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The barrier risk to the ecological connectivity of plant diversity in karst landscapes in Guizhou Province, China

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Ecological connectivity in landscapes is crucial for plant diversity conservation. The barrier risk to ecological connectivity represents the risk to ecological connectivity loss or weakening, resulting from the barrier to biological information exchange among habitats. Therefore, clarifying the barrier risk to the ecological connectivity of plant diversity in space can reveal the spatial impacts of reduced ecological connectivity on plant diversity. This study analyzed effects of karst peak, river network, arable land, and impervious surface on plant diversity in karst natural, countryside, urban, and island landscapes in Guizhou Province with fragile environment. Then, we calculated the barrier distance of ecological connectivity to reveal the barrier risk to the ecological connectivity of plant diversity in space. The results showed that karst peak was the source of high plant diversity, and plant diversity could diffuse about 400 m around karst peaks. River network and arable land enhanced the connectivity among karst peaks to maintain plant diversity, and the effect on enhancing the connectivity was about 300 m and 450 m, respectively, while the weakening effect of impervious surface on connectivity was about 350 m. Based on the distance for plant diversity diffusing around karst peaks, the barrier distance of ecological connectivity was determined by the combination type of river network, arable land and impervious surface in landscapes. From low to high, the barrier risk to the ecological connectivity of plant diversity was about 1,110 m in the combination of river network and arable land, about 790 m in the combination of river network, arable land and impervious surface, about 520 m in the combination of arable land and impervious surface, about 400 m in the combination of river network and impervious surface. Our findings clarify the barrier risk to the ecological connectivity of plant diversity in space, and provide a scientific basis for plant diversity conservation from the perspective of ecological connectivity.

KEYWORDS

plant diversity, ecological connectivity, barrier risk, remote sensing, karst regions

1 Introduction

As an important component of biodiversity, plant diversity contributes to ensuring human survival and ecosystem stability (Shen et al., 2022). Plant diversity is threatened by habitat decrease and ecological connectivity loss driven by the increasing economic development and urbanization (Bergès et al., 2020; Damiens et al., 2021; Perrin et al., 2022). Habitat loss and fragmentation reduce structural and functional connectivity, leading to plant population density decrease (Herrerías-Diego et al., 2008) and barrier to biological information exchange (Dong et al., 2020). Weakened ecological connectivity among habitats reduces ecological corridors in landscapes (Huang et al., 2022), and undermines the integrity of ecosystem in a region (Kietzka et al., 2021), which increases barriers between habitats creating islands that increase extinction probability (Tian et al., 2022). The barrier risk to ecological connectivity represents the risk of ecological connectivity loss or weakening, which is a threat to plant diversity. Therefore, evaluating the barrier risk to ecological connectivity is important for plant diversity conservation (Li et al., 2022c).

Changes in habitat patterns not only limit the migration ability of animals and plants (Balbi et al., 2019; Liccari et al., 2022), but also reduce the ecological connectivity within landscapes (Uroy et al., 2019), leading to a high barrier risk to the ecological connectivity of plant diversity. Many studies have revealed the mechanism of the barrier risk to the ecological connectivity of plant diversity in terms of landscape pattern and spatial response (Huang, 2011). For example, plant diversity gradually becomes rich with decreases in human interference along the urban–rural gradient due to reduction of the barrier risk to ecological connectivity (Jha et al., 2019). It is easier to form rich plant diversity in areas with a low barrier risk to ecological connectivity compared with urban areas with severe habitat fragmentation, such as the countryside with good habitat integrity (Yang et al., 2021). Rivers, wetlands and mountains are important corridor that can weaken the barrier risk to ecological connectivity even in urban landscapes (Zhang et al., 2022b; Wang et al., 2022). In contrast, impervious surface in human dominated landscapes threaten ecological connectivity from the perspective of landscape pattern and biological information exchange (Cui et al., 2020; Dai et al., 2021), explaining, to some extent, observed differences in plant diversity between urban and rural areas. However, current research on the barrier risk to the ecological connectivity of plant diversity mainly focus on the spatial response of plant diversity to its influencing factors (Li et al., 2022a). How far the distance that causes barrier risk to ecological connectivity remains unknown because of the limitation in plant dispersal among habitats. Analyzing the barrier distance of ecological connectivity is of great significance for revealing the barrier risk to ecological connectivity in landscapes, and plant diversity conservation in areas with rapid socioeconomic development.

As one of the 32 biodiversity landmarks in the world (Myers et al., 2000), about 10,255 species have been discovered in karst regions in Guizhou Province, China, and over 38% of Chinese endemic species inhabit these regions (Liu et al., 2018a). The rich plant diversity is sensitive to external influences, making the Guizhou karst regions a hot spot for research on plant diversity (Chen et al., 2022). Since 2012, poverty alleviation and rural revitalization have been implemented in succession. Rapid social

development has exacerbated problems such as rocky desertification and rural to urban land conversion in Guizhou Province (Zhao and Hou, 2019; Han and Song, 2020), leading to increasingly negative impacts of the barrier risk to ecological connectivity. Meanwhile, the South China Karst is the largest distribution region of karst landforms in the world (Zhang et al., 2021). The staggered distribution of karst peaks and depressions causes significant spatial heterogeneity in human interference and underlying surface (Wang et al., 2019), resulting in spatial differences in ecological connectivity. Therefore, it is appropriate to analyze the barrier risk to the ecological connectivity of plant diversity in Guizhou Province, with rich biodiversity, rapid society development and strong topography heterogeneity.

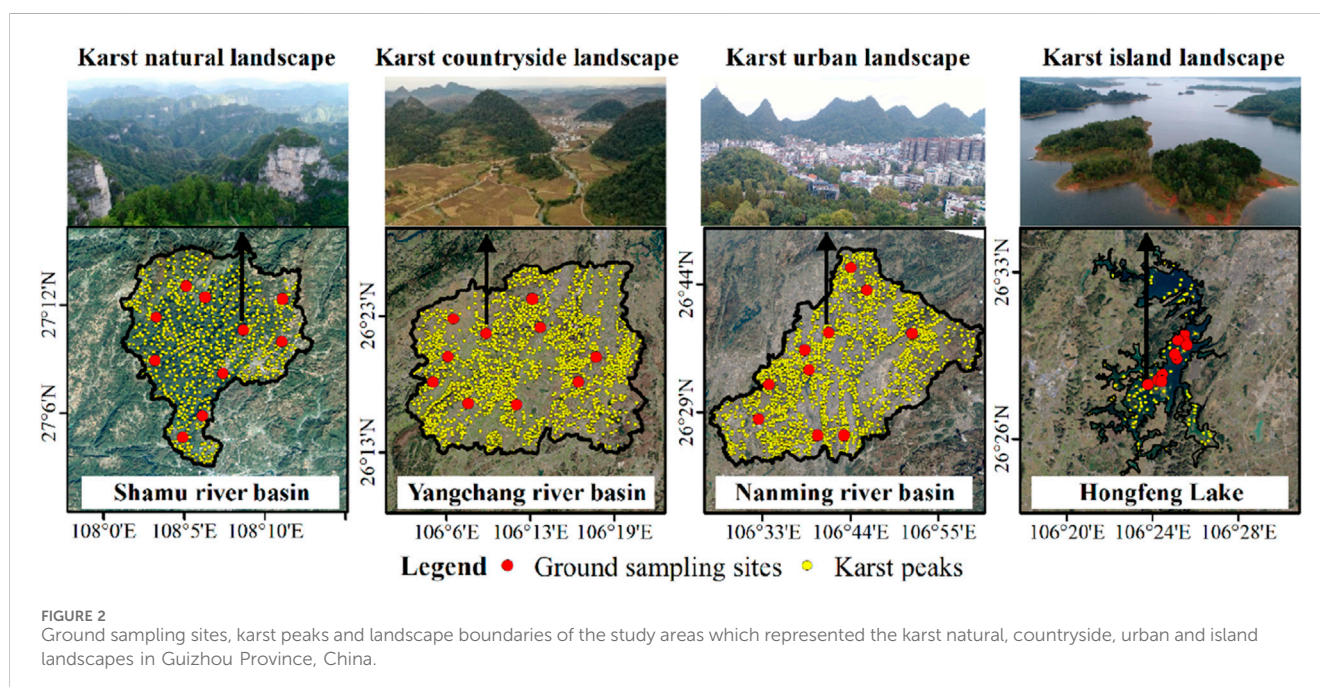
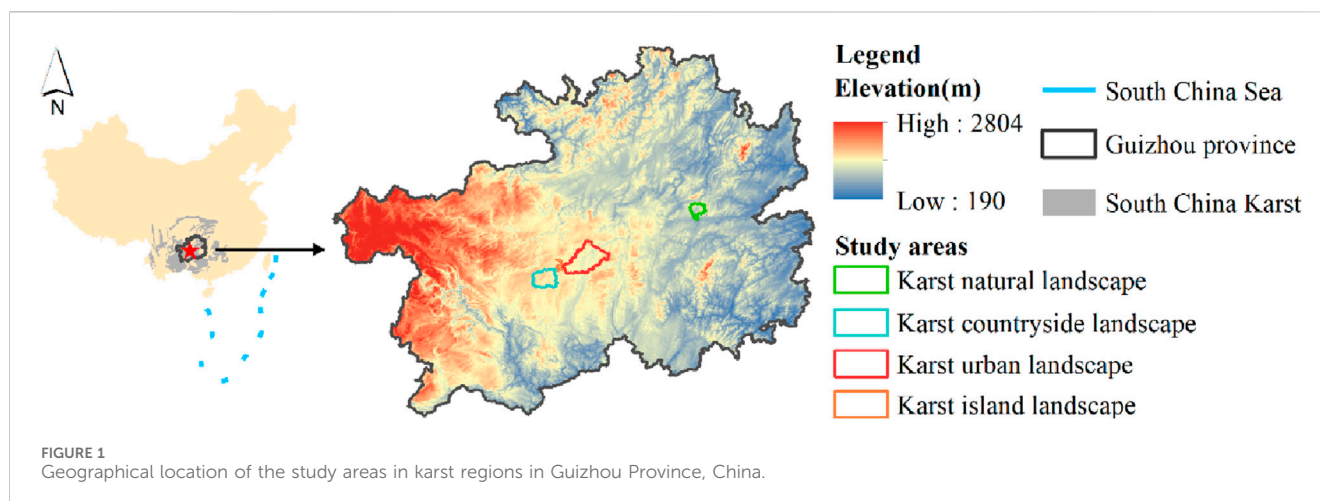
To spatially reveal the barrier risk to the ecological connectivity of plant diversity in karst regions, this study selected karst natural, countryside, urban, and island landscapes in Guizhou Province as the study areas, and used ground sampling data, unmanned aerial vehicle (UAV) and satellite remote sensing images. The objectives of this study are: (1) Obtain the differences in plant diversity among the four karst landscapes with different ecological connectivity; (2) Identify the factors affecting plant diversity in karst regions, and analyze the their effects on ecological connectivity; (3) Determine the influence distance of these factors on plant diversity from the perspective of ecological connectivity; (4) Calculate the barrier distance of ecological connectivity, and reveal the barrier risk to the ecological connectivity of plant diversity in karst landscapes.

2 Methods and materials

2.1 Study area

Guizhou Province is located in the core area of Southwest China, a region with largest continuous karst landform in the world (Chen et al., 2021), covering an area of about 160,000 km² (Figure 1). This region is one of the most rapidly urbanized in China, growing to 38 million people in the last 20 years (Yang et al., 2022a). The climate is subtropical monsoon (Xue et al., 2023). The suitable hydrothermal environment enriches the plant resources in Guizhou Province, and make a wide distribution of evergreen-deciduous broad-leaved mixed forest. Among them, the evergreen plants mainly include the *Quercus*, *Neolitsea*, *Sloanea*, and the deciduous plants are mostly the *Cornus*, *Cerasus*, *Carpinuspubescens*, and *Platycarya* (Li et al., 2022b).

The Shamu River Basin, Yangchang River Basin, Nanming River Basin and Hongfeng Lake in Guizhou Province are taken as the study areas of karst natural, countryside, urban and island landscapes (Figure 2). Among them, the Shanmu River Basin is located in the Shibing Nature Reserve, and is a typical karst natural landscape, with forest coverage over 90% and rich biodiversity (Tang et al., 2017). The Yangchang River Basin is located in the rural transitional zone between Guiyang city and Anshun city, with an area of 605.61 km². Vegetation is dominated by crops and shrubs due to agricultural cultivation-led human activities, while forests are concentrated in karst peaks (Pan et al., 2023). The Nanming River Basin is located in Guiyang city and its surrounding areas, with an area of 1131.26 km². Human disturbance in the Nanming River Basin is strong. Construction land and arable land occupy most of dissolved depressions, causing the vegetation mostly grass and



shrubs (Li et al., 2022b). Hongfeng Lake is an artificial plateau lake constructed in 1958s and is located between the Yangchang River Basin and Nanming River Basin. Islands in the lake are formed by karst peaks emerging from the lake surface. Vegetation on islands is mainly shrubs and a small amount of forest (Lou et al., 2021).

A total of 40 ground sampling sites were established to obtain the plant diversity data in karst natural, countryside, urban and island landscapes with socioeconomic development from low to high (Table 1).

2.2 Plant diversity and remote sensing data

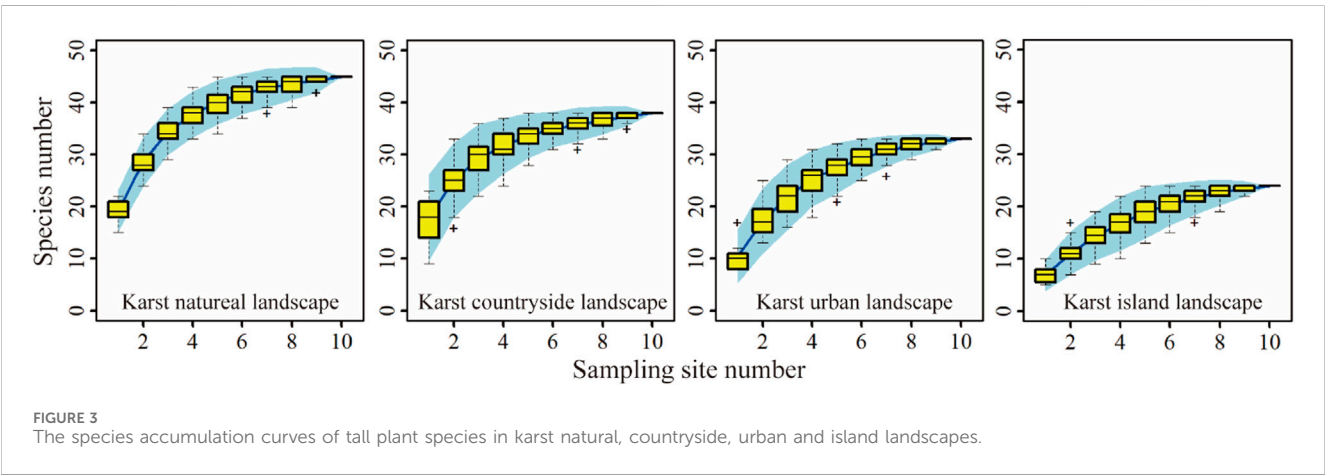
Plant diversity of each ground sampling site was obtained through the aerial photography of UAV due to the steep terrain of karst peaks. In each of the sampling sites, UAV was used to take low-flying aerial photos, and a total of 10,174 UAV images were

obtained. UAV images were processed by Pix4D software to generate the digital orthophoto map with a spatial resolution of about 3 cm. Then, plant species and individuals in the canopy were counted by visual interpretation. According to investigation results, the species accumulation curve of tall plant species tended to converge in the four karst landscapes (Figure 3), showing the sampling for tall plant species could represent the richness of tall plant in landscapes. The evergreen trees, such as *Cryptomeria fortune*, *Juniperus formosana*, *Juniperus chinensis*, *Taxus chinensis*, *Cephalotaxus sinensis*, *Cunninghamia lanceolata*, and the deciduous trees, such as *Salix wilsonii*, *Juglans regia*, *Platycarya longipes*, *Castanea mollissima*, *Broussonetia papyifera*, were relatively common in the sampling sites. In addition, the shrubs mainly include *Cotinus*, *Viburnum*, *Rubus*, *Rosa*, and *Chimonanthus*.

In the field survey, three 400 m² plots were set at the edge of karst peak in each sampling site to validate the identification accuracy for

TABLE 1 Location of the ground sampling sites in karst natural, countryside, urban and island landscapes in Guizhou Province, China.

Karst natural landscape			Karst countryside landscape			Karst urban landscape			Karst island landscape		
Site	Latitude	Longitude	Site	Latitude	Longitude	Site	Latitude	Longitude	Site	Latitude	Longitude
N1	27.15	108.05	C1	26.30	106.09	U1	26.56	106.65	I1	26.51	106.42
N2	27.14	108.12	C2	26.27	106.20	U2	26.63	106.87	I2	26.50	106.42
N3	27.22	108.08	C3	26.30	106.28	U3	26.47	106.54	I3	26.51	106.41
N4	27.19	108.05	C4	26.32	106.30	U4	26.75	106.74	I4	26.48	106.40
N5	27.21	108.10	C5	26.27	106.14	U5	26.44	106.72	I5	26.47	106.40
N6	27.10	108.10	C6	26.33	106.11	U6	26.63	106.69	I6	26.50	106.42
N7	27.18	108.14	C7	26.37	106.12	U7	26.53	106.57	I7	26.49	106.41
N8	27.08	108.08	C8	26.39	106.22	U8	26.60	106.64	I8	26.50	106.41
N9	27.08	108.08	C9	26.36	106.23	U9	26.44	106.67	I9	26.47	106.39
N10	27.17	108.18	C10	26.35	106.16	U10	26.71	106.77	I10	26.47	106.40



plant species by UAV. The number of tree and shrub species was identified and recorded in plots, and the number of trees and shrubs individuals was counted with a diameter at breast height greater than 2.5 cm.

Landsat 8 images could provide surface reflectance information from visible light to near-infrared band with a spatial resolution of 30 m. Fractional vegetation coverage (FVC) was calculated by the Landsat 8 images that was the same period as field survey. Landsat 8 images could be downloaded from the United States Geological Survey (USGS) (<https://earthexplorer.usgs.gov>).

Land cover data were from the China Land Cover Dataset (CLCD) (Yang and Huang, 2021) and could be derived from the Google Earth Engine (<https://developers.google.cn/earth-engine>). The temporal and spatial resolutions of CLCD were 1 year and 30 m respectively. CLCD divided the land use into 9 types, including arable land, forest, shrub, grassland, water, snow or ice, barren, impervious surface and wetland. Three-phase CLCD images (1990, 2005, 2020) were used to detect the changes in land use and calculate the density of arable land and impervious surface.

The Shuttle Radar Topography Mission (SRTM) DEM data were widely used due to high precision (Bhang and Schwartz, 2008). With a spatial resolution of 30 m, SRTM1 V3.0 DEM data were for two uses in this study. The first was to determine the subbasin in karst landscapes using the Hydrology Tools in ArcGIS 10.6 software. The second was to identify the karst peaks by combining them with Landsat 8 images. SRTM1 V3.0 DEM data were derived from the USGS.

Details of the dataset used in this study was in Table 2.

2.3 Methods

2.3.1 Plant diversity calculation

Alpha and beta diversity were used to measure the plant diversity of sampling sites. Alpha diversity reflected the species richness and evenness within a certain spatial range (Tuomisto, 2010). Hill number index was the index that considered the number of species and the evenness between species and individuals by

TABLE 2 Descriptions of the datasets in this study.

Dataset	Data type	Data time	Purpose	Source
Ground sampling data	Plant species and individual number	November 2020	Identification accuracy of plant diversity by UAV	Field survey
Unmanned aerial vehicle (UAV) images	Digital orthophoto map	November 2020	Plant species and individual number	UAV
Landsat 8 images	Reflectivity of red and near-infrared bands	12 November 2020	Fractional vegetation cover	United States geological survey
China land cover dataset	Land cover type	1990, 2005, 2020	Changes in land cover, and density of arable land and impervious surface	Google earth engine
Shuttle radar topography mission 1 V3.0 dataset	Digital elevation model	-	Subbasins and karst peaks	United States geological survey

different q values (Chao et al., 2014). Formula of the Hill number index was presented by Eq. 1.

$${}^qH = \left(\sum_{i=1}^S p_i^q \right)^{1/(1-q)} \quad (1)$$

Where p_i represented the proportion of plant species i and S was the total number of plant species in a sampling site. When q tends to 1, the limit of Hill number index was the Shannon's entropy exponent, and the Shannon diversity index (SHDI) could be obtained by Eq. 2. For $q = 2$, the Hill number index was equal to the Simpson reciprocal index (de Bello et al., 2014). The 1H , 2H and 3H was used for plant alpha diversity evaluation, because the sensitivity of Hill number index was from rare species to dominant species with q increased (Tan et al., 2022).

$$SHDI = - \sum_{i=1}^S p_i \ln p_i \quad (2)$$

The larger the SHDI was, the higher the species richness of the sampling site and the more uniform the number of individuals. SHDI was also used for spatial pattern evaluation of plant alpha diversity (Li et al., 2022b).

Beta diversity represented the differences in species composition between habitats or sampling sites (Fortin et al., 2020). Sørensen's index of dissimilarity was used to characterize the beta diversity and indicate the degree of biological information exchange between sampling sites. The calculation of Sørensen's index of dissimilarity was presented as Eq. 3 (Sperandii et al., 2019).

$$\beta = \frac{S_i + S_j}{2S_c + S_i + S_j} \quad (3)$$

where S_i represented the number of unique species in sampling site i , S_j represented the number of unique species in sampling site j , and S_c represented the number of common species between two sampling sites. The lower the β index was, the smaller the differences in species composition between two sampling sites and the better the ecological connectivity among habitats.

2.3.2 Spatial pattern estimation of plant diversity

Spatial pattern of plant diversity could be estimated based on the strong correlation between plant diversity and FVC (Li et al., 2022a). The normalized difference vegetation index (NDVI) was calculated

by Eq. 4 and the reflectance of near-infrared and red bands from Landsat 8 images.

$$NDVI = \frac{NIR - R}{NIR + R} \quad (4)$$

where NIR and R represented the surface reflectance of the near-infrared and red bands, respectively. Then, the pixels were decomposed into vegetation and non-vegetation parts by the pixel dichotomy model. The percentage of vegetation part in pixel was estimated to be the FVC by Eq. 5 (Liu et al., 2018b).

$$FVC = \frac{NDVI - NDVI_{soil}}{NDVI_{vegetation} - NDVI_{soil}} \quad (5)$$

where $NDVI_{soil}$ and $NDVI_{vegetation}$ were the NDVI of pure bare soil and vegetation pixels, respectively. Finally, spatial pattern of plant diversity could be obtained by establishing the statistical relationship between FVC and SHDI.

2.3.3 Quantifying the barrier risk to the ecological connectivity of plant diversity in spatial distance

Determining the barrier distance of ecological connectivity included identifying the influencing factors of plant diversity and calculating their influence distance on plant diversity. To identify the influencing factors, karst peaks were determined by human-machine interactive interpretation through Landsat 8 images and DEM data. Karst landscapes were divided into several subbasins based on DEM data, and the calculation of river network density was shown as Eq. 6.

$$RND = \frac{L}{A} \quad (6)$$

where L was the length of river in subbasin (km), and A was the area of subbasin (km^2). Taking the subbasin as basic unit, density of arable land and impervious surface could be calculated by Eq. 7.

$$D = \frac{A}{A_s - A_p} \quad (7)$$

where A was the area of arable land or impervious surface in the subbasin (km^2), A_s was the area of subbasin (km^2), and A_p was the area of karst peaks (km^2).

To determine the spatial influence of karst peak, river network, arable land and impervious surface on plant diversity, buffer zones was established in increments of 100 m around karst peaks and river

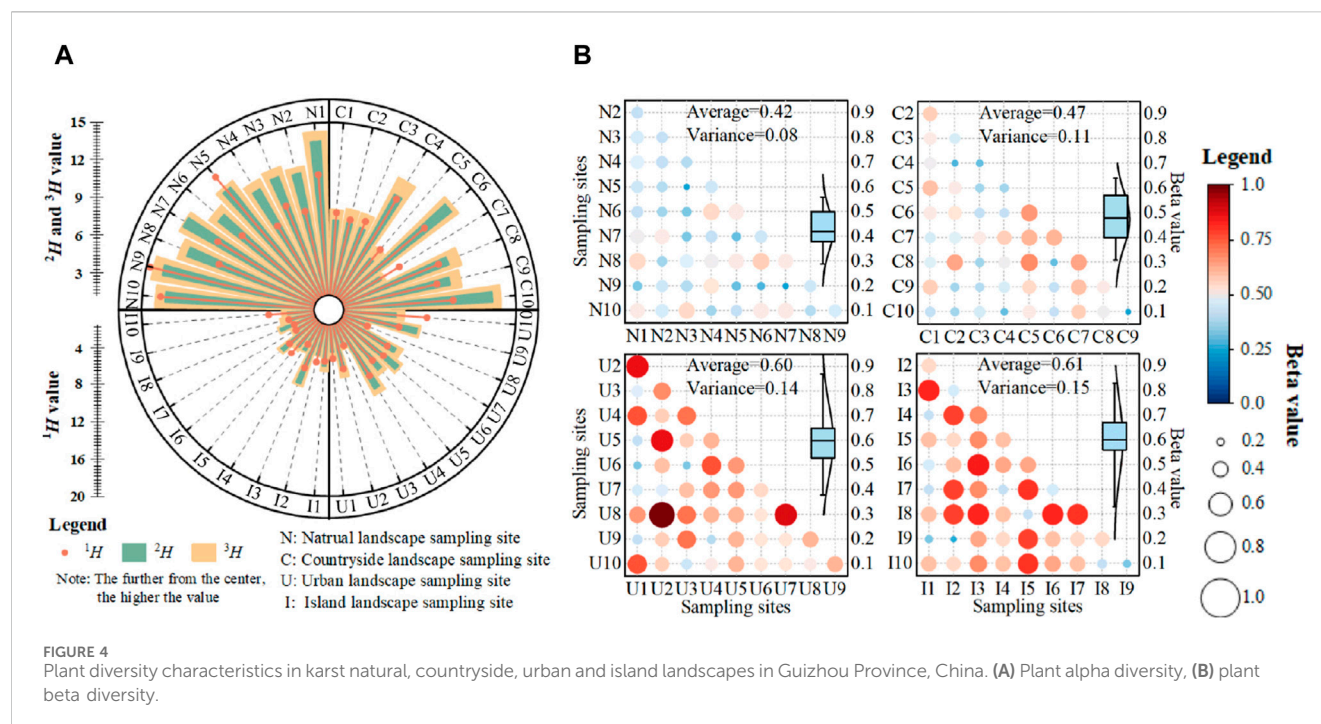


FIGURE 4
Plant diversity characteristics in karst natural, countryside, urban and island landscapes in Guizhou Province, China. (A) Plant alpha diversity, (B) plant beta diversity.

networks to obtain the changes in SHDI. The distance where changes in SHDI tended to 0 was determined as the spatial limit for karst peak and river network influencing plant diversity. Similarly, the spatial influence of arable land on ecological connectivity were obtained by changes in SHDI with the distance among karst peaks, while that of impervious surface were obtained by changes in SHDI with the nearest distance between karst peaks and impervious surfaces. Then, the barrier distance of ecological connectivity could be determined by the combination type of karst peak, river network, arable land and impervious surface in landscapes.

2.3.4 Statistical analysis for data cluster and coefficient estimation

The natural breaks method was a data cluster-based grouping method (Wei et al., 2020), and could group data by making smallest difference within group and largest difference between groups (Bai et al., 2022). The natural breaks method was used to divide the density of river network, arable land and impervious surface into three levels to explore their influence on plant diversity; The local Moran's index reflected the spatial aggregation type of data by homogeneity, heterogeneity, and autocorrelation (Song and Song, 2022). The spatial aggregation of karst peaks could be obtained by the local Moran's index in terms of plant diversity; Information entropy was a measure of information disorder degree. The smaller the information entropy was, the greater the amount of information and the greater the coefficient (Zou et al., 2006). Thus, the entropy method was used to calculate the coefficients when river network, arable land and impervious surface were combined to form the barrier distance of the ecological connectivity of plant diversity.

3 Results

3.1 Characteristics of plant diversity and its spatial pattern in karst landscapes

Plant alpha diversity showed a gradual decrease among karst natural, countryside, urban and island landscapes according to UAV survey (Figure 4A). Plant alpha diversity was the highest in karst natural landscape, due to the Hill number index (1H , 2H and 3H) obviously higher than that of the other karst landscapes. Although plant alpha diversity in karst countryside landscape was slightly lower than that of karst natural landscape, plant diversity was still maintained at relative high level, and the average 1H , 2H and 3H could reach a value of 11.3, 9.7 and 8.7, respectively. In contrast, plant alpha diversity decreased significantly in urban and island landscapes due to the lower component of vegetation in sampling sites.

In addition, karst natural and countryside landscapes maintained a good similarity of plant species compositions and biological information exchange, while differences in species composition was obvious in karst urban and island landscape (Figure 4B). The average beta value increased from 0.42 to 0.47 in karst natural and countryside landscapes to 0.60 in karst urban landscape, and reached the maximum value of 0.61 in karst island landscape.

The strong correlation between FVC and SHDI was found (Figure 5A). The coefficient of determination (R^2) reached 0.85, showing FVC could well describe the variations in SHDI. p -value was lower than 0.01, indicating the significant positive linear correlation between FVC and SHDI due to passing the 99% significance test. Then, the spatial pattern of SHDI could be estimated by FVC (Figure 5B). Although the proportion of area

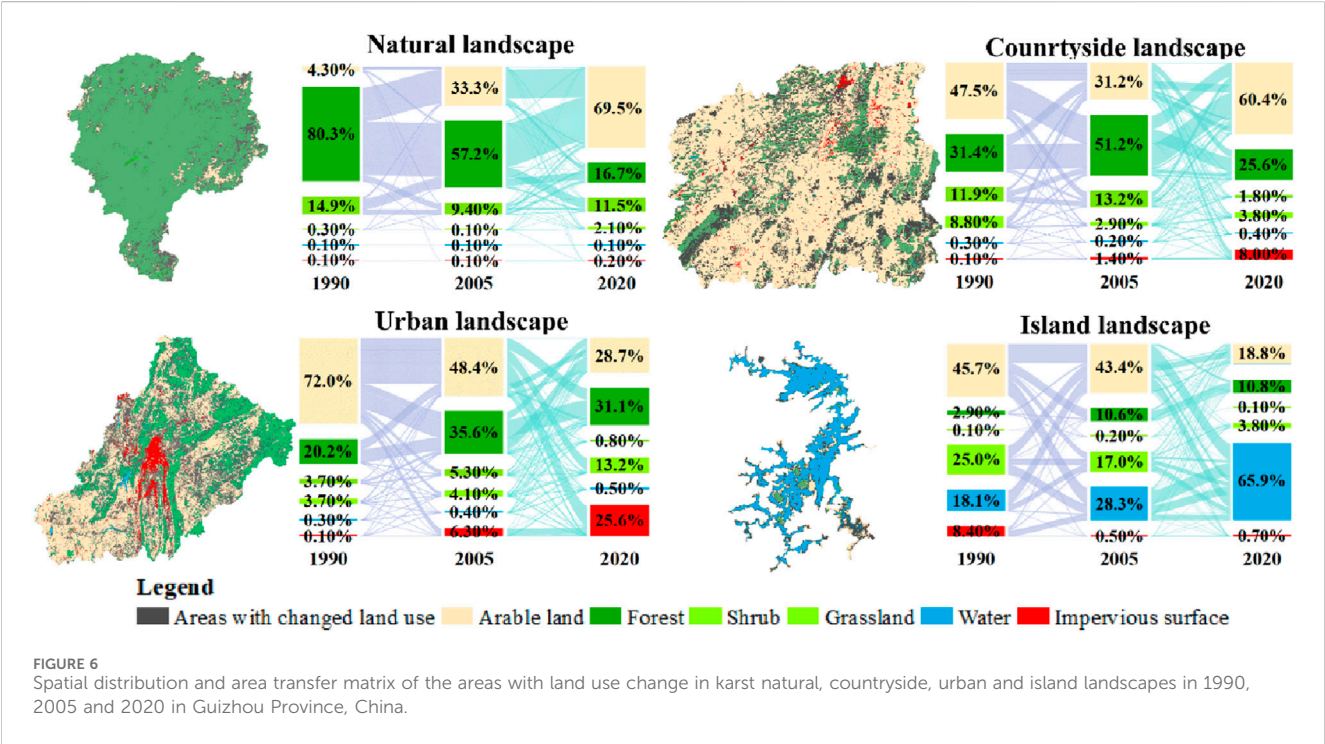
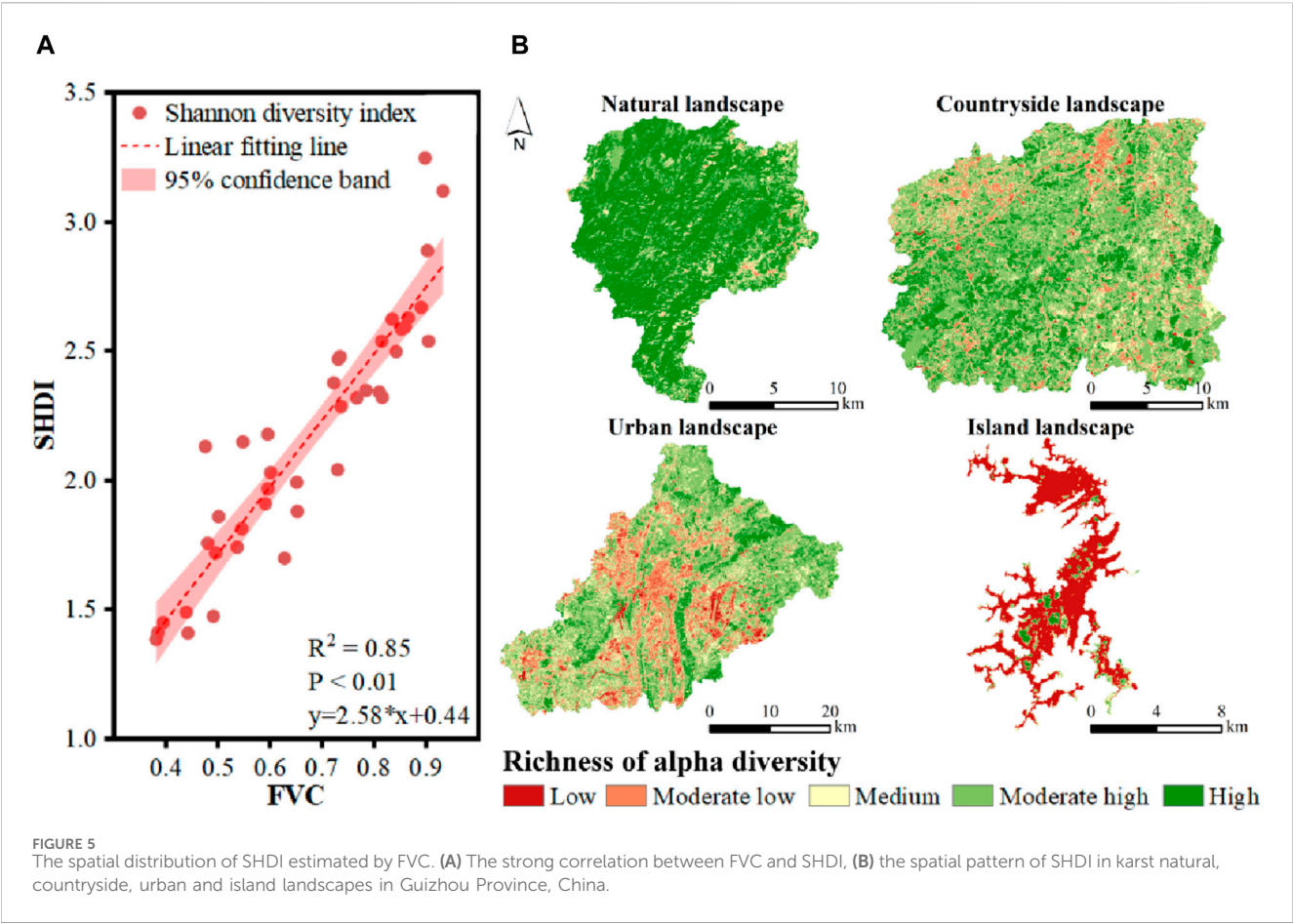
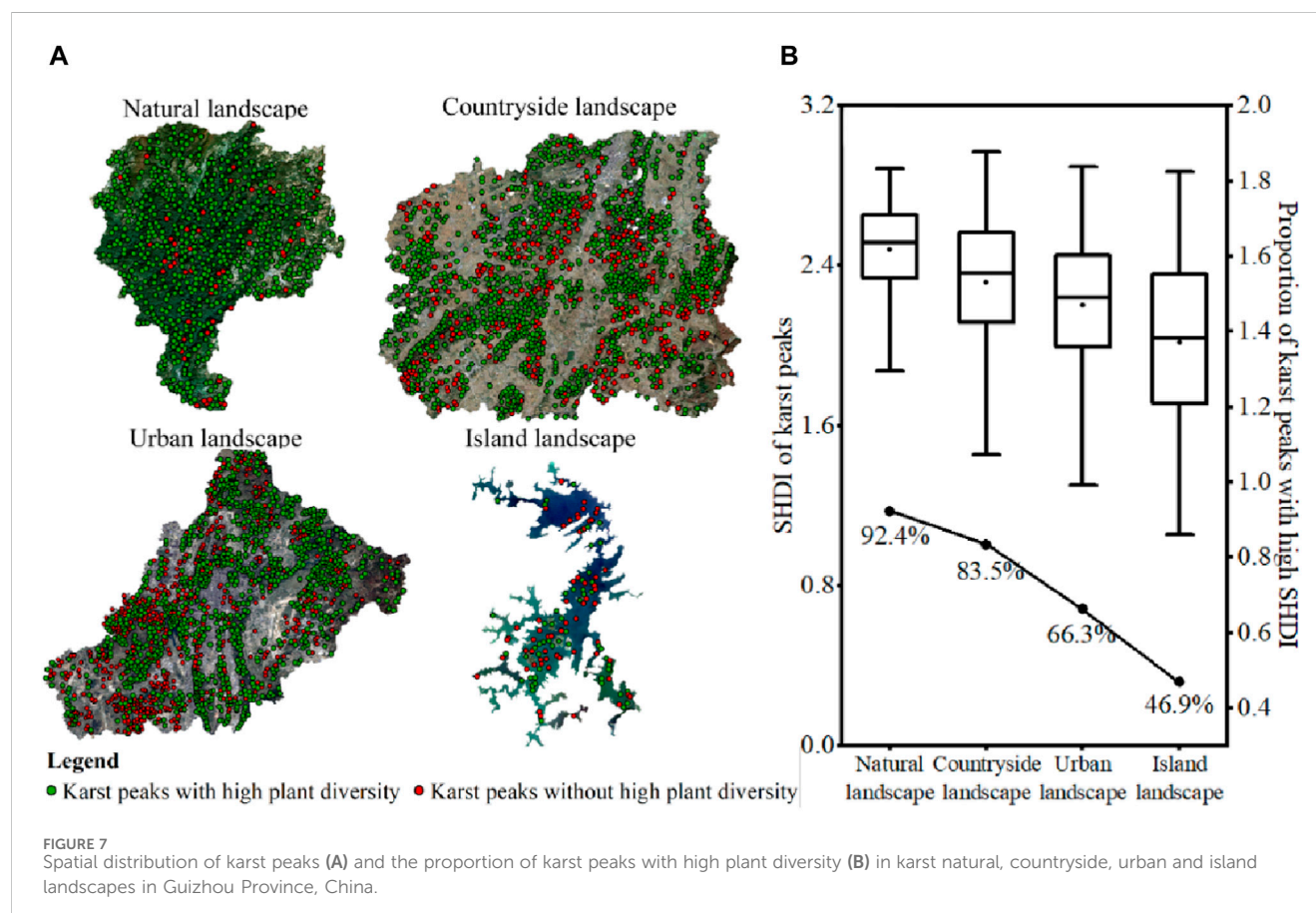


TABLE 3 Differences in karst peak density and river network density in karst natural, countryside, urban and island landscapes in Guizhou Province, China.

	Natural landscape	Countryside landscape	Urban landscape	Island landscape
Karst peak density (pcs/km ²)	2.82	2.58	1.50	2.23
River network density (km/km ²)	0.81	0.62	0.47	-



with high plant diversity in karst countryside landscape was lower than that of karst natural landscape, the spatial fragmentation remained low. In contrast, the areas with high plant diversity were seriously spatially fragmented in karst urban landscape, leading to overall decreases in plant diversity. In karst island landscape, vegetation was only scattered on the island. Therefore, the integrity of karst natural and countryside landscape was better than that of karst urban and island landscape in terms of the spatial pattern of areas with high plant diversity.

3.2 Effects of underlying surface factors on plant diversity in karst landscapes

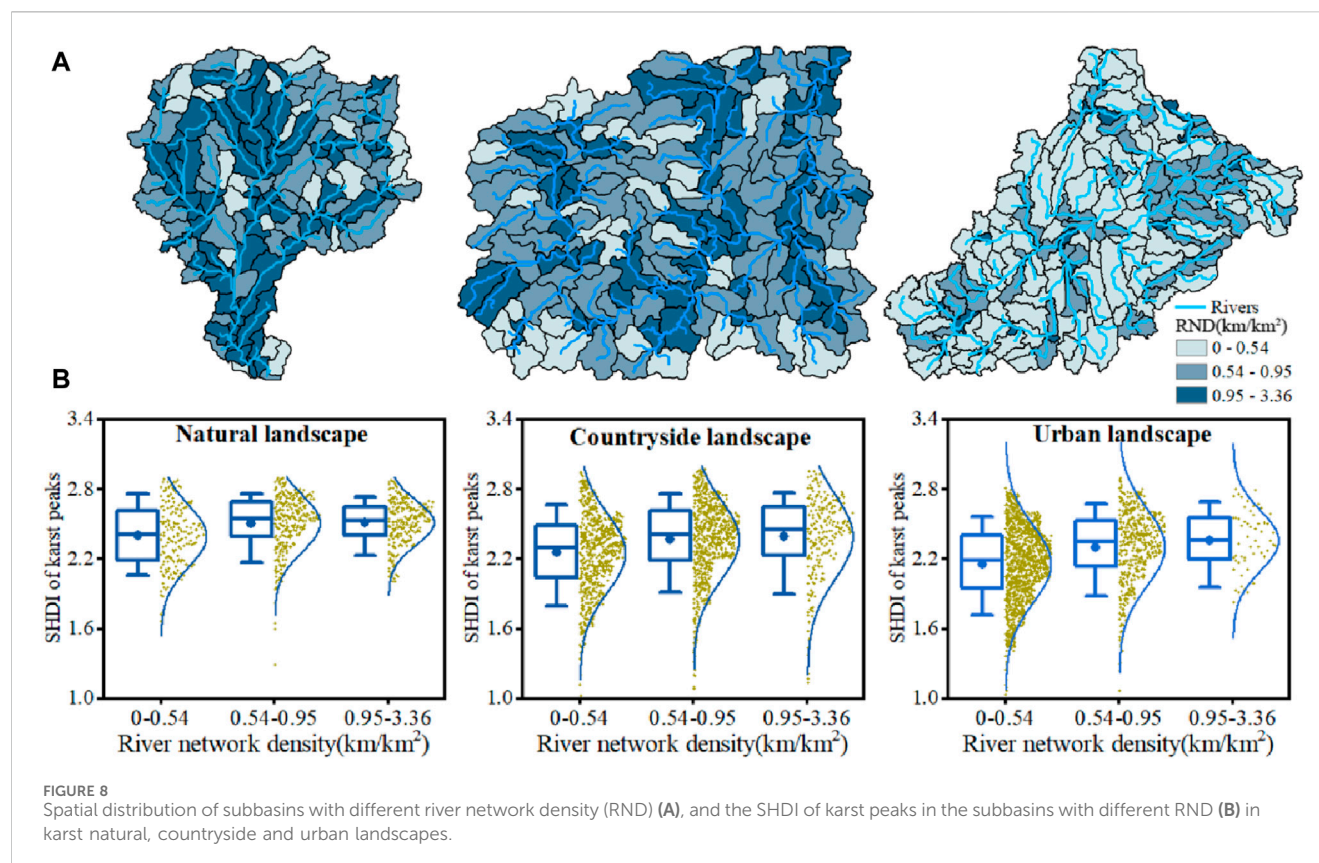
Arable land had positive impact on plant diversity, while impervious surface had negative impact, according to the conversion relationship of land use in karst natural, countryside, urban and island landscapes (Figure 6). During the last 30 years, plant diversity maintained rich in spite of a small amount of forest

converting to arable land in karst natural landscape. Although arable land was dominant, plant diversity still remained relative rich in karst countryside landscape. Plant diversity was low in karst urban landscape, because a large amount of arable land was converted into impervious surfaces.

In addition, karst peaks and river networks had positive impacts on plant diversity according to Table 3. Karst peak density and river network density both decreased from karst natural, countryside to urban landscapes, which was consistent with the decreases in plant diversity among karst natural, countryside and urban landscapes.

3.2.1 Karst peak as the source of plant diversity diffusion

Karst peak was the source of high plant diversity, and plant diversity could diffuse around karst peak. A total of 701, 1,564, 1,701, and 113 karst peaks were identified in karst natural, countryside, urban and island landscapes, respectively (Figure 7A), and the SHDI of all karst peaks were obtained (Figure 7B). Firstly, the average SHDI of karst peaks decreased among karst natural, countryside,



urban and island landscapes, which was consistent with the differences in SHDI among the four karst landscapes. Secondly, the proportion of karst peaks with high plant diversity could also reach 66.3% and 46.9% even in karst urban and island landscapes, respectively. Third, gradient decreases in plant diversity were consistent with the decreasing trend in karst peak density among karst natural, countryside, urban and island landscapes. The above three factors together indicated that karst peak was the region with high plant diversity in karst landscapes.

3.2.2 Effects of river networks, arable land and impervious surfaces on connectivity

River networks could promote the formation of high plant diversity through enhancing the ecological connectivity among karst peaks (Figure 8). The proportion of subbasins with high river network density (0.95–3.36 km/km²) decreased among karst natural, countryside and urban landscapes, consistent with the decreases in SHDI from karst natural, countryside to urban landscape (Figure 8A). Furthermore, the SHDI of karst peaks all experienced an increasing trend to different degrees with increases in river network density in subbasins in the same landscape (Figure 8B).

Arable land enhanced the ecological connectivity among karst peaks, while impervious surface could weaken the ecological connectivity (Table 4). In subbasins with the same grade of river network density, the SHDI of karst peaks showed an increasing trend with the increases in arable land density, indicating a positive correlation between the SHDI of karst peaks and arable land. It

could be inferred that arable land positively influence the SHDI of karst peaks by enhancing the ecological connectivity among karst peaks, since the depressions where arable land mainly distributed were the transition zones among karst peaks. In contrast, impacts of impervious surface was opposite to that of arable land, which could cause the barrier to ecological connectivity among karst peaks.

3.3 Determining the spatial influence on plant diversity

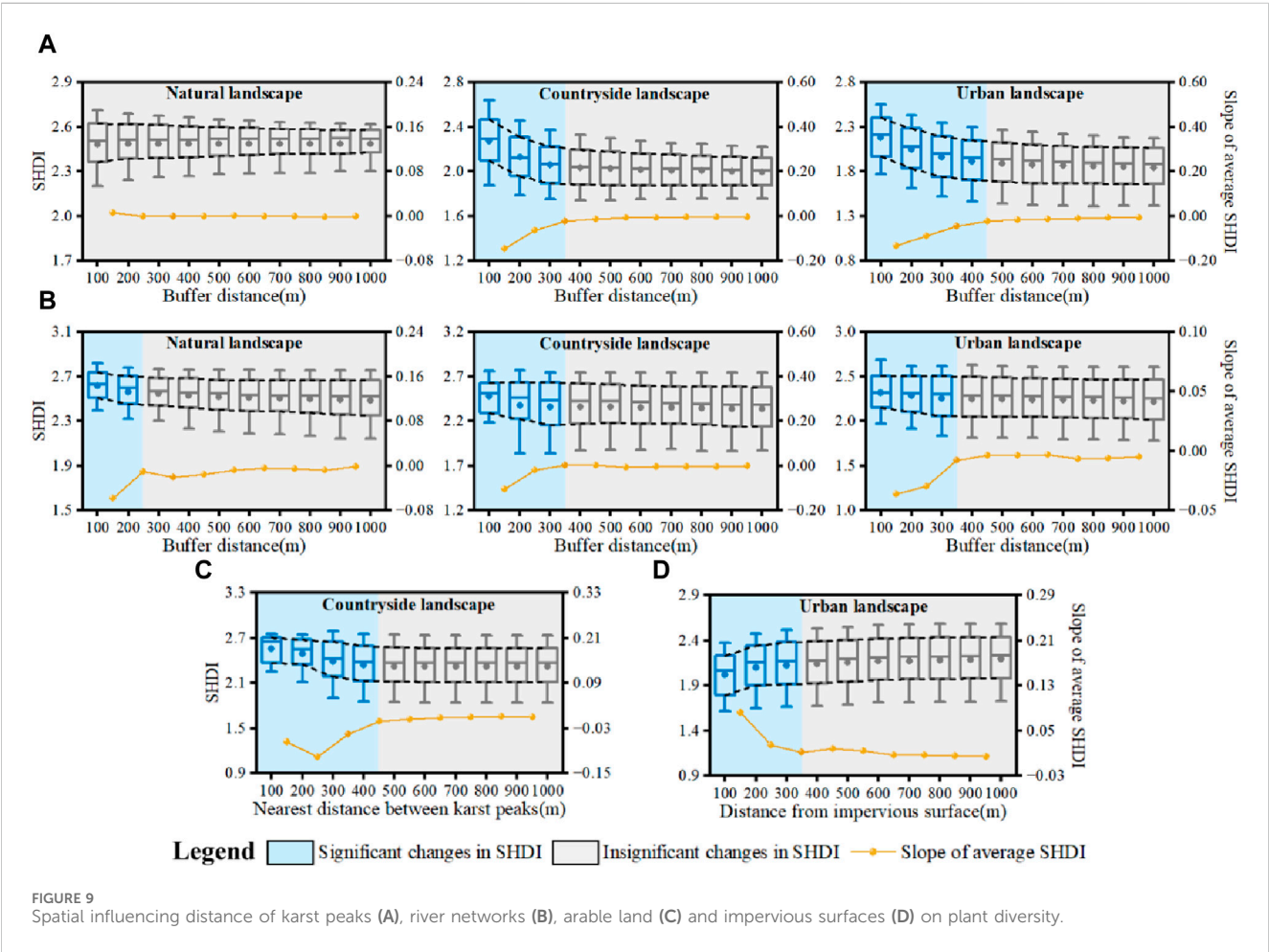
The spatial distance for plant diversity diffusing around karst peaks was about 400 m (Figure 9A). The average SHDI showed a significant decreasing trend with the increasing distance from karst peaks. Distance for plant diversity diffusing around karst peaks reached the limit between 300 m and 400 m in karst countryside landscape, and between 400 m and 500 m in karst urban landscape. Changes in SHDI were no longer obvious with the increasing distance after exceeding the limit.

According to the slope of changes in SHDI of karst peaks in different river network buffer zones (Figure 9B), river network could enhance the ecological connectivity among karst peaks until reaching the distance of 200–300 m, 300–400 m and 300–400 m in karst natural, countryside and urban landscapes, respectively. Therefore, the effect of river network on enhancing the ecological connectivity was about 300 m.

Similarly, there was also a distance limit about 450 m that arable land could influence the ecological connectivity among karst peaks.

TABLE 4 Relationship between SHDI and arable land and impervious surface in subbasin with the same grade of river network density.

Landscape type	River network density (km/km ²)	Arable land density (km ² /km ²)			Impervious surface density (km ² /km ²)		
		0–0.59	0.59–0.84	0.84–1.0	0–0.05	0.05–0.15	0.15–0.4
Countryside landscape	0–0.54	2.02	2.23	2.25	2.24	2.25	2.17
	0.54–0.95	2.16	2.24	2.37	2.37	2.31	2.29
	0.95–3.36	2.31	2.38	2.40	2.41	2.38	2.35
Urban landscape	0–0.54	2.14	2.15	2.16	2.16	2.10	2.17
	0.54–0.95	2.18	2.32	2.33	2.31	2.29	2.19
	0.95–3.36	2.07	2.23	2.38	2.39	2.28	2.07



Because decrease in SHDI of karst peaks tended to 0 when the distance reached about 400–500 m (Figure 9C). For impervious surface, the SHDI of karst peaks gradually increased with the increasing distance from impervious surface, showing a weaker effect of impervious surfaces on ecological connectivity (Figure 9D). When the distance from karst peak to impervious surface reached about 350 m, changes in SHDI of karst peaks were no longer significant.

3.4 Evaluation of the barrier risk to the ecological connectivity of plant diversity

Plant diversity could diffuse around karst peak. The impacts of river network, arable land, and impervious surface on plant diversity were reflected by changing the ecological connectivity among karst peaks. All these factors influenced the ecological connectivity with a spatial distance limit. Therefore, the barrier distance of ecological

TABLE 5 The barrier distance of the ecological connectivity of plant diversity formed by four combinations of karst peak, river network, arable land and impervious surface.

	The barrier distance of the ecological connectivity of plant diversity (m)		
	River network	Impervious surface	Arable land + impervious surface
River network	-	400 (0)	790 (390)
Arable land	1110 (710)	520 (120)	-

Numbers in brackets represent the connection distance formed by the corresponding combination of river network, arable land and impervious surface.

connectivity was formed according to karst peak and the combination of river network, arable land, and impervious surface in landscapes, and thus revealed the barrier risk to the ecological connectivity of plant diversity.

The barrier distance of ecological connectivity was calculated in Table 5. The combination of arable land and river networks could influence plant diversity by enhancing ecological connectivity among karst peaks within about 710 m, which was significantly higher than the other combinations with impervious surface, such as the combination of impervious surfaces and river networks (0 m), the combination of impervious surfaces and arable land (120 m) and the combination of impervious surfaces, river networks and arable land (390 m) (Figure 10A).

20 plant diversity aggregation regions were determined as the validation regions by the local Moran’s I index (Figure 10B). The combination type of river networks, arable land and impervious surfaces in each validation region was identified (Figure 10C). In karst natural and countryside landscapes, high plant diversity aggregation was dominant, while low plant diversity aggregation of karst peaks was dominant in karst urban and island landscapes.

When the distance among karst peaks was lower than the barrier distance of ecological connectivity, ecological connectivity among karst peaks maintained well, and formed high plant diversity in landscapes. Otherwise, plant diversity tended to be low (Figure 10C). In validation regions with high plant diversity aggregation, the distance among karst peaks was generally lower than the barrier distance of ecological connectivity, indicating a well ecological connectivity among karst peaks. In contrast, karst peaks tended to be isolated in validation regions with low plant diversity aggregation due to the overall distance among karst peaks higher than the barrier distance of ecological connectivity, thus resulting in the low plant diversity of karst peaks.

4 Discussion

4.1 Mechanisms of underlying surface factors influencing plant diversity

Karst peaks could affect plant diversity because terrain heterogeneity was highly correlated with plant diversity (Stein et al., 2014). The topographic relief of karst peaks caused spatial heterogeneity in soil physical and chemical properties, such as soil water content, pH value and soil calcium (Zhang et al., 2014). Differences in spatial distribution of soil physical and chemical properties affected the growth suitability of plants, leading to the spatial heterogeneity of plant species and richness (Zhang et al., 2013), and thus the increase in plant diversity. In addition, human

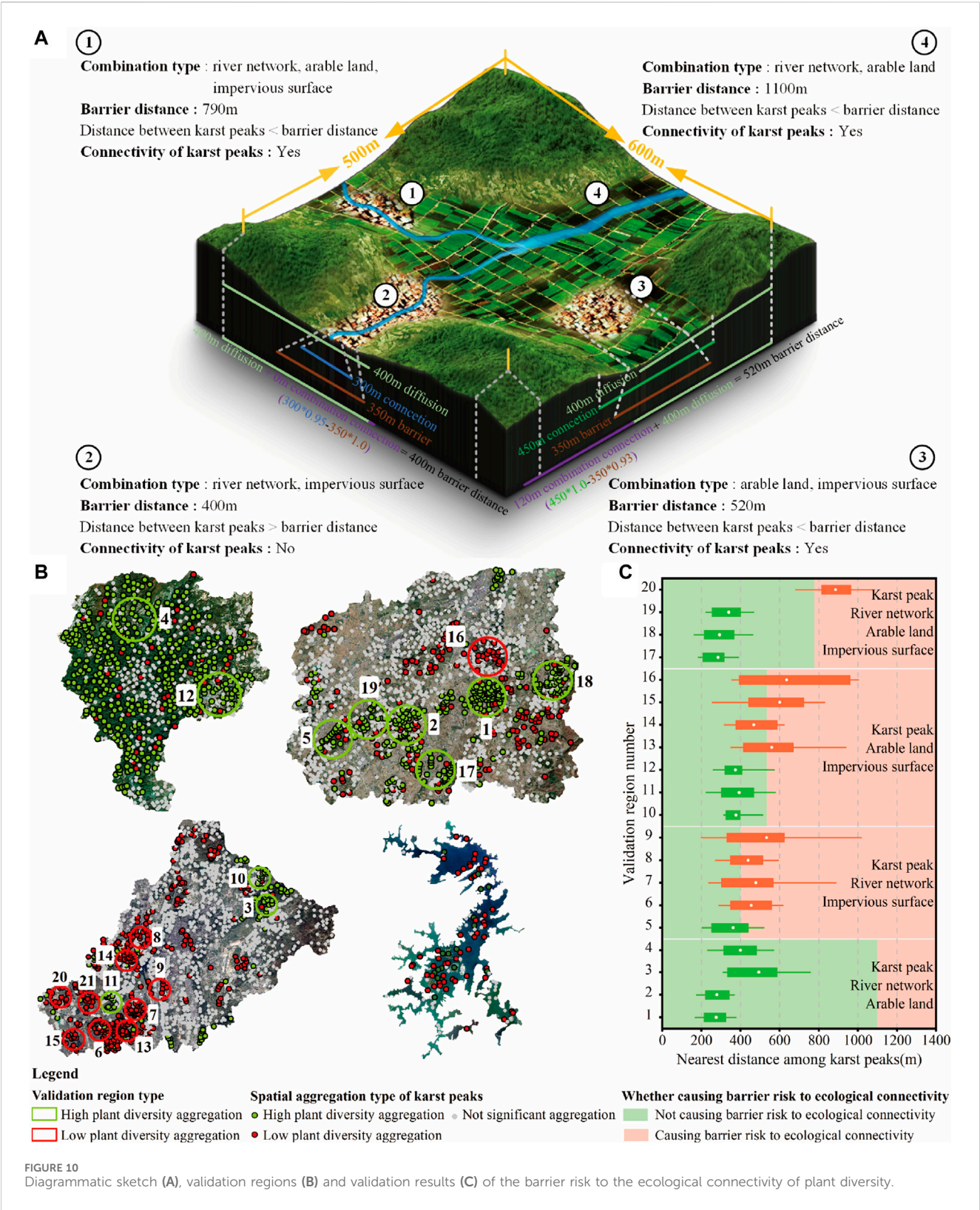
disturbance was an important driver for plant diversity decrease (Li et al., 2022b). The steep slope prevented the human disturbance on karst peaks to some extent. Meanwhile, karst peaks were generally considered one of the regions with the richest plant diversity in karst landscapes (Yang et al., 2021). The above factors indicated karst peaks maintained the rich plant diversity in karst landscapes.

Rivers could affect the ecological connectivity to influence plant diversity by environmental suitability and riparian vegetation zone. On the one hand, a suitable hydrothermal environment was necessary for plant life activities (Yao et al., 2021). Hydrological conditions could change the direction and grade of plant succession by the available water for plant (Zou et al., 2022). Rivers not only controlled the surface water supply to plants but were also the main migration carriers of necessary nutrients for plants (Li et al., 2022a). On the other hand, the impact of rivers on riparian vegetation was significant, because plant diversity along rivers was generally higher than that in areas far from rivers (Zhang et al., 2022a). In addition, rivers were also a positive factor for constructing the resistance surface to derive ecological corridors (Cui et al., 2020). This showed a positive influence of rivers on ecological connectivity and plant diversity.

Arable land and impervious surfaces had the opposite impacts on plant diversity due to the differences in spatial pattern and vegetation composition. First, strong human interference in impervious surfaces made plant species and richness subject to human control. In contrast, the mosaic structure of fallow land, hedges, and shrubs in arable land increased the heterogeneity of the landscapes (Chen and Zhang, 2021), and contributed to maintaining rich plant species diversity (Turtureanu et al., 2014). Second, impervious surfaces were generally distributed in a spatial aggregation pattern (Yang et al., 2022b). Large impervious surface patches cut off the ecological connectivity between habitats (Crouzeilles et al., 2021). Arable land was distributed mainly in the transition zones among karst peaks or between karst peaks and impervious surfaces. It helped to weaken the negative impacts of impervious surfaces, and enhance ecological connectivity among karst peaks (Yang et al., 2021). Thus, arable land had a positive impact on plant diversity by influencing ecological connectivity among karst peaks, while the impacts of impervious surface were opposite.

4.2 Reliability analysis for the barrier risk to the ecological connectivity of plant diversity

Plant dispersal among habitats was of great significance for plant diversity formation and maintenance (Liccari et al., 2022). According to current research, the dispersal distance of acorn



species ranged from 3 m to 550 m in the eastern Iberian Peninsula, Spain (Pons and Pausas, 2007). 15 tree and shrub species were evaluated in Saipan, and their dispersal distance maintained at about 500 m (Rehm et al., 2019). In addition, the dispersal distance of more than 200 plant species was within 1 km investigated by Thomson et al. (2011). Even in tropical regions where seeds spread farther away, the farthest dispersal distance of tree species was mostly at the level of hundreds of meters (Chen et al., 2019). As shown in Table 5, the barrier distance of ecological connectivity also remained at the level of hundreds of meters, which was close to the dispersal distance of

most plants. Therefore, it was feasible to use the barrier risk to ecological connectivity to indicate the ecological connectivity of plant diversity among habitats.

Plant dispersal ability was limited in space (Morgan and Venn, 2017). However, the dispersal distance of plants could be influenced by environment factors, such as karst peak, river network, arable land and impervious surface, leading to differences in the barrier risk to the ecological connectivity of plant diversity. In countryside landscape in Guizhou Province, the average distance was about 400 m among karst peaks with rich plant diversity (Yang et al., 2021), within the barrier distance of the four different combination types in Table 5. In the same regions, areas with high plant diversity rarely occurred within about 500 m from towns (Yang et al., 2021), consistent with the 400 m and 520 m barrier distance that included impervious surface in Table 5. For river networks, the gradient difference in plant diversity was greater than the distance of 100 m in riparian zones (Zhang et al., 2022a), within the 300 m ecological connectivity enhancement distance among karst peaks. In summary, karst peaks tended to form high plant diversity when the distance among karst peaks was lower than the barrier distance of ecological connectivity, and *vice versa*.

Although the main limitation of this study was the difficulty to sample short plants by UAV due to the difficulties in plot investigation at karst peaks and the occlusion of tall plant canopy, the dispersal distance of tall plants was generally longer than that of short plants (Thomson et al., 2017). The barrier distance of tall plants could cover the influence distance by karst peak, river network, arable land, and impervious surface on short plants. It showed the maximum spatial response distance of plant diversity to the barrier risk to ecological connectivity. Therefore, it was reliable to evaluate the barrier risk to the ecological connectivity of plant diversity by the tall plants which could be sampled by UAV.

5 Conclusion

Analyzing the barrier risk to the ecological connectivity of plant diversity was crucial for balancing plant diversity conservation and socioeconomic development in karst regions. This study revealed spatial impacts of the barrier risk to ecological connectivity on plant diversity in karst regions, and the main conclusions were as follows:

1. Karst peak, river network and arable land had maintenance effects on plant diversity. Karst peak was the source of plant diversity diffusion. River network and arable land enhanced connectivity among karst peaks, while impervious surface had the barrier effect on connectivity.
2. In space, plant diversity could diffuse about 400 m around karst peaks. River network and arable land could enhance the connectivity among karst peaks by a distance about 300 m and 450 m, respectively, while the barrier effect of impervious surface on connectivity was about 350 m.
3. Combination of river network, arable land and impervious surface determined the barrier risk to the ecological connectivity of plant diversity. From low to high, the barrier distance was about 1,110 m in the combination of river network and arable land, about 790 m in the combination of river network, arable land and impervious surface, about

520 m in the combination of arable land and impervious surface, about 400 m in the combination of river network and impervious surface.

Our findings concretized the barrier risk to the ecological connectivity of plant diversity, which could provide a planning basis for plant diversity protection in the karst regions with rapid socioeconomic development and large population. For the global karst regions whose development and population were not as fast and large as Guizhou Province, much attention should be paid to the barrier risk to ecological connectivity to protect plant diversity when society develops fast in future.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

Author contributions

BZ: Conceptualization, Formal Analysis, Investigation, Methodology, Visualization, Writing—original draft. HL: Conceptualization, Investigation, Supervision, Writing—review and editing. SY: Conceptualization, Data curation, Funding acquisition, Investigation, Supervision, Validation, Writing—review and editing. CL: Data curation, Investigation, Methodology, Validation, Visualization, Writing—review and editing. ZP: Investigation, Validation, Visualization, Writing—review and editing. YZ: Investigation, Software, Visualization, Writing—review and editing. HaL: Investigation, Visualization, Writing—review and editing. YY: Supervision, Writing—review and editing. JG: Investigation, Writing—review and editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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