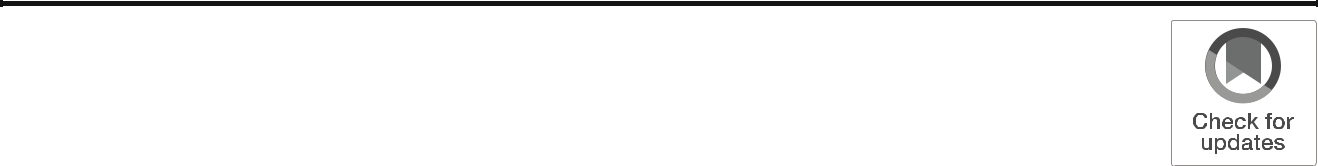
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https://doi.org/10.1007/s11252-020-01040-z



Impacts of the remnant sizes, forest types, and landscape patterns of surrounding areas on woody plant diversity of urban remnant forest patches

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* Springer Science+Business Media, LLC, part of Springer Nature 2020

Abstract

Remnant forests in urban areas are hotspots of urban biodiversity. However, the survival and integrity of many remnant forests are currently at risk. Better knowledge of the interactions between remnant forests and urban environments is urgently needed for guiding the conservation effort. In this study, we intend to answer the question: how do patch attributes and landscape patterns of surrounding environments affect the taxonomic diversity of woody plants in urban forest remnants? We surveyed the woody plant species in 240 sample plots in 54 remnant forest patches in Guiyang City, China. We analyzed the taxonomic diversity of woody plants and the effects of influencing factors using multi-level taxonomic diversity indicators and the generalized dissimilarity modeling. The results showed that shrubs had higher within-patch α-diversity than that of trees. However, adult trees had higher among-group β-diversity than those of shrubs and saplings/seedlings. The vegetation type of the patch had more influence than other factors on the compositional dissimilarity of adult trees and sapling/seedling among patches. The patch size had the highest impact on the compositional dissimilarity of shrubs. Besides, small patches had a higher rate of compositional turnover in all woody plants. The percentage of impervious surfaces in surrounding areas and the spatial distance from each other were the main influencing factors for adult trees and saplings/ seedlings, respectively. Based on our results, we recommend that more attention should be paid to preserve the small remnant forest patches and protect sampling/seedlings to maintain the taxonomic diversity of urban remnant forests.

Keywords Remnant forests . Woody plants . Taxonomic diversity . Compositional dissimilarity . Urban matrix

Introduction

Remnant forests in urban areas are natural or semi-natural forests that remained through the urbanization process that

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s11252-020-01040-z>) contains supplementary material, which is available to authorized users.

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has never been cleared for urban use (Zipperer [2002](#page9)). Urban remnant forests are hotspots of biodiversity. They help to pre-serve native plant species (Kowarik and von der Lippe [2018](#page9)) and provide food and shelter to urban wildlife (Barth et al.

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[2015](#page9)). Also, they generate ecosystem services that are impor-tant to urban residents (Fahey and Casali [2017](#page9); Niemelä et al. [2010](#page9)). Despite these benefits, their long-term sustainability is threatened by intensive anthropogenic forces in urban envi-ronments such as changes in biogeochemical cycles (Alberti [2010](#page9); Carreiro and Tripler [2005](#page9)), and habitat fragmentation (Stiles and Scheiner [2010](#page9)).

Habitat fragmentation is a major threat to urban remnant forests because it not only leads to direct loss of forest habitats but can also modify the structure and functions of the remain-ing forest patches. Increased isolation of forest remnants changes the community assemblages of forest plants. Species with limited dispersal capacity or low fecundity grad-ually drop out from the community assemblages (Bonte et al. [2012](#page9); Jesus et al. [2012](#page9)). Besides, habitat fragmentation re-duces pollinator services, which favors plants with self-fertilization (Aguilar et al. [2006](#page9)). Habitat fragmentation also alters gene flow patterns and results in decreased genetic di-versity of plants (Van Rossum [2008](#page9)). The change of plant community assemblages further causes impacts on the insect community composition (Williams [2011](#page9)) and the abundance and species richness of birds living in the remnant forests (Sewell and Catterall [1998](#page9)).

Many factors mediate the impact of habitat fragmentation on species diversity of remnant forests in the urban environ-ment. Sizes of forest remnants have been found to correlate with the plant species diversity positively (Malkinson et al. [2018](#page9); Stiles and Scheiner [2010](#page9)). Large remnants often support more individuals, which can lower the risk of local extinction (MacArthur and Wilson [1967](#page9); Scheiner and Willig [2005](#page9)). It is because large remnants contain a greater diversity of habitat types than small ones, so more plant species can grow there (Scheiner [2003](#page9); Scheiner and Willig [2005](#page9)). Besides the size, the geometrical shape of a remnant is also an important medi-ating factor. Remnants with complex geometric shapes can facilitate species exchange with adjacent habitats (Stamps et al. [1987](#page9)). Moreover, the plant diversity of the remnant forests correlates negatively with the urbanization levels of surrounding environments (Caryl et al. [2013](#page9)). Sealed surfaces such as paved roads can weaken the ecological function of seed dispersers by impeding long-distance seed dispersal (Niu et al. [2018](#page9)).

While existing studies offer valuable information on how habitat fragmentation affects the species diversity of urban remnant forests, several issues need to be addressed. First, existing studies mainly focused on the variation of taxonomic α-diversity in the remnant forests (Malkinson et al. [2018](#page9); Ramalho et al. [2014](#page9); Stiles and Scheiner [2010](#page9)). Studies that examined the β-diversity of urban remnant forests are rare (Heckmann et al. [2008](#page9)). The lack of studies on the β-diversity of remnant forests may not serve urban conservation well because urbanization can increase α-diversity at one site but lower β-diversity across sites (Lososová et al. [2012](#page9)).



Second, existing studies seldom differentiate the response of trees at different ontogenetic stages to urbanization. To treat trees at different ontogenetic stages as one group may mask the long-term response of trees to urbanization (Ribeiro et al. [2016](#page9)). The species composition of saplings/seedlings reflects the sustainability of forests in the future (Valiente-Banuet and Verdú [2007](#page9)). Furthermore, except for a few studies (Malkinson et al. [2018](#page9)), existing studies focused primarily on the impacts of attributes of remnant forest patches (e.g., size and shape) on species diversity but seldom considered the influence of the landscape pattern of surrounding environments.

In this study, we intend to address the question: how do patch attributes and landscape patterns of surrounding envi-ronments affect the taxonomic diversity of woody plants in urban forest remnants? We chose a rapidly urbanized city located in the subtropical climate zone ─ Guiyang, China ─ as our study site. The specific objectives of our study include:

1. to quantify the taxonomic diversity of woody plants in the remnant forest at different spatial scales; (2) to analyze the impacts of patch attributes and landscape patterns of surround-ing environments on the taxonomic diversity of woody plants in the remnant forest.

Methods

Study area

Guiyang City is a city located in southwest China. The admin-istrative area of the city is bounded between 106°30′ to 106°59′E and 26°10′ to 26°49’ N. The city sits on a well-developed karst landform, which creates opportunities to pre-serve many natural and semi-natural forest patches during the urbanization as the topography is too steep to support urban development. Guiyang has a subtropical humid temperate cli-mate. The primary natural vegetation type of the city is sub-tropical evergreen broadleaf forests. Since 1996, the city has experienced rapid urban expansion. The built-up area of the city has increased from 74 km2 in 1996 to 359 km2 in 2017, while the population has increased from 1.35 million to 3.59 million at the same time (Guiyang Municipal Bureau of Statistics [1997](#page9); Guiyang Municipal Bureau of Statistics [2018](#page9)).

Field survey

In order to obtain information on the species diversity of woody plants in the remnant forests in Guiyang, we conducted a field survey between October and December 2018. The sample sites were first selected by origin (i.e., only forests classified as natural selected), followed by categorizing the forest patches based upon three attributes: vegetation type,

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impervious surface, and patch size. More details were present-ed as follows.

We first selected out naturally originated forest patches by referring to the forest resources inventory data of Guiyang (Guiyang Ecological Environment Bureau [2005](#page9)). The inven-tory is conducted every ten years by the Guiyang Municipal Bureau of Ecological Environment. The data contains the sizes, stand volumes, locations, types, origins, and major tree species of all forest stands in Guiyang. The origin of forest stands was classified as “natural”, “planted”, and “aerial-seeding” stands. We exported the shapefile of forest stands as a KML file to Google Earth and manually selected the patches with a natural origin that has been entirely or partially surrounded by impervious areas by 2015. A total of 191 forest patches were identified using this method.

We derived the percentages of impervious surfaces within a buffer of 500 m around each patch from a land cover map of Guiyang obtained from Huang et al. ([2018](#page9)). The land cover map was generated using Landsat 8 data. It contains six land cover classes: tree/shrub, grass, water, impervious surface, bare soil, and crop. The data has a ground resolution of 30 m and was projected using the WGS84 Web Mercator projection. We classified the percentages of impervious sur-faces in buffered areas into three levels, <20%, 20%–50%, and > 50%. According to Wickham et al. ([2010](#page9)), these values represent developed and open areas, developed areas with low density, and developed areas with medium to high density, respectively.

We further divided the forest patches based on their sizes and main vegetation types. Two size classes, smaller than 10 ha and larger than 10 ha, were used in this study. The size of 10 ha was considered a critical threshold value of the size of the urban green space (Ramalho et al. [2014](#page9)). We determined the vegetation type of each patch based on the dominant spe-cies recorded in the inventory data. Patches were classified as broadleaf forest stands, coniferous forest stands, and mixed forest stands. Pinus massoniana is the dominant canopy spe-cies in the coniferous forest stands. Species from the Fagaceae and Lauraceae families are main overstory trees in the broad-leaf forest stands. The mixed forest stands are mainly consisting of P. massoniana, Quercus spp., Carpinus spp., and Cyclobalanopsis spp.

We randomly selected three patches for each combination of size, degree of urbanization, and vegetation type as sample sites. A total of 54 patches (18 groups, three replications) were chosen from the 191 remnant forest patches at the end. The locations of these 54 remnants were shown in Fig. [1](#page9).

Following the sampling method used in Threlfall et al. ([2016](#page9)), we lay out two, four, six, and eight sample plots in forest patches with sizes at 1–5 ha (22 patches), 5–10 ha (5 patches), 10–50 ha (20 patches) and > 50 ha (7 patches), respec-tively. In total, 240 sample plots (20 m by 20 m) were located inside 54 patches. Each plot was kept at least 25 m from the

edge of the forest patch. In the field, information on the plot and woody plant species were collected (Table [1](#page9)). The classification of a woody plant species to tree or shrub species was done by referring to the Flora of Guizhou (Chen [2004](#page9)). We followed the recommendation in Fang et al. ([2009](#page9)) to treat an individual tree with a diameter at breast height (DBH) smaller than 3 cm as saplings/seedlings. We labeled the species that are commonly used for landscaping by referring to a list of ornamental plant species compiled for Guiyang (Wang and Yu [2010](#page9)).

Estimate taxonomic diversities

We used the equivalent number of species to represent taxo-nomic diversity at multiple spatial scales (Pavoine et al. [2016](#page9)). The equivalent number was defined as “the number of equally likely and maximally dissimilar species needed to produce the given value of quadratic entropy (Ricotta and Szeidl [2009](#page9))”. The taxonomic diversity of woody plants in 54 remnant patches were calculated at four levels: within patches (α-di-versity), among patches within groups (β1-diversity), among groups (β2-diversity) and at the whole study area (γ-diversity) (Table [2](#page9)).

The equivalent number for α-diversity within patches was calculated using Eq. ([1](#page9)) and ([2](#page9)).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Eα ¼ | 1 |  |  | ð1Þ |  |
|  |  |  |  |
| 1−Qα |  |  |
|  | N M | | S | ð2Þ |  |
| Qα ¼ ∑ ∑ wim | | | ∑ pkimplimdkl |  |
|  | i¼1 m¼1 | | k;l¼1 |  |  |

where N is the number of groups (N = 18). M is the number of patches in each group (M = 3). wim is the weight attributed to patch m in group i. In the same group, we think all the patches contributed equally to the group, so we give the equal weight to each patch in the same group, that is wim=1/MN for patch m in group i. pkim is the relative abundance of species k in patch m of group i. plim is the relative abundance of species l in patch m of group i. S is the number of species. dkl is the dissimilarity between species k and species l. The taxonomic dissimilarities between two species were defined by Pavoine et al. ([2016](#page9)): 0.25 for species in the same genus, 0.5 for species in the same family but different genera, 0.75 for species in the same order but different families, and 1 for species at different orders.

The equivalent number for β1-diversity among patches within groups was calculated following Eq. ([3](#page9)) and ([4](#page9)).

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Eβ1 ¼ | | |  | 1−Qα | | |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | ð3Þ |  |
| 1−Qα−Qβplot | | | | | | |  | i |  |  |  |  |  |  |  |  |  |  |  |
|  | β1 ¼ i | 1 | | iþ m;n | 1wi | | wi |  |  |  |  | k;∑l 1 | | kim lin | kl− 2 | | k;∑l 1 | kim lim | kl− 2 | | k;∑l 1 kin lin kl! | |  |
|  |  | N | | M i wim win | | | | | | | |  | S |  | 1 | | S |  | 1 | | S |  |  |
| Q |  | ∑ w | | ∑ |  |  |  |  |  |  |  |  |  | p p d |  |  |  | p p d |  |  |  | p p d |  |
|  |  | þ |  | þ | | | | ¼ | |  |  | ¼ |  |  | ¼ |  |
|  |  | ¼ |  | ¼ |  |  |  |  |  |  |  |  |  |  |

ð4Þ



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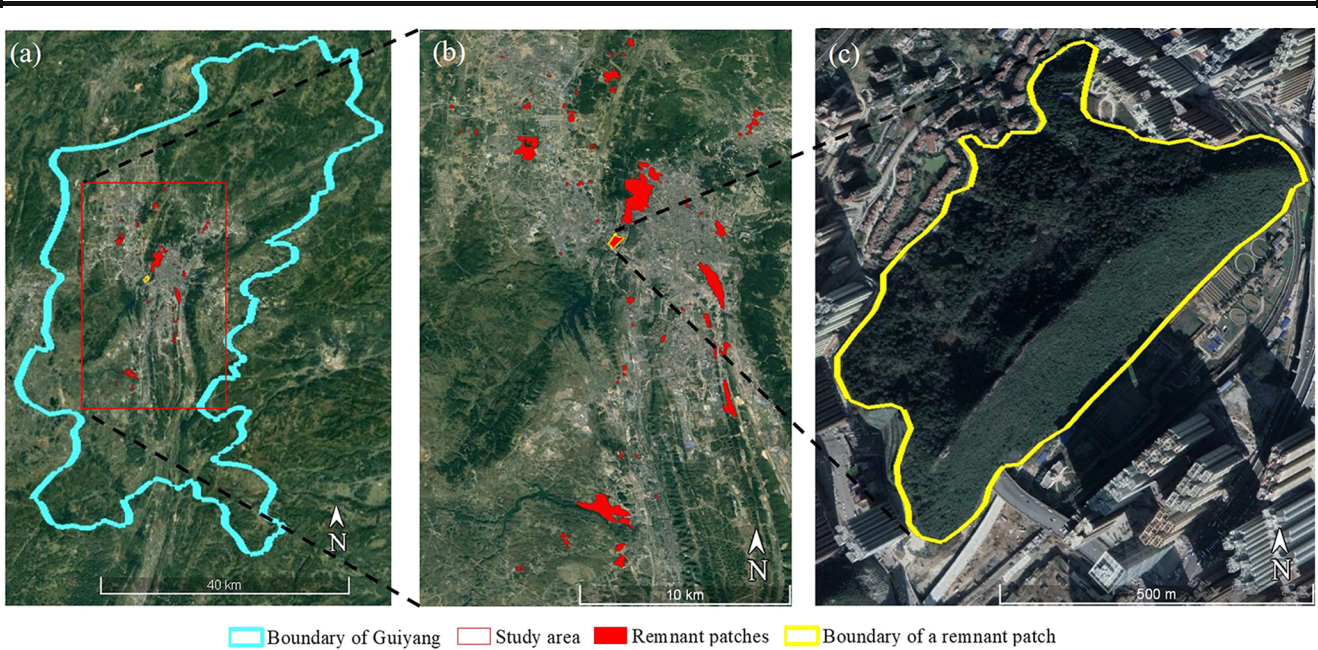


Fig. 1 The location of the study area. (a) The administrative boundary of Guiyang (blue outline) and the study area (red outline); (b) locations of the 54 forest patches as shown on Google Earth; (c) an example of a remnant forest patch

where wi+ is the weight attributed to group i. Similarly, we think all the groups contributed equally to the overall diversi-ty, so we give them equal weight to each group, that is wi+=1/ N for any group i. win is the weight attributed to patch n in group i. pkin is the relative abundance of species k in patch n of group i. plin is the relative abundance of species l in patch n of group i.

The equivalent number for γ-diversity at the study area was calculated using Eq. ([5](#page9)) and ([6](#page9)).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Eγ ¼ | 1 |  | ð5Þ |  |
|  |  |  |
| 1−Qγ |  |
|  | S | | ð6Þ |  |
| Qγ ¼ ∑ pkþþplþþdkl | | |  |

k;l¼1

where pk + + is the relative abundance of species k. pl + + is the relative abundance of species l.

The equivalent number for β2-taxonomic diversity among groups was calculated using Eq. ([7](#page9)).

|  |  |  |  |
| --- | --- | --- | --- |
| Eβ2 ¼ | 1−Qα−Qβ1 | ð7Þ |  |
| 1−Qγ |  |

In order to test the significance of differences in species composition, we rescaled the β components using Equation ([8](#page9)) and ([9](#page9)), and then applied the permutation tests to the nor-malized E\*\*β1 and E\*\*β2 components.

|  |  |  |  |
| --- | --- | --- | --- |
| Eβ\*\*1 ¼ | Eβ1−1 | ð8Þ |  |
|  |  |
| M −1 |  |
| Eβ\*\*2 ¼ | Eβ2−1 | ð9Þ |  |
| N −1 |  |

Analyze the factors affecting compositional dissimilarity of woody plants

Two patch attributes (the patch size and the vegetation type) and two indicators of the landscape patterns (the percentage of impervious surface in surrounding areas and the spatial dis-tance between patches) were used as predictors in this study. The Jaccard dissimilarity indicators of woody plant species between paired patches were calculated to represent the com-positional dissimilarity. Compositional dissimilarity means the difference in species composition among different com-munities (Legendre et al., [2005](#page9)). The generalized dissimilarity

Table 1 Information recorded in each sample plot



|  |  |  |
| --- | --- | --- |
| Category | Indicator | |
|  |  |  |
| Plot | Geographic coordinates; Altitude; Slope; Aspect | |
| Adult trees | Species name; DBH; Number of individuals; Ornamental species or not | |
| Saplings/seedlings | Species name; DBH; Number of individuals; Ornamental species or not | |
| Shrubs | Species name; the percentage of canopy cover; Ornamental species or not | |
|  |  |  |

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Table 2 Introduction of taxonomic diversity at four levels

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Diversity | Definition | Stratum | Number | |
|  |  |  | of | |
|  |  |  | stratum | |
|  |  |  |  |  |
| α-diversity | Dissimilarities | Individual patch | 54 |  |
|  | among species |  |  |  |
|  | from distinct |  |  |  |
|  | patches |  |  |  |
| β1-diversity Dissimilarities | | Patches in a group with | 18 |  |
|  | among patches | the same vegetation |  |  |
|  | from distinct | type, the size class, and |  |  |
|  | groups | the impervious area |  |  |
|  |  | class |  |  |
| β2-diversity Dissimilarities | | The group | 3 |  |
|  | among groups |  |  |  |
| γ-diversity | Diversity of all | A landscape with all | 1 |  |
|  | patches and | patches |  |  |
|  | groups combined |  |  |  |
|  | together |  |  |  |
|  |  |  |  |  |

modeling (GDM) (Ferrier et al. [2007](#page9)) was used to estimate the influences of the selected factors on the compositional dissim-ilarity. Following Ferrier et al. ([2007](#page9)), we derived three I-spline basis functions and calculated the value of each patch against each of the functions for each predictor. The absolute difference in the value of each I-spline basis function for all possible pairs of patches was then calculated. The matrix of the Jaccard dissimilarity indicators was used as the response matrix, and the absolute difference of I-spline basis functions as explanatory matrices in the GDMs to express the change in compositional dissimilarity along the gradient of a predictor. The percentage of change in deviance between the model fit with and without any one of variables was used to represent the relative importance of that predictor on affecting the var-iation of compositional dissimilarity. The vegetation type was modeled as a categorical variable.

All data analysis in this study was carried out using R version 3.5.3 (R Core Team [2019](#page9)). The matrix of taxonomic distance among species was calculated using the ade4 pack-age (Dray et al. [2018](#page9)). The equivalent numbers of species were calculated, and the permutation test was conducted using the adiv package (Pavoine [2017](#page9)). The GDM was conducted using gdm package (Manion et al. [2018](#page9)).

only in adult trees, only in sapling/seedlings, and in both adult trees and sapling/seedlings, respectively. In the shrub layer, a total of 126 species were identified. Native species accounted for 95.7% of all identified species, and 29% have been used as ornamental species in Guiyang (Table [3](#page9)). A list of species and abundances can be found in the supplementary material (Table [S1](#page9)).

The sampled coniferous forest, mixed forest, and broadleaf forest patches had different mean stem densities, basal areas, and dbh (Table [4](#page9)). Detailed descriptions of each individual patch can be found in Table [S2](#page9).

The hierarchical taxonomic diversity of woody plants was shown in Table [5](#page9). There were no significant differences among patches within a group (β1-diversity) for all the types of woody plants. However, the dissimilarities among groups (β2-diversity) were statistically significant for adult trees and saplings/seedlings.

The relative importance of predictors

The results of GDM showed that together the four predictors could explain 11.5%, 8.9%, 9.9%, 10.2%, and 14.8% of the variation in the compositional dissimilarity of adult trees, sap-lings/seedlings, trees, shrubs, and woody plants, respectively. The vegetation type and the patch size had higher relative importance than other variables (Table [6](#page9)).

The partial response graph of the GDMs shows how the rate of compositional turnover varies along the gradient of an explanatory variable. Compositional turnover is the change in species composition (Legendre et al., [2005](#page9)). The maximum height in the y-axis indicates the total amount of composition-al turnover associated with the variable, holding all other var-iables constant. The results indicated that the rates and total amount of compositional turnover were different for woody plants, tree species, adult trees, and sapling/seedlings, and shrubs (Fig. [2](#page9)).

Discussion

The remnant forest in Guiyang provides habitats to a large number of woody plant species, especially native species.

Results

Taxonomic diversity of woody plants of the remnant forest

We recorded a total of 305 woody plant species in the 54 remnant forest patches (Table [2](#page9)). Among the 179 identified tree species, 34 species, 50 species, and 95 species were found

Table 3 Number of species in different layers

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Traits |  | Adult tree | Sapling/seedling |  | Shrub | |
|  |  |  |  |  |  |  |
| Origin | Native | 123 | 141 | 121 | |  |
|  | Exotic | 6 | 4 | 5 | |  |
|  | Total | 129 | 145 | 126 | |  |
| Ornamental use | | 30 | 29 | 50 | |  |
|  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |



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Table 4 Mean stem density, basal area, and dbh of the three types of forest patches. Standard errors are shown in parentheses

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Characteristic | Coniferous | Mixed | Broadleaf | |
|  |  |  |  |  |
| Mean stem density (stem/ha) | 1025(150) | 1175(75) | 1525(125) | |
| Mean basal area (m2/ha) | 25.6(2.1) | 19.9(1.5) | 18.8(1.1) |  |
| Mean DBH (cm) | 16.8(1.3) | 12.8(0.6) | 11.5(0.5) |  |
|  |  |  |  |  |

We recorded 305 woody plant species, and 95.7% of these species were native species. On the contrary, only 117 woody plant species were found in planted urban green spaces in Guiyang, while over 40% of them were exotic species (Wang and Yu [2010](#page9)). This vast difference is because a few woody plant species, especially exotic species with high or-namental value, are frequently used in urban tree planting in China (Yan and Yang [2017](#page9)). The result showed that the rem-nant forest plays a vital role in conserving native woody plant species in a rapidly urbanized environment like Guiyang. Other studies had a similar finding. For example, native spe-cies account for over 90% of woody plant species found in the urban remnant forest in Puerto Rico (Lugo-Perez and Sabat-Guernica [2011](#page9)).

We found that the within-patch α-diversity of shrubs (Eα=4.48) was higher than that of trees (Eα=3.94). The lower Eα of trees may be due to their larger sizes, higher demands for living space, more extended growth period, and slower regen-eration than shrubs (Körner [2012](#page9)). The within-patch α-diver-sity of sapling/seedlings (Eα=3.61) was higher than that of adult trees (Eα=2.50). This pattern may be explained by the process of self-thinning occurring in the remnant forest patches, which prevent some species in the sapling/seedling layer to grow into adult trees (Schnitzler and Borlea [1998](#page9)).

All types of woody plants had non-significant composi-tional dissimilarities among patches within the same group (β1-diversity). This result showed that remnant patches with the same vegetation type, similar sizes, and similar percent-ages of surrounding impervious surfaces tend to have similar species composition of woody plants, no matter where they were located. The compositional dissimilarity among groups

(β2-diversity) of shrubs was lower than that of tree species. The lower β2-diversity and the higher percentage of ornamen-tal species in the shrub layer may indicate a homogenization effect possibly caused by the invasion of ornamental shrub species into the remnant forest patches. About 40% of shrub species found in the remnant forests were also used as orna-mental species, while this percentage for tree species was only 21%. Our finding was in contrast to the finding of early stud-ies that shrub species composition was more sensitive to the change of spatial patterns than tree species (Echeverría et al. [2007](#page9); Moffatt et al. [2004](#page9)).

The β2-diversity was significant for both adult trees and saplings/seedlings. This indicated that the patch size, the vegetation type, and the composition of land cover types in surrounding areas impacted the tree species composition of remnant patches. Heckmann et al. ([2008](#page9)) found that the species composition of trees differed significantly along the urban gra-dient. Here our result showed that the difference could not be attributed to urban gradient alone. In addition, the β2-diversity of adult trees was higher than that of sapling/seedlings. Saplings/seedlings are more vulnerable to human disturbances than adult trees (Ribeiro et al. [2016](#page9)). It is believed that species found in the sampling/seedling layer are more likely to be gen-eralists and have high urban tolerance. Urban tolerance is the ability of a species to tolerate soil compaction, water shortage, restricted small rooting space, and higher temperatures in cities (Nock et al. [2013](#page9)). In our study, 26% of tree species in the sapling/seedling layer can be classified as urban tolerant species according to the criteria specified in Roloff et al. ([2009](#page9)) (See Table [S3](#page9) for more details). The occurrence of 14 urban tolerant species in 18 groups was more than 50% (Table [S3](#page9)). This homogenization effect may partially explain the finding that the species composition of the saplings/seedings was more sim-ilar between patches than that of adult trees. This finding justi-fied the necessity to differentiate the ontogenetic stages of trees in studies. Because adult trees are longer-lived, so the rapid urbanization is a more important determinant of tree sapling/ seedling. This legacy effect may influence the future tree com-position in urban remnant forests if the impact of urbanization impedes the recruitment of canopy tree species significantly.

Table 5 Hierarchical taxonomic diversity (inside the parenthesis are P-values of the permutation tests)

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  |  |  | Adult tree | Sapling/ | Tree | Shrub | |
|  |  |  |  |  | seedling |  |  |  |
|  |  |  |  |  |  |  |  |  |
| Among groups | | | Eβ2 | 2.14 | 1.94 | 1.99 | 1.45 |  |
|  |  |  | E\*\* | 0.07(0.001) | 0.06(0.007) | 0.06(0.002) | 0.03(0.194) | |
|  |  |  | β2 |  |  |  |  |  |
| Among patches within groups | | | Eβ1 | 1.35 | 1.63 | 1.52 | 1.59 |  |
|  |  |  | E\*\* | 0.17(0.26) | 0.31(0.25) | 0.26(0.065) | 0.30(0.297) | |
|  |  |  | β1 |  |  |  |  |  |
| Within patches | | | Eα | 2.50 | 3.61 | 3.94 | 4.48 |  |
| Total | | | Eγ | 7.20 | 11.41 | 11.92 | 10.37 |  |
|  |  |  |  |  |  |  |  |  |



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Table 6 Relative importance (%) of predictors estimated using the GDMs

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Explained variable | Adult tree | Sapling/ Seedling | Tree | Shrub | Woody plant | |
|  |  |  |  |  |  |  |
| Patch size | 33.49 | 8.03 | 25.12 | 40.53 | 36.35 |  |
| Vegetation type | 48.00 | 61.67 | 51.28 | 38.43 | 40.32 |  |
| Percentage of impervious surface | 6.29 | 6.12 | 0.00 | 0.00 | 0.00 |  |
| Spatial distance | 12.17 | 19.04 | 20.10 | 18.68 | 20.82 |  |
| Overlap | 0.05 | 5.14 | 3.50 | 2.36 | 2.51 |  |
|  |  |  |  |  |  |  |

The GDM results further indicated that the effects of patch attributes and landscape patterns of surrounding environments varied among different types of woody plants. We found that the vegetation type of the remnant forest patch affected the compositional dissimilarity of sapling/seedlings among patches (61.67%) more than those of adult trees (48%) and shrubs (38.43%). Vegetation type influences the seed source from local canopy trees, the germination process, and habitat availability of sapling/seedlings (Olejniczak et al. [2018](#page9)). Therefore, the vegetation type accounted for a large portion of the variation in the species composition of saplings/seed-lings. The variation in the species composition of adult tree species in the same group was low because the vegetation type was mainly determined by the dominant species in adult trees. Early studies have found that the vegetation type can affect the compositional dissimilarity of woody plants (Akinyemi et al. [2019](#page9); Zhang et al. [2016](#page9)). We further showed that the magni-tude of influence was different for different types of woody plants.

The patch size has a higher relative importance in affecting the compositional dissimilarity of shrubs (40.53%) than for adult trees (33.49%) and sapling/seedlings (8.03%). A possi-ble mechanism through which the patch size influences the compositional dissimilarity of a plant community is to provide different light conditions to plants in interior and edge zones, especially for the understory plants (Harper et al. [2005](#page9)). The low impact on the composition similarity of sapling/seedlings may be due to their tolerance to a low-light condition at this ontogenetic stage. Also, we found that the slope of curves was steeper when the size of the patch was smaller (Fig. [2c, d, e](#page9)), which indicated that the rates of compositional turnover along the patch size for woody plant species, tree species, and shrub species increased faster when the patch size was smaller. This finding might be due to the fact that small patches often pos-sess some unique species (Wintle et al. [2018](#page9)). While the im-portance of large patches in maintaining the α-diversity has been well noted in other studies (Capmourteres and Anand [2016](#page9); Nielsen et al. [2014](#page9)), our results showed the importance of preserving the small patches in order to maintain the β-diversity of the entire urban remnant forest.

The influence of landscape patterns of surrounding areas on the compositional dissimilarity of woody plants was de-tectable but considerably lower than these of patch attributes. The percentage of impervious surfaces in surrounding areas

influenced the compositional dissimilarity of adult trees (6.29%) and sapling/seedlings (6.12%) more than that of shrubs (0%). Existing studies found that the increase of im-pervious cover in surrounding areas leads to homogenization of species composition due to the decrease of specialists and the increase of commonly shared species (Uchida et al. [2018](#page9)). Our result showed that this effect was relatively small and primarily associated with tree species. Furthermore, the rates of compositional turnover along the percentage of impervious surfaces for adult trees and sapling/seedlings reached asymp-tote when the percentage of impervious surfaces reached about 35%. This indicated that the influence of surrounding impervious areas on the compositional dissimilarity of trees in remnant forests stayed at a certain level when the percentage of the impervious area was high. A possible explanation is that the homogenization effect by surrounding areas reached the balance with the intrinsic dynamics of the woody plant com-munity (Zelnik et al. [2018](#page9)). However, more studies are needed to test this explanation.

The relative importance of spatial distance on the composi-tional dissimilarity of adult trees (12.17%) was less than sapling/seedlings (19.04%) and shrubs (18.68%). Spatial dis-tances affect the species composition of patches through spa-tially structured speciation or seed dispersal patterns (König et al. [2017](#page9)). Therefore, the spatial distance was more closely associated with the compositional dissimilarity of sapling/ seedlings because the seed dispersal affected sapling/seedlings more directly than adult trees. The GDM analysis showed that the four predictors explained less than 15% of the variation in the data. The seemly low explanation power by the four pre-dictors is expected because the species diversity of remnant forests is affected by myriad exogenous and endogenous factors (Hahs and McDonnell [2007](#page9); Heckmann et al. [2008](#page9); Ramalho et al. [2014](#page9)). However, our analysis confirmed that the effects of the four predictors were significant and detectable.

Our findings have some implications for conserving rem-nant forests in rapidly urbanized regions: (1) It is equally im-portant to preserve large remnant patches and small remnant patches. Our results showed that while large patches had higher α-diversity than that of small patches, small patches are important to maintaining the taxonomic β-diversity among patches. Also, small patches often face higher risks than larger patches to be developed. (2) More attention should be paid to sapling/seedlings in the remnant forests. Although



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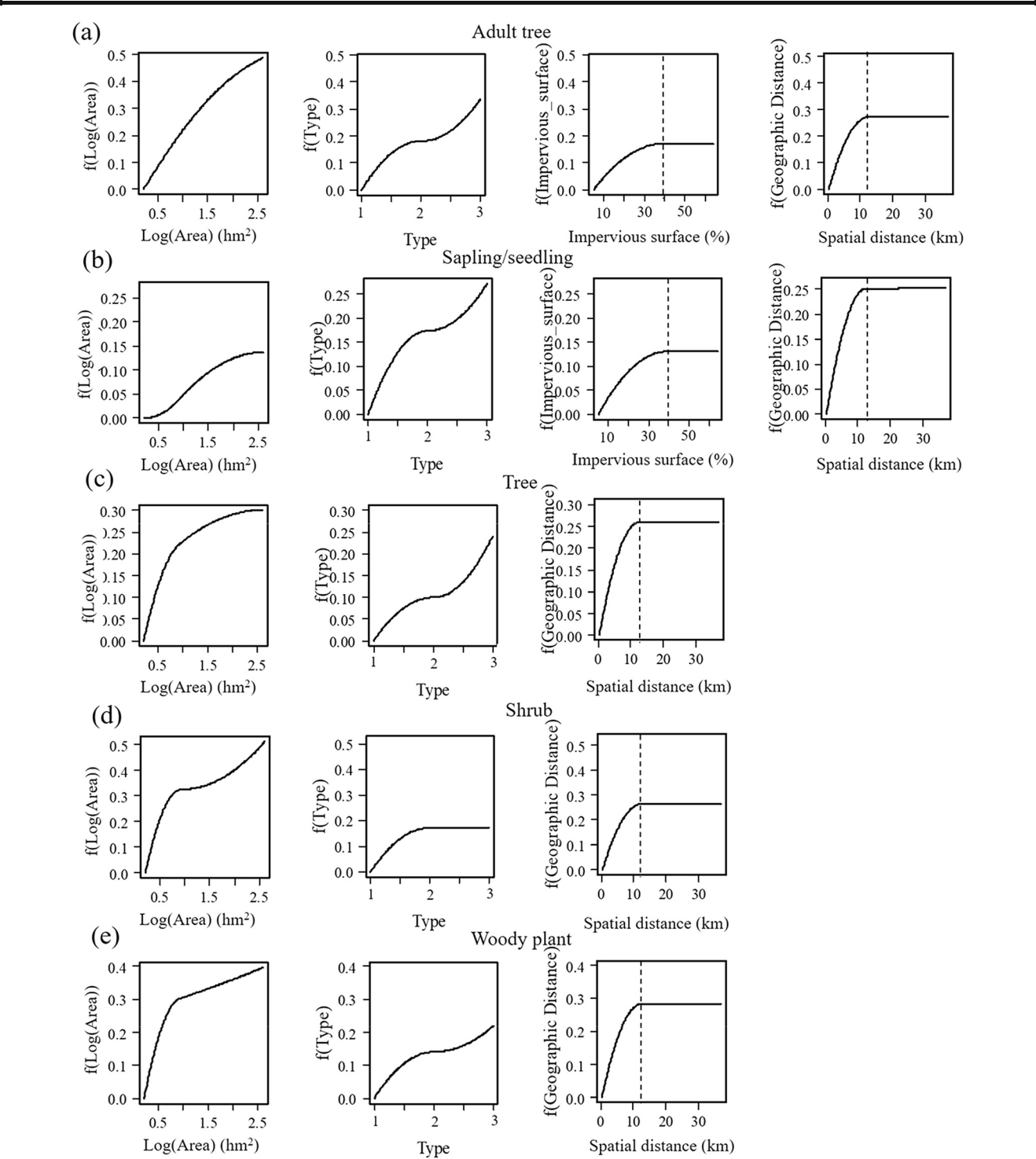


Fig. 2 Partial response graph of the GDMs for (a) adult trees, (b) sapling/ seedlings, (c) trees, (d) shrubs, and (e) woody plants. Type 1 for coniferous forest stands, 2 for mixed forest stands, and 3 for broadleaf

forest stands. The percentage of impervious surface areas was not a significant factor for shrub and all woody plants

the sapling/seedling layer in the remnant forests had higher α-diversity than that of adult trees, its β-diversity was lower. Conservation programs only focused on preserving the diver-sity of adult trees may neglect the risk of homogenization in the future.



While our study provides useful information for conserving remnant forests in urban environments, there are some limita-tions that should be noted. We used 500 m as the buffer dis-tance to study the impact of landscape patterns of surrounding areas on species diversity of remnant patches. A range of

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buffer distances can be used to examine the impact at different spatial scales. In addition, we only considered the geographic distance in this study. Distance metrics that incorporate the heterogeneity of urban matrix (e.g., least-cost distance) may characterize the resistance to species dispersal better. Despite these limitations, to look into the divergent impacts on differ-ent types of woody plants and to treat the landscape patterns of surrounding areas explicitly in the analysis have helped us to gain a better understanding of the interactions between the remnant forest and the urban environment. As most studies on this topic were conducted in cities located in the temperate climate zone, an additional benefit of our study is that the applicability of findings from existing studies to other regions can be tested.

Conclusion

Knowledge of the woody plant species diversity of remnant forests in urban areas and the factors influencing the diversity is crucial for their conservation. In this study, we quantified the taxonomic diversity of woody plants in a remnant urban forest at multiple levels. We analyzed the relative importance of patch attributes and the landscape pattern of surrounding environments on the compositional dissimilarity of woody plants. Our results revealed a divergent pattern of influences on different types of woody plants. Based on our results, we recommended to preserve small remnant patches and pay more attention to the species composition of the sapling/ seedling layer in order to maintain the β-diversity of remnant forest. Our study provides useful information on preserving the plant diversity of remnant urban forests in rapidly urban-ized regions. Future studies can build upon our study to further explore the influence of the urban matrix on remnant forests.

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