Postprint: Floristic Geography of Woody Plants in the Gulinqing Karst Forest Dynamics Plot, Yunnan

Authors: Liu Qun, Chen Wenhong, Huang Hong, Yang Chong, Fan Changli, Zhang Jinguo, Shui Yumin

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Abstract

This study investigates the 25-ha Gulinqing karst forest dynamics plot in Yunnan, employing methods of plot census, specimen collection and identification, floristic analysis, Jaccard similarity coefficient, and PCA analysis to explore the floristic characteristics and status of the Gulinqing plot and its geographical relationships with the Bubeng plot in Yunnan and the Nonggang plot in Guangxi. The results show that: (1) There are approximately 406 species (including infraspecific taxa and excluding lianas) of woody plants with DBH $ $1 cm, belonging to 238 genera and 78 families. (2) In this plot, families containing 2–5 species and families containing 1 species are dominant, accounting for 37.18% and 34.62% of the total number of families, respectively; genera containing 2–4 species and genera containing 1 species are dominant, accounting for 30.25% and 65.13% of the total number of genera, respectively. (3) Analysis of distribution types at the family and genus levels reveals that families exhibit 9 distribution types and 7 variants, with the "pantropical distribution" type being the most predominant, accounting for 50.77%, and the ratio of tropical to temperate floristic elements (R/T) is 4.42; genera exhibit 11 distribution types, dominated by "tropical Asian elements," followed by "pantropical elements" and "Old World tropical elements," accounting for 33.47%, 18.22%, and 13.98%, respectively, with an R/T of 10.25. (4) Comparison of Jaccard similarity coefficients for family and genus composition among the Gulinqing, Bubeng, and Nonggang plots shows that Gulinqing and Bubeng have the highest similarity coefficients for both families and genera (0.674 and 0.395, respectively), while Bubeng and Nonggang have the lowest similarity coefficients for both families and genera (0.575 and 0.297, respectively). (5) PCA analysis of generic floristic spectra yields results similar to those of generic similarity coefficient analysis, but familial PCA analysis results differ from familial similarity analysis results, with familial PCA analysis indicating greater geographical connections between

Gulinqing and Nonggang. In summary, this plot exhibits rich family and genus composition, pronounced tropical nature, ancient floristic origin, obvious transitional status, and extensive floristic connections. However, comparison of species composition and floristic spectra cannot yield consistent geographical relationship results among the three aforementioned regions.

Full Text

Preamble

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Floristic Geography of Woody Plants in the Gulinqing Karst Forest Large Plot, Yunnan Province

LIU Qun[1,2], CHEN Wenhong[1], HUANG Hong[1,3], YANG Chong[1], FAN Changli[1], ZHANG Jinguo[4], SHUI Yumin[1*]

[1]Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650201, China
[2]School of Ecology and Environmental Science, Yunnan University, Kunming 650091, China
[3]University of Chinese Academy of Sciences, Beijing 100049, China
[4]Maguan Gulinqing Provincial Nature Reserve Management and Protection Bureau, Wenshan 663701, Yunnan, China

Abstract: Based on the 25 ha karst forest large plot in Gulinqing, Yunnan, this study employed plot investigation, specimen collection and identification, floristic analysis, Jaccard similarity coefficients, and PCA to explore the floristic characteristics and status of the Gulinqing plot and its geographical relationships with the Bubeng plot in Yunnan and the Nonggang plot in Guangxi. The results showed: (1) There were approximately 406 species (including infraspecific taxa, excluding woody vines) of woody plants with DBH $\geq$ 1 cm, belonging to 238 genera and 78 families. (2) Families with 2–5 species and families with 1 species dominated, accounting for 37.18% and 34.62% of total families respectively, while genera with 2–4 species and genera with 1 species dominated, accounting for 30.25% and 65.13% of total genera respectively. (3) Analysis of areal-types revealed 9 types and 7 variations at the family level, with pantropic distribution being the most common (50.77%), and a tropical to temperate flora ratio (R/T) of 4.42. At the genus level, 11 areal-types were identified, dominated by tropical Asian elements (33.47%), followed by pantropic (18.22%) and Old World tropical elements (13.98%), with an R/T ratio of 10.25. (4) Jaccard similarity coefficients showed the highest family and genus similarity between Gulinqing and Bubeng (0.674 and 0.395 respectively), while Bubeng and Nonggang showed the lowest similarity (0.575 and 0.297 respectively). (5) PCA of generic floristic spectra yielded similar results to the Jaccard similarity analysis, but familial PCA results differed, indicating closer geographical connections between Gulinqing and Nonggang at the family level. In conclusion, the plot exhibits rich familial and generic composition, pronounced tropical characteristics, ancient floristic origins, evident transitional status, and extensive floristic connections. However, comparisons of species composition and floristic spectra did not yield consistent geographical connection patterns among the three regions.

Keywords: floristic spectrum, floristic geography, Gulinqing, Southeast Yunnan, tropical karst forest

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First Author: LIU Qun (1998–), Master's student, specializing in floristic geography, (E-mail) liuqun@mail.kib.ac.cn.
Corresponding Author: SHUI Yumin, Ph.D., Researcher, specializing in floristic geography, taxonomy, and ecology, (E-mail) ymshui@mail.kib.ac.cn.

Introduction

Floristic geography is the science that investigates the composition, distribution patterns, distribution laws, formation mechanisms, and evolutionary history of floras in a given region or worldwide (Ying, 1997). Flora refers to the total assemblage of plant taxa in a specific area during a particular period, representing the long-term development and evolution of plants under certain natural historical conditions, especially geological history (Wu & Wang, 1983). Based on these concepts, flora constitutes the research object of floristic geography. While flora focuses on species composition and distribution, floristic geography additionally explores the origins and evolutionary processes of floristic elements by integrating geological history (Li, 2008; Wu & Yang, 2022). Studying the areal-types of families and genera in a region can reveal its floristic origins, species migration and differentiation history, and provide a comprehensive inventory of plant resources (Wu et al., 2006). Because generic morphological characteristics are relatively stable, geographical distributions are relatively fixed, and they reflect plant differentiation and evolutionary history, generic areal-types are typically used to characterize regional floristic properties and features (Li & Zhang, 2022). Currently, floristic geography is transitioning from macro- to micro-scale research, entering a stage of multidisciplinary integration and multi-method collaborative development. Macroscopically, research explores factors influencing floristic patterns from perspectives of geological history, ecological environment, plant communities, and large-scale spatial patterns. Microscopically, studies reveal the origins and evolutionary mechanisms of floristic elements through phylogenetic trees and molecular mechanisms of speciation, or combine macro- and micro-approaches to elucidate the formation, evolution, and spatial differentiation of floras (Sun, 2017; Sun et al., 2017).

Forest dynamic plots are established to study biodiversity maintenance mechanisms, species coexistence mechanisms, and community succession patterns. Research on these plots primarily focuses on species composition and structure, floristic characteristics, spatial distribution patterns, community assembly mechanisms, population survival and regeneration, coevolution between species and habitats, plant-microbe interactions, seed rain and litter dynamics, and negative density-dependent mechanisms of species coexistence (Pei, 2011; Feng et al., 2016; Mi et al., 2016, 2022; Ma, 2017; Zheng, 2018). To date, over 70 large forest dynamic plots have been established globally, with approximately 26 in China and nearly 60 auxiliary plots of 1–5 ha (Anderson-Teixeira et al., 2015; Wu et al., 2022; http://www.cncdiversitas.cn/zyxm/cforbio/js/). Many Chinese plots have documented and analyzed the floristic characteristics of woody plants, covering a range from cold-temperate to tropical zones (Ye et al., 2008; Zhu et al., 2008; Liu et al., 2011; Yang et al., 2011; Xu & Jin, 2012; Lu et al., 2013; Diao et al., 2016; Wang, 2016; Xie, 2017; Xie et al., 2019; He et al., 2021; Wu et al., 2021). Among these, tropical plots include Bubeng and Nabanhe in Xishuangbanna (Yunnan), Nonggang in Guangxi, and Jianfengling in Hainan, all located on the northern margin of tropical regions and suitable for longitudinal comparisons with the Gulinqing plot (Lan et al., 2013; Wang et al., 2014; Xu et al., 2015; Shi et al., 2021).

The 25 ha Gulinqing karst forest plot represents a karst depression landform, harboring many typical "rock-loving" tree species as well as "soil-loving" species, with strong habitat heterogeneity. Due to its unique climatic conditions, habitat types, and floristic characteristics, the region has attracted numerous scholars since Cai Xitao collected plant specimens there in 1932, followed by researchers including Liu Yuhu, Wu Sugong, Sun Hang, and Peng Hua (Bao et al., 1998). Chen Feipeng, Hu Yujia, and Li Biao from Sun Yat-sen University, in collaboration with the Wenshan Forestry Bureau, collected approximately 3,300 specimens stored at the SYS herbarium (Li, 1987). Shui Yumin and his team extensively surveyed forest areas in Gulinqing Township, collecting over 3,000 specimens and enriching regional vegetation surveys (Zhang, 2007).

However, previous botanical surveys lacked systematic approaches and employed limited methodologies. The region's complex biogeographical position in a border tropical area, substantial species uncertainty, inadequate survey intensity, and insufficient evidence for its floristic status made it difficult to systematically reflect local floristic characteristics and position. Building on previous investigations, this study established a 25 ha permanent karst forest monitoring plot in a karst depression approximately 600 m north of the timber inspection station in Gulinqing Township, Maguan County, Yunnan, in 2021, providing a foundation for systematic survey and in-depth floristic analysis. Based on plot survey data, we compiled a plant inventory and statistically analyzed the areal-types of all woody plant families and genera to explore floristic properties. Floristic analysis typically examines generic patterns and compares them with surrounding regions to assess geographical connections (Li & Sun, 2017). According to floristic regionalization of China, the 25 ha Gulinqing karst forest monitoring plot is located in the Paleotropical Kingdom, within the transition zone between the northern Beibu Gulf region and the Yunnan-Myanmar-Thailand region of the Malaysian subkingdom, near the Honghe Fault Zone. The role of this fault zone in demarcating these regions remains unstudied (Shui et al., 2003; Wu et al., 2010; Chen et al., 2014). This study compares the floristic relationships between the Gulinqing plot and the Bubeng plot (Yunnan-Myanmar-Thailand region) and the Nonggang plot (Beibu Gulf region) (Liang et al., 1988; Zhu, 1993; Lan et al., 2014; Wang et al., 2016) to explore Gulinqing's floristic connections.

Using the 25 ha Gulinqing karst forest plot as the study area, this research employs CTFS forest dynamic plot survey methods and floristic geography approaches, utilizing Jaccard similarity coefficients and PCA analysis to address: (1) the floristic properties of the Gulinqing plot; (2) its transitional biogeographical status; and (3) its geographical connections with the Bubeng plot (Yunnan-Myanmar-Thailand region) and the Nonggang plot (Beibu Gulf region).

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1. Materials and Methods

1.1 Study Area Overview

The 25 ha Gulinqing karst forest plot is located in Bojia Village, Gulinqing Township, southwestern Maguan County, Wenshan Prefecture, southeastern Yunnan, approximately 600 m from the timber inspection station, at the border between Hekou and Maguan counties (Zhu et al., 2007; Liu et al., 2019). Situated south of the Tropic of Cancer at 104°15 E, 22°36 N, the plot ranges from 530–613 m in elevation with 83 m vertical relief. Southeastern Yunnan faces Vietnam across a river and represents the northern margin of Southeast Asian tropical rainforests (Zhu et al., 2007). The region has a mean annual temperature of 22.8 °C, 1,802 hours of sunshine, and annual rainfall reaching 1,764 mm. Influenced by airflows from the Beibu Gulf and Bay of Bengal, the climate is hot and humid year-round with 86% mean annual relative humidity and a "double rainy season" pattern (Zhang et al., 2015; Li et al., 2018). Based on this rainfall pattern and vegetation classifications, the tropical rainforest belongs to the tropical humid rainforest subtype (Wu et al., 1987; Wu, 1995), though some scholars argue it should be classified as tropical seasonal rainforest due to monsoon climate influence and deciduous components (Schimper, 1903; Zhu & Tan, 2023). The substantial vertical relief creates a typical karst landform with high rock outcrop rates and a central depression surrounded by higher elevations (Maguan County Local Records Compilation Committee, 1995; Kong, 2008). Shielded by the Himalayas, the area was rarely affected by ancient geological extreme events, preserving numerous relict plants and earning the reputation as a "mysterious green treasure south of the Tropic of Cancer" (Shui et al., 2005). The region is also a core area of the ancient endemic center of southeastern Yunnan and one of China's three major biodiversity centers (Zhang, 2013). Its unique geographical location harbors particularly rich biodiversity and rare/endangered species, making systematic research and conservation of this tropical rainforest critically important.

1.2 Plot Establishment and Inventory Compilation

The 25 ha Gulinqing karst forest plot was established following CTFS (Center for Tropical Forest Science) standards, measuring 500 m × 500 m and divided into 625 subplots of 20 m × 20 m, designated as GLQ0101–GLQ2525. Each 20 m × 20 m subplot was further divided into sixteen 5 m × 5 m quadrats. All woody plants (excluding woody vines) with DBH $\geq$ 1 cm at 1.3 m height were tagged, with branches $\geq$ 1 cm below breast height receiving branch tags (Condit, 1998). Plant surveys were conducted seasonally from 2022–2023, with four major intensive surveys recording species, tree height, DBH, location, habitat, and special conditions. Unidentifiable plants were collected as specimens for indoor identification; specimens that could not be identified morphologically were subjected to molecular identification. Species nomenclature followed previous surveys of Maguan Gulinqing (Shui & Chen, 2006; Zhu et al., 2007; Shui et al., 2020), *Seed Plants of Karst Regions in China (Vol. 1, Southeast Yunnan)* (Shui & Chen, 2006), *Wild Seed Plants of Xishuangbanna, Yunnan* (Zhu & Yan, 2012), and *Guangxi Nonggang Karst Seasonal Rainforest—Tree Species and Their Distribution Patterns* (Wang et al., 2016). Online resources including iPlant (http://www.iplant.cn/), Chinese Virtual Herbarium (https://www.cvh.ac.cn/, CVH), and Plant Photo Bank of China (http://ppbc.iplant.cn/, PPBC) were consulted for species information, identification, and standardization of family, genus, and species names, resulting in the *Inventory of Woody Plants in the 25 ha Gulinqing Karst Forest Plot* (Appendix 1). Families and genera for the comparative Bubeng and Nonggang plots were updated according to the latest APG IV system (Appendices 2 and 3).

1.3 Floristic Analysis

Using the iPlant database and the latest APG IV system, plant inventories for Gulinqing, Nonggang, and Xishuangbanna were standardized. Revised areal-types for families and genera were statistically analyzed following Wu et al. (2006) and Stevens (2001 onwards) for families, and *A Dictionary of the Families and Genera of Chinese Vascular Plants* (Li et al., 2018) and *The Families and Genera of Chinese Vascular Plants* (Li et al., 2020) for genera.

1.4 Analysis of Geographic Connections Among Floras

Geographic connections were assessed through Jaccard similarity coefficients of families and genera among Gulinqing karst forest plot (GLQ), Nonggang karst seasonal tropical rainforest plot (NG), and Xishuangbanna's Bubeng tropical seasonal rainforest plot (BB). Following Whittaker (1972), Jaccard similarity was calculated as Jaccard = C/(A+B-C), where C represents shared taxa between two regions, and A and B represent total taxa in each region. Higher coefficients indicate greater similarity.

Floristic spectra (percentage representation of each floristic element) were compared among plots (Ma et al., 1995), calculated as FER = (FEi/T) × 100, where FEi is the number of taxa for the i-th floristic element and T is the total number of taxa. Cosmopolitan elements were excluded, and distribution types 2–15 were quantified through floristic spectra calculation and visualized using PCA in Origin 2021.

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2. Results

2.1 Statistical Analysis of Family and Genus Richness

Systematic survey of the 25 ha Gulinqing karst forest plot documented 78 families, 238 genera, and 406 species of woody plants.

2.1.1 Family-Level Richness Analysis Family richness analysis (Table 1) revealed three families with >20 species: Lauraceae (34 species), Rubiaceae (28 species), and Moraceae (22 species), representing 3.85% of total families and 20.69% of total species. These are cosmopolitan or pantropic families. Eight families contained 11–20 species: Fabaceae (19), Annonaceae (17), Meliaceae (16), Euphorbiaceae (14), Phyllanthaceae (13), Rutaceae (11), Primulaceae (11), and Lamiaceae (11), accounting for 10.26% of families and the highest proportion of species (27.59%), mostly cosmopolitan or pantropic. Eleven families had 6–10 species (14.10% of families, 22.17% of species), including Acanthaceae (10), Malvaceae (9), Urticaceae (9), Sapindaceae (9), Araliaceae (9), Magnoliaceae (8), Salicaceae (8), Fagaceae (8), Ebenaceae (8), Myrtaceae (6), and Burseraceae (6), showing diverse areal-types including pantropic, north temperate and south temperate disjuncted, East Asian (tropical, subtropical) and tropical South American disjuncted, and East Asian and North American disjuncted. Families with 2–5 species were most numerous (39 families, 37.18% of total), comprising 22.91% of species, including Rosaceae (5), Celastraceae (5), Anacardiaceae (5), Connaraceae (5), Apocynaceae (4), Proteaceae (4), Dipterocarpaceae (3), Clusiaceae (3), Cannabaceae (3), Icacinaceae (3), and Stemonuraceae (2), predominantly pantropic. Families with 1 species were the second most common (27 families, 34.62%), representing 6.65% of species, including Capparaceae, Pittosporaceae, Theaceae, Aquifoliaceae, Gentianaceae, Lecythidaceae, and Tapisciaceae, with diverse areal-types dominated by pantropic distribution.

2.1.2 Genus-Level Richness Analysis Genus richness analysis (Table 2) showed one genus with >10 species: *Ficus* (15 species, 0.42% of genera, 3.69% of species), a cosmopolitan genus with broad ecological amplitude and strong adaptability. Ten genera contained 5–10 species (4.20% of genera, 14.78% of species), including *Diospyros*, *Ardisia*, *Polyalthia*, and *Litsea*, mostly pantropic, Old World tropical, East Asian (tropical, subtropical) and tropical American disjuncted, tropical Asian to tropical Australasian, and East Asian–North American disjuncted. Genera with 2–4 species were most numerous (72 genera, 30.25% of total, 43.35% of species), including *Michelia*, *Artocarpus*, *Dalbergia*, *Aphanamixis*, *Garcinia*, *Manglietia*, and *Viburnum*, predominantly tropical Asian, pantropic, Old World tropical, East Asian (tropical, subtropical) and tropical American disjuncted, tropical Asian to tropical Australasian, and East Asian–North American disjuncted. Single-species genera dominated (155 genera, 65.13% of total, 38.18% of species), including *Deutzianthus*, *Dipterocarpus*, *Parashorea*, *Lirianthe*, *Pometia*, and *Polygala*, mostly tropical Asian, pantropic, Old World tropical, East Asian (tropical, subtropical) and tropical American disjuncted, and tropical Asian to tropical Australasian.

2.2 Areal-Type Statistics

2.2.1 Family Areal-Types Family areal-types comprised 9 types and 7 variations (Table 3). Pantropic distribution was most prevalent (50.77%), including Euphorbiaceae, Annonaceae, Malvaceae, Acanthaceae, Meliaceae, Sapotaceae, Sapindaceae, and Ebenaceae—dominant families in tropical rainforests. East Asian (tropical, subtropical) and tropical South American disjuncted families included six families (9.23%): Aquifoliaceae, Elaeocarpaceae, Gesneriaceae, and Araliaceae. North temperate distribution and its variations accounted for 12.31%, including Cannabaceae, Juglandaceae, Fagaceae, Cornaceae, and Salicaceae, which were not dominant in the plot. The ratio of tropical (types 2–7) to temperate (types 8–15) floristic elements (R/T) was 4.42 at the family level.

2.2.2 Genus Areal-Types Genus areal-types are particularly significant. Analysis revealed 11 areal-types (Table 4), with tropical Asian elements being most abundant (79 genera, 33.47%), including *Manglietia*, *Michelia*, *Artocarpus*, *Aphanamixis*, *Nothapodytes*, *Desmos*, *Chukrasia*, *Actinodaphne*, *Trivalvaria*, *Chisocheton*, *Parashorea*, and *Sarcosperma*. Pantropic distribution ranked second (43 genera, 18.22%), including *Ficus*, *Diospyros*, *Ardisia*, *Sterculia*, *Beilschmiedia*, *Salacia*, *Drypetes*, *Ziziphus*, *Schefflera*, and *Homalium*. Old World tropical elements were third (33 genera, 13.98%), including *Canarium*, *Syzygium*, *Pavetta*, *Maesa*, *Tarenna*, *Bridelia*, *Cleistanthus*, *Antiaris*, and *Flueggea*. Tropical Asian to tropical Australasian distribution ranked fourth (30 genera, 12.71%), including *Actephila*, *Breynia*, *Trigonostemon*, *Aglaia*, *Neonauclea*, and *Horsfieldia*. East Asian (tropical, subtropical) and tropical South American disjuncted elements ranked fifth (16 genera, 6.78%), including *Litsea*, *Meliosma*, *Microtropis*, *Caryodaphnopsis*, *Ilex*, *Lycianthes*, *Turpinia*, and *Sapindus*. Among types 8–15, few genera were present, but East Asian and North American disjuncted and East Asian distributions comprised substantial proportions (3.39% and 2.54% respectively), including *Gleditsia*, *Castanopsis*, *Nyssa*, *Firmiana*, *Vernicia*, and *Eriobotrya*. The generic R/T ratio was 10.25, indicating strong tropical affinities.

2.3 Comparative Study with Bubeng and Nonggang Plots

Preliminary data showed the Gulinqing 25 ha plot (530–613 m elevation, 83 m relief, 104°15 E, 22°36 N) had 44.73% rock outcrop and 78 families, 238 genera, and 406 woody species (excluding vines, see Appendix 1). The Nonggang plot (15 ha, 180–370 m, mean 260 m, 190 m relief, 106°57 E, 22°25 N) had 68.80% rock outcrop and 55 families, 154 genera, and 218 woody species (Wang et al., 2016) (Appendix 2). The Bubeng plot (20 ha, 709–869 m, 160 m relief, 101°34 E, 21°36 N) had latosol soils, thick soil layers, and 71 families, 200 genera, and 428 woody species (Ci, 2018; Zhang et al., 2018) (Appendix 3).

2.3.1 Similarity Coefficients of Family and Genus Composition Jaccard similarity coefficients (Table 5) showed the highest familial similarity between Gulinqing and Bubeng (0.674), followed by Gulinqing and Nonggang (0.583), with Bubeng and Nonggang showing the lowest similarity (0.575). Generic similarity was also highest between Gulinqing and Bubeng (0.395), followed by Gulinqing and Nonggang (0.315), with Bubeng and Nonggang lowest (0.297). Thus, Jaccard similarity analyses yielded consistent results at both family and genus levels.

2.3.2 PCA of Family and Genus Floristic Spectra PCA was performed on floristic spectra of families and genera from the three plots (Table 6). The first two principal coordinates explained >80% of variance. For families, Coordinate 1 explained 63.70% and Coordinate 2 explained 36.30% (cumulative 100%). For genera, Coordinate 1 explained 85.05% and Coordinate 2 explained 14.95% (cumulative 100%), indicating effective dimensionality reduction.

PCA results (Figure 1 [Figure 1: see original paper]) showed that at the family level, Gulinqing and Nonggang were closest, indicating higher similarity in familial floristic spectra, followed by Gulinqing and Bubeng, with Bubeng and Nonggang most distant—contradicting familial Jaccard similarity results (Figure 1A). At the genus level, Gulinqing and Bubeng were closest, showing highest similarity, followed by Gulinqing and Nonggang, with Bubeng and Nonggang most distant—consistent with generic Jaccard results (Figure 1B). Thus, PCA yielded different patterns for families and genera.

3. Discussion and Conclusion

The high species richness of families, genera, and species in this plot likely relates to diverse limestone-sandstone habitats, reflected in rock outcrop rates: Gulinqing 44.73%, Nonggang 68.80%, and Bubeng (non-karst, soil-dominated) (Table 8). The rock-soil composite habitat nurtures unique species preferences, enhancing diversity. Soil environments support richer plant life than rock environments, giving Gulinqing and Bubeng higher species richness than Nonggang.

Family richness analysis revealed that families with >20 species and those with 11–20 species were dominant, comprising plot-advantaged families including Lauraceae, Moraceae, Rubiaceae, Annonaceae, Fabaceae, Meliaceae, and Euphorbiaceae. These cosmopolitan or pantropic families have undergone adaptive differentiation, substantially supplementing local species richness. Genus analysis showed that genera with 2–4 species and monotypic genera dominated, including both newly migrated genera (not yet differentiated) and relict genera (evolutionarily terminal). Relict genera such as *Lirianthe* and *Manglietia* suggest Gulinqing may be their origin center, surviving due to minimal or no impact from polar glaciation, corroborating its status as an ancient endemic center.

Familial areal-type analysis identified 9 types and 7 variations, indicating extensive and complex geographical connections related to its transitional position. Pantropic families dominated, demonstrating pronounced tropical characteristics. North temperate and East Asian distributions also contributed substantially, evidencing deep historical connections with temperate regions, particularly East Asia. Generic areal-type analysis identified 11 types, with tropical Asian elements dominant, likely resulting from Indian-Eurasian plate collision and infiltration of tropical Asian elements after the Tertiary, consistent with Zhu (2018). Pantropic and Old World tropical elements ranked second and third, confirming pronounced tropical properties and ancient origins, supporting the status of southeastern Yunnan as an ancient endemic center (Li et al., 2002). The substantial proportion of tropical Asian to tropical Australasian elements suggests the area was once oceanic, retaining some Australasian floristic components after uplift during the Yanshan orogeny (Shui et al., 2020). East Asian elements also contributed significantly, indicating connections with East Asian flora and confirming the transitional nature of southeastern Yunnan as a corridor for southward penetration of East Asian flora (Zhu, 2013).

All three plots showed dominant tropical components in R/T values. Gulinqing's R/T values were higher than Nonggang's but lower than Bubeng's, showing clear longitudinal patterns: Bubeng > Gulinqing > Nonggang (Table 8). Tropical Asian elements also decreased longitudinally from west to east, suggesting the Indian-Eurasian collision center may have been located in or west of southern Yunnan.

Familial similarity and PCA analyses revealed an interesting discrepancy: despite higher Jaccard similarity between Gulinqing and Bubeng, familial PCA indicated closer geographical connections between Gulinqing and Nonggang. This likely reflects different geological backgrounds, with southern Yunnan's Bubeng and southeastern Yunnan's Gulinqing hosting different plant groups (Zhu, 2011). The closer familial connection between Gulinqing and Nonggang may reflect more ancient geological ties, as both belong to the same geological karst plate (Ma, 2002). Generic analyses showed Gulinqing and Bubeng had both higher similarity coefficients and closer PCA distances, possibly due to 30° clockwise rotation of the Simao-Lanping geological plate and southward shift of southeastern Yunnan, causing migration of some taxa to southern Yunnan (Zhu & Yan, 2003; Zhu, 2015). This geological event may explain the higher similarity between Bubeng and Gulinqing. Additionally, Bubeng's soil-dominated environment (without harsh karst limestone) supports rich diversity and "soil-loving" plant groups similar to those in Gulinqing, where stable soil environments provide most species while rock habitats contribute fewer. Gulinqing-Nonggang similarity ranked second, with Bubeng-Nonggang lowest, though differences were small. Nonggang's homogeneous karst limestone habitat results in lower diversity, explaining its lower similarity with Gulinqing. However, shared species between Nonggang and Gulinqing are likely rock-dwelling specialists, and Gulinqing's rock-soil composite habitat creates conditions for its transitional floristic status. Integrating latitude/longitude, similarity coefficients, PCA results, R/T values, and rock-soil habitat heterogeneity, Gulinqing occupies an intermediate position between the Yunnan-Myanmar-Thailand region (Bubeng) and the Beibu Gulf region (Nonggang), with its transitional status clearly related to proximity to the Honghe deep fault zone. We propose that besides demarcating southern and southeastern Yunnan, the Honghe Fault may also serve as a boundary between the Yunnan-Myanmar-Thailand and Beibu Gulf regions (Shui et al., 2003; Zhu, 2011).

In summary, the 25 ha Gulinqing karst rainforest plot exhibits pronounced tropical characteristics with minimal East Asian elements, leaning more toward the Paleotropical Kingdom. Its ancient origin is evidenced by substantial Old World tropical components and numerous ancient families and genera, confirming its ancient floristic nature. Its transitional status is evident in geographical location, habitat conditions, similarity coefficients, PCA results, and R/T values, all positioning it between the Yunnan-Myanmar-Thailand region (Bubeng) and the Beibu Gulf region (Nonggang). Generic PCA indicates closer recent geographical connections with Bubeng, while familial PCA suggests more ancient geological connections with Nonggang. All evidence points to a clear transitional nature. However, whether species-level analyses will corroborate these patterns requires further investigation.

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Appendices

Appendix 1 Statistics on the list of woody plants with a diameter at breast height $ $1 cm in the 25 ha large sample plot of Gulinqing, Yunnan

Appendix 2 Statistics on the list of woody plants with a diameter at breast height $ $1 cm in the 15 ha large sample plot of Nonggang, Guangxi

Appendix 3 Statistics on the list of woody plants with a diameter at breast height $ $1 cm in the 20 ha large sample plot of Bubeng, Yunnan

Note: Figure translations are in progress. See original paper for figures.