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RESEARCH ARTICLE





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Environmental filtering and spatial processes shape the beta diversity of liana communities in a valley savanna in southwest China

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Abstract

Questions: Lianas contribute substantially to the diversity and function of ecosystems. What is the relative importance of environmental filtering and spatial processes on structuring liana beta diversity at taxonomic, functional and phylogenetic levels? Is there any synergy between these drivers (environmental factors and spatial distance) on shaping these three dimensions of beta diversity in a savanna liana community?

Location: A dry-hot valley savanna in Yunnan Province, southwest China.

Methods: We established 30 20 m \times 20 m plots in the savanna to collect data on the distribution of 22 liana species, 19 functional traits, and plot-level soil nutrients, elevation, and slope. The relative contributions of these environmental factors and spatial distance to liana taxonomic, functional and phylogenetic dissimilarity were analyzed using multiple regression on distance matrices. We also tested which environmental factors influence the beta diversity of liana community using permutational multivariate analysis of variance.

Results: Both environmental and spatial distances were significantly correlated with taxonomic, functional and phylogenetic dissimilarity. Spatial distance explained more variation in taxonomic beta diversity than environmental factors. But for both nearest-neighbour functional and phylogenetic distance $D_{nn'}$, environment explained relatively more variation than space did. Moreover, the proportion explained by environmental variables was ranked in decreasing order as follows: functional $D_{nn'}$, phylogenetic $D_{nn'}$, and taxonomic beta diversity. We found soil pH had the highest contribution to taxonomic and functional beta diversity, while soil total nitrogen contributed most to phylogenetic beta diversity.

Conclusions: This study revealed that liana taxonomic, functional and phylogenetic beta diversity in the studied hot-dry savanna ecosystem is affected and maintained by both environmental filtering and spatial processes. Moreover, the functional and phylogenetic diversities were more strongly subject to environmental filtering. Our study provides information on the mechanisms underlying liana diversity

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KEYWORDS

community assembly, deterministic processes, functional beta diversity, liana diversity, phylogenetic beta diversity, savanna ecosystem, stochastic processes, taxonomic turnover

1 | INTRODUCTION

Savannas are an important component of terrestrial ecosystems, occurring in Africa, Asia, South America, and Australia, covering nearly one third of the world's land surface (Huntley & Walker, 1982; Silva & Bates, 2002). Savannas have high species richness and endemism owing to their unique climate conditions (Myers *et al.*, 2000; Furley, 2006). The climate, soil, topography, fire, herbivores and anthropogenic disturbances interact to form the highly variable and complex savanna system, even at local scales (Staver *et al.*, 2019; Staver *et al.*, 2011). Therefore, it is a challenge to predict the effects of environmental and spatial factors on diversity in savanna ecosystems (Staver *et al.*, 2019; Staver *et al.*, 2011), although understanding how those factors affect savanna diversity is necessary for improving the conservation of this globally widespread biome (Staver *et al.*, 2019).

Lianas are one of the key growth forms in tropical and subtropical forests (Schnitzer & Bongers, 2002), which are important for providing canopy connectivity, food sources, and habitats for animals (Schnitzer & Bongers, 2002; Odell et al., 2019). Previous studies have shown that lianas employ acquisitive strategies, i.e. lianas have higher specific leaf area, wider vessel diameter, higher hydraulic efficiency, but lower cavitation resistance to drought than co-occurring trees (Zhu & Cao, 2009; Campanello et al., 2016; Chen et al., 2017). As such, they can alter forest structure and composition by competing for resources with trees, thus affecting tree growth, recruitment, and mortality, and also resulting in reduced carbon sequestration and ecosystem functioning (van der Heijden et al., 2015; Schnitzer, 2018). The resource acquisition traits of lianas may be responsible for the observation that the abundance and biomass of lianas are increasing in tropical forests (Wright et al., 2004; Yorke et al., 2013). Although there are many studies focused on lianas in forests (Schnitzer & Bongers, 2011; van der Heijden et al., 2015; Schnitzer, 2018), knowledge about the mechanisms that drive the structure, function, and dynamics of liana communities is still scant, let alone of liana communities in savanna ecosystems.

Beta diversity describes variation in species composition among sites (Whittaker, 1960) and has been widely used to study community assembly (Anderson *et al.*, 2011; Kraft *et al.*, 2011; Legendre & De Cáceres, 2013). Many studies have also incorporated phylogenetic and functional information (Swenson, 2011; Swenson *et al.*, 2011, 2012; Yang *et al.*, 2015; Asefa *et al.*, 2017) into the traditional beta diversity metrics. Two types of mechanisms, deterministic process, emphasizing the importance of environmental filtering, and spatial process, stressing dispersal limitation, have been proposed to explain community assemblages (Hubbell, 2001; Legendre *et al.*, 2009; McFadden *et al.*, 2019; van Breugel *et al.*, 2019). Quantifying the variation of species composition along environmental and spatial distance contributes to understanding the relative importance of these two processes (Legendre *et al.*, 2009; Anderson *et al.*, 2011; Arellano *et al.*, 2016b), despite that their relative importance has been found to vary considerably in different tree communities (Legendre *et al.*, 2009; Swenson *et al.*, 2012; Myers *et al.*, 2013; Wang *et al.*, 2015; Yang *et al.*, 2015; van Breugel *et al.*, 2019).

In those few studies on liana beta diversity (López-Martínez et al., 2013; Menegat et al., 2019), the focus has been on taxonomic beta diversity, as in many studies on forest tree diversity (Legendre et al., 2009; Baldeck et al., 2013; Myers et al., 2013). Taxonomyfocused beta diversity may sometimes be insufficient because all species are treated as evolutionarily independent and ecologically equivalent and species-environment relationships could be misrepresented (Swenson, 2011; Swenson et al., 2011). For example, Wang et al. (2015) demonstrated that both habitat filtering and dispersal limitation, rather than dispersal limitation alone, influenced phylogenetic and functional beta diversity in two temperate forests. Hence, exploring community assembly beyond the species level is necessary for understanding the co-occurrence of species with certain traits and phylogenetic relatedness along environmental gradients. In addition, it has been reported that soil properties can be regarded as major drivers of variation in plant species composition. For example, Arellano et al. (2016a) summarized the soil/floristic composition in tropical forests and showed that the relative importance of soil characteristics followed the list: available base content, texture, pH, total C and N, available P, available AI, and available micronutrients. However, knowledge about the effects of soil variables on liana taxonomic, functional and phylogenetic beta diversity in savanna ecosystems is lacking.

Liana studies in savannas have so far mainly focused on species diversity (de Oliveira *et al.*, 2014; Brito *et al.*, 2017; Meyer *et al.*, 2020) and on exploring interactions between lianas and trees (Sfair *et al.*, 2010, 2015, 2018). Beta diversity in lianas is not well understood. That is true even for lianas in forest ecosystems, in which liana beta diversity is compared with that of trees, shrubs or herbaceous plants and partitioned into the effect of environmental filtering and spatial distance (Macía *et al.*, 2007; Gallagher & Leishman, 2012; López-Martínez *et al.*, 2013; Murphy *et al.*, 2016). The only study comparing tree, palm and liana community assembly is from a savanna in Brazil (Menegat *et al.*, 2019). It reports that both environmental and spatial distances play important roles in structuring liana beta diversity, but the number of liana species included in

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the study is only four, making it difficult to generalize the result. A multidimensional biodiversity approach including taxonomic, functional and phylogenetic dimension has not yet been applied to the study of liana diversity. Moreover, there is lack of understanding on the relative contributions of heterogeneity in soil resources, topography, and spatial distance in shaping liana beta diversity in savanna ecosystems.

In this study, we investigated the factors structuring liana taxonomic, functional and phylogenetic beta diversity in a dry-hot valley savanna ecosystem in Yunnan Province, southwest China. We attempted to address the following questions: (1) what is the relative importance of environmental filtering and spatial distance on structuring liana beta diversity at taxonomic, functional and phylogenetic levels; and (2) is there any synergy between these drivers (environmental factors and spatial distance) on shaping these three dimensions of beta diversity in a savanna liana community? Answers to these questions will help to quantify the relative importance of environmental heterogeneity and spatial processes in shaping liana taxonomic, functional and phylogenetic beta diversity. Given the harsh environmental condition induced by frequent drought stress in our dry-hot valley savanna, we are particularly interested in identifying the critical factors in environmental heterogeneity for a savanna liana community and in testing whether environmental heterogeneity dominates its phylogenetic and functional beta diversity.

2 | METHODS

2.1 | Site and species

We conducted this study at the Yuanjiang Savanna Ecosystem Research Station (23°27'56" N, 102°10'40" E, altitude 481 m) of Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, which is located in Yuanjiang County, Yunnan Province, southwest China (Appendix S1). According to the meteorological records for this station (2012-2017), the annual mean temperature is 24.7°C and the annual mean precipitation is 733 mm, with a pronounced six-month dry season (November-April). The annual mean pan evaporation is ca. 2,220 mm, nearly three times the precipitation. We calculated the aridity index following Nastos et al.(2013), to be 0.33, indicating a semi-arid climate at our site. The dominant trees are Lannea coromandelica and Polyalthia cerasoides, the dominant shrub is Campylotropis delavayi, and the dominant herb is Heteropogon contortus. We randomly established 30 20 m × 20 m plots, separated by a distance ≥20 m. All lianas ≥0.5 cm in diameter at breast height were measured, tagged, and identified at the species level. Following liana census standard protocols by Gerwing et al. (2006) and by Schnitzer et al. (2008), we defined individual lianas as rooted in the plots, and each stem was counted as an individual if it was independently rooted. In total, 945 liana individuals were recorded, representing 22 species belonging to 20 genera and 11 families (Table 1). Hiptage benghalensis var. tonkinensis was excluded

TABLE 1 Species selected in this study

Species	Family	Number of individuals
Abrus pulchellus	Leguminosae	200
Secamone sinica	Apocynaceae	143
Cissus repanda	Vitaceae	134
Jasminum seguinii	Oleaceae	84
Bauhinia championii	Leguminosae	64
Pterolobium macropterum	Leguminosae	57
Bauhinia comosa	Leguminosae	49
Bridelia stipularis	Phyllanthaceae	48
Smilax china	Smilacaceae	46
Cryptolepis buchananii	Apocynaceae	44
Passiflora henryi	Passifloraceae	19
Myriopteron extensum	Apocynaceae	16
Dregea volubilis	Apocynaceae	14
Argyreia osyrensis var. cinerea	Convolvulaceae	7
Loeseneriella merrilliana	Celastraceae	4
Phyllanthus reticulatus	Phyllanthaceae	3
Cyclea wattii	Menispermaceae	3
Abrus precatorius	Leguminosae	3
Capparis cantoniensis	Capparaceae	2
Hiptage benghalensis var. tonkinensis	Malpighiaceae	2
Gymnema sylvestre	Apocynaceae	2
Cajanus mollis	Leguminosae	1

from the statistical analyses due to lack of trait data. In total, our analysis included 21 species.

2.2 | Functional traits

We measured 19 functional traits (Table 2; Appendix S2) for the 21 species based on standardized protocols proposed by Pérez-Harguindeguy et al. (2013). These traits represent the different dimensions of the functional niche with respect to carbon economy, nutrient acquisition, water economy in leaves and stems among liana species. Specifically, we measured leaf thickness, specific leaf area, leaf dry matter content, stomatal density, vein density, nitrogen (N) concentration, phosphorus (P) concentration, potassium (K) concentration, ratio of nitrogen and phosphorus, stable carbon isotopic discrimination, mass-based maximum photosynthetic rate, stomatal conductance, photosynthetic N use efficiency, photosynthetic P use efficiency, photosynthetic water use efficiency, wood density, hydraulically weighted vessel diameter, vessel density, and theoretical hydraulic conductivity (see Appendix S3 for details of measurement methods). We selected 3-5 individuals for each species to measure the leaf and stem traits during the rainy season. We used the species mean values of traits to represent each liana species. We standardized the trait data by subtracting mean value and dividing by its

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TABLE 2 The loadings of 19 functional traits on the first four principal		Trait	PC 1	PC 2	PC 3	PC 4
components for 21 liana species in Yuanjiang savanna	Carbon economy	Leaf thickness	0.138	0.026	-0.184	0.020
		Mass-based maximum photosynthetic rate	-0.370	0.011	0.169	-0.254
		Specific leaf area	-0.194	-0.265	0.022	-0.210
		Leaf dry matter content	0.289	0.208	0.205	0.137
	Nutrient economy	N concentration	-0.054	-0.364	-0.25	-0.170
		P concentration	-0.272	-0.068	-0.398	0.089
		K concentration	-0.035	-0.405	-0.295	0.017
		N/P ratio	0.249	-0.279	0.175	-0.154
		Photosynthetic N use efficiency	-0.338	0.161	0.263	-0.165
		Photosynthetic P use efficiency	-0.235	0.060	0.390	-0.325
	Water economy	Stomatal density	-0.037	0.335	-0.163	-0.226
		Stable carbon isotope discrimination	0.126	-0.326	-0.102	-0.342
		Stomatal conductance	-0.247	0.259	-0.275	-0.108
		Intrinsic photosynthetic water use efficiency	0.194	-0.259	0.332	0.183
		Vein density	0.002	0.163	-0.199	-0.045
		Wood density	0.311	0.215	-0.113	0.055
		Vessel diameter	-0.276	-0.059	0.048	0.468
		Vessel density	0.226	0.217	-0.235	-0.229
		Theoretical hydraulic conductivity	-0.272	-0.036	-0.053	0.435
		Proportion of variance explained	27.10%	19.85%	14.39%	11.75%

Note: See Appendix S3 for trait definitions and units.

standard deviation before conducting further analyses. A principle components analysis (PCA) was conducted to reduce the dimensionality of the multivariate traits to a few major orthogonal axes of a functional trait space. The first four PCA axes accounted for over 73.1% of the variation (Table 2) and were used to compute a Euclidean distance matrix. All analyses were conducted using functional trait dendrograms generated by both the four PCA axes and the raw trait distance matrix.

2.3 | Environmental variables

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Soil nutrients and topography (elevation and slope) were used as environmental variables to explain liana beta diversity. Soil samples were collected at the end of the rainy season, in 2015. Five soil samples (0–20 cm) were collected at the four corners and the center of each plot. In total, we took 150 soil samples. The fresh soils placed in plastic bags were sent to the laboratory in Xishuangbanna Tropical Botanical Garden. In the laboratory, one sub-sample was used to measure pH values as soon as possible using a potentiometer after water extraction (soil/water: 1/2.5). Another sub-sample was then dried, smashed, sieved using 1 and 0.15 mm mesh and stored in plastic bags for analyses of soil total N, total P, total K, hydrolysable N, available P, available K, and organic matter. Soil total N was analyzed by the micro-Kjeldahl method, and hydrolysable N was determined by an automatic steam distilling unit. After digestion in HNO₃-HClO₄ solution, we utilized an inductively coupled plasma atomic emission spectrometer (iCAP6300, Thermo Fisher Scientific, USA) to determine the soil total P and K. Available P and available K were determined using a 0.03 mol/l NH_4F and 0.025 mol/l HCl solution, and a neutral 1 mol/l CH₃COONH₄ solution, respectively. Soil organic matter was determined using an oxidized H₂SO₄-K₂Cr₂O₇ solution. Elevation was calculated at the centre of each 20 m \times 20 m plot. Slope was calculated as the mean angular deviation from horizontal for each of four triangular planes formed by connecting three corners. Because the environmental variables have high collinearity (Appendix S4), we constructed a PCA analysis-based correlation matrix of the environmental variables. The first three principal components, which accounted for 80.53% of the total variation, were used for subsequent analyses (Table 3).

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TABLE 3 The loadings of ten environmental variables on the first three principal components for $30\ 20\ m\times 20\ m$ plots from the savanna studied

Environmental variables	PC 1	PC 2	PC 3
pН	-0.202	0.549	-0.215
Total N	-0.429	-0.171	0.079
Total P	-0.405	-0.104	0.107
Total K	0.159	-0.422	0.077
Hydrolysable N	-0.429	-0.046	0.166
Available P	-0.168	0.578	0.037
Available K	-0.263	-0.019	-0.679
Organic matter	-0.430	-0.160	0.101
Altitude	-0.243	-0.338	-0.386
Slope	-0.245	0.065	0.530
Proportion of variance explained	49.1%	20.75%	10.68%

2.4 | Spatial variables

We utilized GPS to record latitude and longitude of each plot and then calculated the spatial distance between plots. We used the deg2dec function in the "spa" package of R software to transform the coordinates to distance. A principal coordinates of neighbour matrices analysis (PCNM) is proposed to produce orthogonal spatial variables covering a wide range of spatial scales, allowing modelling any type of spatial structures (Borcard & Legendre, 2002). We first constructed a matrix of Euclidean distances among the sampling sites. We then selected those PCNM variables with positive eigenvalues using the forward selection proposed by Blanche and Legendre (2008) based on a double stopping criterion. By this step, we retained the distance among close neighbours under the defined threshold, and computed a principal coordinates of the truncated distance matrix. Finally, we kept the positive eigenvectors [Moran's I > E(I)] as the spatial explanatory variables in regression. We used the PCNM function in the R package "PCNM" (Borcard & Legendre, 2002) to generate a suite of spatial variables. In total, we obtained 20 PCNM eigenvalues to represent the spatial distance. Furthermore, we conducted forward selection by using the "packfor" package (Dray, Legendre, & Blanchet, 2009) in R software. The positive PCNMs were eventually retained as spatial explanatory variables to analyze the liana beta diversity.

2.5 | Phylogenetic tree reconstruction

We retrieved four DNA markers (*rbcL*, *matK*, *trnH-psbA*, ITS) from GenBank for each of the 22 species (Appendix S5). Firstly, we performed alignments on each marker using Aliview software (Larsson, 2014). Secondly, for each marker, we utilized jModeltest 2.1.10 to estimate the best-fit model of nucleotide evolution by the corrected Akaike Information Criterion (AIC), with the best model having the lowest AIC value (Darriba *et al.*, 2012). Thirdly, we used SequenceMatrix 1.7.8 (Vaidya *et al.*, 2011) to concatenate the DNA sequences into a single supermatrix. We finally performed Bayesian analyses in MrBayes 3.2.6 (Ronquist *et al.*, 2012) to construct the consensus tree. Convergence of the consensus tree was estimated by Tracer 1.7.1 (Rambaut *et al.*, 2018). We chose *Amborella trichopoda* as our outgroup. The consensus phylogenetic tree of the 22 focal species with bootstrap support probability values can be found in Appendix S6.

2.6 | Taxonomic, functional and phylogenetic beta diversity metrics

We used dissimilarity indices based on the proportion of shared and unique fractions of species counts and distinctive parts to calculate taxonomic, functional and phylogenetic beta diversity. We transformed species abundance by Hellinger's transformation, which down-weights the influence of common species in dissimilarity calculation (Legendre & De Cáceres, 2013), using the *decostand* function in the "vegan" package (Oksanen *et al.*, 2013). We then calculated the abundance-weighted Bray-Curtis dissimilarity index using the *vegdist* function in the "vegan" package for taxonomic beta diversity.

To quantify functional and phylogenetic beta diversity, we calculated two commonly used metrics representing two main mathematically independent classes of functional (or phylogenetic) beta diversity metrics (Swenson, 2011). The first functional (or phylogenetic) metric was measured using the abundance-weighted mean pairwise trait (or phylogenetic) distance (D_{pw}). The second functional (or phylogenetic) metric was the abundance-weighted mean nearest-neighbour trait (or phylogenetic) distance (D_{nn}) (Rao, 1982). The detailed equations are as follows:

$$D_{pw'} = \frac{\sum_{i=1}^{n_{k_1}} f_i \overline{\delta}_{ik_2} + \sum_{j=1}^{n_{k_2}} f_j \overline{\delta}_{jk_1}}{2}$$
(1)

$$D_{nn'} = \frac{\sum_{i=1}^{n_{k_1}} f_i min\delta_{ik_2} + \sum_{j=1}^{n_{k_2}} f_j min\delta_{jk_1}}{2}$$
(2)

where n_{k_1} is the number of species in community k_1 ; n_{k_2} is the number of species in community k_2 ; $\overline{\delta}_{ik_2}$ represents the mean pairwise trait or phylogenetic distance from species *i* in community k_1 to all species in community k_2 , and $\overline{\delta}_{jk_1}$ is the mean pairwise phylogenetic or trait distance between species *j* in community k_2 to all species in community k_1 ; f_i and f_j are the relative abundance of species *i* in community k_1 and species *j* in community k_2 . Similarly, $\min \delta_{ik_2}$ is the nearest phylogenetic neighbour or trait distance between species *i* in community k_1 to all species in community k_2 , and $\min \delta_{jk_1}$ is the nearest phylogenetic neighbour or trait distance between species *j* in community k_2 to all species in community k_1 . To test whether the observed functional and phylogenetic beta diversity deviated from random expectation, we conducted a null model analysis (Swenson, 2011; Swenson *et al.*, 2012) by randomly shuffling taxon names across the tips of the trait or phylogeny FIGURE 1 Flow chart describing the liana taxonomic, functional, and phylogenetic beta diversity data as well as the statistical analyses to evaluate the relative roles of environmental and spatial distance in partitioning the liana community at three dimensions. For details see the Method section [Colour figure can be viewed at wileyonlinelibrary. com]



dendrogram 999 times to randomize trait similarity or phylogenetic relationships among species, given unchanged branch length and tree topology. A standardized effect size of functional or phylogenetic $D_{\rm pw'}$ (SES $D_{nn'}$) or $D_{nn'}$ (SES $D_{nn'}$) was quantified by the difference between average functional or phylogenetic distances in the observed communities vs. the null distribution, then divided by the standard deviation of the null data using the SES.mpd and SES.mntd functions in the R package "picante" (Kembel et al., 2010). Negative SES D_{pw} or SES D_{pm} values indicated functionally (or phylogenetically) clustered, or lower observed $D_{nw'}$ or $D_{nn'}$ metrics than expected. We utilized the *comdist* and comdistnt functions in the "picante" package to calculate D_{nw}, and $D_{\rm nn'}$ metrics. $D_{\rm nw'}$, a "basal" metric, is better to detect major compositional turnover from community to community. D_{nn}, a "terminal"

metric, is useful for detecting subtle turnover in composition from subplot-to-subplot that may not be detected by pairwise metrics (Swenson et al., 2012).

2.7 | Variation partitioning of taxonomic, functional and phylogenetic beta diversity

To determine the relative importance of environmental variables (proxy of environmental filtering) and spatial variables (representing the spatial processes, of which dispersal limitation is a major mechanism) in structuring liana beta diversity, we partitioned the variation in beta diversity to the effects of the environment, space and their



FIGURE 2 Distribution of standard effective size for abundance-weighted mean pairwise phylogenetic and functional distances (SES D_{nw}) and standard effective size for abundanceweighted mean nearest taxon phylogenetic and functional distances (SES D_{nn'}). Functional SES D_{nw'} and SES D_{nn}, are based on functional PCA results. Bars to the left of the red zero line indicate phylogenetic and functional turnover is lower than expected. The proportions of SES values below zero were as follows: (a) 70%; (b) 50%; (c) 66.67%; and (d) 50% [Colour figure can be viewed at wileyonlinelibrary.com]

interaction (Figure 1). We utilized multiple regressions on distance matrices (MRM) (Lichstein, 2007), a kind of extension of the partial Mantel Test, which can be used to determine the relative power of environmental and spatial distance in explaining taxonomic, functional, and phylogenetic beta diversity. The "environmental" in the bar plot represents the variance explained exclusively by environment, and "spatial" represents the variance explained exclusively by space. The "shared" is the variance explained simultaneously by environment and space. The "residuals" is 1 minus the total variation explained by the environmental, spatial and shared. Considering the collinearity among edaphic and climatic variables, we used the first three environmental principal components as the independent explanatory variables (Table 3). Based on the first three PCA components, we constructed a Euclidean distance matrix of environmental variables. The response variable is the taxonomic, functional, and phylogenetic beta diversity, and the independent variables are environmental and spatial distance in MRM analyses. The MRM analyses were carried out using the *MRM* function in the "ecodist" package (Goslee & Urban, 2007) in R. If environmental distance was significantly correlated with dissimilarity distance, we went a step further to test which environmental variables were more important in determining liana taxonomic, functional, and phylogenetic beta diversity. To select environmental variables, we conducted permutational MANOVA analyses using the "vegan" package. In this analysis, the response variable is liana beta diversity, and explanatory variables are the original environmental variables. The R^2 and Pr (>*F*) were calculated followed the method for non-parametric multivariate analysis of variance (Anderson, 2001). If two variables had a correlation coefficient \geq 0.8, we retained one variable in the regression model. For instance, total N was highly correlated with total P, hydrolysable N, and organic matter, with correlation coefficients being 0.92, 0.95 and 0.99, respectively. We just retained total N to avoid collinearity (see Appendix S4 for all the pairwise Pearson's correlation coefficients of the environmental variables).

All analyses in this study were carried out in the R programming environment v.5.3.3 (R Core Team, 2019).

3 | RESULTS

The distributions of effect size for abundance-weighted mean pairwise and nearest-neighbour phylogenetic and functional distances (SES $D_{pw'}$ and SES $D_{nn'}$) are shown in Figure 2. More than 50% of the effect sizes (range 50-70%) are negative. Similar results were found for the effect sizes of raw phylogenetic and functional distances (Appendix S7). In general, both environmental distance and spatial distance were significantly correlated with taxonomic dissimilarity $(R^2 = 0.159, p = 0.001)$, phylogenetic $D_{pp'}$ ($R^2 = 0.137, p = 0.001$) and $D_{pw'}$ ($R^2 = 0.084$, p = 0.001), and functional $D_{nn'}$ ($R^2 = 0.146$, p = 0.001), and $D_{nw'}$ ($R^2 = 0.075$, p = 0.002) based on functional PCA data, according to results of multiple regressions of distance matrices (MRM) (Figure 3; Appendix S8). For the functional $D_{nn'}$ ($R^2 = 0.141$, p = 0.001) and $D_{nw'}$ ($R^2 = 0.065$, p = 0.002) based on raw trait data, the results are similar (Appendix S8; Appendix S9). The explanatory power of spatial distance ($R^2 = 0.121$) in taxonomic beta diversity was higher than that of environmental distance ($R^2 = 0.094$; Figure 3). But for both phylogenetic and functional D_{nn}, metrics, environmental distance ($R^2 = 0.100$ and $R^2 = 0.112$, respectively) had a relatively higher proportion of explained variation than that of spatial distance $(R^2 = 0.085 \text{ and } R^2 = 0.085, \text{ respectively})$ (Figure 3; Appendix S8). Overall, the proportion explained by environmental variables was ranked as follows: functional $D_{pp'}$ ($R^2 = 0.121$) > phylogenetic $D_{pp'}$ $(R^2 = 0.100) >$ taxonomic beta diversity $(R^2 = 0.094)$ (Figure 3).

According to the results from the *adonis* analysis, soil pH, total N, available K, and slope had significant influences on taxonomic beta diversity (Table 4). Moreover, pH ($R^2 = 0.163$, p = 0.002), total N ($R^2 = 0.179$, p = 0.001), and available K ($R^2 = 0.078$, p = 0.023) were significantly associated with phylogenetic $D_{nn'}$ pH, total N, and slope had significant correlations with functional $D_{nn'}$ (Table 4). For functional $D_{nn'}$ metrics based on raw data, in addition to pH ($R^2 = 0.185$, p = 0.001), total N ($R^2 = 0.139$, p = 0.002), and slope ($R^2 = 0.087$, p = 0.006), available K ($R^2 = 0.075$, p = 0.014) also had significant effects (Appendix S10).

4 | DISCUSSION

Our study quantifies liana taxonomic, functional, and phylogenetic beta diversity and decomposes their variation at a local scale for



FIGURE 3 Bar chart showing variation partitioning results by analyses of multiple regressions of distance matrices. Here, functional $D_{nn'}$ and $D_{pw'}$ are calculated based on the first four PCA components of trait data [Colour figure can be viewed at wileyonlinelibrary.com]

inferring mechanisms governing liana community assembly in a dryhot valley savanna ecosystem in southwest China. We found that environmental filtering and spatial processes jointly shaped liana beta diversity in taxonomic, functional, and phylogenetic dimensions. As predicted, environmental variables had a significant influence on liana beta diversity.

We found that environmental factors, such as soil pH, total N, available K, and slope were significantly correlated with three liana beta diversities (Table 4; Appendix S10). Soil pH may modify nutrient availability of P and K by controlling their chemical forms (John et al., 2007). Slope was also correlated to total N, total P, hydrolysable N, and organic matter (Appendix S4), suggesting that slope may mediate soil nutrient availability (Weintraub et al., 2015; Chadwick & Asner, 2016). Taken together, these results imply that soil nutrients and topography (e.g. slope) are important factors driving liana community assembly in the studied savanna, in accordance with other liana studies in Amazonian rain forest (Macía et al., 2007) and tropical dry forest in Yucatan (López-Martínez et al., 2013). Besides, given the fact that slope was related to soil water availability (Balvanera et al., 2002; Rockström & de Rouw, 1997), combined with slope having a significant association with liana beta diversity, we presume water availability is an important factor affecting the liana community assemblages in this savanna, even though soil water was not directly measured in our study.

Our results showed that environmental variables had a relatively larger influence than spatial variables on functional and phylogenetic beta diversity (Figure 3; Appendix S8). We also

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	Species beta diversity		Phylogenetic Dnn'		Functional Dnn'	
Explanatory variables	R ²	Pr (>F)	R ²	Pr (>F)	R ²	Pr (>F)
pH	0.141	0.001	0.163	0.002	0.203	0.001
Total N	0.097	0.001	0.179	0.001	0.129	0.004
Total K	0.048	0.066	0.009	0.679	0.028	0.279
Available P	0.040	0.126	0.034	0.237	0.039	0.158
Available K	0.064	0.019	0.078	0.023	0.058	0.057
Altitude	0.035	0.180	0.022	0.383	0.022	0.383
Slope	0.071	0.013	0.045	0.133	0.079	0.025
Residuals	0.504		0.470		0.442	

TABLE 4 Results of permutational MANOVA (adonis) where species dissimilarity, phylogenetic D_{nn} , and functional D_{nn} , respectively based on PCA results are regressed onto environmental variables. The R^2 and Pr (>*F*) were calculated followed the method for non-parametric multivariate analysis of variance (Anderson, 2001)

Note: Bold value indicates significant variable (p < 0.05).

found the values of functional and phylogenetic beta diversity were more often to be negative in the studied savanna (Figure 2; Appendix S7), meaning that the observed functional and phylogenetic beta diversity were clustered or generally lower than expected from random assembly null model, consistent with findings that environmental filtering dominates in temperate and tropical forests (Swenson et al., 2012; Yang et al., 2015). Furthermore, the importance of environmental distance in explaining liana beta diversity decreases from functional and phylogenetic to taxonomic. These results show that functional and phylogenetic beta diversity are better at detecting the role of habitat filtering than spatial processes, which is in line with the findings of tree communities (Swenson et al., 2011, 2012; Wang et al., 2015). Habitat may serve as an ecological filter by sieving the natural histories and functional strategies of species, resulting in different habitats having biota with distinct ecological trait combinations (Lebrija-Trejos et al., 2010; Asefa et al., 2017). Based on our trait PCA results (Table 2), the first three axes represent the water conservation and nutrient use efficiency, with the fourth axis representing water transportation efficiency. Therefore, habitat filtering that selected functional traits relating to water and nutrient use efficiency is probably a main driver for liana functional and phylogenetic beta diversity in this valley savanna. This makes sense given the aridity index and soil nutrient status of the site.

In addition to the effect of habitat filtering, our study showed that spatial processes were also important in liana community assembly in this dry-hot savanna (Figure 3; Appendix S8), as is also true in other liana communities (Macía *et al.*, 2007; López-Martínez *et al.*, 2013; Murphy *et al.*, 2016; Menegat *et al.*, 2019). Moreover, we found that spatial processes explained a higher proportion of variation in the taxonomic beta diversity than environmental filtering, in contrast to the results of López-Martínez *et al.* (2013) and Menegat *et al.* (2019) in which environmental filtering was found to be more important for liana taxonomic beta diversity. Considering the sampling scale here, the possible reason could be that limited dispersal plays an important role in determining species distributions at local scales (<1 km²) (Dalling *et al.*, 2002).

The shared fraction explained by spatially structured environmental variables was 15.9%, 14.6% and 13.7% in taxonomic, functional and phylogenetic beta diversity, respectively, which is higher than that only explained by environment or space, consistent with another study (Chain-Guadarrama et al., 2012). This shared proportion is often difficult to interpret (Arellano et al., 2016b). The variation partitioning analyses showed that 62.6%, 65.7% and 67.8% variance in taxonomic, functional and phylogenetic beta diversity remained unexplained (Appendix S8). There may be three reasons for these unexplained variations. Firstly, it is argued that the MRM method may greatly underestimate the overall variance explained by the environmental and spatial variables (Legendre, 2008), although it has been widely used (Zhang et al., 2013; Song et al., 2017; Yang et al., 2015). Secondly, these unexplained components represent stochastic processes or variables not measured in the present study (De Cáceres et al., 2012; Baldeck et al., 2013). For example, soil moisture, Al, cationic exchange capacity and micronutrients are suggested to influence the plant community (Balvanera et al., 2002; Arellano et al., 2016b; Meyer et al. 2020) but were not measured in this study. In our field data collection design, we used slope as a proxy of soil moisture (Rockström & de Rouw, 1997; Balvanera et al., 2002; see Discussion above). We admit missing soil moisture and other soil variables represents a limitation of our study. Future studies incorporating these environmental variables may better explain the variance in liana beta diversity. Thirdly, we did not include any seed functional traits, which are proxy for the dispersal ability of lianas (Muller-Landau et al., 2008); future studies including seed traits should improve our understanding of the role of dispersal limitation in liana community assembly.

Our study provides vital information on mechanisms underlying savanna liana diversity maintenance, which is necessary to shed new light on liana community assembly and dynamics in these vulnerable ecosystems, and to inform conservation management. Based on our findings that taxonomic, functional and phylogenetic beta diversity in this dry-hot savanna ecosystem are affected by both environment and space, we suggest to consider both spatial and environmental variables when selecting protected areas to conserve liana diversity in terms of the three beta diversity dimensions. Menegat *et al.* (2019) compared the relative importance of environment and space on the taxonomic beta diversity of three plant functional groups in Brazilian savanna, concluding that environments play a different role in determining the taxonomic beta diversity of different plant groups. In the light of their study, we suggest testing whether the role of environment differs in determining functional and phylogenetic beta diversity between lianas and other plant groups in savanna ecosystems. Besides, more attention should be paid to liana growth form in the context of global climate change scenarios, considering our relatively limited knowledge of liana diversity maintenance and community assembly in the vulnerable savanna ecosystems.

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AUTHOR CONTRIBUTIONS

HDW and JLZ conceived and designed the study; HDW and JLZ collected the data;YBZ analysed the data and wrote the first draft of the manuscript. JY, XYS, FH and JLZ critically reviewed the manuscript. All authors contributed critically to drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data used in this study are provided in Appendices S11–S14 of the Supporting Information.

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SUPPORTING INFORMATION

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

Appendix S1. Geographic location of the study site

Appendix S2. Descriptive statistic summary of trait of 21 species Appendix S3. Measurement methods for plant traits

Appendix S4. Pearson's correlation between soil chemical properties, elevation, and slope across 30 20 m \times 20 m plots in Yuanjiang valley savanna

Appendix S5. GenBank accessions used to estimate the phylogeny of 22 focal species

Appendix S6. Consensus phylogenetic tree based on MrBayes analysis for 22 focal species

Appendix S7. Distribution of standard effective size for abundance-weighted mean pairwise functional distance and standard effective size for abundance-weighted mean nearest taxon functional distance based on raw trait data

Appendix S8. Results of multiple regression where species dissimilarity, phylogenetic $D_{nn'}$, and functional $D_{nn'}$ based on PCA and raw traits data are regressed onto spatial and environmental distance matrices

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Appendix S9. Bar chart showing variation partitioning results by analyses of multiple regressions on distance matrices (MRM). Here, functional $D_{nn'}$ and $D_{pw'}$ are calculated based on raw functional traits data

Appendix S10. Results of permutational MANOVA (adonis) where functional $D_{nn'}$ based on raw data are regressed onto environmental variables

Appendix S11. Species composition data

Appendix S12. Functional trait data

Appendix S13. Environmental variable data

Appendix S14. Spatial variable data

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