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Original Research

Spatial Patterns and Environmental Drivers of Nationally Protected Gymnosperms in Guangxi, Southern China

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Abstract

Accurate knowledge of the distribution patterns and environmental determinants of threatened plants is essential for effective conservation prioritization. We conducted a regional assessment of nationally protected gymnosperms in Guangxi, southern China, a karst-dominated region spanning tropical–subtropical climatic transitions. Based on 213 georeferenced records for 35 taxa (6 families, 15 genera), we examined species richness, elevational patterns, and climatic associations at a regional scale across Guangxi (using a 50 km × 50 km spatial grid). Of these taxa, 15 are listed as national Class I protected species and 22 are categorized as Critically Endangered (CR), Endangered (EN), or Vulnerable (VU) according to the IUCN Red List, with most showing declining global population trends. Two Guangxi endemics and 11 karst-obligate species indicate high conservation irreplaceability. Species richness was concentrated in the central-northern Guilin–Liuzhou karst corridor and southwestern border regions, with a maximum of 13 taxa per 50-km grid cell. Occurrences were strongly biased toward low elevations, with 50.2% of records below 200 m. Principal component analysis identified temperature, particularly winter minimum temperature and seasonality, as the dominant environmental gradient (46.88% of explained variance), followed by precipitation-related factors (26.58%). These patterns, together with severe habitat fragmentation and anthropogenic pressures in lowland karst landscapes, underscore the urgent need for spatially targeted, climate-informed conservation actions in this globally important biodiversity region.

Keywords: Karst ecosystems, conservation biogeography, climate drivers, endemic species, southern China

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Introduction

Gymnosperms represent one of the most ancient and evolutionarily distinctive lineages of vascular plants, playing irreplaceable roles in maintaining ecosystem structure, function, and evolutionary heritage [1-3]. Despite their relatively low species richness compared with angiosperms, gymnosperms contribute disproportionately to phylogenetic diversity and provide critical ecological services, including carbon sequestration, soil stabilization, and habitat provision for diverse faunal assemblages [4]. Many gymnosperm lineages are also of considerable cultural, medicinal, and economic importance, particularly in East and Southeast Asia [5]. However, a substantial proportion of extant gymnosperms are currently threatened by habitat loss, climate change, overexploitation, and illegal trade, making them a focal group for biodiversity conservation at both national and global scales [1, 6, 7].

China harbors one of the world's richest assemblages of gymnosperm species, including numerous relictual and endemic taxa that survived past climatic oscillations [8]. As a result, gymnosperms have long been recognized as a priority group in China's biodiversity conservation strategies, with many species listed under national protection schemes [9]. Understanding the spatial distribution patterns and environmental constraints of these protected gymnosperms is therefore fundamental for improving conservation planning, identifying priority areas, and anticipating potential risks under ongoing environmental change [10, 11]. Nevertheless, despite their recognized importance, the ecological and biogeographic determinants shaping the regional distribution of nationally protected gymnosperms remain insufficiently explored, particularly at subnational scales where conservation actions are most directly implemented.

Guangxi Zhuang Autonomous Region (hereinafter referred to as Guangxi), located in southern China, represents a biogeographically unique and conservation-relevant region for gymnosperms [12, 13]. Situated at the intersection of the tropical and subtropical zones and forming part of the transition belt between East Asia and Southeast Asia, Guangxi exhibits pronounced climatic gradients, complex topography, and extraordinary habitat heterogeneity [14]. The region is especially renowned for its extensive karst landscapes [15], which are characterized by shallow soils, high rock exposure, fragmented habitats, and strong environmental filtering. These conditions have promoted the persistence of specialized plant lineages and contributed to high levels of endemism [16], while simultaneously increasing ecological vulnerability [15]. For gymnosperms, which often exhibit narrow ecological tolerances and limited dispersal capacity, such environmental complexity may exert strong controls on spatial distribution, elevational range, and niche differentiation.

In recent decades, Guangxi has experienced rapid socioeconomic development accompanied by land-use change, infrastructure expansion, and increasing human disturbance [17, 18], all of which pose growing threats to native vegetation and particularly to slow-growing, long-lived gymnosperm species [19]. Although several nature reserves have been established in the region [20], conservation effectiveness remains uneven, and knowledge gaps persist regarding whether existing protection efforts adequately encompass the environmental niches and spatial hotspots of nationally protected gymnosperms. Addressing these gaps requires not only inventories of species occurrences but also a mechanistic understanding of how climatic and topographic factors shape current distribution patterns.

Previous studies on gymnosperm conservation in China have largely focused on species-level population ecology [21], phylogenetics [2, 22], or predictive species distribution modeling at national or continental scales [6, 19]. While these approaches have yielded valuable insights, they often emphasize potential distributions rather than observed ecological differentiation and may overlook fine-scale environmental constraints that are highly relevant for regional conservation planning. In addition, many studies treat gymnosperms as a taxonomically homogeneous group [23], without explicitly considering functional or biogeographic attributes such as karst specialization, regional endemism, or differences in conservation status. Such attributes, however, are likely to be closely linked to environmental sensitivity and extinction risk, particularly in environmentally heterogeneous regions like Guangxi.

An emerging body of conservation biogeography research emphasizes the importance of integrating species traits, environmental gradients, and spatial patterns to identify vulnerability and guide conservation prioritization [24-26]. From this perspective, analyzing how protected species with different ecological affinities occupy multidimensional environmental space can provide deeper insights than distribution prediction alone. For instance, species restricted to karst habitats or confined to narrow climatic envelopes may face disproportionate risks under climate variability or habitat degradation, even if they currently occur within protected areas [27, 28]. Similarly, regionally endemic species may exhibit distinct environmental preferences compared with more widespread taxa, implying different management needs [29]. Despite their relevance, such comparative analyses remain scarce for nationally protected gymnosperms in southern China.

Another critical yet underexplored aspect concerns elevational patterns. Elevation integrates multiple environmental gradients, including temperature, moisture, and disturbance regimes, and has long been recognized as a key determinant of plant diversity and distribution [30, 31]. For long-lived gymnosperms, elevational range size may reflect historical refugia, dispersal limitation, and climatic tolerance [32]. Identifying elevation-related patterns in species richness and niche breadth can thus inform both in situ conservation and potential assisted management strategies [33]. However, comprehensive evaluations of elevational and climatic constraints on protected gymnosperms at the regional scale are still lacking for Guangxi.

We synthesize a comprehensive dataset of georeferenced occurrence records for nationally protected gymnosperms in Guangxi, coupled with detailed climatic, elevational, and ecological attribute information, and apply spatial and multivariate analytical approaches to disentangle the key drivers shaping regional distribution patterns. The objectives of this study are to (i) quantify spatial patterns of species richness and identify conservation priority areas; (ii) characterize elevational distribution patterns and assess climatic drivers structuring gymnosperm occurrences; and (iii) provide evidence-based recommendations for conservation planning and climate-adaptive management in this biodiversity hotspot facing accelerating anthropogenic pressures.

Materials and Methods

Study Area

Guangxi (approximately 20°54′-26°24′ N, 104°26′-112°04′ E) lies in southern China and borders Vietnam to the southwest, covering ~237,600 km² (Fig. 1). Guangxi sits at the interface of tropical Southeast Asia and subtropical East Asia and includes strong latitudinal and elevational gradients. Its topography ranges from near sea level to >2,000 m and comprises low mountains, hills, basins, plains, and extensive karst terrain (peak clusters, towers, sinkholes, and limestone outcrops). Karst areas are characterized by shallow soils, high rock exposure, rapid drainage, and marked microclimatic contrasts, producing a highly fragmented habitat mosaic that can promote local specialization while increasing vulnerability to disturbance [14, 15].

The study area is characterized by a typical subtropical to tropical monsoon climate [34], with

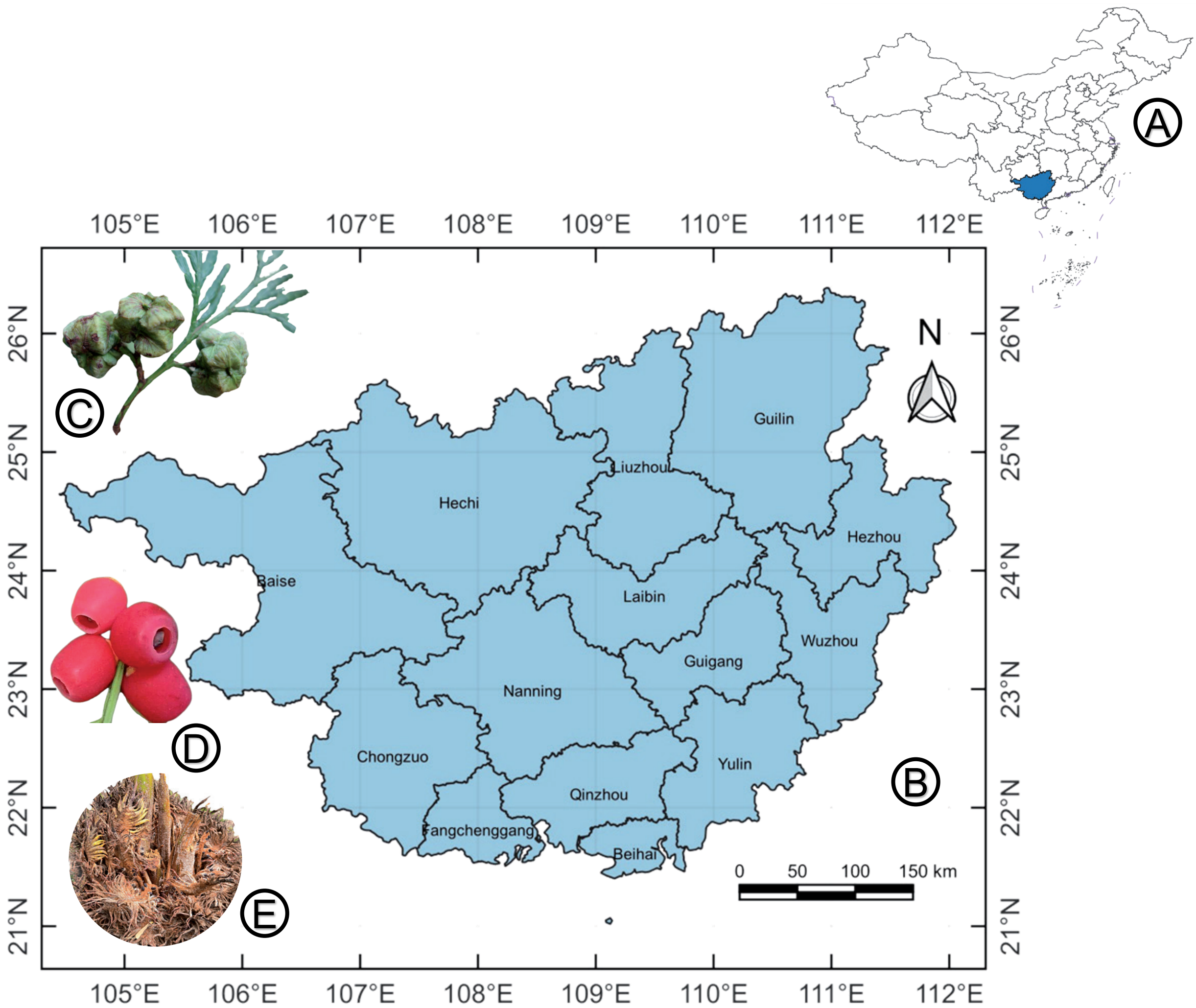

Fig. 1. Location of the study area and representative nationally protected gymnosperm species in Guangxi. Panel (A) shows the geographic position of Guangxi within China; Panel (B) displays the administrative divisions of Guangxi, including its 14 prefecture-level cities; Panels (C)–(E) show the seed cones of *Fokienia hodginsii*, *Taxus wallichiana* var. *mairei* and *Cycas debaoensis,* respectively.

a mean annual temperature (MAT) ranging from 16.0°C to 24.4°C and a mean annual precipitation (MAP) ranging from 1,000 mm to 2,800 mm, exhibiting strong spatial and seasonal variability across the region. This combination of climatic gradients and karst-related habitat constraints makes Guangxi an informative region for examining how environmental filtering shapes the distribution of nationally protected gymnosperms.

The dominant vegetation in Guangxi exhibits clear latitudinal and edaphic variations, transitioning from subtropical evergreen broad-leaved forests in the north to tropical monsoon evergreen broad-leaved forests and rain forests in the south [35]. Notably, due to the extensive distribution of peak-cluster depressions and towers, karst evergreen and deciduous broad-leaved mixed forests constitute a major and unique habitat type, which hosts a high proportion of habitat-restricted and endemic gymnosperms. In montane regions (such as the Mao'er and Yuanbao Mountains) [22], transitional coniferous–broad-leaved mixed forests and localized subalpine coniferous forests serve as critical refugia for ancient and endangered conifers.

Species Occurrence Data Compilation

We compiled comprehensive occurrence records for all nationally protected gymnosperm taxa occurring in Guangxi based on the List of National Key Protected Wild Plants [9, 36] (jointly issued by the National Forestry and Grassland Administration and the Ministry of Agriculture and Rural Affairs of China, with the latest revision officially implemented in September 2021). Species occurrence data were compiled from four sources: (1) field surveys by the authors during 2020-2025; (2) digitized specimens from major Chinese herbaria (e.g., IBK, PE, IBSC) accessed through national data portals (http://www.nsii.org.cn); (3) peer-reviewed literature and regional floras [12]; and (4) verified records from biodiversity databases and nature-reserve monitoring programs. To guarantee data accuracy and incorporate first-hand ecological observations, our research team conducted extensive field surveys across major forest reserves, forest parks, and karst landscapes in the study region. Of the occurrence records compiled for this study, 42 were original records collected directly through our field line-transect surveys and GPS tracking, with the surveys focusing particularly on localized micro-populations of critically endangered endemics (e.g., *Glyptostrobus pensilis*, *Cycas* spp.).

All occurrence records underwent rigorous quality control to ensure spatial and taxonomic accuracy. Records were excluded if (1) georeferencing uncertainty exceeded 5 km; (2) coordinates fell outside Guangxi's boundaries or in implausible habitats (e.g., marine areas); (3) taxonomic identification was uncertain or outdated nomenclature could not be reliably resolved; or (4) records represented cultivated or introduced individuals rather than naturally occurring populations. Taxonomic nomenclature followed the Flora of China and was cross-checked against current online plant name resources (e.g., World Flora Online), with recent taxonomic revisions incorporated where applicable. Duplicate records from the same locality were retained only when representing temporally distinct observations (>5 years apart) to capture potential distributional changes. The final dataset comprised 213 spatially unique occurrence records representing 35 gymnosperm taxa.

Conservation Status Assessment

National protection categories (Class I or Class II) for each taxon were assigned according to the official List of National Key Protected Wild Plants. Additionally, we compiled IUCN Red List threat categories and global population trend assessments from the IUCN Red List of Threatened Species database (https://www.iucnredlist.org, accessed July 2025). For species with multiple assessments, we used the most recent evaluation. Taxa were classified according to IUCN categories: Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), Data Deficient (DD), Extinct in the Wild (EW), and Extinct (EX). Population trends were categorized as decreasing, stable, or unknown based on IUCN assessments.

We identified taxa with restricted distributions based on two key ecological criteria: (1) Guangxi-endemic (GE) species, defined as taxa whose entire known global range is restricted to Guangxi, based on a comprehensive review of the "Flora of Guangxi" [37], regional botanical literature [12], and recent taxonomic treatments; and (2) karst-obligate (KO) species, defined as taxa strictly dependent on limestone karst habitats, following criteria established in karst vegetation studies and species-specific ecological research [12, 38]. Karst-obligate designation required evidence of exclusive occurrence on calcareous substrates with characteristic karst landforms (e.g., peak-cluster depressions, karst hills, limestone outcrops) and physiological adaptations to high calcium availability, shallow alkaline soils, and drought-prone conditions typical of karst environments.

Spatial Distribution Analysis

To visualize geographic patterns of species richness, we divided Guangxi into a grid of approximately 50 km × 50 km cells (0.5° × 0.5° in geographic coordinates) using QGIS 3.42.0 [39]. Species richness for each grid cell was calculated as the total number of unique taxa with occurrence records within that cell. Grid cells were classified into richness categories (1-13 taxa) and visualized using a color gradient to identify diversity hotspots and spatial patterns. The 50-km resolution was selected to balance adequate sampling coverage with meaningful biogeographic resolution, given the heterogeneous distribution of karst landscapes and elevational gradients across Guangxi.

Elevational Distribution Analysis

Elevation for each occurrence was extracted from the Shuttle Radar Topography Mission (SRTM) digital elevation model [40]. To characterize elevational distribution patterns, we classified all occurrence records into six 200-m elevational bands: 0-200 m, 200-400 m, 400-600 m, 600-800 m, 800-1,000 m, and 1,000-1,200 m. The 200-m interval was chosen based on preliminary analysis indicating sufficient ecological differentiation along elevational gradients in Guangxi's subtropical karst landscapes. We calculated the number and percentage of occurrence records within each elevational band to identify dominant patterns and assess whether distributions exhibited lowland concentration, mid-elevation peaks, or broad elevational ranges. Although elevations in Guangxi extend above 1,200 m, protected gymnosperm occurrences were extremely sparse at higher elevations, and the analysis focused on the 0-1,200 m range where the vast majority of records occurred.

Climatic Data Acquisition and Analysis

To characterize climatic constraints on gymnosperm occurrences, we extracted 19 bioclimatic variables (Bio1-Bio19) from WorldClim v2.1 at a 2.5′ spatial resolution [41]. WorldClim bioclimatic variables represent biologically meaningful temperature and precipitation metrics derived from monthly climate data, including annual trends (e.g., annual mean temperature, annual precipitation), seasonality (e.g., temperature seasonality, precipitation seasonality), and extreme or limiting environmental factors (e.g., temperature of the coldest and warmest months, precipitation of the wettest and driest quarters).

Principal component analysis (PCA) was performed on the matrix of 19 bioclimatic variables across all 213 occurrence records to reduce dimensionality and identify the dominant environmental gradients structuring species distributions. Prior to PCA, all variables were standardized to zero mean and unit variance to ensure equal weighting regardless of original measurement units. PCA was conducted using PAST 5.2 [42]. We retained principal components (PCs) with eigenvalues >1.0 following Kaiser's criterion, and reported eigenvalues, percentage of variance explained, and cumulative variance for the first four PCs. Variable loadings (correlations between original variables and PCs) were examined to interpret the ecological meaning of each principal component, with loadings >|0.25| considered substantial contributors to each axis. The first two principal components, which collectively explained the majority of variance, were interpreted as representing the primary climatic gradients – specifically temperature-related factors and precipitation patterns – that constrain the distributions of protected gymnosperms in Guangxi's subtropical karst landscapes.

Results

Species Composition and Richness Patterns

A total of 35 nationally protected gymnosperm taxa (including species and varieties) are recorded in Guangxi (Table 1), representing a substantial component of China's protected gymnosperm diversity in this biogeographic transition zone. These taxa span 6 families and 15 genera, with Cycadaceae (9 taxa), Pinaceae (10 taxa), Cupressaceae (5 taxa), and Taxaceae (5 taxa) being the most speciose. Based on the List of National Key Protected Wild Plants, 15 taxa are designated for national Class I protection (highest priority), while the remaining 20 are Class II. Class I taxa are heavily concentrated in Cycadaceae (e.g., *Cycas debaoensis*, *Cycas multipinnata*, *Cycas balansae*) and include select Pinaceae and Taxaceae representatives (e.g., *Abies yuanbaoshanensis*, *Glyptostrobus pensilis*, *Taxus wallichiana* var. *mairei*), reflecting their extreme rarity and vulnerability in Guangxi's landscapes.

IUCN Red List evaluations indicate that 5 taxa are Critically Endangered (CR), 7 are Endangered (EN), 10 are Vulnerable (VU), 5 are Near Threatened (NT), and 8 are Least Concern (LC), with no taxa assessed as Extinct, Extinct in the Wild, or Data Deficient. Global population trends are largely declining (26 taxa), with only 2 stable and 7 unknown, underscoring pervasive threats including habitat loss, illegal harvesting, and anthropogenic disturbances in karst-dominated areas.

In particular, 2 taxa are Guangxi-endemic (GE), with their entire known global range restricted to the region (*A. yuanbaoshanensis*, *Cycas ferruginea*). Additionally, 11 taxa are karst-obligate (KO), strictly dependent on limestone karst habitats with their associated edaphic and microclimatic challenges (e.g., *Cycas bifida*, *C. debaoensis*, *Pinus wangii*). One taxon (*C. ferruginea*) exhibits both GE and KO attributes. These restricted-distribution taxa are particularly susceptible to localized impacts and warrant prioritized conservation actions, such as enhanced reserve networks and ex situ propagation.

The spatial distribution of species richness for nationally protected gymnosperms in Guangxi is highly heterogeneous across approximately 50 km × 50 km grid cells (Fig. 2). The highest diversity occurs in the central-northern and northeastern parts of the province, where several cells support 12-13 taxa (darkest blue shading), creating a distinct hotspot roughly centered around the Guilin–Liuzhou region and extending northward toward the Hunan border and eastward toward the Guangdong boundary. A secondary zone of elevated richness (9–11 taxa, medium to dark blue) is evident in the southwestern karst-dominated area near the Vietnam border, particularly encompassing Chongzuo, Baise, and Debao. In marked contrast, species richness remains low in the southern coastal lowlands and southeastern regions (predominantly 1-4 taxa, light blue to white), as well as in the far western and northwestern margins (mostly

Table 1. Nationally protected gymnosperm species occurring in Guangxi, China: conservation status, IUCN assessments, population trends, and endemism/karst-obligate characteristics.

Scientific name	Family	Protection category [a]	IUCN [b]	Global population trends [c]	Guangxi-endemic / Karst-obligate [d]
Cycas balansae	Cycadaceae	I	EN	Decreasing	
Cycas bifida	Cycadaceae	I	VU	Decreasing	KO
Cycas debaoensis	Cycadaceae	I	CR	Decreasing	KO
Cycas dolichophylla	Cycadaceae	I	NT	Decreasing	KO
Cycas ferruginea	Cycadaceae	I	NT	Decreasing	GE/KO
Cycas guizhouensis	Cycadaceae	I	VU	Decreasing	
Cycas multipinnata	Cycadaceae	I	CR	Decreasing	KO
Cycas segmentifida	Cycadaceae	I	EN	Decreasing	
Cycas sexseminifera	Cycadaceae	I	LC	Decreasing	KO
Abies yuanbaoshanensis	Pinaceae	I	CR	Decreasing	GE
Abies ziyuanensis	Pinaceae	I	EN	Decreasing	
Cathaya argyrophylla	Pinaceae	I	VU	Stable	
Keteleeria davidiana var. *calcarea*	Pinaceae	II	LC	Unknown	
Keteleeria fortunei var. *cyclolepis*	Pinaceae	II	LC	Stable	
Keteleeria fortunei var. *oblonga*	Pinaceae	II	CR	Unknown	
Keteleeria pubescens	Pinaceae	II	LC	Unknown	
Pinus kwangtungensis	Pinaceae	II	NT	Unknown	
Pinus wangii	Pinaceae	II	EN	Decreasing	KO
Pseudotsuga brevifolia	Pinaceae	II	VU	Decreasing	KO
Calocedrus macrolepis	Cupressaceae	II	NT	Unknown	
Calocedrus rupestris	Cupressaceae	II	EN	Decreasing	KO
Chamaecyparis hodginsii	Cupressaceae	II	VU	Unknown	
Glyptostrobus pensilis	Cupressaceae	I	CR	Decreasing	
Xanthocyparis vietnamensis	Cupressaceae	II	EN	Decreasing	
Podocarpus chinensis	Podocarpaceae	II	LC	Decreasing	
Podocarpus macrophyllus	Podocarpaceae	II	LC	Decreasing	
Podocarpus neriifolius	Podocarpaceae	II	LC	Decreasing	
Podocarpus pilgeri	Podocarpaceae	II	LC	Unknown	
Cephalotaxus hainanensis	Cephalotaxaceae	II	EN	Decreasing	
Cephalotaxus oliveri	Cephalotaxaceae	II	VU	Decreasing	
Amentotaxus argotaenia	Taxaceae	II	NT	Decreasing	
Amentotaxus yunnanensis	Taxaceae	II	VU	Decreasing	KO
Pseudotaxus chienii	Taxaceae	II	VU	Decreasing	
Taxus calcicola	Taxaceae	I	VU	Decreasing	KO
Taxus wallichiana var. *mairei*	Taxaceae	I	VU	Decreasing	

Note: [a] Conservation status was determined according to the List of National Key Protected Wild Plants (jointly issued by the National Forestry and Grassland Administration and the Ministry of Agriculture and Rural Affairs of China, with the latest revision officially implemented in September 2021). [b, c] Conservation status (threat categories) and population trends follow the assessments published in the IUCN Red List of Threatened Species database (International Union for Conservation of Nature, accessed via https://www.iucnredlist.org). The abbreviations stand for the following: Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), and Least Concern (LC). [d] GE — Guangxi-endemic: Species that are strictly endemic to the Guangxi Zhuang Autonomous Region; KO — Karst-obligate: Species that are obligately restricted to karst (limestone) habitats.

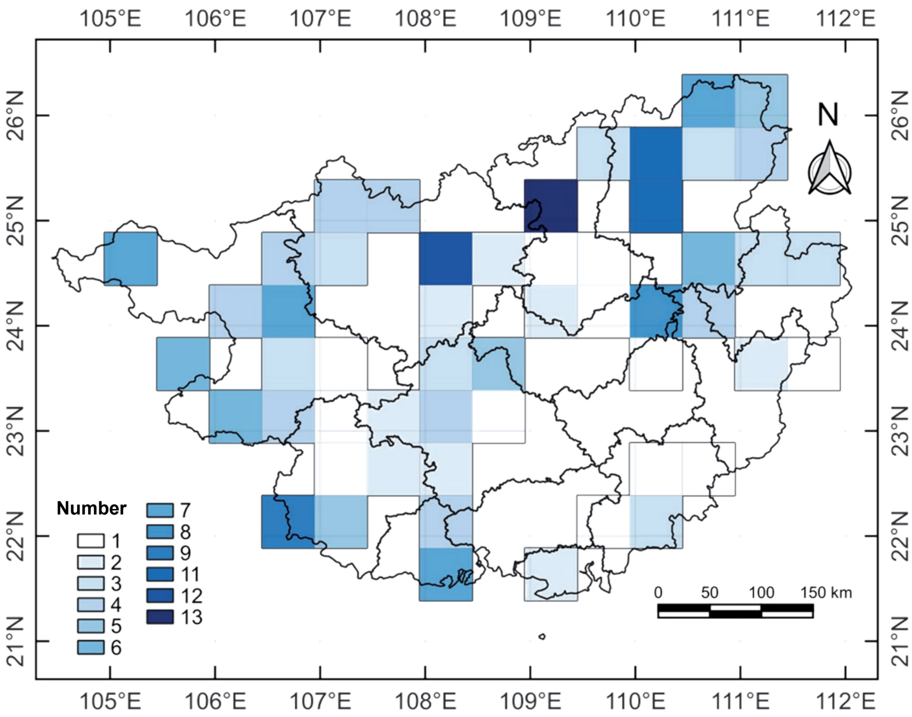

Fig. 2. Distribution pattern of species richness mapped in about 50 km × 50 km grid cells. The colors in the cells indicate different abundance levels of gymnosperm species in Guangxi.

1-6 taxa). Substantial portions of the province, especially in the south and southeast, contain only 1-3 taxa or none at all. Overall, protected gymnosperm diversity peaks in the central-northern karst and montane-interior zones and decreases sharply toward the southern and coastal lowlands, with the maximum richness per cell reaching 13 taxa.

Elevational Distribution Characteristics

The majority of occurrences (107 records, 50.2% of the total of 213) are concentrated in the lowest elevational band (0-200 m) (Fig. 3), reflecting the strong preference of many protected gymnosperms – particularly karst-obligate cycads (*Cycas* spp.) and certain conifers – for lowland karst landscapes characterized by limestone hills, peak-cluster depressions, and associated microhabitats.

Occurrence frequency declines markedly with increasing elevation: the 200-400 m band hosts 31 records (14.6%), the 400–600 m band 34 records (16.0%), the 600-800 m band 22 records (10.3%), the 800-1,000 m band 9 records (4.2%), and the 1,000-1,200 m band 10 records (4.7%).

Climatic Drivers of Distribution

To identify the primary climatic gradients influencing the distribution of nationally protected gymnosperms in Guangxi, a principal component analysis (PCA) was conducted on 19 WorldClim bioclimatic variables (Bio1-Bio19) and elevation. The first four principal components (PCs) collectively explained 97.17% of the total variance (Table 2), providing an efficient dimensionality reduction of the highly collinear climatic dataset. PC1 accounted for 46.88% of the variance (eigenvalue = 8.91), PC2 for 26.58% (eigenvalue = 5.05), PC3 for 18.14% (eigenvalue = 3.45), and PC4 for 5.57% (eigenvalue = 1.06).

Loadings of the climatic variables on the first four PCs (Table 3) highlight the dominant environmental axes. PC1 exhibited strong positive loadings (>0.25) on several temperature variables, including Bio11 (Mean Temperature of Coldest Quarter, 0.31), Bio6 (Min Temperature of Coldest Month, 0.30), Bio3 (Isothermality, 0.30), Bio9 (Mean Temperature of Driest Quarter, 0.26), Bio1 (Annual Mean Temperature, 0.26), and Bio8 (Mean Temperature of Wettest Quarter, 0.25). Negative loadings of similar magnitude were observed for Bio4 (Temperature Seasonality, –0.31), Bio7 (Temperature Annual Range, –0.30), Bio17 (Precipitation of Driest Quarter, –0.28), Bio14 (Precipitation of Driest Month, –0.27), and Bio19 (Precipitation of Coldest Quarter, –0.25). These contrasting patterns indicate that PC1 primarily represents a cold tolerance and temperature seasonality gradient, separating warmer, less seasonal lowland sites with higher winter minima and drier dry-season conditions from cooler, more seasonal mid- to high-elevation environments.

PC2 (26.58%) was dominated by positive loadings on precipitation variables, most notably Bio12 (Annual Precipitation, 0.38), Bio13 (Precipitation of Wettest Month, 0.34), Bio16 (Precipitation of Wettest Quarter, 0.32), Bio14 (0.25), Bio17 (0.24), Bio18 (Precipitation of Warmest Quarter, 0.24), and Bio19 (0.25), alongside

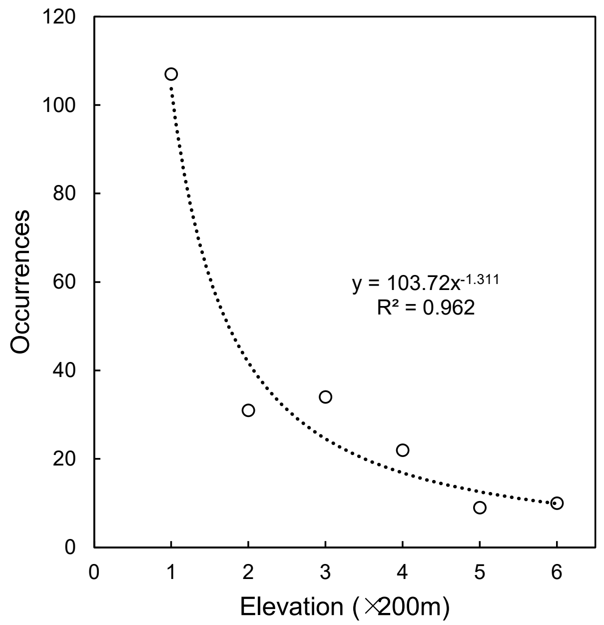

Fig. 3. Vertical distribution patterns of the gymnosperm species in Guangxi in relation to species richness. There are six elevational bands ranging from 0 to 1,200 m, each spanning 200 m.

moderate contributions from temperature variables such as Bio10 (Mean Temperature of Warmest Quarter, 0.28). This axis clearly captures a precipitation amount gradient, distinguishing wetter sites influenced by strong monsoon inputs from drier locations, often associated with rain-shadow effects or karst-specific hydrological constraints.

PC3 and PC4, explaining 18.14% and 5.57% of the variance respectively, capture secondary gradients related to seasonal temperature extremes (PC3) and diurnal temperature range combined with precipitation seasonality (PC4). However, their explanatory power is clearly subordinate to that of the first two components, which together account for 73.46% of the total variance and represent the principal climatic gradients structuring species distributions.

The PCA results clearly indicate that temperature is the dominant driver of environmental variation (PC1), primarily reflecting winter minimum temperature, isothermality, and temperature seasonality, whereas precipitation is the secondary driver (PC2), mainly capturing total annual rainfall and wet-season intensity. Together, these two axes explain 73% of the total variation and substantially outweigh the remaining components, suggesting that the distribution (or habitat suitability) of protected gymnosperms in Guangxi is chiefly constrained by cold winters and limited rainfall.

Table 2. Eigenvalues and variance explained by principal components derived from climatic and elevational variables.

Principal components	Eigenvalues	Variance explained (%)	Accumulation (%)
PC 1	8.91	46.88	46.88
PC 2	5.05	26.58	73.46
PC 3	3.45	18.14	91.60
PC 4	1.06	5.57	97.17

Table 3. Loadings of climatic variables on the first four principal components.

Climatic variables [a]	PC 1	PC 2	PC 3	PC 4
Bio1	0.02	-0.26	0.17	0.69
Bio2	0.30	-0.17	-0.04	0.16
Bio3	-0.31	0.07	0.12	0.19
Bio4	-0.01	0.23	0.43	0.24
Bio5	0.30	0.15	0.12	-0.14
Bio6	-0.30	-0.01	0.16	0.29
Bio7	0.25	0.17	0.20	0.13
Bio8	0.26	0.21	0.18	-0.14
Bio9	0.07	0.28	0.39	0.10
Bio10	0.31	0.12	0.12	-0.09
Bio11	-0.05	0.38	-0.24	0.10
Bio12	-0.01	0.34	-0.30	0.27
Bio13	-0.27	0.25	0.04	-0.06
Bio14	0.28	-0.07	-0.23	0.30
Bio15	0.07	0.32	-0.33	0.24
Bio16	-0.28	0.24	0.04	-0.04
Bio17	0.19	0.24	-0.32	0.09
Bio18	-0.25	0.25	0.05	-0.09
Bio19	0.02	-0.26	0.17	0.69

Discussion

Patterns of Gymnosperm Diversity in Guangxi's Karst Landscapes

Our comprehensive survey revealed that Guangxi harbors 35 nationally protected gymnosperm taxa, representing a substantial proportion of China's protected gymnosperm diversity within a relatively compact biogeographic region [9]. This remarkable richness underscores Guangxi's critical role as a refugium and diversity center for ancient plant lineages at the intersection of tropical and subtropical floristic zones [43]. The dominance of Cycadaceae, Pinaceae, and Taxaceae reflects both historical biogeographic processes and contemporary ecological filtering mechanisms [44, 45]. Cycads, as living fossils with Mesozoic origins, have persisted in Guangxi's karst landscapes due to the topographic complexity and microhabitat heterogeneity that buffer against climatic extremes and provide refugia during periods of environmental change [43, 46]. The high diversity of Pinaceae, conversely, reflects the region's elevational gradients and transitional position between lowland subtropical forests and montane temperate communities, facilitating the coexistence of taxa with divergent climatic requirements [47].

The heavily skewed conservation status – with 15 taxa classified under national Class I protection and 22 taxa categorized as Critically Endangered, Endangered, or Vulnerable under IUCN criteria – highlights the precarious status of gymnosperm populations in this region. The concentration of Class I taxa within Cycadaceae (including *C. debaoensis*, *C. multipinnata*, and *C. balansae*) and the presence of critically endangered endemics such as *Abies yuanbaoshanensis* and *Glyptostrobus pensilis* reflect extreme range restrictions, small population sizes, and high vulnerability to anthropogenic disturbances. Notably, 26 of 35 taxa exhibit declining global population trends, signaling pervasive and accelerating threats that transcend protected area boundaries. This pattern aligns with broader concerns regarding gymnosperm conservation globally [1, 48], where habitat fragmentation, illegal harvesting, and climate change synergistically erode population viability.

The identification of two Guangxi-endemic species (*A. yuanbaoshanensis* and *Cycas ferruginea*) and 11 karst-obligate taxa carries profound conservation implications. These restricted-distribution species represent irreplaceable evolutionary heritage and ecosystem functions unique to Guangxi's landscapes. Karst-obligate gymnosperms, adapted to edaphically extreme environments characterized by shallow alkaline soils, high calcium concentrations, and pronounced drought stress during the dry season, exemplify ecological specialization that simultaneously confers persistence in harsh habitats and vulnerability to habitat degradation [49, 50]. The dual designation of *C. ferruginea* as both Guangxi-endemic and karst-obligate elevates its conservation priority, as localized threats – such as limestone quarrying, agricultural expansion, or infrastructure development – could precipitate global extinction.

Spatial Heterogeneity and Diversity Hotspots

The pronounced spatial heterogeneity in species richness, with peak diversity (12-13 taxa per grid cell) concentrated in the central-northern and northeastern regions, particularly around the Guilin–Liuzhou karst corridor [43], reveals the non-random distribution of protected gymnosperms across Guangxi's landscapes. This primary hotspot encompasses the most extensive and well-developed peak-cluster karst formations in southern China, characterized by tower karst, cone karst, and peak-cluster depressions that create an intricate mosaic of microclimates, substrate types, and moisture regimes [51]. The topographic complexity inherent to this region likely facilitates niche partitioning among taxa with varying moisture, light, and edaphic requirements [52], thereby supporting higher local diversity than that found in more homogeneous landscapes.

Furthermore, the central-northern hotspot coincides with relatively lower human population densities than those in coastal and southern Guangxi [53], suggesting that reduced anthropogenic pressure has allowed more intact gymnosperm assemblages to persist. The establishment of several nature reserves in this region, including Huaping National Nature Reserve, Maoershan National Nature Reserve, and Yuanbaoshan Nature Reserve, has likely contributed to the conservation of rare gymnosperms, although our results indicate that diversity extends beyond current protected area networks [20]. The secondary diversity zone in southwestern Guangxi, particularly in the Chongzuo-Baise-Debao region near the Vietnam border, represents another critical conservation area characterized by extensive karst landscapes and transboundary connectivity with biodiversity-rich areas in northern Vietnam [54]. This region harbors multiple karst-obligate cycads and serves as a corridor for species with broader Southeast Asian distributions.

The sharp decline in species richness toward the southern coastal lowlands and southeastern regions likely reflects multiple interacting factors. These areas are dominated by non-karst sedimentary and igneous substrates that exclude karst-obligate taxa comprising a substantial proportion of Guangxi's protected gymnosperms. At the same time, the warmer and more humid conditions at low southern latitudes may exceed the thermal tolerances of certain temperate-affiliated conifers (e.g., some Pinaceae species) that reach their southern range limits in Guangxi [55, 56]. Southern Guangxi has experienced more intensive land use conversion for agriculture, aquaculture, and urban development [18, 57], resulting in extensive habitat loss and fragmentation that disproportionately impact large-statured, slow-growing gymnosperms with limited dispersal capabilities and long generation times.

The concentration of diversity in specific hotspots, coupled with large areas of low richness, suggests that conservation strategies must move beyond uniform protection approaches toward spatially targeted interventions. Enhanced protection, restoration, and monitoring should focus on the central-northern karst corridor and southwestern transboundary region, where conservation investments are likely to yield maximal returns in terms of species coverage and ecosystem representation.

Elevational Distributions and Lowland Concentration

The strong concentration of gymnosperm occurrences in the lowest elevational band (0-200 m, comprising 50.2% of all records) diverges from classical elevational diversity patterns documented for many plant groups in tropical and subtropical mountains, where diversity typically peaks at mid-elevations [58]. This lowland dominance aligns with the ecological specialization of numerous taxa to warm, humid subtropical monsoon conditions prevalent at lower altitudes, where shallow calcareous soils, rapid drainage, and high calcium availability favor habitat-restricted species. This lowland bias reflects the ecological dominance of karst-obligate cycads and certain lowland conifers that are physiologically adapted to warm, seasonally dry conditions and calcareous substrates prevalent in Guangxi's lowland karst valleys and depressions [59, 60]. The extensive lowland karst landscapes provide abundant suitable habitat patches, despite their fragmented nature, allowing karst-specialists to maintain relatively widespread distributions compared to more narrowly endemic montane taxa.

However, the lowland concentration of protected gymnosperms raises critical conservation concerns, as lowland habitats face disproportionately intense anthropogenic pressures compared to montane areas [61]. Agricultural expansion, urbanization, infrastructure development, and limestone quarrying for cement production are concentrated at lower elevations where terrain is more accessible and economically valuable. Consequently, lowland-restricted gymnosperms experience higher rates of habitat loss, fragmentation, and edge effects than do montane species. The declining population trends documented for the majority of lowland cycads corroborate these concerns and suggest that current protection measures may be insufficient to counteract ongoing degradation.

The steep decline in occurrences above 600 m, with minimal representation above 1,000 m, is consistent with broader patterns observed in the subtropical karst ecosystems of southern China. In these environments, topographic heterogeneity, edaphic constraints, and climatic gradients, including decreasing temperature and increasing orographic effects with altitude, impose strong filters on species distributions. This pattern likely reflects both severe climatic constraints and the limited extent of high-elevation karst habitats in Guangxi. Only a few isolated mountain peaks exceed 1,500 m, and these support distinct montane conifer assemblages that include cold-tolerant taxa such as *Abies* species and *Taxus* varieties. The rarity of high-elevation gymnosperms in our dataset underscores their sky-island distributions and heightened extinction risk under climate warming scenarios, which are predicted to drive upslope range shifts and reduce available habitat area for montane specialists. The modest secondary peak in the 400-600 m band may represent transitional ecotones where lowland karst taxa intermix with mid-elevation forest species, creating locally elevated diversity through environmental heterogeneity [62]. In particular, the slightly higher number of occurrences in this band than in adjacent bands may reflect localized suitability for certain mid-elevation specialists, such as some Pinaceae or Cupressaceae taxa adapted to transitional zones between lowland karst forests and montane habitats. However, occurrences remain sparse above 800 m, likely due to cooler temperatures, reduced precipitation reliability in higher karst terrains, and limited suitable substrate availability for obligate calcicoles or karst-restricted gymnosperms.

From a conservation perspective, the elevational distribution patterns highlight the need for stratified protection strategies that address the distinct threats and ecological requirements of lowland versus montane gymnosperms [61, 63]. Lowland conservation must emphasize habitat restoration, connectivity enhancement, and sustainable land-use planning to mitigate fragmentation [64], while montane conservation should focus on establishing climate refugia, monitoring population responses to warming [65], and potentially implementing assisted migration for critically threatened sky-island endemics.

Climatic Drivers and Environmental Constraints

The PCA results provide compelling evidence that temperature-related variables, particularly winter minimum temperature and temperature seasonality (PC1, 46.88% of variance), constitute the primary climatic axis structuring gymnosperm distributions in Guangxi. This pattern reflects the strong intercorrelations among bioclimatic variables in subtropical monsoon climates, where temperature and precipitation regimes are modulated by latitudinal, elevational, and orographic factors. This finding aligns with fundamental physiological principles governing gymnosperm biogeography [66, 67], as many taxa exhibit limited cold tolerance due to their evolutionary origins in warmer paleoclimates and the physiological constraints imposed by evergreen foliage and exposed ovules. The strong negative loadings of temperature seasonality and annual range on PC1 indicate that protected gymnosperms are concentrated in areas with mild, less seasonal thermal regimes – characteristic of subtropical lowland karst valleys buffered by topographic shelter and proximity to oceanic influences [68].

The positive loadings of winter minimum temperature (Bio6) and coldest quarter temperature (Bio11) on PC1 suggest that frost avoidance represents a critical threshold determining gymnosperm occurrence. Indeed, many Guangxi subtropical conifers are intolerant of prolonged freezing temperatures [69], which can cause tissue damage, reproductive failure, and mortality. The buffering effect of karst topography, where deep valleys and enclosed depressions trap warm air and moderate temperature extremes, likely enables cold-sensitive taxa to survive at higher latitudes than would be possible in non-karst landscapes [70]. This microclimatic buffering may have facilitated the Pleistocene survival of thermophilous gymnosperms in Guangxi, contributing to its role as a glacial refugium.

Precipitation, as represented by PC2 (26.58% of variance), emerges as the secondary driver of distribution patterns, with annual precipitation and wet-season rainfall distinguishing wetter from drier sites. Although Guangxi receives abundant monsoon precipitation overall, substantial spatial variation exists due to orographic effects, rain-shadow patterns, and karst hydrology [51, 68]. Karst landscapes receive high rainfall, yet rapid drainage through subsurface conduits and limited soil water retention often lead to moisture stress during dry periods. This hydrological paradox, characterized by high precipitation coupled with drought vulnerability [71], imposes strong selective pressures favoring drought-adapted taxa with deep root systems, efficient water use, and mechanisms for surviving seasonal water deficits.

Climate-informed conservation planning should prioritize the identification and protection of climate refugia, which are areas where topographic complexity, hydrological characteristics, or other factors buffer against regional climate trends and maintain suitable microclimates [72]. In Guangxi's karst landscapes, such refugia likely include deep valleys, north-facing slopes, cave entrances, and areas with perennial subsurface moisture. Integrating climate vulnerability assessments with spatial distribution data can guide the expansion of protected area networks to encompass sites with high microclimate diversity and connectivity, thereby enhancing the resilience of gymnosperm populations to climate change.

Conservation Implications and Management Priorities

The convergence of high diversity, severe threat status, and concentrated distributions in lowland karst habitats necessitates urgent conservation interventions. The current protected area network in Guangxi exhibits critical gaps in coverage [20], particularly in southwestern karst regions and lowland valleys supporting karst-obligate cycads. Systematic conservation planning using complementarity-based site selection should identify priority areas for reserve establishment or expansion that maximize representation of unprotected taxa and genetically distinct populations [73]. For critically endangered endemics such as *A. yuanbaoshanensis* and *C. debaoensis*, integrated in situ and ex situ strategies provide essential safeguards [74]. Botanical gardens, germplasm banks, and seedling nurseries, coupled with population reinforcement and restoration programs, offer the best prospects for long-term persistence. Cycad conservation is particularly complicated by illegal collection for horticultural trade, necessitating enhanced enforcement, community engagement, and demand reduction efforts [75].

Habitat restoration and connectivity enhancement in fragmented lowland karst landscapes are equally critical. Karst gymnosperms, particularly cycads with specialized pollination systems and limited seed dispersal, are vulnerable to genetic erosion and inbreeding depression in small, isolated populations [76]. Establishing corridors linking isolated populations and restoring degraded sites can enhance landscape connectivity and facilitate gene flow, thereby improving population viability [77]. These habitat-focused interventions must be complemented by community-based conservation initiatives that engage local stakeholders in monitoring, protection, and sustainable livelihood development. Many gymnosperm populations occur on communal lands where local communities depend on karst resources for agriculture, grazing, and non-timber forest products. Participatory conservation models that provide economic incentives, build local capacity, and respect traditional land use practices are more likely to achieve durable outcomes than top-down enforcement approaches [78].

Long-term monitoring programs employing standardized protocols for population demography, genetic diversity, reproductive success, and threat assessment are essential for evaluating conservation effectiveness and adapting management strategies [79]. The predominantly declining population trends documented in this study underscore the urgency of early detection systems and rapid response interventions. Integrating remote sensing, citizen science, and technologies such as drone-based monitoring can enhance surveillance efficiency across Guangxi's rugged karst terrain [80]. These monitoring efforts should inform adaptive management frameworks that respond to changing conditions, incorporate new scientific knowledge, and coordinate actions across governmental agencies, research institutions, and local communities to ensure the long-term persistence of Guangxi's irreplaceable gymnosperm heritage [81].

Conclusions

This study provides a comprehensive assessment of spatial patterns, elevational distributions, and environmental drivers of nationally protected gymnosperms in Guangxi, revealing a flora of exceptional conservation significance characterized by high endemism, severe threat status, and concentration in climatically and edaphically specialized habitats. The identification of discrete diversity hotspots, predominant lowland distributions, and climate-mediated range constraints offers critical insights for spatially targeted conservation planning and climate-adaptive management. The pervasive population declines documented across the majority of taxa signal urgent conservation needs that demand coordinated action among governmental, scientific, and community stakeholders. By integrating protected area expansion, habitat restoration, ex situ conservation, community engagement, and adaptive management informed by ongoing research and monitoring, it is possible to secure the long-term persistence of Guangxi's irreplaceable gymnosperm heritage and the broader karst ecosystems they inhabit. Ultimately, the fate of these ancient lineages will depend on society's commitment to reconciling biodiversity conservation with sustainable development in one of China's most biodiverse and geologically distinctive regions.

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AI Usage Disclosure

The authors used DeepSeek solely for language polishing and stylistic refinement of the manuscript. No generative AI tools were used for data analysis, data interpretation, image or figure preparation, or the generation of scientific content.

Conflict of Interest

The authors declare no conflict of interest.

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