

Article

Multiple Ecological Drivers Determining Vegetation Attributes across Scales in a Mountainous Dry Valley, Southwest China

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Abstract: Identifying the ecological processes determining spatial variation in community composition and structure is a central issue in arid areas, especially in the face of climate change. This study aims to estimate how environmental and spatial processes jointly determine vegetation attributes across scales in the Min dry valley, one of the dry valleys in Hengduan Mountainous region suffering severe ecological degradation. A total of 48 plots along slope transects were investigated at three sites along the dry valley, with vegetation and environmental information gathered. Distance-based Moran's eigenvector maps (dbMEM) was used to extract local spatial variables, while geographic coordinates were used as regional spatial variables. We used redundancy analysis (RDA) and variation partitioning to detect the relative importance of environmental and spatial processes in influencing community composition and vegetation structure (including biomass, coverage, height, density, α and β diversity), and to identify the most determinant environmental variables at different spatial scales. Results showed that both environmental and spatial processes accounted for significant and comparable variations in both vegetation composition and structure. Local spatial variables provided significant and comparable contribution as regional spatial variables to vegetation composition, while provided more contribution than regional spatial variables to vegetation structure. Topography had an overriding effect relative to soil on both vegetation composition and structure. Multi-scale analyses showed elevation was the most important variable (associated with soil moisture and nutrient) at the regional scale; while microtopography, especially slope aspect and shape, dominated at the local scale. We also demonstrated how vegetation composition and structure varied along environmental gradients. The study revealed the overriding role of topography in determining vegetation attributes in this mountainous dry valley, highlighting the advantage of multi-scale spatial analysis for better understanding spatial variation in vegetation pattern and with their important implications for biodiversity conservation and ecological management in the arid mountain areas.

Keywords: community composition; vegetation structure; topography; spatial scale; mountainous arid areas

1. Introduction

Spatial variation in community composition and structure and its underlying drivers are essential issues in community ecology, as they have significant practical implications for biodiversity conservation and ecological restoration particularly in the face of climate change [1,2]. The dichotomous debate between the two main hypotheses, niche-based theory [3,4] and neutral theory [5,6], for controlling community assembly is ongoing for decades. The niche-based theory (i.e., environmental process)

suggests that species distribution and community composition are largely determined by niche-based processes, such as environmental filtering, biotic interactions, and interspecific trade-offs, while the neutral theory (i.e., spatial process) suggests that species are ecologically equivalent and community dynamics are governed by stochastic processes of dispersal, ecological drift, and speciation. Until recently a reconciliation has emerged that niche differentiation and neutral processes jointly determined community assembly [7–11]. However, their relative importance varied depending on habitats, target species groups, and scale [7,12–14]. For example, the relative importance of environmental processes for community assembly increased in harsher environment relative to benign environment [14,15]. Additionally, the spatial process contributed more to the spatial variation in composition for species with lower dispersal ability than those with higher dispersal ability [13,16]. Nevertheless, determining the relative importance of environmental and spatial processes is still of high importance for identifying the community assembly mechanism for a given natural ecosystem.

Particularly, spatial scale, defined in terms of two components: grain and extent, has an overriding influence on our perception of community assembly mechanism [17,18]. Spatial Grain is the size of sampling unit, while spatial extent describes the sampling area encompassing all the sampling units [19,20]. Generally, increasing spatial grain leads to decreased spatial variation in community composition and decreased importance of niche-based process, while increasing spatial extent leads to increased spatial variation in community composition and increased importance of niche-based process [18,21–24]. Benefitting from the advanced spatial analysis approach based on eigenfunctions of spatial distance matrix [25–27], now community ecologists can dissect the spatial variation of community structure across series scales (from broad to small scale) [22,28] and identify specific determinant factors at each spatial scale [29–31]. For example, Menezes, et al. [29] found climatic filters were most responsible at the broad scale while edaphic filters were more important at the fine scale for shaping species composition of a subtropical coastal grasslands. Therefore, current community ecology is shifting to a new era where multiple processes are operating simultaneously across multiple scales when concurrently considered [32].

In contrast to the numerous studies conducted in tropical and temperate ecosystems [12,21–24,33], studies conducted in arid ecosystem are rather few with respect to the scale-dependency of ecological drivers [34,35]. Drylands, one of the key terrestrial biomes, covering 41% of earth's terrestrial area with more than 38% of the human population [36], provide important ecological services and are among the most sensitive ecosystems to climate change [37,38]. They are mainly constrained by resource limitation, especially water and nutrient insufficiency, with numerous studies reporting significant response of species distribution and vegetation structure to environmental heterogeneity, especially soil and topography [39–42]. However, the paucity of studies examining the effect of spatial scale on the community structure and diversity pattern, have undermined our understanding of community assembly especially when the arid area is combined with strong substrate complexity (but see Pashirzad, et al. [34] and Smith and Stark [35]). Therefore, in this study, taking the spatial variables into account, we investigated how multiple ecological determinants operating across different spatial scales can influence species distribution and community structure in arid ecosystem.

The dry valleys of the Hengduan Mountains region, southwest China, are a striking geographical landscape, widely distribute in the main rivers and their tributaries in this region, notably along the upper Yangtze (Jinsha), Dadu, Yalong, Min, Lancang (Mekong), Nu (Salween), and Yuan (Red) and their tributaries [43]. With much less rainfall, higher temperature and evaporation comparing to their neighboring areas, these dry valleys are among the most fragile and degraded ecosystems in Southwest China. The dry valley in the upper reaches of Min River, the first-order branch of the Yangtze River, is one of these dry valleys, located on the transition zone from the Tibetan Plateau to the Sichuan Basin (30°44'–32°24' N, 102°41'–103°58' E) [43]. The high mountain-deep valley featured topography not only results in the strong foehn effect (which gives rise to arid local climate) [43], but also leads to high spatial variation in vegetation composition through the complex substrate heterogeneity [44], making it a perfect arid ecosystem to studying the underlying processes and factors controlling community

assembly in arid areas. Moreover, previous studies used soil property as environmental predictors for vegetation distribution [45–47]. However, they ignored that topography has critical effect on soil and vegetation development in arid mountainous area [42]. Thus, in the present study topography will be considered in addition to soil properties.

This study aimed to estimate how environmental and spatial processes jointly influence the variation in community composition, as well as vegetation structure (i.e., biomass, height, coverage, density, and diversity) which fundamentally determines the ecological function [48], in the dry valley of the upper reach of Min River. Given the significant role of topography in mountainous arid area [42], this study takes topography into consideration to account for variation in vegetation pattern. Meanwhile, benefitting from multiscale spatial analysis advanced methodology [32], we detected the spatial variation at different spatial scales (here, in terms of spatial extent). Consequently, we divide environmental variables into soil and topography subsets, and spatial processes into regional (i.e., the whole valley) and local (i.e., sampling site) scales. We addressed several questions: (1) What is the relative importance of environmental and spatial processes, of topography and soil property and of regional and local spatial processes, in explaining the variation in vegetation composition and structure? (2) Which environmental variables are most relevant in controlling the observed patterns of vegetation composition and structure at different scales? (3) How do the vegetation composition and structure vary along environmental gradients?

2. Method

2.1. Study Area

The study area is located in the central part of the dry-warm valley in the upper reaches of the Min River (alt. 1300–2200 m; lat. 30°44′–32°24′ N; long. 102°41′–103°58′ E), covering the Wenchuan, Maoxian, and Lixian counties in Sichuan province, Southeast China. It has mean annual temperature of 11.2–12.9 °C mean annual precipitation of 409–462 mm (with 70–80% occurring throughout May–October), and mean annual evaporation of 1300–1800 mm [49]. Typically, the shallow cinnamon soil (10–30 cm) has a clay loam with coarse texture and low fertility with phyllite parent material [43]. This area had history of a drastic anthropogenic activities, especially deforestation, which has taken place for at least a thousand years and greatly intensified during the last century, resulting in severe forest degradation and consequent soil and water erosion as well as mountain hazards [43]. Vegetation belongs to winter drought scrubs mainly consisting of small-leaf arid shrubs [50] and distributed in a mosaic of vegetated patches, isolated plants and bare surfaces. It is dominated by drought-tolerant shrub species, such as *Sophora davidii* (Franch.) Skeels, *Bauhinia brachycarpa* var. *microphylla* (Oliv. ex Craib) K. et S. S. Larsen, and *Indigofera bungeana* Walp. accompanied by herbaceous species, such as *Ajania breviloba* (Franch. ex Hand.-Mazz.) Ling et Shih, *Sedum wenchuanense* S. H. Fu, and *Heteropogon contortus* (L.) P. Beauv. ex Roem. et Schult. [43].

2.2. Data Collection

This study is based on field investigation dataset collected during August 2006 in the central part of the Min River dry valley. Three sites were selected along the dry valley representing different vegetation types: Shidaguan at the upper end is dominated by short dry shrubs and grasses on both the north and south-facing slope; Feihong at the middle mainly consisting of sparse dry dwarf shrubs on north-facing slopes and sparse grasses on south-facing slopes; and Wenchuan at the southern end has some small trees growing on the north-facing slopes and only sparse shrubs on the south-facing slopes (Figure 1 and Table 1). At each site, forming a “V” shape, two transects were set along north- and south-facing slopes. Sample plots of 5 × 5 m² were set up along the transects at altitude intervals of about 20 m. In each plot, all woody species were identified and measured of abundance, coverage (%), and height (cm). The importance value (I.V.) of each species was calculated as sum of the relative

abundance, coverage and height of each species. A total of 48 plots formed the study dataset. Species nomenclature followed the Flora of China (<http://foc.efora.cn/>).

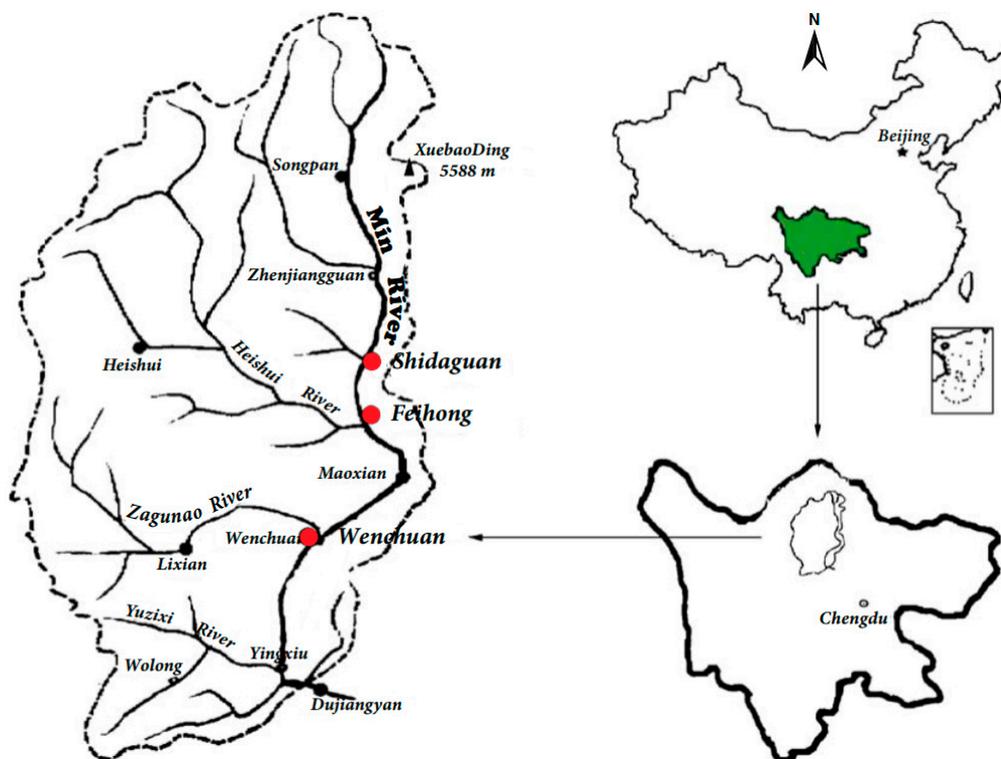


Figure 1. Location of sampling sites along the dry valley in the upper reaches of Min River (modified from Lu, et al. [47]).

Table 1. Brief description of the study sites.

Site	Latitude	Longitude	Elevation (m)	Temperature (°C)	N ¹
Shidaguan	31.8980°	103.6962°	2027	8.7	23
Feihong	31.7993°	103.7394°	1853	11.9	12
Wenchuan	31.4698°	103.5756°	1433	13.5	13

¹ N: number of sampling plots.

For each sampling plot, a total of 11 environmental variables were measured including topographical characteristics: elevation (ele- m), slope degree (deg-°), shape (shp- concave, flat or convex), position (pos- upper, middle or bottom of the slope) and aspect (asp- north or south-facing slope), and edaphic properties: soil moisture (SM-%), organic content (ORG-%), available nitrogen (NA- mg·kg⁻¹), available potassium (KA- mg·kg⁻¹), available phosphorus (PA- mg·kg⁻¹), and pH. The elevation and slope degree were measured using an altitude meter and a clinometer, respectively. Within each sampling plot, soil moisture content was measured from the surface soil (0–15 cm) at nine points using a portable Time Domain Reflectometry (TDR) [47]. Given the temporal variation in SM after rainfall event, the measurement was conducted on sunny days within a two-week period (at least three days after the latest rainfall event). For soil chemical analyses, soil samples (0–15 cm) were collected using cores (5 cm diameter) from five random soil profiles of each plot, air-dried, thoroughly mixed and passed through a 2 mm sieve to remove gravel and debris. Laboratory analyses of soil chemical properties followed Lu, et al. [47]. Geographical coordinates (longitude and latitude degree) were recorded for each plot and converted into Universal Transverse Mercator's (UTM) coordinates.

2.3. Vegetation Structure Metrics

Woody species biomass ($\text{Mg}\cdot\text{ha}^{-1}$), coverage (%), density, and average height (cm) were estimated for all sampling plots. For each species, aboveground biomass of 3–5 standard individuals were harvested, oven-dried at 80 °C until all the water was evaporated, and the dry mass were weighted, then an average value was calculated to represent the species biomass expectation. The biomass of each plot was estimated by the sum of biomass of all constituent species weighted by their relative abundance. Coverage (%) was the visual estimate of percentage canopy cover of each sampling plot. Density was the total number of individual woody plants per plot. Plot average height (height) was the mean species height weighted by their relative abundances.

Three α diversity (species richness (S), Fisher's α diversity, and Simpson index) and three β diversity metrics (Sorensen, Bray-Curtis, and Chao) were estimated for all sampling plots. Species richness (S) was estimated based on presence data. Fisher's α diversity and Simpson index were estimated based on abundance data [51]. Fisher's α is a parameter of Fisher's log series model [52], which has been recommended as a sample-size-independent estimator of richness predicting the number of species represented by a single individual [51]. For Simpson index, $D_{\text{Simpson}} = 1 / \sum_1^S p_i^2$, where S is the number of species, p_i is the proportion of individuals found in the i th species ($p_i = n_i/N$), n_i is the number of individuals of species i in the sample, and N is the total number of individuals sampled. β diversity was estimated at the local (plot) level by calculating the average pairwise dissimilarity between the focal plot and all the other plots within the same transect; this estimate is a variation of β diversity measurement of grid system [53] in accord with the sampling design in the present study and allows to be used by classical statistic method. The pairwise dissimilarity was calculated using Sorensen, Bray-Curtis, and Chao indices, respectively. Sorensen [54] is one of the most widely used incidence-type indices derived from three components: the number of species shared by two assemblages and the number of species unique to each. Bray-Curtis [55] is a modified version of the Sorensen index and is based on abundance data. Chao [56] is an abundance-based index taking into account the number of unseen species pairs to adjust for under-sampling bias. All the metrics were calculated using R package "vegan" [57].

2.4. Spatial Variables

Based on the sampling design, we considered and developed two groups of spatial variables representing spatial variation at regional (i.e., the whole valley) and local (i.e., the sampling site) scales. We used geographic coordinates (X and Y of UTM coordinates) of sampling sites as spatial variables to capture the global trend at regional scale, which is usually used to detect the linear trend at broad scale. We used distance-based Moran's eigenvector maps (dbMEM) [27] to generate spatial variables at local scale, which can be directly used as explanatory variables in regression or canonical analysis models. In brief, the dbMEM method builds pairwise geographical distance matrix among sampling plots, which is truncated at the smallest distance that keeps all points connected in a single network. Then, a principal coordinate analysis (PCoA) is carried out and the eigenvectors associated with positive eigenvalues are retained as spatial variables which are independent and could model spatial structure from broad to fine scales. Following the procedure of Declerck, et al. [58], we built dbMEM variables for each spatial cluster (i.e., sampling site; Figure 1) independently and assembled them into a staggered matrix, arranging dbMEM variables in blocks corresponding to each site. Within these blocks, plots from the other site were assigned the value zero [58]. Seven eigenvectors with positive eigenvalues were obtained representing structures of all relevant scales and used as potential spatial variables (hereafter, dbMEM variables) in canonical ordination. The `create.dbMEM.model` function of R package "adespatial" [59] was used to constructs the combined staggered matrix of dbMEM spatial eigenvectors.

2.5. Data Analysis

Redundancy analysis (RDA) [60] was used to identify the processes and variables controlling community composition and vegetation structure pattern. For community composition, the response data was species composition based on the species important value (IV), while for vegetation structure, the response data were structure variables including biomass, height, coverage, density, and α and β diversity metrics. Explanatory variables included environmental and spatial variables.

We separated environmental variables into soil and topography, and spatial variables into X-Y coordinates and dbMEM variables, for four explanatory subsets. In order to select only the most important factors for the parsimonious model, forward selection [61] was independently conducted on soil, topography and dbMEM variables, based on significant level α and R^2_{adj} of the global model. Specifically, the forward-selection of environmental variables (soil and topography subsets separately) was run on the undetrended response variables, while the selection of the dbMEM variables was run on the response variables that have been detrended by the X-Y coordinates (if the trend was significant) [62]. After variable selection, collinearity among selected variables was tested by variance inflation factor (VIF) and variable was removed if $VIF > 10$. Consequently, the selected environmental variables were used to compose the final explanatory subsets-soil and topography, and the selected dbMEM variables composed the final local spatial subset. Further, soil and topography together composed final environmental subset, while X-Y coordinates and dbMEM subset composed the final spatial subset. The above procedure was conducted for community composition and vegetation structure, respectively. Then, to estimate the relative contribution of each explanatory subset to the variation in community composition and vegetation structure, RDA and variation partitioning [63,64] were implemented based on both two and four explanatory subsets, respectively. Global and unique explanation of each explanatory subset was estimated, and the significance test was conducted by permutation test with 999 runs. Finally, to demonstrate how vegetation attributes varied along environmental gradient, RDA was conducted only on environmental variables for community composition and vegetation structure, respectively, and the ordination diagram along the first several canonical axes were visualized.

To identify the most relevant environmental variables at different spatial scales, first, we conducted RDA of community composition and vegetation structure only on spatial variables at regional and local scales, respectively. Then, for each spatial scale, we conducted RDA of the fitted canonical values of community composition and vegetation structure on environmental variables, respectively, followed by forward selection procedure as above. At last, ANOVA was used to each final RDA model to examine the significance of each environmental variable for each scale.

Prior to RDA, different data transformations were conducted on the two response datasets, community composition and vegetation structure. Species important value (IV) in the community composition analysis were Hellinger transformed [65], which preserves the Hellinger distance among sites and is appropriate for community composition data. Only the most abundant species with occurrence frequency $> 5\%$ (i.e., occupation > 2 plots), total of 32 species, were used in the analysis of community composition to remove the noise effect. All numerical environmental and vegetation structure variables were standardized to zero mean and unit variance prior to data analysis.

All statistical analyses were performed in R v3.3.5 [66], using the `rda`, `varpart` and `ordiR2step` functions of the package “vegan” [57], the `forward.sel` function of the package “adespatial” [59].

3. Results

A total of 52 woody species belonging to 34 genera and 19 families were recorded, among which Fabaceae was the largest family represented with 12 species accounting for 24% of total species.

3.1. Community Composition

For community composition, soil variables (SM, ORG, PA, and KA) and all topography variables (asp, ele, deg, shp, and pos) were forward selected in the final redundancy analysis (RDA) model. As for spatial variables, forward selection retained geographic coordinates (i.e., X and Y) and local spatial variables, dbMEM1, 2 and 6 (corresponding to Shidaguan, Feihong, and Wenchuan, respectively) in the final model. Collectively, environmental and spatial processes explained 61% of total variation (Table 2). Partial RDA showed significant partial contribution of each of the environmental and spatial subsets ($p < 0.001$, Table 2), as well as each of the four explanatory subsets to the composition variation after controlling for the other three explanatory subsets ($p < 0.001$ or $p = 0.004$, Table 2).

Table 2. Results of redundancy analysis (RDA) and variation partitioning of community composition and vegetation structure based on two and four explanatory subsets. (topo, topography; env, environmental process; spa, spatial process; XY, geographic coordinates; dbMEM, dbMEM variables).

	Community Composition				Vegetation Structure			
	R^2_{adj}	Df	F	p	R^2_{adj}	Df	F	p
Total	0.610	16	5.596	0.001	0.727	15	9.357	0.001
Based on Four Subsets								
soil	0.254	4	5.001	0.001	0.336	4	6.941	0.001
soil/(topo+XY+dbMEM)	0.028	4	1.625	0.004	0.012 ^{NS}	4	1.411	0.096
topo	0.403	7	5.529	0.001	0.498	5	10.320	0.001
topo/(soil+XY+dbMEM)	0.108	7	2.502	0.001	0.076	5	3.053	0.001
XY	0.208	2	7.185	0.001	0.218	2	7.535	0.001
XY/(soil+topo+dbMEM)	0.062	2	3.611	0.001	0.081	2	6.047	0.001
dbMEM	0.184	3	6.410	0.001	0.361	4	7.639	0.001
dbMEM/(soil+topo+XY)	0.068	3	2.990	0.001	0.099	4	4.252	0.001
Based on Two Subsets								
env	0.476	11	4.880	0.001	0.559	9	7.610	0.001
env/spa	0.190	11	2.857	0.001	0.144	9	3.411	0.001
spa	0.420	5	7.817	0.001	0.583	6	11.951	0.001
spa/env	0.134	5	3.477	0.001	0.169	6	4.918	0.001

NS, non-significant.

The results of variation partitioning are presented in Table 2 and Figure 2a. Environmental and spatial subsets contributed comparable explanation to community composition, accounting for 48 and 42% of the total variation respectively; moreover, 60% of environmental explanation was spatially structured, and 68% of spatial explanation was environmentally controlled. Further variation partitioning of environmental subset showed topography played dominate role in controlling community composition: topography subset explained 40% of the total variation with a uniquely explained amount of 22% after controlling for the co-occurring fraction with soil subset (i.e., overlap fraction), while soil subset explained 25% of the total variation with a unique explained amount of 7%. In contrast, geographic coordinates (accounting for 21% of the variation) and dbMEM variables (accounting for 18% of the total variation) provided comparable explanation to total variation (Table 2, Figure 2a), indicating both regional and local spatial processes strongly influencing community composition.

The identification of most relevant environmental variables influencing community composition at different spatial scales is presented in Table 3. At the regional scale, ele, SM, shp, ORG, and KA were identified as the significant environmental variables controlling community composition, among which elevation provided the highest unique explanation (almost three times more than the second one (shp or ORG)) (Table 3), indicating its dominant effect on specie distribution. At local scale, asp, shp, deg, and pos were the significant environmental variables. Aspect and shape had much more explanation than slope degree and position (Table 3), indicating their dominant roles at the local scale.

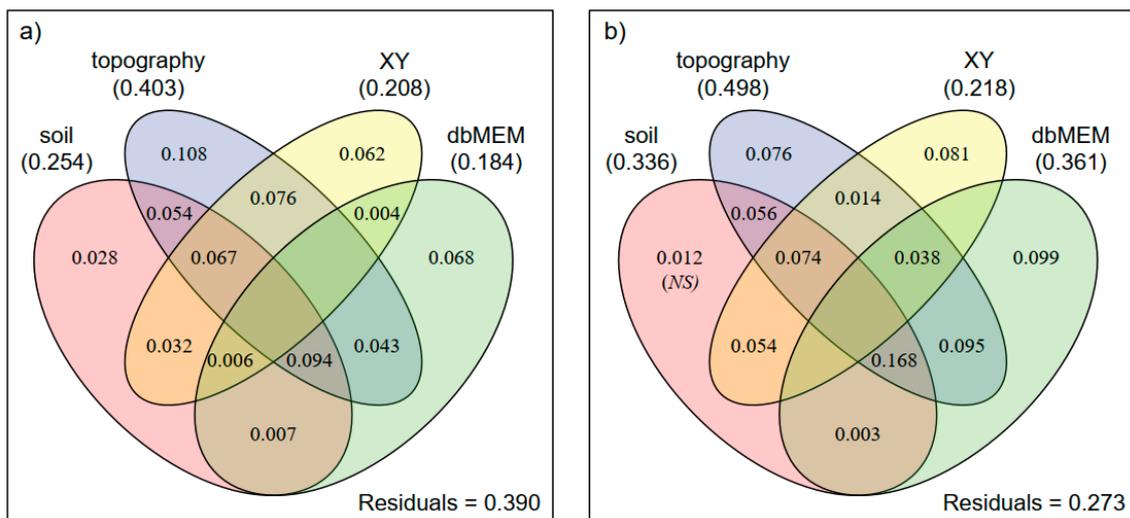


Figure 2. Variation partitioning for (a) community composition and (b) vegetation structure based on soil, topography, regional (XY), and local (dbMEM) spatial processes. (Non-significant: NS; Numbers in brackets are R^2_{adj} explained by the specific processes).

Table 3. Result of scale-specific identification of relevant environmental variables based on ANOVA test of redundancy analysis model.

		Community Composition				Vegetation Structure			
		Df	Variance	F	Pr (>F)	Df	Variance	F	Pr (>F)
Regional scale	ele	1	0.041	47.956	0.001	1	0.185	39.876	0.001
	shp	2	0.013	8.093	0.001	2	0.068	7.378	0.001
	SM	1	0.009	11.421	0.001	1	0.054	11.558	0.001
	ORG	1	0.013	14.784	0.001	1	0.071	15.195	0.001
	KA	1	0.005	5.993	0.002	1	0.026	5.705	0.006
	Residual	41	0.035			41	0.19		
		Df	Variance	F	Pr (>F)	Df	Variance	F	Pr (>F)
Local scale	ele	—	—	—	—	1	0.021	3.81	0.029
	asp	1	0.044	20.781	0.001	1	0.252	44.826	0.001
	shp	2	0.043	10.374	0.001	2	0.254	22.568	0.001
	deg	1	0.011	5.341	0.002	1	0.055	9.772	0.001
	pos	2	0.01	2.368	0.023	—	—	—	—
	Residual	41	0.086			42	0.236		

Redundancy analysis (RDA) of community composition in environmental space results are presented in Table 4. The first five significant canonical axes accounted for 87% of the explained variation, and the intra-set correlations showed larger magnitudes with topographic variables (asp, shp, ele, and deg) indicating the dominant role of topography in determining species distribution (Table 4). The ordination diagrams along the first four canonical axes were illustrated in Figure 3. Axis 1 and 2 combined accounted for 23% of the total variation. Axis 1 was mostly correlated with asp ($r = 0.865$), followed by KA ($r = -0.686$) and shp ($r = 0.567$) (Table 4); it well separated the sampling plots from north and south aspect which located on the left and right side of the axis, respectively (Figure 3). Species found on north aspect included *Quercus baronii* Skan, *Lespedeza thunbergii* (DC.) Nakan, *Cotinus coggygia* Scop., and *Jasminum humile* L., while species occurred at south aspect included *Caryopteris bicolor* (Roxb. ex Hardw.) Mabb., *Caryopteris terniflora* Maxim., *Sophora davidii*, *Bauhinia brachycarpa* var. *microphylla*, *Indigofera bungeana*, and *Lespedeza virgata* (Thunb.) DC.. Axis 2 was strongly correlated with ele ($r = 0.663$), shp ($r = 0.551$) and PA ($r = 0.547$) (Table 4). Generally, sampling plots were well positioned along the elevation gradient, and some species occurred at lower elevations such as *Leptodermis purdomii* Hutchins., *Desmodium elegans* DC., and *Pertya sinensis* Oliv., while some

at higher elevations such as *Quercus baronii* and *Caryopteris glutinosa* Rehd. (Figure 3). Axis 3 and 4 accounted for 13% of total variation (Table 4). Axis 3 was highly correlated with shp ($r = 0.721$) and SM ($r = 0.708$), while axis 4 was mostly correlated with shp ($r = 0.544$) and deg ($r = 0.438$). Species *Ajanía nubigena* (Wall.) Shih, *Caryopteris bicolor*, *Indigofera amblyantha* Craib, and *Leptodermis purdomii* were at convex slopes with low soil moisture (Table 4), while *Quercus baronii* and *Caryopteris glutinosa* occurred at concave slopes.

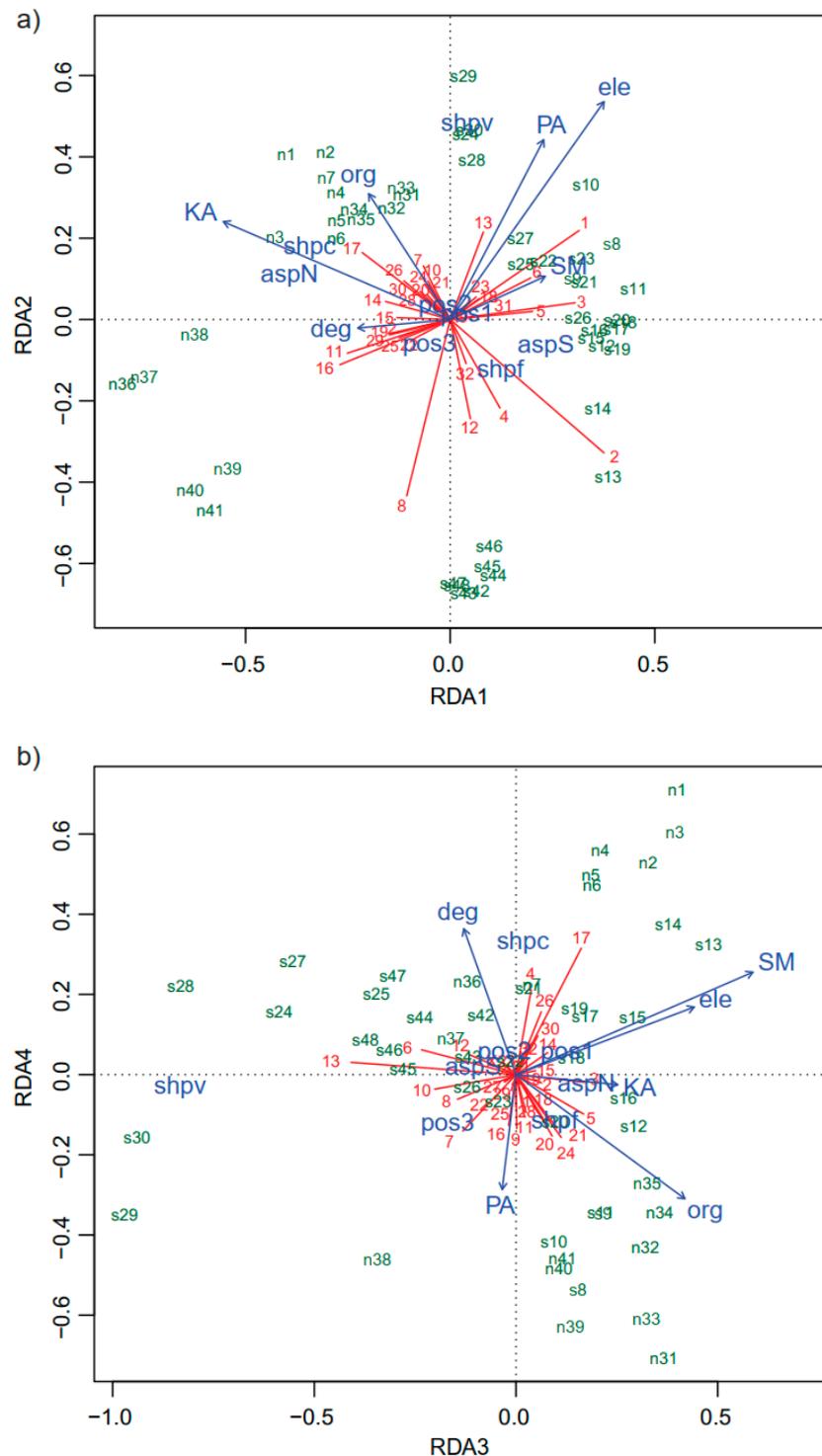


Figure 3. Redundancy analysis (RDA) of community composition on environmental variables on the first four canonical axes: (a) axis1 and 2, (b) axis 3 and 4. (ORG, organic matter; SM, soil moisture; PA,

available phosphorous; KA, available potassium; ele, elevation; aspN/S, north/south aspect; shpc/f/v, shape concave/flat/convex; deg, slope degree; pos1/2/3, position up/middle/down. Site code ni and si indicate plot is on north and south aspect respectively. Species code: 1, *Onosma sinicum* Diels; 2, *Caryopteris terniflora* Maxim.; 3, *Sophora davidii* (Franch.) Skeels; 4, *Bauhinia brachycarpa* var. *microphylla* (Oliv. ex Craib) K. et S. S. Larsen; 5, *Indigofera bungeana* Walp.; 6, *Caryopteris bicolor* (Roxb. ex Hardw.) Mabb.; 7, *Caryopteris forrestii* Diels; 8, *Leptodermis purdomii* Hutchins.; 9, *Daphne tangutica* Maxim.; 10, *Indigofera amblyantha* Craib; 11, *Jasminum humile* L.; 12, *Lespedeza virgata* (Thunb.) DC.; 13, *Ajania nubigena* (Wall.) Shih; 14, *Lespedeza thunbergii* (DC.) Nakai; 15, *Cotinus coggygria* Scop.; 16, *Pertya sinensis* Oliv.; 17, *Quercus baronii* Skan; 18, *Rosa hugonis* Hemsl.; 19, *Zanthoxylum simulans* Hance; 20, *Campylotropis macrocarpa* (Bge.) Rehd.; 21, *Daphne penicillata* Rehd.; 22, *Desmodium elegans* DC.; 23, *Lespedeza floribunda* Bunge; 24, *Spiraea henryi* Hemsl.; 25, *Berberis sargentiana* Schneid.; 26, *Caryopteris glutinosa* Rehd.; 27, *Lonicera japonica* Thunb.; 28, *Sageretia pycnophylla* Schneid.; 29, *Spiraea salicifolia* L.; 30, *Bauhinia brachycarpa* Wall. ex Benth.; 31, *Krascheninnikovia ceratoides* (L.) Gueldenst.; 32, *Daphne modesta* Rehd.

3.2. Vegetation Structure

The relationships among vegetation structure metrics showed biomass, height, coverage were significantly correlated (except for $r_{\beta.cover} = 0.100$, $p = 0.500$, Table 5), and all had no significant correlation with density (Table 5). The α diversity metrics had no significant correlation with β diversity, biomass, height and coverage, except for a weak correlation between richness and coverage ($r_{S.cover} = 0.354$, $p < 0.05$, Table 5). The β diversity metrics had significant correlations with biomass and height (except for $r_{Bray-Curtis.biomass} = 0.147$, $p = 0.317$, Table 5). Density had significant negative correlation with all α diversity metrics (except for $r_{richness.density} = -0.152$, $p = 0.301$) and β diversity metrics (except for $r_{Sorensen.density} = -0.152$, $p = 0.304$) (Table 5).

For vegetation structure, soil variables, ORG, KA, PA, and SM, and all topography variables except for position were forward selected in the final RDA model. Geographic coordinates (X and Y), and local spatial variables, dbMEM1, 2, 6 and 7 (corresponding to Shidaguan, Feihong, and Wenchuan respectively) were selected in model of vegetation structure. Together, the environmental and spatial variables explained 73% of total variation (Table 2). Partial RDA showed significant contribution of each of environmental and spatial process to vegetation structure ($p < 0.001$, Table 2); it also showed significant partial effect of all the four explanatory subsets except for soil subset ($R^2_{adj} = 0.012$, $p = 0.096$) on vegetation structure after controlling for the other three explanatory subsets (Table 2).

The results of variation partitioning are presented in Table 2 and Figure 2b where environmental and spatial subsets contributed comparable explanation to vegetation structure, accounting for 56 and 58% of the total variation respectively; moreover, 74% of environmental explanation was spatially structured, and 71% of spatial explanation was environmentally controlled. Further variation partitioning of environmental subset showed topography played a dominate role in controlling vegetation structure: topography subset explained 50% of the total variation with a uniquely explained amount of 22% after controlling for the co-explained fraction with soil subset, while soil subset explained 33% of the total variation with a unique explained amount of 6%. Comparison between geographic coordinates (X and Y) and local spatial variables (dbMEM variables) indicated both provided significant unique explanations to the final model ($p < 0.001$, Table 2), and local spatial variables provided almost half (66%) more explanation than regional spatial subset ($R^2_{adj.XY} = 0.218$, $R^2_{adj.dbMEM} = 0.361$, Table 2). See Figure 2b for variation partitioning based on the four explanatory subsets.

The identification of determinant environmental variables in controlling vegetation structure at different spatial scales showed almost the same result as that of community composition, except for elevation instead of position which was found to be the significant variables at local scale (Table 3). Similarly, elevation was found the most explanatory variable at regional scale, while aspect and shape dominated at local scale (Table 3).

Table 4. Result of RDA of community composition and vegetation structure on environmental variables.

	Community Composition					Vegetation Structure			
	RDA1	RDA2	RDA3	RDA4	RDA5	RDA1	RDA2	RDA3	RDA4
Eigenvalue	0.121	0.096	0.069	0.056	0.043	3.053	1.844	0.879	0.454
Variation explained	0.129	0.102	0.074	0.060	0.046	0.265	0.160	0.076	0.039
Cumulative variation explained	0.129	0.232	0.305	0.366	0.412	0.265	0.425	0.502	0.541
Intra-set correlation coefficient									
Organic matter (ORG)	−0.246	0.383 **	0.505 ***	−0.373 **	−0.438 **	−0.563 ***	−0.372 **	−0.343 *	0.619 ***
Available phosphorus (PA)	0.283	0.547 ***	−0.041	−0.345 *	0.229	−0.028	0.195	−0.382 **	0.249
Available potassium (KA)	−0.686 ***	0.298 *	0.304 *	−0.030	0.171	−0.739 ***	−0.230	−0.407 **	−0.155
Soil moisture (SM)	0.287 *	0.131	0.708 ***	0.308 *	0.246	−0.504 ***	0.197	0.522 ***	0.138
Elevation (ele)	0.465 ***	0.663 ***	0.533 ***	0.203	0.090	−0.436 **	0.348 *	0.216	0.383 **
Degree (deg)	−0.280	−0.026	−0.156	0.438 **	−0.566 ***	−0.215	0.466 ***	−0.144	0.242
Aspect (asp)	0.865 ***	0.239	0.388 **	0.059	0.140	0.790 ***	0.323 *	0.380 **	0.114
Shape (shp)	0.567 ***	0.551 ***	0.721 ***	0.544 ***	0.166	0.651 ***	0.559 ***	0.735 ***	0.404 *
Position (pos)	0.106	0.109	0.336	0.207	0.281	—	—	—	—

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table 5. Correlations among vegetation structure variables. p -value of significance test Pearson correlation coefficients are listed above and below diagonal, respectively.

	Biomass	Cover	Height	Density	S	Fisher	Simpson	Sorenson	Bray-Curtis	Chao
Biomass		0.009	0.000	0.597	0.245	0.644	0.191	0.000	0.317	0.028
Cover	0.371 **		0.023	0.250	0.014	0.067	0.195	0.500	0.847	0.176
Height	0.736 ***	0.327 *		0.239	0.697	0.698	0.856	0.000	0.001	0.000
Density	0.078	0.169	−0.173		0.301	0.000	0.021	0.304	0.000	0.000
S	−0.171	0.354 *	0.058	−0.152		0.000	0.000	0.334	0.993	0.611
Fisher	−0.068	0.267	0.058	−0.515 ***	0.664 ***		0.000	0.087	0.519	0.499
Simpson	−0.192	0.190	0.027	−0.332 *	0.774 ***	0.772 ***		0.196	0.884	0.539
Sorenson	0.489 ***	0.100	0.730 ***	−0.152	−0.142	−0.250	−0.190		0.000	0.000
Bray-Curtis	0.147	−0.029	0.463 ***	−0.583 ***	−0.001	0.095	0.022	0.707 ***		0.000
Chao	0.317	0.199	0.624 ***	−0.486 ***	0.075	0.100	0.091	0.835 ***	0.881 ***	

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Redundancy analysis (RDA) of vegetation structure in environmental space results are presented in Table 4. The first four significant canonical axes explained 54% of the total variation and the intra-set correlations showed larger magnitudes with topographic variables indicating the dominant role of topography in determining vegetation structure (Table 4). The ordination diagram along the first two axes (accounting for 43% of the total variation, Table 4) was illustrated in Figure 4, which showed different patterns of vegetation structure variables along the environmental gradients. Axis 1 was strongly correlated with asp ($r = 0.790$), KA ($r = -0.739$), shp ($r = 0.651$) and ORG ($r = -0.563$); the sampling plots were well separated by aspect (Figure 4), and all biomass, height, coverage, β and α diversity were generally higher at the north aspect which was associated with higher ORG and KA. Axis 2 was significantly correlated with all topographic variables, ele ($r = 0.348$), deg ($r = 0.466$), asp ($r = 0.323$) and shp ($r = 0.559$), and soil ORG ($r = -0.372$) (Table 4); α diversity metrics were negatively correlated with degree and elevation, and high at flat shape (Figure 4). Strikingly, high density occurred at convex slope and south aspect (especially plot s24–30, Figure 4).

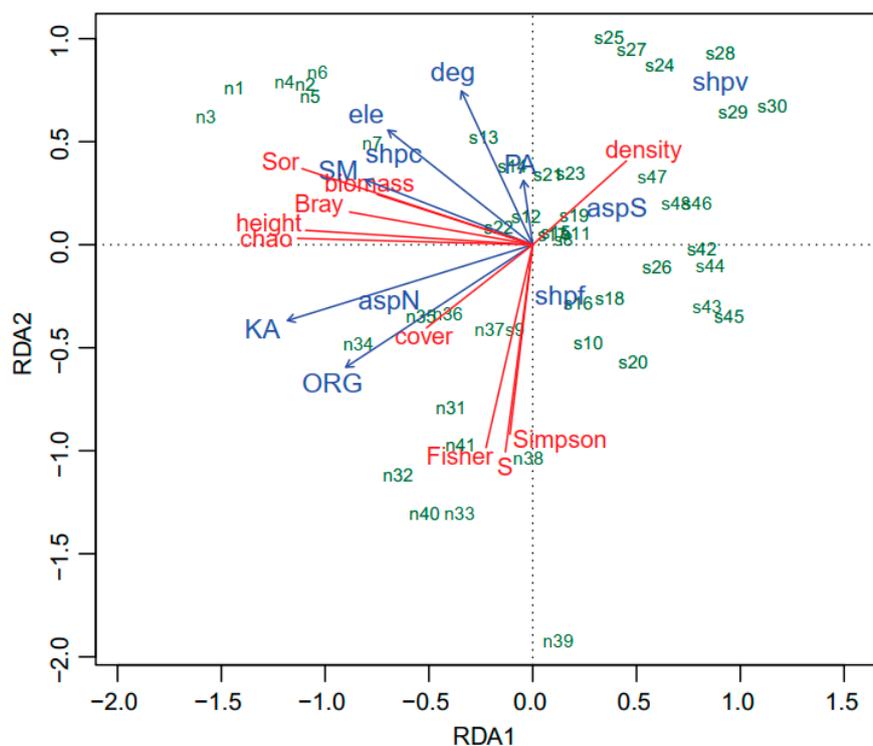


Figure 4. Redundancy analysis (RDA) of vegetation structure on environmental variables on the first two canonical axes. (Sor, Sorensen; Bray, Bray-Curtis; ORG, organic matter; PA, available phosphorous; KA, available potassium; ele, elevation; aspN/S, north/south aspect; shpc/f/v, shape concave/flat/convex; deg, slope degree).

4. Discussion

We found significant contributions of both environmental and spatial processes in driving the vegetation composition and structure in the dry valley of Min River. Specifically, topography was found to be imposing dominant environmental constraints over soil property on vegetation attributes, with elevation dominating at the regional scale while microtopography dominating at the local scale. We also demonstrated how vegetation composition and structure varied along environmental gradients.

Both environmental and spatial processes showed significant and comparable explanation for community composition (Table 2), supporting the current hypothesis that niche-based and neutral processes jointly determine community assembly [9]. Additionally, we determined that topography played a dominant role over soil in environmental explanation of community composition (Table 2).

These findings are consistent with other studies revealing the determinant effect of topography on vegetation [41,67,68], but inconsistent with studies that showed soil property mostly determined vegetation pattern [40,45,69]. Besides the different natures of the ecosystems studied, the observed inconsistency could also result from the lack of standardized sampling protocol, different environmental variables selection, and different analytical methods used across these studies. Nevertheless, we would interpret our result based on the mechanism of how topography influences vegetation. In fact, topography is a proxy of environmental gradients which indirectly influence vegetation through its modification of the local environment such as microclimate and soil property [70–73]. This could be seen by the result of variation partitioning between soil and topography subsets- the large overlap fraction (45% of topography and 71% of soil explanation) could reflect the strong topographic effect on soil property. For example, Xu, et al. [45] and Ma, et al. [46] found soil moisture was strongly determined by topographic variables in the same studied dry valley. On the other hand, the solely topographic explanation could reflect a topography-induced microclimate other than soil property such as air temperature and humidity which directly influence plant growth [70,71,74].

In the present study, all topography variables measured were included in final parsimonious model, indicating they all significantly contributed to the formation of various microhabitats occupied by different species. Specifically, elevation was identified to be dominant at the regional scale while aspect and shape dominated at the local scale. At the whole dry valley, elevation spanned 800 m from the lowest Wenchuan to the highest Shidaguan, causing local climate variation with decreased aridity and temperature [75] and also accompanied with increased soil moisture and nutrient (Figure 3). Species distribution showed that *Quercus baronii* and *Caryopteris glutinosa* occurred at high elevation while *Leptodermis purdomii*, *Desmodium elegans*, and *Pertya sinensis* at low elevation. At the local scale, we found microtopography, with aspect and shape as dominant variables, determined community composition (Table 3). Different solar radiation received resulted in creating different microclimate and soil properties between north and south aspects, which, in turn, are occupied by distinct vegetation types [76,77]. Generally, the south aspect is hotter and dryer and occupied by xeric species while the north aspect is cooler and moisture and associated with mesic species [78,79]. In our study, the result of RDA showed clear separation of sampling plots between north and south aspects (Figure 3a), indicating significantly distinct species composition. For example, *Quercus baronii*, *Lespedeza thunbergii*, *Cotinus coggygria*, and *Jasminum humile* mostly occurred on north aspect while *Caryopteris bicolor*, *Caryopteris terniflora*, *Sophora davidii*, *Bauhinia brachycarpa* var. *microphylla*, *Indigofera bungeana*, and *Lespedeza virgata* mainly occurred on south aspect. Similar pattern was widely found in semiarid areas demonstrating coexistence of distinct aspect-delimited ecosystems in very close proximity [78,79]. Slope shape as well as position and degree could influence soil property through the change of sediment movement and water condition [80]. For example, we found lowest and highest soil moisture at convex and concave configurations respectively (result not shown), which was consistent with previous studies [81]. Specifically, abundant *Ajania nubigena* was found occupying the convex slope at Feihong's south aspect (the harshest habitat), which is the dominant species as it is resistant to extreme drought and soil leanness and also is a soil-conserving species suitable for eco-restoration [82,83]. Overall, topographic variables were dominant influences at both regional and local scales for species distribution and community composition through modification of local climate (e.g., aridity condition) and amelioration of the environmental harshness, and consequently increased floristic heterogeneity.

Environmental processes also significantly explained vegetation structure variation with topography providing much higher explanation than soil properties (Table 2, Figure 2b). It is interesting that we found the same scale-specific environmental determinants of vegetation structure as that of community composition: elevation (dominant variable) associated with soil moisture and nutrient at regional scale, and microtopography (aspect and shape as dominant variables) at local scale (Table 3). Specifically, different vegetation structure metrics showed different responses to environmental gradients. High biomass, coverage and height occurred at high elevation, north aspect, and concave configuration, all of which were modest habitats associated with high soil moisture and nutrient

availability. This pattern was also found in previous studies in Min dry valley and congruent with the pattern of semiarid trans-Himalaya valley and hilly grassland at Inner Mongolia [82,84,85]. However, it is counter-intuitive that plant density was found to be higher at south aspect, which incidentally suffered the most stressful aridity. This was actually resulted from the extraordinary high individual abundance of the dominant species, *Ajania nubigena*, at the south-facing slope in Feihong (see the ordination in Figure 4, plot s24–30), which was simultaneously accompanied with the lowest α diversity in the whole valley (Figure 4). In contrast to Feihong, plant density was significantly lower at the south aspects of the other two sites, Wenchuan and Shidaguan. As for diversity components, α and β diversity showed different responses to environmental gradients. Firstly, we found no significant correlations between α diversity metrics and biomass (as well as height and cover; Table 5), consistent with previous studies indicating non-significant species-productivity relationship at the local scale [86,87]. Meanwhile, we found α diversity decreased with elevation (i.e., with higher soil moisture and nutrient), which might be due to the higher competition exclusion in modest environment [88]. In fact, the second lowest α diversity occurred at the north aspect in Shidaguan (the site at highest elevation) (Figure 4, plot n1–7), which had the most benign condition of the whole valley and was associated with the tallest plant (a signal of light competition in modest environment) and community biomass (Figure 4). Similar pattern was also found by Badano, et al. [78] who found higher species richness on xeric than on mesic slopes due to the decrease in importance of negative interactions from mesic to xeric habitats. In contrary, β diversity increased with elevation, at north aspect and concave configuration, and this was consistent with other studies [15,89] suggesting that higher productivity leads to higher β diversity.

Although environmental processes accounted for a large proportion of variation in both community composition and vegetation structure, spatial process additionally resulted in 28 and 33% increased of the total explanation, respectively (Table 2, Figure 2), indicating that significant spatial structured variation of vegetation pattern occurred independent of environmental gradients. Significant linear trend at the regional scale was found for both vegetation composition and structure, indicating that a spatial structure at a broader scale than the sampling extent [26], and the identification of scale-specific environmental determinant suggested it is mainly due to elevational gradient. Moreover, the local scale spatial variables provided comparable explanation as regional scale variables for community composition but much higher explanation than the regional scale variables for vegetation structure (Table 2, Figure 2), highlighting the importance of local spatial process in determining vegetation structure. A large proportion of spatial explanation was shared by environmental variables, i.e., the space-environment overlap fraction, which reflects the spatially structured environmental constraints on vegetation attributes. This was well evidenced by the investigation of determinant environmental variables at different scales, which found elevation and soil property influencing vegetation pattern at the regional scale while microtopography at the local scale.

The interpretation of the pure spatial fraction must be viewed with caution, as it could be attributed to neutral processes or unmeasured spatially structured environmental variables. As an adaptive strategy to the spatially heterogeneous environments, numerous field studies found plant species to have low dispersal ability, i.e., short dispersal distance, in arid environments [90]. However, the study of the soil seed bank in Min dry valley by Li, et al. [91] showed rather low similarity (Sorensen < 30%) between the soil seed bank and associated vegetation in species composition, which seemed not to support the dispersal limitation hypothesis. Nevertheless, Li, et al. [91]'s study was conducted using different sampling design and took all plant species into account. Therefore, it might lead to biased conclusion about the dispersal strategy of woody species. Further studies are required to validate this conclusion. Alternatively, we believe the pure spatial fraction could result from unmeasured environmental variables, such as direct solar insolation and soil texture, which critically influence plant growth and species distribution in mountainous arid area [39,69,92]. Specifically, Chang, et al. [93] claimed that the improvement of environment measures could decrease the relative explanation of spatial variables in species distribution. Furthermore, Jones, et al. [94] revealed that data quality

and model choice had a profound effect on conclusions about the total explanation and the relative contributions of environment and space, and highlighted the need for separating methodological artefacts from the real ecological differences.

5. Conclusions

We investigated how environmental and spatial processes jointly determined vegetation attributes across scales in the Min dry valley. Specifically, based on the multi-scale spatial analysis conducted, we estimated the relative importance of: (1) total environmental and spatial processes, (2) topography and soil, and (3) regional and local spatial processes, and identified the scale-specific environmental determinants for vegetation composition and structure. Our result showed both environmental and spatial processes had significant and comparable effects on vegetation attributes. Topography played overriding role than soil property in determining vegetation attributes in this mountainous dry valley, with elevation dominating at the regional scale while slope aspect and shape at the local scale. We also detected spatial variation in species composition and the different responses of vegetation structure variables along environmental gradients. To the best of our knowledge, this study is among the first that incorporated multi-scale spatial analysis in investigating the ecological processes controlling vegetation attributes in mountainous arid areas. The study strengthened our understanding of vegetation pattern and the underlying processes in arid area. We hope that our study would inspire future work on assessing the underlying mechanism of vegetation pattern not only in the dry valleys of Hengduan Mountains region but also other mountainous arid areas worldwide. It also enlightened us to strengthen conservation strategies and ecological restoration with respect to spatial scales and specific vegetation attributes, such as productivity and different biodiversity components.

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