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Research Article

Amphibian Biodiversity and Distribution Changes From the Paleozoic in China

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Vertically exploring the animals' biodiversity and distribution change trajectories and horizontally demonstrating their association with the existing floral structures are critically required to integrally analyze their biodiversity changes and predict their future survival trends. Here, we study the distribution of amphibian fossils since the Paleozoic and their extant taxa in China. They have been regarded as very sensitive to environmental changes and ecologically fragile. We also explore their association with vascular and nonvascular plants. The results indicate that amphibians appeared in the Late Paleozoic in Northern China, currently Xinjiang, Ningxia, Gansu, and Henan provinces. Their dispersion and radiation during the Mesozoic period were from three isolated centers. A future development during the Cenozoic was toward South and Southwest China. Southwest and coastal regions are major biodiversity-bearing areas, corresponding to abundant vascular and nonvascular floral structures. They, however, rely more on vascular plants that present the most extraordinary biodiversity index and the most outstanding national repositories in Southwest China. Thus, the conservation strategies for amphibians in China must prioritize the region, especially Yunnan and Sichuan, as well as the coastal region. Avoiding further human disruption is a conservation policy in the central region, and less investment in the northwest and northeast, where amphibian biodiversity and distribution have met a bottleneck due to further desertification of the environment and ecology.

Keywords: amphibian and floral structures; conservation strategies of amphibians; fossil and extant amphibians in China; vascular and nonvascular plants

1. Introduction

Amphibians are a class of vertebrates, including frogs, toads, salamanders, and cecilians. They are characterized by their ability to live in terrestrial waters, undergoing a metamorphosis from larval to adult forms [1]. Depending on the life cycle stage, they typically have moist skin, allowing them to breathe through the skin instead of using lungs or gills. They play essential roles in ecosystems due to their sensitivity to environmental and ecological changes—they are often considered indicator species in monitoring pollution and habitat degradation [2, 3]. On the other hand, since their unique environmental and ecological demands of waters and confined ability of geographic migration, they have been regarded as model species in analyzing land and geographic modification during the evolutionary development [4].

The amphibia in China is supposed to appear in the late Devonian, 382.7–372.2 mya, during the Paleozoic era [5], following the appearance of the first forests that took shape on land after remarkable radiation and dispersion of vascular plants in the Silurian and Devonian, which significantly promoted the evolution and distribution of the vertebrates [6, 7]. They became dominant land vertebrates, but experienced a significant extinction before the Jurassic (201.3–145 mya) [5]. Geographically and evolutionarily, they then experienced substantial changes in biodiversity and distribution during the Mesozoic and Cenozoic [8–11].

Evolutionary development and the relationships among modern amphibians are still far from understood due to the scarcity of fossils and specialized anatomical variability [5]. Some famous fossils include primitive salamanders in the Jurassic–Cretaceous, the earliest known fossil from North China (Liaoning, Hebei, and Inner Mongolia), implying an Asian origin of crown taxa [12, 13]. A frog fossil from the early Cretaceous (145 million to 100 million years ago) in East Asia was found in the Zhonggou Formation of Jiuquan Basin, Gansu Province, Northwestern China, implying its unique contribution to amphibian origin and evolution [14]. Other amphibian fossils are mainly concentrated in the Jehol Biota at the Gezidong and Jiaxikou localities, Eastern Inner Mongolia, which is regarded as "Moqi Fauna" of fossil bed, indicating an early Cretaceous diversification [15] and other places, such as Sihetun (Liaoning), Daohugou (Inner Mongolia), Skuikouzi (Liaoning), and Paozhanggou (Hebei). They originated in the late Jurassic/early Cretaceous in the Mesozoic [16].

Contemporarily, China is rich in amphibians, including salamanders, cecilians, and anurans (frogs and toads), with numerous rare and endemic species; there are more than 400 species, classified into 76 genera, 13 families of the three orders, in which 242 (60%–62.8% of the total species) are endemic to China [17, 18]. Thus, China, especially its south and southwest, is a global hot spot for amphibian diversity [19–21].

The geographic distribution of amphibians in China has been a hot topic according to diversity spots. It is categorized into six regions at the national level: 1) southwest (Yunnan, Sichuan, and Tibet); 2) southeast (Guangdong, Anhui, Jiangsu, Zhejian, Fujian, Hong Kong, and Jiangxi); 3) northeast (Ningxia, Jilin, Liaoning, Heilongjiang, and Shangdong); 4) central and east (Guangxi, Guizhou, and Hunan); 5) central to northwest (Hubei, Gansu, and Shaanxi); 6) Hainan Island [21]. They are geographically confined to the three major centers [22]—Mts. Hengduan in Yunnan, Nanling in Southern China, and the Mts. Wuyi links Fujian and Jiangxi. Various environmental types define them as Southern, Southwestern, and Central China [23, 24].

However, the study illustrating fossil biodiversity and distribution, changed from the late Paleozoic to the current has not been seen, except for some studies focusing on contemporary regional profiles, such as the Mt. Emei in Sichuan [25], Sichuan province [26, 27], Hunan Province [28], the Tibetan Plateau [29], Tianping Mountain, Hunan Province [30], Eastern China [31], Yunnan [32], and Qinling [33]. However, the relationships between their biodiversity, distribution, and floral systems (vascular and nonvascular plants) have not been explored.

In other words, those studies focus on the existing environmental and ecological profiles and landscapes to analyze amphibian biological biodiversity and distribution without tracing back their evolutionary development process. Such a tracing back effort is critically required to retrospectively explore the evidence and information to explain their current biodiversity and distribution profiles and search for evolutionary and historical factors that have shaped such changes. Such information and evidence are critically needed in generating tangible conservation strategies.

On the other hand, those approaches are principally based on amphibian biodiversity or richness in categorizing distribution areas. Even though some studies analyzed the relationship between their biodiversity and distribution patterns, referring to changes in climate and ecology, the association between such issues and floral distribution patterns, both vascular and nonvascular plants, is critically needed—an integral approach to comprehending amphibian evolutionary development and future survival prosperity.

Thus, the primary purposes of this study include: 1) schematically illustrating the fossil distribution of the amphibians from the late Paleozoic to Cenozoic in China, based on which their origin and radiation centers can be identified; 2) presenting their contemporary diversity profiles and geographic distribution, referring to floral structures; 3) proposing their conservation priority perspectives referring to floral distribution outlines.

2. Material and Methods

This research contains four databases: 1) Fossil locations recorded in different geographic epochs, from the Devonian in the Paleozoic to the Pleistocene in the Cenozoic, collected from a comprehensive literature review. A total of 419 fossil records in three orders, eight families, were found at 48 sites; 2) the existing geographic distribution of the amphibians in China, published in 2024 from the Life Catalogues of China (http://www.sp2000.org.cn/download). They include three orders (Anura, Caudata, and Gymnophiona), 14 families, and 614 species; 3) floral repositories of China containing vascular and nonvascular plant species recorded in 2024 (http://www.sp2000.org.cn). A total of 42,641 vascular and 3947 nonvascular plant species (subspecies) were analyzed. Amphibian and plant species with incomplete records and a lack of information on geographical distribution were excluded. Additionally, records from islands such as Taiwan, Hong Kong, and Macao were not included, except for Hainan Island, due to ambiguity in the definitions of marine and terrestrial taxa for these areas.

We group amphibian fossils found in China into the three major eras, Paleozoic, Mesozoic, and Cenozoic, and then, explore their evolutionary development trajectories. According to Chen et al. [34], vascular plants in China are included in the phylum Tracheophyta. Others, containing Phyla, Bryophyta, Chlorophyta, Rhodophyta, Anthocerotophyta, and Marchantiophyta, are regarded as nonvascular plants.

The reason for separating flora into vascular and nonvascular plants is that the two types have different functions in the ecosystem structure [35, 36], so it is attractive to determine which type of plants the Chinese amphibians are more dependent on.

As for the extant amphibian and plant distribution in China, there is excellent biodiversity in various regional geographic landscapes [21, 37]. However, in general, the whole terrestrial land of China is divided into five regions: northwest (Inner Mongolia, Ningxia, Gansu, Shaanxi, Qinghai, Xinjiang, and Tibet); southwest (Sichuan, Chongqing, Yunnan, Guizhou, and Guangxi); central (Shanxi, Henan, Anhui, Hubei, Hunan, and Jiangxi); costal (Hebei, Shandong, Jiangsu, Zhejiang, Fujian, Guangdong, Hainan, and the three metropolis cities of Beijing, Tianjin, and Shanghai); northeast (Heilongjiang, Jilin, and Liaoning). Such regionalization, which shows a significant variation in land size, has been successfully used to explore mammal and plant geographic variations in China [38, 39].

Thus, to identify whether an abundant amphibian biodensity/richness in a specific region is because of its larger geographic size instead of the higher quality of habitats for amphibian adaptation, we use an index to remove such land size differentiation (RSDI) [39].

$$\text{Provincial amphibian density (RSDI)}: \text{RSDI} = N/A \times 1000,$$

where N is the number of amphibian species in a given province and A is the province's area (km^2). Thus, RSDI measures species density in a specific region.

The same index applies to vascular and nonvascular plants separately.

Another index (RSTD) is employed to identify the regions bearing a significant national proportion of amphibian repositories in China:

$$\text{Regional distribution proportion of national repositories (RSTD)}: \text{RSTD} = N/T \times 100,$$

where N is the species number of amphibians in a given region and T is the total recorded number of the whole nation, including five regions. It is greater than the total number of species in the country since one species can appear in different regions.

Those two indices also apply to vascular and nonvascular plants separately.

A successful application of those indices has been clarified in a study aimed at exploring regional fauna–flora diversity and conservation strategy in China [39].

The Spearman's rank correlation test was used to indicate the relationship among amphibians, vascular plants, and nonvascular plants.

3. Results

3.1. Fossil Distribution of Amphibians. Figure 1 presents the amphibian fossil dispersion from the late Paleozoic to the Cenozoic in China. The database indicates that fossils unearthed in the late Paleozoic include one in Gansu, one in Xinjiang, two in Henan, and one in Ningxia. Those discovered in the Mesozoic can be clustered into three regions: the first in Xinjiang and Gansu; the second in northeast China, including Hebei, Hubei, Liaoning, and Inner Mongolia; the third in Shanxi, Sichuan, and Yunnan. The fossils discovered during the Cenozoic period are in Beijing, Shandong, Shanxi, and Guangdong.

3.2. Association of Amphibians and Flora. Regarding the RSDIs of amphibians, vascular, and nonvascular plants, the amphibian RSDI shows a significant correlation with vascular plants ($p < 0.001$) and nonvascular plants ($p = 0.002$), separately. As for amphibians, the southwest presents the highest density, followed by the coastal, central, northeast, and northwest (Figure 2). Concerning vascular plants, the southwest has the highest density, followed by coastal, central, northeast, and northwest. As for nonvascular plants, southwest keeps the highest density, accompanied by coastal, central, northeast, and northwest. Conclusively, the southwest has been identified as maintaining the highest amphibian and plant richness and the northeast has the lowest.

As for RSTD, the amphibian shows significant correlation with vascular plant ($p < 0.001$) and nonvascular plant ($p = 0.012$), separately. The extant amphibians in the southwest rank fourth, accounting for more than 30% of the national repositories (Figure 3). The central and coastal regions come in third, with a share between 20% and 30%, followed by the northwest in second rank, with a share between 11% and 20%. The northeast has the lowest proportion of amphibians, with less than 11%, placing it in the first rank.

The same rank applies to plants. For vascular plants, the southwest takes the fourth rank, the northwest and coastal are categorized into the third, and the central and northeast are regarded as second and first, respectively.

The regional ranking of the nonvascular plants was found in the southwest > the coastal > the northwest, the central > the northeast.

4. Discussion

This study explores amphibians' origin and areas of dispersion by combining fossil distribution locations from the late Paleozoic to Cenozoic and presents their contemporary geographic distribution patterns. Such results allow us to explore their change trajectories in biodiversity and distribution from the Paleozoic to the present. It also illustrates the close relationship between the existing amphibians and different floral composition parts, allowing us to predict their prospective evolutionary developmental trajectories and survival profiles. Such an effort provides robust scientific evidence and information for making conservation strategies for amphibians in China.

4.1. Evolutionary Dispersion and Radiation. The geographic structure of China during the late Paleozoic was quite different

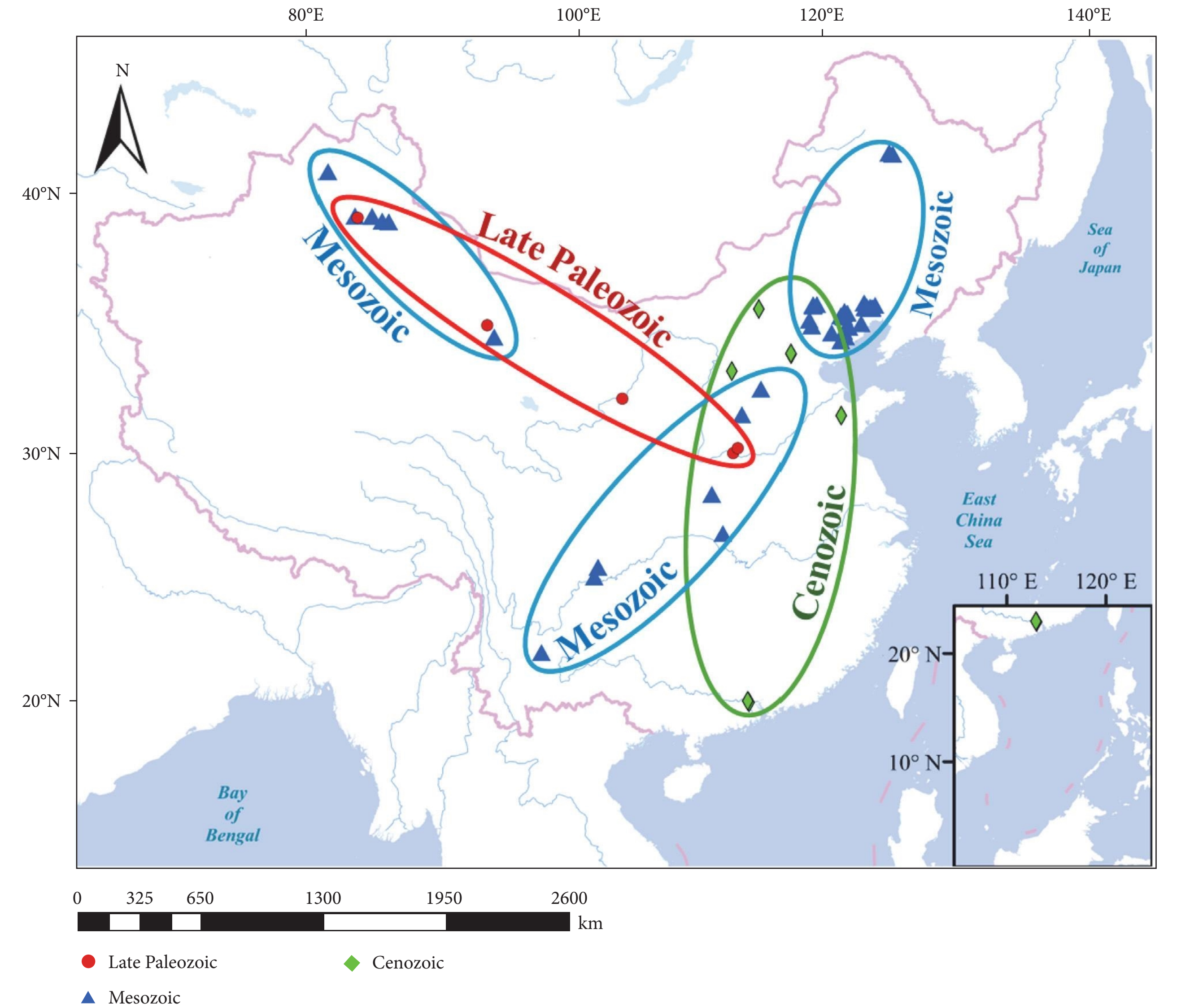

Figure 1: Amphibian fossil distribution from the Late Paleozoic to Cenozoic in China.

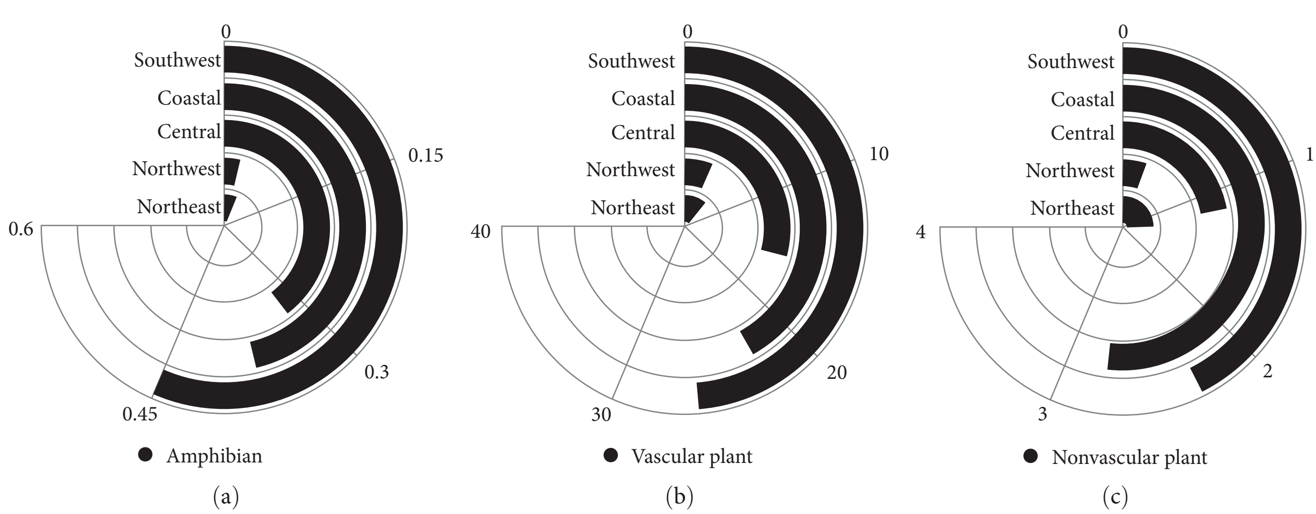

Figure 2: Biodiversity index (RSDI) of amphibians (a), vascular (b), and nonvascular (c) plants.

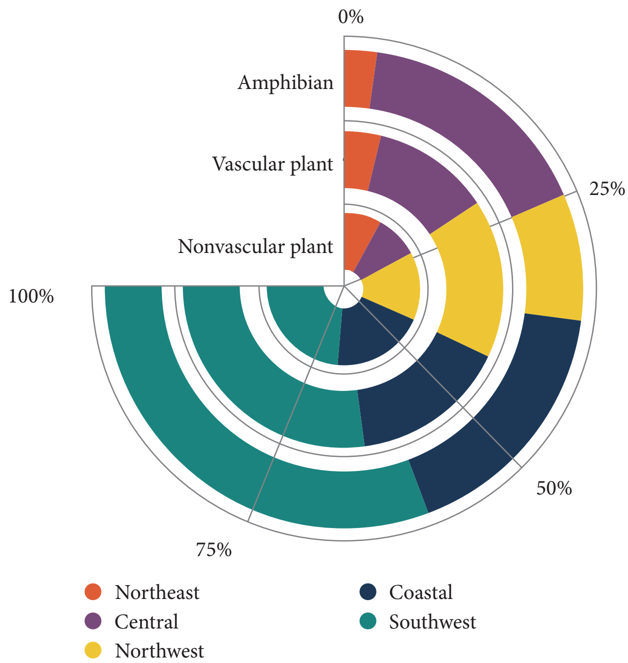

FIGURE 3: National repository display of amphibians, vascular, and nonvascular plants.

from what it is today. The abundant coral fauna found in Baoshan in Southwest China in the late Paleozoic [40] and the wonder of Chengjiang Marine Biota formed during the Cambrian indicate that South China during the Paleozoic was under the water [41]. Marine environments dominated the area of current South China, part of the South China Block (or Yangtze Plate), which had a shallow and warm sea [42].

However, Northern China had formed another great craton—the North China Craton (NCC), and its adjacent areas experienced a series of complex tectonic changes during the late Paleozoic to early Mesozoic, caused by the collision between the Central Asian Orogenic Belt, the NCC, and the subduction of the Yangtze Plate [43]. Different belts also surrounded the craton [44], implying that Northern China during the period was quite changeable, with significant geological movements and large parts of the NCC still underwater. That featured extensive coal-forming swamps and forests home to large plants and primitive amphibians with dense vegetation and wetlands [5, 45]. That may explain why amphibian fossils in the late Paleozoic are isolated in Northern China (Figure 1).

As indicated in Figure 1, referring to fossil ages, amphibians originated in northern China, currently Xinjiang, Ningxia, Gansu, and Henan provinces. Due to fossil scarcity, the issues of amphibian origin and radiation still need to be debated. A study based on molecular elements indicates that Lissamphibia first emerged about 330 million years ago in the Carboniferous in the Paleozoic [5]. The oldest fossils recorded are from the Permian in the late Paleozoic (299–252 mya), which is different from the data recorded in this study, during the Devonian (419–359 mya) in the same era in Ningxia.

During the Mesozoic (~252–66 million years ago), China's geographic structure was highly dynamic due to tectonic activities, volcanic events, and the shifting of continental plates, featuring increased atmospheric CO_2 content and flourishing forests in polar paleolatitudes [46]. The marked extensive tectonic activity included Indosinian Orogeny [47] and Yanshanian Orogeny [48]. On the other hand, the era experienced the remarkable formation of large basins and mountain ranges, such as the Yanshan Belt and the Songliao Basin in Northeast China [49], the Sichuan Basin in Southwest China [50], and the Guizhou triangle linked to the Youjiang foreland basin in the southwest [51]. Ecological characteristics in basins are different from those of the terrestrial environment. They are the depressions or low-lying areas where water collects, forming lakes, rivers, or wetlands, and these environments foster distinct ecosystems—the unique aquatic ecosystems in which fish, amphibians, and invertebrates prefer to thrive. Some basins in Northern China during the early Mesozoic, such as the Ordos Basin, must have played significant roles in amphibian evolutionary development [52]. That may explain why there were three origin and radiation centers for amphibians during the Mesozoic (Figure 1): Northeast China and Central and Southwest China.

The geographic structure of China in the early Cenozoic (Paleocene) was generally very similar to what it is today [53]. It was a time of dynamic tectonic and environmental changes, especially regarding the rise of the Tibetan Plateau [54], the formation of significant mountain ranges in the west, the Yunnan–Guizhou Plateau, and Western Highlands [55], the most critical events caused by the collision between the Indian and Eurasian plates [56]. Such significant changes may explain the absence of amphibian fossils in the Tibetan Plateau, and only two amphibian fossils in South China and none in Southwest China during the Cenozoic period. That must be closely related to the gigantic geographic uplift and movement in the regions where the fossils of amphibians and other animals have deeply been buried, which has occurred to other animals, such as primates [57, 58].

Based on Figure 1 and referring to the database, Figure 4 illustrates the possible biodiversity and distribution changes of amphibians from the late Paleozoic to the Cenozoic in China. The oldest fossil was recorded in Ningxia during the Devonian (big black dot), from which amphibians moved northwest to Xinjiang and Qinghai and east to the southeast to now Central China, where they radiated to the northeast, southwest, and coastlines. The Bohai Sea and Yellow Sea, surrounded by Liaoning, Beijing, Tianjin, and Shandong, formed during the period [43, 44], so amphibians dispersed along the coastline.

The appearance of amphibians in the Devonian was explicitly backed up by unique geodiversity characterized by significant changes in both terrestrial and marine biospheres [59], triggered by the booming diversification of earliest forests, the so-called "greening of earth surface" [60], with abundant nektonic animals, such as cephalopods, favored by amphibians as food, the so-called "predator revolution" [61, 62] or the "Devonian Nekton Revolution," a significant shift in marine ecosystems. This evolution fundamentally transformed ocean ecosystems, introducing greater mobility, new predator–prey dynamics, and diversifying aquatic life forms [63]. The Devonian also featured critical evolutionary development of great diversity, such as the land plant microfossils, which had a much

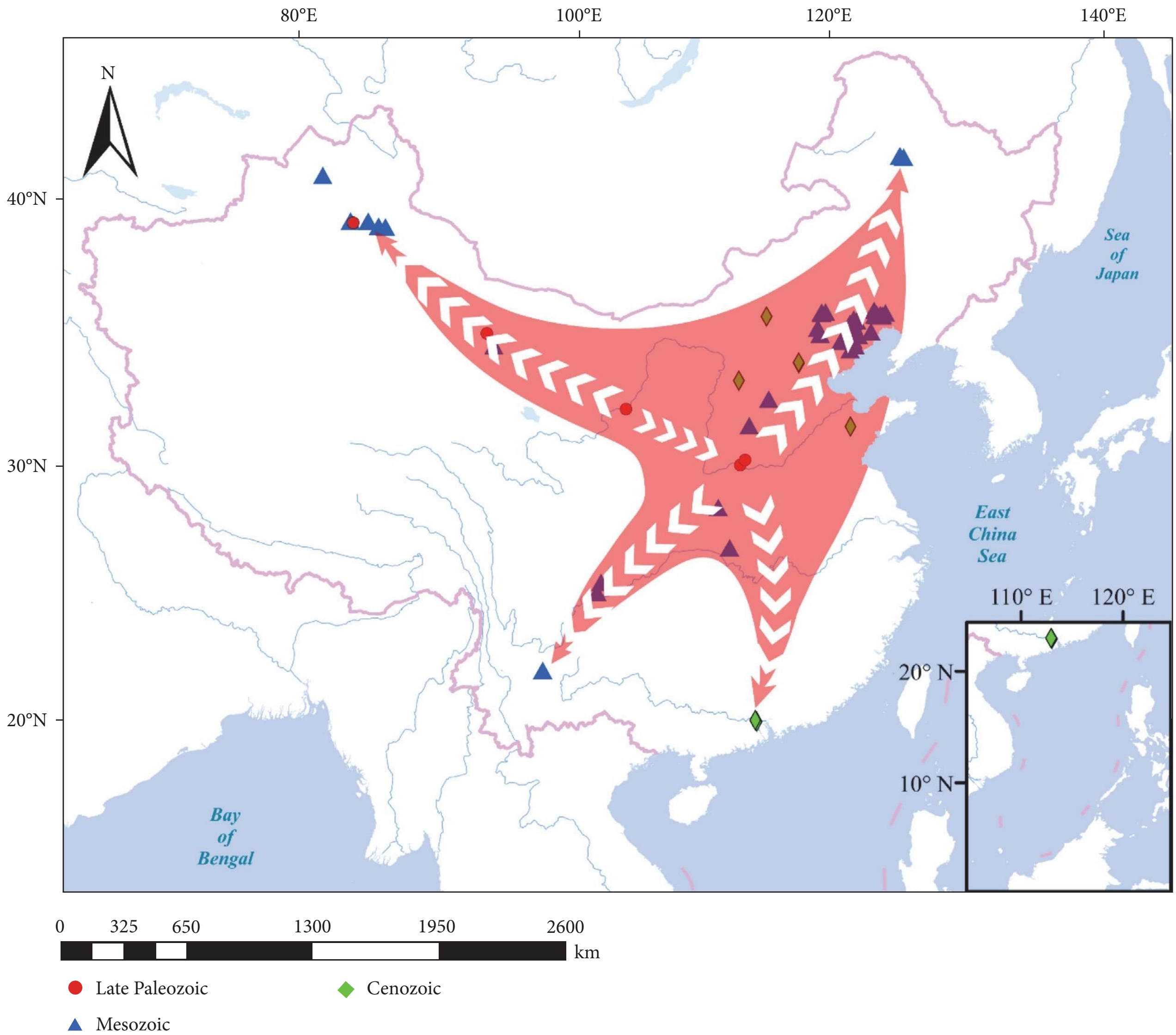

FIGURE 4: Proposed radiation procedure of the amphibians from the late Paleozoic to Cenozoic in China.

broader spread than land plant megafossils [64]. In other words, the Devonian in the Paleozoic was a time of profound evolutionary progress and ecosystem complexity, laying much of the groundwork for terrestrial ecosystems in which some lower vertebrates, such as amphibians, flourished and continued in the following periods [65].

4.2. The Shifted Biodiversity Profiles. The evolutionary change of the amphibians in China is significant, as shown by the comparison between Figures 1 and 2. They used to dominate Northern, Northeast, and Central China during the Paleozoic and Mesozoic (Figure 1), and moved to South China during the Cenozoic (Figure 4). Their extant taxa are principally distributed in the southwest and coastlines (Figure 2a). Most importantly, northwest and northeast, which played essential roles in their origin and radiation, now bear the poorest biodiversity (RSDIs; Figure 2a) and a much smaller national repository, especially northeast (Figure 3).

Such remarkable changes, especially the shift from north to south, must be associated with prominent geographic and biological modifications in Northern, Northeast, and Central China.

In North China, the Mesozoic terrestrial tectonic changes involved five remarkable periods, including the middle Triassic, the late Triassic to middle Jurassic, the late Jurassic to early Cretaceous, the middle–late early Cretaceous, and the late Cretaceous, triggered by regional punctuated tectonic events that occurred during these evolutionary stages [8]. Such gigantic modifications finally resulted in the mass extinction of dinosaurs during the late Cretaceous [66].

During the Mesozoic, especially in its late period, Northern China experienced significant geological and biological changes, witnessing dominant dinosaur fauna, primitive birds, mammals, pterosaurs, insects, and plants (angiosperms), which also appeared in northeastern Asia, the Korean Peninsula, Japan, and the Far East of Russia [8].

The following prominent geographic changes during the Cenozoic included the acceleration of the Tibetan Plateau [67], which may have prominently shaped amphibians' geographic distribution. Another significant tectonic reform during the era was the formation and quick uplift of the Qinling Mountains in Central China, initially generated due to the collision between the North and South China blocks in the Paleozoic, starting the formation of a geographical boundary between North and South China [68]. Consequently, many animals began their shifts from north to south and retreats from east to west, especially during the Neogene and Quaternary, such as primates [57], the Ailuropoda–Stegodon fauna [69], and other mammals [70]. The same scenarios occurred to amphibians. Such significant evolutionary development has been associated with significant shifts of tropical and subtropical forests from the north to the south of China and the glacial formation [71], resulting in the extraordinary appearance of vascular and nonvascular plant biodiversity in the southwest and coastal regions, providing high-quality habitats for amphibians, especially in Southwest China (Figure 2). According to Figure 3, corresponding to vascular and nonvascular plants, a significant proportion of amphibians is found in the southwest (40.99%) and coastal (22.76%).

Thus, this study indicates that the southwest is the best region for amphibians, considering its highest biodiversity and bearing the most excellent national repositories of vascular and nonvascular plants, which the coastal follows. Such results correspond to what we have reported on a larger scale srudy of regional variation in fauna and flora biodiversity of China [39, 57], in which southwest and coastal regions have the most significant terrestrial faunal–floral biodiversity.

Southwest China has evolutionarily presented the most diversified faunal and floral structures since the Pliocene. It has been regarded as their sanctuary during the Quaternary, especially in the period of glaciation; it contains all of the mammalian orders (11 in number) in China and is one of the global biodiversity hotspots [72–74], with a critical convergence–divergence center of the animals and humans [57]. Thus, it is unsurprising that this region has the highest biodiversity of amphibians and vascular plants and the second highest nonvascular plants. It also contains the most significant number of national repositories of amphibians and plants (Figure 3).

The next ideal region for amphibian biodiversity and distribution is the coastal. The region even demonstrates the highest biodiversity of nonvascular plants, higher than the southwest (Figure 2). It has more diversified ecosystems, including tropical and subtropical forests, and abundant wetlands linking with rivers and oceans of the South and East China Seas [75], plus humid, semihumid, and warm temperate ecosystems in subtropical and tropical zones, much preferred by amphibians [76], so that the region provides abundant invertebrates and lower vertebrates, such as Gastropoda, Arachnida, and Insecta [38, 39]—they are the preferred food for amphibians.

According to the reviewer of this paper, amphibian distribution in the coastal region could be divided into two main areas: the northern coast, including Hebei, Shandong, Jiangsu, Zhejiang, Beijing, Tianjin, and Shanghai, and the southern coast, which includes Fujian, Guangdong, and Hainan. Thus, we were required to explore whether there is significant differentiation between the two regarding RSDIs and RSTDs. The statistical results indicate that the variation in RSTDs reaches a significance level at $p < 0.005$, but not RSDIs ($p = 0.207$). The southern coast has 14.28% of the national total, exceeding that of the northern coast, with a value of 8.49%. The results indicate that the southern coast has a significantly higher national repository of amphibians than the north. This phenomenon must be associated what has been discussed above, such as significant drift of amphibians from north to south during the Cenozoic (Figure 4), and promiment shifts of tropical and subtropical forests from north to south during the Pliestocene.

It has been reported that Central China had environments and ecosystems like those in the coastal and the southwest [39]. Unfortunately, following the appearance of modern Chinese, initiated in the Yellow River Valley in the early Holocene, represented in the Neolithic Yang-Shao culture, then, extended to Central China before radiation to the northeast, coastal, and southern regions [77, 78]. Consequently, the environment and ecology in Central China started to be devastated, so many animal taxa, especially mammals, have become extinct [57, 79, 80]. That can explain why the region displays lower levels of amphibian and plant diversity compared with the southwest and coastal (Figure 2) and a small proportion of national repositories (Figure 3). The most remarkable threats to the amphibians and other animals in the region must have occurred in the most recent Chinese history, between the 18th and 20th centuries, in which China experienced rapid agricultural and economic development that depended heavily on land conversion and featured prominent social chaos and wars, such as the Opium Wars, Sino–Japanese War, part of the Second World War, and Civil Wars [81–84]. Another significant environmental and ecological devastation occurred in post-war China, featuring substantial increases in human population and transaction procedures from an agrarian country to an industrial nation after the 1950s [85, 86].

Although the northwest occupies China's most significant land proportion (50% of China's land area), it maintains deficient biodiversity levels of amphibians and plants (Figure 2). This region, characterized by the highest elevation of the Himalayas and plateaus of Tibetan and Loess, which started uplift in the middle Miocene [87], and significantly accelerated in the late Pliocene or early Pleistocene [88], have triggered significant topography, ecology, and climate changes, resulting in prominent desertification and monsoon-dominated cold and dry weather. Thus, it presents very poor faunal and floral biodiversities [39, 57], including amphibians analyzed in this study.

The northeast has the poorest diversity of amphibian and vascular plants and the smallest proportion of national repositories among the five geographic regions (Figures 2 and 3). This area also features the lowest biodiversity of mammals [39]. The region's environment and ecology have been significantly degraded due to permafrost and periglacial phenomena, beginning before the Pleistocene with dry and alkaline or saline soil, especially in the meadow steppes [38]. Such degradation has been further deepened following more extensive human activities, mainly deforestation after the 1950s—an annual forest loss of 1014 km^2 between 1958 and 1980 resulted in thousands of environmental fragmentations [89]. It has played a leading role in the logging industry since the 1950s in China—5.21 million m^3 of timber were generated by 1977, half of the nation's total [90].

4.3. Association With Flora. According to Figure 2a the amphibians' biodiversity and geographic distribution in China are principally driven by vascular plants dominating the southwest and the coastal regions. They also present a significant proportion of national floral repositories (Figure 3). That must be related to the unique functions of vascular plants in maintaining a stable ecosystem by maintaining soil stability and providing more extensive and solid forest and bush habitats that support the stability of animals. They drive nutrient cycles on a large scale and play a critical role in moderating climate change, especially regarding terrestrial and arboreal taxa, and they are essential as oxygen providers for aquatic systems, which amphibians prefer [35, 91, 92]. Meanwhile, nonvascular plants play a more localized role and feature short life cycles. They are strictly confined to moist and shaded environments provided by vascular plants [36, 93].

However, vascular and nonvascular plants contribute uniquely to biodiversity and ecosystem functionality, with vascular plants typically having a broader ecological footprint [94]. That may explain why amphibians prefer the southwest, where nonvascular plant biodiversity is lower than in the coastal region.

4.4. Conservation Implication. Due to extensive human-induced activities, especially in Central China, and severe climate changes, the biodiversity and distribution of amphibians in China could lose 20% of their original ranges in the following years [95]. Considering its highest biodiversity and the most significant national repositories of amphibians and vascular plants, Southwest China must be prioritized for amphibian conservation. It is also a critical amphibian region with important endemic amphibian taxa [21], especially in Sichuan [96]. Yunnan is unique in the region; it has 191 amphibian species, 49 genera, 12 families, and three orders, accounting for 32.5% of China's national repository. Unfortunately, 25.6% have been classified as threatened taxa [32].

On the other hand, a model demonstrating the potential climate effects on China's amphibian distribution indicates that about 95% of current amphibian species would be in higher altitudes in the 2050s or 75% in the west of their current range in the 2070s [95]. They are the areas featuring Southwest China. The second conservation attention should be paid to Coastal and Central China, referring to the results explored in Figures 2 and 3.

Data Availability Statement

All the required data are uploaded as supporting information.

Ethics Statement

This article complies with the Committee on Publication Ethics (COPE).

Disclosure

All authors have read and agreed to the published version of the manuscript.

Conflicts of Interest

The authors declare no conflicts of interest.

Author Contributions

Kang Huang, Baoguo Li, and Ruliang Pan designed and executed the experiments and carried out project administration. Hao Pan wrote the original draft. Ruliang Pan, Hao Pan, and Gaigai Guo revised the manuscript. Gaigai Guo, Jing Wang, Gu Fang, Yuli Li, and Rong Hou collected the data. Kang Huang, Gang He, Songtao Guo, and Pei Zhang carried out the formal analysis. Kang Huang and Baoguo Li organized the funding acquisition. Hao Pan and Gaigai Guo have equal contributions to the work and are considered co-first authors.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

Supporting Information 1. S1. Attachment of amphibian fossils location: Description of the precise locations where amphibian fossils were found in China.

Supporting Information 2. S2. RSTD and RSDI: The RSTD and RSDI for amphibian, vascular plant, and nonvascular plant across 31 regions in China

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