Three Parallel Rivers of Yunnan Protected Areas”. It is rich in natural landscapes and biodiversity, with intact temperate coniferous forests (especially *Picea* forests and *Abies* forests). In recent years, these forests have been fragmented by road construction and agricultural development (Fig. 5) (Li et al., 2008; Liu et al., 2019a; Miettinen et al., 2014). Forest landscape fragmentation can have extremely negative impacts on biodiversity (Hua et al., 2016; Liu et al., 2019a; Wang et al., 2019). If forest fragmentation in the study area continues to increase, it could threaten local biodiversity and undermine the plant diversity conservation efforts that have been achieved. Therefore, government departments and stakeholders should be working to formulate policies for forest landscape restoration and management (Diao et al., 2021). Furthermore, as protected area systems need to be larger and more numerous than they currently are, we must include plant diversity and forest landscape outside of protected areas. The western part of Yulong County and the central to southern parts of Shangri-La County should be included in the existing reserve system to protect higher plant diversity and the intact forest landscape.

Biodiversity surveys in China have long been conducted primarily as administrative units and have accumulated a wealth of data. Most of the data are recorded with counties as the basic unit; counties are also the fundamental unit for the current administration in China (Liu et al., 2021a; Wu et al., 2016). Considering the importance of historical data, to facilitate the management and utilization of biodiversity data, construction of a county-based biodiversity database is recommended. Field surveys and specimen collection are important means of understanding and documenting the world's species (Yang et al., 2013). Through two seasons of specimen collection, 120% more plant species were found in Yunlong County than the number recorded in the *Flora of Yunnan* (Chen et al., 2013). In-depth county-based plant diversity field surveys are needed on the level of administrative units, especially in those counties where there is large disparity between the number of species present and collected specimens.

5. Conclusion

NYST is a world hotspot for higher plant diversity, with nearly one-third of China's higher plant species and rich endemic plants. It is necessary to expand the area of protected areas in Yulong County and Shangri-La County to fill the conservation gaps. Species of Orchidaceae and *Rhododendron* in the study area need to be a priority for protection and monitoring.

Although much work has been invested in biodiversity surveys in China, the data on species distributions are not sufficiently detailed. Along with biodiversity surveys, suitable sample sites should be selected to establish fixed sample lines as permanent observation points for biodiversity monitoring. Through regular monitoring of sample sites, time-series data can be obtained to form a regional and national biodiversity monitoring network system. In addition, attention needs to be given to preserving the genetic diversity of higher plant species and to improving the management quality of protected areas. More cross-disciplinary collaboration among landscape ecologists, botanists, zoologists, and statisticians is needed to establish effective nature reserves.

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.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02396](https://doi.org/10.1016/j.gecco.2023.e02396).

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