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Research Paper

Beta diversity of urban spontaneous plants and its drivers in 9 major cities of Yunnan province, China

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HIGHLIGHTS

- The exponent (*z*) of the SAC model was used in urban ecosystems to characterize beta diversity.
- We found the species composition of native plants was more heterogeneous than non-natives.
- The beta diversity of all species groups was best explained by alpha diversity and urbanization.
- Urban spontaneous plants diversity was determined by both the current state and historical processes of urbanization.

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ABSTRACT

Urbanization has significantly reshaped regional biodiversity structure globally. Previous studies suggested that urban communities of spontaneous plants are well adapted to the urban environment. However, a perspective of urbanization that accounts for the joint impacts of the current state (as expressed by urbanization intensity) and the historical progress of urbanization (as expressed by urbanization rate) to reveal the mechanisms underlying the biodiversity patterns of spontaneous plants in cities is still lacking. Here we present data and analysis of spontaneous plants sampled in 709 patches within 82 sites of built-up areas from nine cities distributed across climatic and floristic zones in Yunnan province, a biodiversity hotspot in China. We used the exponent (*z*) of a species accumulation curve (SAC) model to characterize beta diversity among patches in a site, and found a higher beta diversity of native species compared with non-natives, indicating that the species composition of native plants is more heterogeneous. The beta diversity of all species groups was best explained by the constant *c* of the SAC (a proxy of alpha diversity), followed by the urbanization intensity (as expressed by the proportion of sealed surface and patches' Shannon diversity index), and urbanization rate (as expressed by the sealed surface expansion rate). Moreover, beta diversity of non-native species was additionally negatively correlated with altitude. Our results suggest that the interplay of natural environmental factors and human-induced urbanization shape diversity of urban spontaneous plants in Yunnan province. Our findings emphasize that urban spontaneous plants diversity is not only a reflection of the current state of urbanization, but also a consequence of historical processes of urbanization.

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1. Introduction

Rapid urbanization drives regional and local environmental changes by altering land use patterns, and is usually associated with the introduction of a large number of exotic plants (Elmqvist et al., 2013). This, in turn, tends to homogenize the species composition in urban areas, and jeopardizes the provision of urban ecosystem services (Muller et al., 2010). The urbanization intensity could thus be an important factor influencing plant biodiversity (Malkinson et al., 2018; Li et al., 2019; Peng et al., 2019; Gao et al., 2021). Additionally, urban biodiversity patterns may be affected by a "lag effect" in the response of plants to environmental changes, that is, the observed biodiversity patterns may be affected by the historical process of urbanization, resulting in a potential "extinction debt" or "invasion debt" of biodiversity (Tilman et al., 1994; Essl et al., 2011; Hahs and McDonnell, 2014). Despite this, most studies to date have focused on the impacts of the current state of urbanization (i.e., urbanization intensity) on urban biodiversity. While, few studies qualitatively analyzed the effects of historical urbanization processes on current biodiversity patterns, such as, studies addressing land use legacies to predict diversity and composition of urban plant communities (Nassauer and Raskin, 2014; Johnson et al., 2015; Johnson et al., 2018). Therefore, considering the joint impacts of the current state and the historical progression of urbanization on biodiversity would provide a more comprehensive theoretical basis for biodiversity conservation in urban areas.

Spontaneous plants are an important component of urban plant communities and biodiversity, as they are neither intentionally cultivated by humans in cities nor part of the natural remnant vegetation (Prach et al., 2001; Cervelli et al., 2013). Urban spontaneous plants are characterized by their high plasticity to environmental change, and their low demand for resources (Chen et al., 2014). The plant communities formed by spontaneous plant species are well adapted to the local environment and provide important habitats for other species (Bonthoux et al., 2019). Moreover, they can respond quickly to urbanization (Smith and Fellowes, 2014), and are thus also good indicators of urbanization processes.

Beta diversity is the variability in species composition among a set of sampling units (Whittaker, 1960). It is mainly determined by regional environmental factors, such as temperature and precipitation regimes (Pinto-Ledezma et al., 2018; Sreekar et al., 2018). Furthermore, urban species diversity depends on migration and interspecific competition (Crawley and Harral, 2001), and is affected by other drivers, such as habitat heterogeneity (Ricklefs, 1977; Stein et al., 2014), edge effects and dispersal limitations (Gao et al., 2021), and biotic homogenization caused by introducing non-native plants (Kühn and Klotz, 2006; Qian et al., 2016). Therefore, to better explain the driving factors of urban beta diversity, we should comprehensively analyze the abovementioned driving factors. A better understanding of drivers of beta diversity would support a more informed application in urban ecology and management measures.

The species-area relationship (SAR) describes the phenomenon of increasing species richness with increasing area and is viewed as one of the most fundamental patterns in ecology (Connor and McCoy, 1979). The Species Accumulation Curve (SAC) fitted by a power law model $S = c \times A^z$, is commonly used to analyze species-area relationships (Gray et al., 2004). According to this relationship, when A (patch size) = 1, then S (species richness) = c, which is essentially the species diversity of a unit area-alpha diversity (Dembicz et al., 2021). The exponent z quantifies the rate of increase in species richness with increasing habitat area (Sreekar et al., 2018). Therefore, one can interpret the z to reveal the relationship between species composition and environmental variables, which can be as a characterization of beta diversity (Dengler et al., 2020; Dembicz et al., 2021). Furthermore, the z of SAC is affected by ecological processes such as environmental filtering, dispersal limitation, and interspecific interactions, which can be applied to illuminate the differences between native and non-native species (He and Legendre, 2002; Rosindell and Cornell, 2009). In addition, due to its control of the sampling area effect (Quinn and Harrison, 1988), it has been widely used to compare beta diversity at different spatial scales in natural ecosystems (Flather, 1996; Gray et al., 2004; Matthews et al., 2016). Since species accumulation curves may be driven by environmental properties, correlations between the z (i.e., the rate of species accumulation) and ecological parameters have been found and used to assess their contributions (Dengler et al., 2020; Dembicz et al., 2021).

The SAC has been used extensively in fragmented and disturbed ecosystems. While urban ecosystems are both fragmented and disturbed, relatively few studies have explored the driving factors behind the rate of species accumulation of spontaneous plants in these ecosystems. In this study, we used the SAC of different groups (i.e., native, non-native and total species) of spontaneous plant species to estimate their z and characterize beta diversity. By using a dynamic view of urbanization impacts on biodiversity, our aims were to disentangle the environmental factors affecting the beta diversity of native and non-native spontaneous plants in urban environments, and compare relative importance of the environmental factors in affecting the beta diversity of native and non-native spontaneous plants.

2. Materials and methods

2.1. Study area

Yunnan province (N 21°8′32'' - N 29°15′8′', E 97°31′39'' - E 106°11′47′') comprises parts of two biodiversity hotspots: the mountains of Southwest China and Indo-Burma (Myers et al., 2000; Williams et al., 2011; Noss et al., 2015). These hotspots are inhabited by more than 18,000 higher plant species, equaling 51.6% of all higher plant species in China (Yang et al., 2004; Qian et al., 2020; Liu et al., 2021). The high floristic richness is attributed to the geologic, topographic, and climatic diversity within the area (Li and Walker, 1986). Additionally, some parts of Yunnan province have been identified as refugia for biodiversity during the Pleistocene (López Pujol et al., 2011). Over the past 30 years, Yunnan province has been undergoing rapid urbanization. It is expected that by 2030, more than 862 km^2 of urban land will be located in or adjacent to biodiversity hotspots. Therefore, the impact of urbanization on biodiversity in this region cannot be ignored (Güneralp et al., 2013).

Our study was carried out in nine cities of Yunnan province, China (Fig. 1). The nine selected cities are distributed along natural gradients of mean annual precipitation (779.8 mm – 1,467.4 mm), mean annual temperature (12.8 °C – 22.1 °C) and mean annual solar radiation duration (1,580.8 h – 2,222.3 h). In addition, the cities range in size between 12.6 and 371.6 km^2 in 2019, and the proportion of the impermeability area within the urban areas ranges between 53 and 90% (Table S1). Altogether, the cities selected in this study provide a widely representation of the varied natural and urban environment in Yunnan province (Table S1).

2.2. Data collection

1) Field surveys

Field surveys of plant species were conducted during the growing seasons (June - October) of 2017, 2018 and 2019. In each city, sampling sites of 500 m radius were set up in every 2 km from the city center to the city outskirts (Fig. 1). At each of the sampling sites, we randomly selected more than 3 accessible green patches for a species richness survey (Fig. S1). The mean patch area varied from 0.15 ha to 2.9 ha in each city (Table S1). In total, 709 patches were surveyed in 82 sites (a mean of nine patches per site). We recorded all plant species in each patch, but only used the spontaneous species in the data analysis. We included urban weeds, urban woody seedlings, and early succession urban woody plants which establish spontaneously in unique habitats (e.

g., abandoned lands or masonry walls) (Huang et al., 2019; Gao et al., 2021). We excluded fully grown trees because of the difficulty in determining whether they were intentionally planted or occurred spontaneously, except for those growing on abandoned lands, roofs and walls (Gao et al., 2021). The spontaneous species were further classified into native, and non-native species according to the *Flora Yunnanica* (Wu, 2006), Exotic Plants in China (He, 2012) and The Checklist of Chinese Invasive Plants (Ma et al., 2013).

2) Environmental variables

We collated a combination of environmental data, including climate variables, and characteristics of urbanization and landscape configuration, to assess potential drivers of spontaneous plant biodiversity. We used the China Meteorological Data Network (https://data.cma.cn) to obtain the mean value of climate variables from 1951 to 2019. For each city, we chose the data from the closest weather station to the city. In total, seven climate variables were included: mean annual precipitation, monthly maximum precipitation, mean annual solar radiation duration, mean annual temperature, hottest month temperature, coldest month temperature and maximum wind speed. Site scale climate data were calculated from the climate data of each city.

The characteristics of the different urban areas were represented by current urbanization state and the historical urbanization process of each site and city. The current state of urbanization, further referred to as urbanization intensity, was quantified using landscape pattern indices, namely the Shannon diversity index of each site ($SHDI.site = -\sum_{i=1}^{m} pi \times \ln pi$, where pi represents the percentage of a particular patch type, and m represents the number of patch types), proportion of sealed surface in each site ($\text{Sealed}_{.\text{site}}$), and average distance of patches within a site to the city boundary ($\text{BD}_{.\text{site}}$). We chose $\text{SHDI}_{.\text{site}}$ to reflect the habitat diversity and heterogeneity of each site (Ramezani and Holm, 2011; Ramezani, 2012). We used $\text{Sealed}_{.\text{site}}$ and $\text{BD}_{.\text{site}}$ to reflect the intensity of urbanization (Malkinson et al., 2018). $\text{BD}_{.\text{site}}$ also represents the average distance to the species pool (Gao et al., 2021). Even if two locations have similar current urbanization states, there may be different urbanization processes that could have resulted in different effects on plants. Additionally, different areas within the same city could exhibit different urbanization processes. For example, downtowns may maintain higher urban development and building density for a long time, while the suburban areas are becoming increasingly developed with impervious surface in recent years. We therefore used two metrics

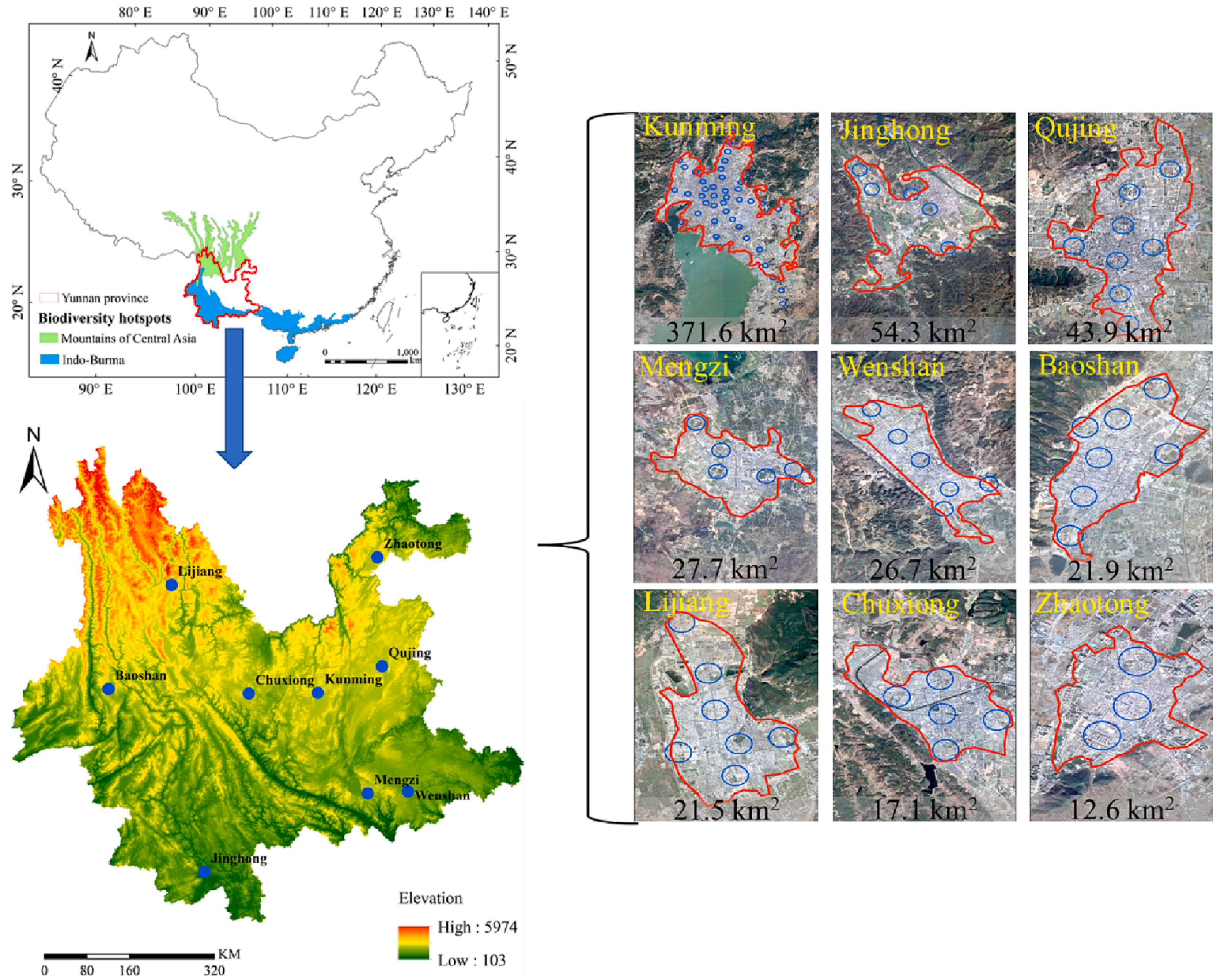

Fig. 1. The distribution of sampling sites in the nine cities of Yunnan province, China Note: the blue circles in the right panels represent sampling sites are equal in area (radius = 500 m); and red polygons are city boundaries; the satellite images are ordered by the size of the urban build-up area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

to quantitatively describe the historical urbanization process at both city and site scale, referred to as urbanization rate at city ($UR_{.city}$) or urbanization rate at site ($UR_{.site}$) scale. Thus, the slopes of the linear regression of the proportion of sealed surface with time from 1989 to 2019 for each city and site have been used as proxies for urbanization rate (steeper slopes indicate more intensive urbanization processes or higher urbanization rate). Additionally, patch number we surveyed in each site (PN) be treated as a confounding variable to proximate the number of habitat islands (Matthews et al., 2014; Matthews et al., 2016; Matthews et al., 2019).

To estimate the above parameters, land cover maps within the administrative boundary of each city for every five years between 1989 and 2019 were derived from cloud-free Landsat TM, ETM and MSS images with a moderate spatial resolution of 30 m. The land covers were classified into five categories: sealed surface, water, barren land, arable land and vegetation, by using the Maximum Likelihood Classification approach which is a supervised classification in ArcGIS 10.3 (ESRI, 2015). To accurately count urbanization intensity, the same method was used to classify high-resolution aerial orthophotos of Google Earth (RGB, 0.14 m resolution, 2018). The city boundary was defined by a threshold of 50% sealed surface detected by using a 1 km × 1 km moving window in Fragstats 4.2.1 to aggregate the sealed surface, and thus to delineate the urban border (McGarigal, 2015).

2.3. Data analysis

To deal with the nonlinearity problem caused by the different survey areas, Gleason index ($Gleasonindex = \frac{S}{\ln A}$, where S is species richness in each city and A is total surveyed area in each city) was used to calculate the species diversity at the city scale (Gleason, 1922).

For a more robust parameter estimation, only sites with more than five patches were selected (54 out of 82 sites) to construct SACs. The patches were bootstrapped 500 times to obtain robust estimates of c and z (Matthews et al., 2016). For example, for the second data point (i.e., two patches) of the SAC of a site, we randomly selected two patches, noting down the combined area and combined richness of this pair. The *mmSAR* package was used for the calculations of c and z (Guilhaumon et al., 2010). SACs were developed separately for species of different groups (native, non-native and total species). Statistically, although both c and z are estimated using the same data, they are two completely unrelated parameters, i.e., any combination between c and z is potentially possible. However, from the ecological standpoint of view, c and z could be interdependent, as between many other measures of alpha and beta diversities (Chao and Jost, 2012). This is because alpha and beta diversities are constrained by the total regional diversity (gama diversity) and for regions with a fixed gama diversity an increase in alpha diversity would inevitably result in a decrease in beta diversity. To account for this interdependence and to reveal the unique effects of various factors on beta diversity that are independent from their effects on the alpha scale, we included c as a predictor in our models of z developed below.

Linear mixed effects models were used to analyze the driving factors of z which is close proxy to beta diversity. Firstly, the independent variables were standardized and centered to unify the dimensionality between the variables. To avoid collinearity between variables, if the correlation coefficient between independent variables was greater than 0.7, only one of the variables was retained in the model. After model construction, the variance inflation factor (VIF) of the model was checked, and variables with VIF greater than 5 were removed from the model one by one until all variables' VIF ≤ 5 (Menard, 2002; Vittinghoff et al., 2006; Gareth et al., 2013). City ID was taken as random effect, and fixed effects were divided into four groups: 1) natural environmental variables (including seven abovementioned climate variables and altitude); 2) Urbanization characteristic variables, including three related to current state of urbanization ($Sealed_{.site}$, $SHDI_{.site}$ and $BD_{.site}$), and two related to historical urbanization process ($UR_{.site}$ and $UR_{.city}$); 3) and the c value in the power law model to represent alpha diversity; 4) and the PN (surveyed patch number in the site) been treated as a confounding variable.

It was found that the within-group error variance and standard deviation of linear mixed effects models was lower than 1.0×10^{-4} (calculated by *VarCorr* function in *lme4* package), and when putting city as random effect, singular issues arose (calculated by *isSingular* function in *lme4* package). Additionally, the AIC value of the linear model deviated by <2 with the mixed model (calculated by *anova* function in *stats* package), and R_c^2 and R_m^2 of mix models were also equal (*r.squaredGLMM* function in *MuMIn* package). Therefore, a linear model was used in this study to simplify the interpretation of the model. Stepwise regression was used to obtain the best model for each group of spontaneous plants, using the *StepAIC* function in the *MASS* package (Guilhaumon et al., 2010). Subsequently, the *check_autocorrelation* function in *performance* package was used to test whether models are autocorrelated. The *shapiro.test* in the *stats* package was used to evaluate the normality of residues in the final model. To further explore the relative contribution of each variable to the model, the total explained variation (R^2) of the model was decomposed to obtain the relative contribution of each variable to the variation of the dependent variable. The R^2 decomposition was performed by using the *booteval.relimp* function in the *Relaimpo* package (Grömping, 2015). All analyses were performed using R 3.4.1 software (RCoreTeam, 2015). The data and codes are provided in the Supplementary information.

3. Results

Across the nine cities, we recorded 1,047 spontaneous plant species from 657 genera of 158 families. Of all species, 769 (73.4%) were native, and 278 (26.6%) were non-native. Of the non-native plants, 143 species were invasive species (51.4%). Half of the top ten most frequent species were invasive plants (*Conyza canadensis*, *Alternanthera philoxeroides*, *Bidens pilosa*, *Lolium perenne* and *Oenothera rosea)*. In total, we recorded 669 herbaceous species (63.9%), 173 shrub species (16.5%), 137 tree species (13.1%) and 68 liana species (6.5%) among the spontaneous species. The Gleason index varied between 16.78 (Zhaotong city, including 12.12 native and 4.66 non-native species) and 29.75 (Lijiang city, including 23.13 native and 6.62 non-native species, see Fig. 2). On average, the Gleason index per city was 23.91 ± 3.95 (SD) for all species, of which 17.07 ± 3.40 for native, and 6.84 ± 1.54 for non-native species.

The SACs constructed at the site scale revealed that *z.native* (mean = 0.45, range 0.24–0.58) > *z.total* (mean = 0.43, range 0.23–0.57) > *z.non-native* (mean = 0.38, range 0.19 ~ 0.56 – Fig. 3). There was no significant difference in beta diversity between total and native species, while beta diversity of non-native species was significantly lower than beta diversity of total and native species (Fig. 3). In other words, the introducing non-native species did not significantly change the pattern of beta diversity at site scale.

The linear regression analysis indicated that c, $Sealed_{.site}$, $UR_{.city}$ and $UR_{.site}$ were the variables that best explained the *z.total*, *z.native* and *z.nonnative* (Table 1). In addition to the variables mentioned above, the best explanatory models also included patch number for *z.total* and *z.native*, and $SHDI_{.site}$ and altitude included for *z.nonnative* (Table 1). The relative contribution of environmental variables to the variation of z showed that the most important explanatory variable for the variation in z of all groups was c (≥71%), whereas the other variables in the model each contributed < 5% (Table 1, Fig. 4).

4. Discussion

Urban spontaneous plants are an important component of urban vegetation and good indicators of urbanization processes, and have been

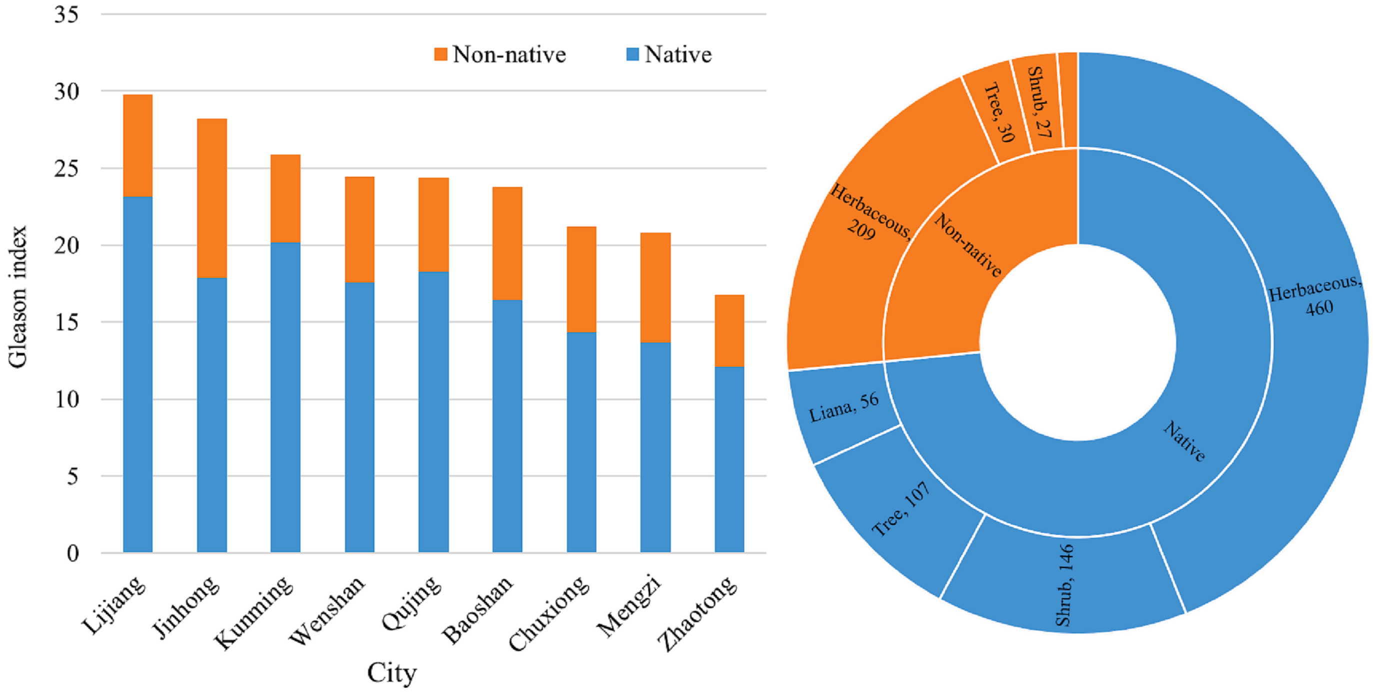

Fig. 2. Overview of Gleason index (left) and composition (right) of spontaneous species in nine cities, Yunnan province, China.

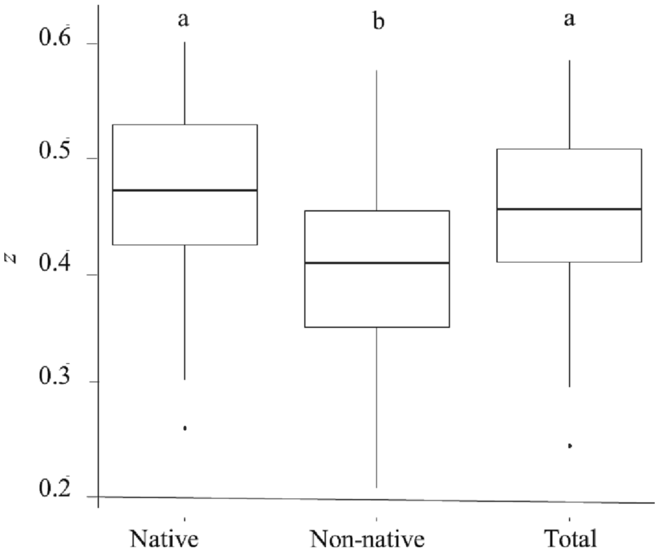

Fig. 3. Boxplot of z for all groups Note: different lower-case letters indicate a significant difference among groups ($p < 0.05$).

Table 1
Linear regression models between z of different group species and environmental variables at site scale.

Group	Factors	Estimate	SE	t value	Df
Total	c	**−0.09**	0.01	−12.13	46
$R^2 = 0.77$	Sealed$_{.site}$	**0.01**	0.01	2.10	46
	PN	0.01.	0.01	1.97	46
	UR$_{.site}$	−0.01.	0.01	−1.63	46
	UR$_{.city}$	**−0.01**	0.01	−2.37	46
Native	c	**−0.09**	0.01	−12.21	46
$R^2 = 0.78$	Sealed$_{.site}$	**0.01**	0.01	2.64	46
	PN	0.01.	0.01	2.01	46
	UR$_{.site}$	−0.01	0.01	−1.37	46
	UR$_{.city}$	−0.01.	0.01	−1.70	46
Non-native	c	**−0.09**	0.01	−13.70	45
$R^2 = 0.82$	Sealed$_{.site}$	**0.02**	0.01	3.09	45
	UR$_{.site}$	**−0.01**	0.01	−2.64	45
	UR$_{.city}$	−0.01.	0.01	−1.78	45
	SHDI$_{.site}$	**0.02**	0.01	3	45
	Altitude	**−0.01**	0.01	−2.56	45

Note: c of SAC in each site, here used to represent alpha diversity; Sealed$_{.site}$: impervious surface ratio of site; PN: patch number in each site; UR$_{.city}$: urbanization rate at city scale; UR$_{.site}$: urbanization rate at site scale; SHDI$_{.site}$: patches' Shannon diversity index; bold font means significance ($p < 0.05$); "." means marginal significance ($0.05 < p < 0.1$).

a focus in urban biodiversity studies (Li et al., 2019; Cheng et al., 2021). However, an understanding of how historical process of urbanization shape current biodiversity patterns is still lacking. In this study, we synthesized natural environmental factors, urbanization characteristic (including the current state of urbanization and historical processes of urbanization), and the c value of the power model (as a proxy of alpha diversity) to investigate how they describe the rate of species accumulation, by assessing the z of species area curves (SAC) in nine cities of Yunnan province, China. Our results indicated that beta diversity of spontaneous plants was significant driven by alpha diversity, following by urbanization factors, i.e., urbanization intensity and urbanization rate. Total explanatory power of urbanization factors on beta diversity of all groups were <9%. Nevertheless, the effect of urbanization rate on beta diversity was opposite to the effect of urbanization intensity, the contribution of both the current and historical process of urbanization should not be ignored in urban biodiversity studies. Additionally, contrary with the findings in most studies that non-native species increased biological homogenization (Lososová et al., 2012; Vitule et al., 2021), our results showed that 26.6 % of non-native spontaneous species introducing did not significantly decrease the beta diversity of the regional species pool.

In this study, we explored to what extent the variation in alpha diversity contributed to explain the variation in beta diversity. We found that alpha diversity was the dominant variable explaining more than 71% of the variation in beta diversity, while the other variables explained <5%. Matthews et al. (2019) found similar results in a global dataset of 151 islands. Thus, our finding suggests that this relationship also holds in urban area. In another study, however, of the Palaearctic

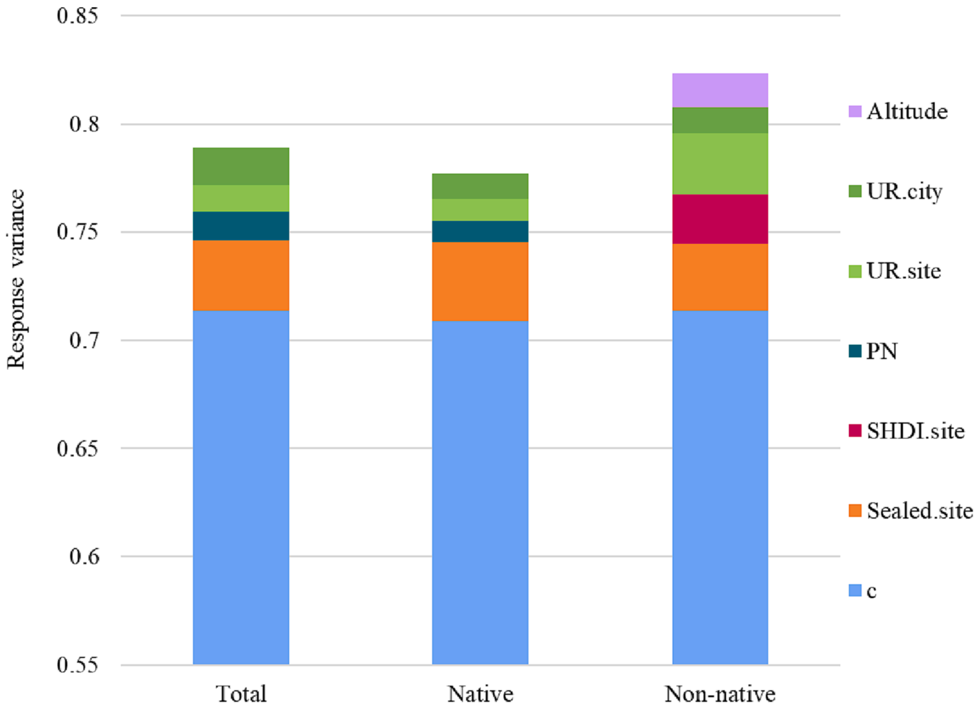

Fig. 4. Explanatory power of environmental variables for *z* of sites Note: *c* value of SAC in each site; $\text{Sealed}_{.\text{site}}$: impervious surface ratio of site; PN: patch number in each site; $\text{UR}_{.\text{city}}$ and $\text{UR}_{.\text{site}}$: urbanization rate at city and site scale; $\text{SHDI}_{.\text{site}}$: patches' Shannon diversity index.

biogeographic realm, alpha diversity and beta diversity for vascular plants showed a U-shaped trend, and alpha diversity explained only 11% of the variation of beta diversity, but was still of the top four explanatory variables (Dembicz et al., 2021). In this study, there was only a relatively low variation in species richness (123 ± 30) and surveyed area (given that all sampling in this study was conducted in a circle within a radius of 500 m). This might potentially explain the strong influence of alpha diversity. Traditionally, the variation of *c* (as proxy of alpha diversity) and *z* (interpreted as beta diversity) in the power models have been examined separately (Fattorini et al., 2017). However, as suggested by Matthews et al. (2019), evaluating these two parameters separately may over-simplify the drivers of beta diversity. Our results again indicated that the effect of alpha diversity should not be ignored when evaluating the drivers of beta diversity.

From the perspective of the current state of urbanization, previous studies indicated that the increasing urbanization intensity causes a large number of native species in urban areas to be replaced by some non-native species with strong dispersal ability, resulting in biological homogenization (Wang et al., 2021). Nevertheless, an increase in urbanization intensity is usually accompanied by fine-scale heterogeneity (McGill and Miller, 2022), resulting in an increase of habitat types per unit area (Dembicz et al., 2021). According to the habitat diversity hypothesis, an increase in habitat diversity will increase species composition differences between patches (Rosenzweig et al., 2003). Furthermore, according to the environmental heterogeneity hypothesis, an increase the heterogeneity should increase the available niche space, provision of refuges and opportunities for isolation and divergent adaptation, and thus enhance species coexistence, persistence and diversification, eventually allowing more species to coexist (Stein et al., 2014). In this study, $\text{Sealed}_{.\text{site}}$ and $\text{SHDI}_{.\text{site}}$ indexes were used to reflect the current urbanization state. Indeed, $\text{Sealed}_{.\text{site}}$ was significantly positively correlated with beta diversity of all species group and $\text{SHDI}_{.\text{site}}$ was significantly positively correlated with beta diversity of non-native plants, consistent with the environmental heterogeneity hypothesis, habitat diversity hypothesis and habitat amount hypothesis (Ricklefs, 1977; Kallimanis et al., 2008; Hortal et al., 2009; Chang et al., 2022). These hypotheses have been confirmed in studies of different groups of organisms in different ecosystems (Nilsson et al., 1988; Mumby, 2001; Fahrig, 2003).We thus conclude that effects of habitat heterogeneity were stronger than the effects of biological homogenization due to the occurrence of non-native species.

An increasing urbanization rate led to more homogeneous species composition between patches. Higher (historical) urbanization rate may have resulted in more frequent and unstable disturbances, rendering colonization by spontaneous species more difficult. Only species with high viability and/or dispersal ability have the chance to colonize and establish, thus accelerating the elimination of urban rare species, and resulting in a relatively smaller beta diversity between patches. Similar results have been found in studies assessing the influence of historical land use processes of urbanization on biodiversity (Ramalho et al., 2014; Qian et al., 2020).

The legacy effect of land use on biodiversity has long been recognized by many ecologists. Plants may have "extinction debt" for historical environmental changes, and land-use legacies may also affect biodiversity (Tilman et al., 1994; Hahs and McDonnell, 2014). In a study in Baltimore, USA, the species composition of plant communities differed between areas with a different land use history, with the beta diversity in park areas being significantly higher than areas that being transformed from parks to residential areas (Johnson et al., 2018). Interestingly, our results show that the beta diversity of total and non-native species groups was significantly explained by urbanization rate, but only marginal significantly for native plants. These results indicate that the effect of urbanization on beta diversity is a dynamic and long-term process. Although, the impact of urbanization on beta diversity was limited as described above, both the current and historical process of urbanization should still be considered in urban biodiversity studies. Since urbanization rate could reflect the frequency of disturbance, the above results may be also interpreted as native plant species being less sensitive to the frequency of disturbance as they are well-adapted to the local climate and disturbance regimes (Shelef et al., 2017). Alternatively, one may argue that with faster urbanization rates the interaction between patches is accelerated. This may speed up the colonization of non-native species in city, and particularly of the invasive species among them, resulting in lower beta diversity of non-native species (Lososová et al., 2012). Such explanation would fit earlier studies on the life-history strategies of invasive species and may explain that impacts of historical urbanization processes (Coutts et al., 2011; Nguyen et al., 2021). In that sense, the interaction between urbanization rates and the occurrence of invasive species threatens beta diversity of urban spontaneous plants.

It is a widely trend that species diversity decreases with altitude (Rahbek, 1995; Kraft et al., 2011). Our study found that the beta diversity of non-native spontaneous plants, unlike the beta diversity of total and native spontaneous plants, significant decreased with altitude. The similar results were also found in researches on the beta diversity of Iranian grasslands, woody plants in forests of China, and spontaneous herbaceous plants in 59 major cities in China (Kraft et al., 2011; Qiao et al., 2012; Moradi et al., 2020; Hu et al., 2022). Changes in altitude may be accompanied with changes in temperature, precipitation and atmospheric pressure, which will result in more stressful environment for plants, resource restrictions limiting plant growth or species pool size (Körner, 2007). As mentioned above, more than half of the non-native plants (51.4%) are invasive in our study which have the strong adaptability, stress resistance and dispersal ability. And those properties enable invasive plants more likely to colonize hash environments (e.g., higher altitude) and gradually increase their regional dominance, eventually lead to a more homogeneous species composition (Štajerová et al., 2017; Alharbi and Petrovskii, 2019). In addition, the non-native plants that are not invasive might not have yet adapted to the local environment, and increased elevation increases their risk of regional extinction. Therefore, strong adaptability of invasive species and low adaptability of non-native plants that are not invasive together led to a lower beta diversity at higher altitude. The beta diversity of native plants did not change significantly with a change in altitude, which may also suggest that native plants and the environment have co-evolved for a long time.

Because it is difficult to obtain high resolution satellite imagery to trace patch age or land use legacy, we only used urbanization rate as a proxy of historical urbanization in our research. Habitat history and land use legacy are also important and should be considered to reflect urbanization history (Kopel et al., 2015; Johnson et al., 2018). Moreover, habitat features (such as urban green space types and land use diversity) are important for evaluating habitat complexity and could be one of the drivers dictating biodiversity patterns (Chang et al., 2022). However, due to the difficulty in obtaining the urban green space types of each patch, the characteristics of patches were not fully included in the analysis in this study. Moreover, limited by the sample size in cities, our research was carried out at the fine-scale. Therefore, variables including topography and city's age which are expected to influence species composition in larger scale (Aronson et al., 2014; Beninde et al., 2015) should include in the research of future.

5. Conclusion

We investigated the driving factors of the exponent (z) of SAC (proxy of beta diversity) of spontaneous plants in 9 major cities of Yunnan province, China and found that: 1) beta diversity of native plants was higher than those of non-native plants at site scales, indicating that the species composition of native plants is more heterogeneous; 2) besides the constant c of SAC (proxy of alpha diversity in the site) and urbanization intensity (proxied by $\text{Sealed}_{\text{.site}}$ and $\text{SHDI}_{\text{.site}}$), beta diversity was also driven by urbanization rate (expressed by $\text{UR}_{\text{.city}}$ and $\text{UR}_{\text{.site}}$); 3) the beta diversity of non-native species was additionally negatively correlated with altitude; 4) factors relating to both current and historical urbanization affect current beta diversity pattern, thus the history of urbanization should be fully considered in urban biodiversity studies. Our results provide insights to the drivers of spontaneous plants diversity in urban area, and a theoretical basis for future urban planning and greening.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

I have shared my data and code at the Attach file step.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2023.104741.

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