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Effect of urbanization on the structure and functional traits of remnant subtropical evergreen broad-leaved forests in South China

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Abstract We investigated the effects of major environmental drivers associated with urbanization on species diversity and plant functional traits (PFTs) in the remnant subtropical evergreen broad-leaved forests in Metropolitan Guangzhou (Guangdong, China). Twenty environmental factors including topography, light, and soil properties were used to quantify the effects of urbanization. Vegetation data and soil properties were collected from 30 400-m^2 plots at 6 study sites in urban and rural areas. The difference of plant species diversity and PFTs of remnant forests between urban and rural areas were analyzed. To discern the complex relationships, multivariate statistical analyses (e.g., canonical correspondence analysis and regression analysis) were employed. Pioneer species and stress-tolerant species can survive and vigorously establish their population dominance in the urban environment. The native herb diversity was lower in urban forests than in rural forests. Urban forests tend to prefer the species with Mesophanerophyte life form. In contrast, species in rural forests possessed Chamaephyte and Nanophanerophyte life forms and gravity/clonal growth dispersal mode. Soil pH and soil nutrients (K, Na, and TN) were positively related to herb diversity, while soil heavy metal concentrations (Cu) were negatively correlated with herb diversity. The herb plant species diversity declines and the species in the remnant forests usually have stress-tolerant functional traits in response to urbanization. The factors related to urbanization such as soil acidification, nutrient leaching, and heavy metal pollution were important in controlling the plant diversity in the forests along the urban–rural gradients. Urbanization affects the structure and functional traits of remnant subtropical evergreen broad-leaved forests.

Keywords Urbanization · Subtropical forest · Pioneer species · Herb diversity · Environmental stress

Abbreviations

PFTs	Plant functional traits
CCA	Canonical correspondence analysis
BYu	Baiyun
PGu	Pugang
LGu	Luogang
SZr	Shizao
SMr	Shimen
BMr	Baimantan

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D Simpson's index
J Pielou index

Introduction

Rapid urbanization has resulted in severe forest degradation and even total destruction worldwide (McKinney 2002). Remnant forests in urban settings serve as refugia for native species and thereby contribute to biodiversity conservation and restoration (Wang et al. 2007). Such remnant forests, however, have only recently received attention from policy makers and scientists (Guntenspergen and Levenson 1997; Hahs and McDonnell 2007). Currently, the effect of urbanization on forests has received worldwide attention (Heckmann et al. 2008; Porter et al. 2001). Species diversity, which plays a critical role in ecosystem productivity and stability, reflects the responses of individual plant species to urban intensity and urban proximity (Johnson et al. 1996). The majority of studies on the impact of urbanization on plant species diversity have focused on the assessment of the pattern of species diversity along the urban–rural gradient, i.e., unimodal, positive monotonic, peaked, and U-shaped (Mackey and Currie 2001).

As suggested by Petchey and Gaston (2002), the concept of plant functional traits (PFTs) is stronger than species diversity in illustrating the response of species to disturbance. Up to now, many studies have investigated how the distribution of different PFTs vary in different land-use types (e.g., urban, agricultural, rural, and forested landscape) (Knapp et al. 2008c) and are related to different landscape characteristics (e.g., patch area and isolation) (Godefroid and Koedam 2003). We already know that plant phenology is shifted in urban plant communities compared to rural plant communities (Luo et al. 2007); species in urban areas have high demands for light and nutrients (Lososová et al. 2006), higher specific leaf area (Knapp et al. 2008c), shorter life span and higher dispersal capacity than species in rural areas (Jacquemyn et al. 2003; Kühner and Kleyer 2008; Kleyer 1999), and prefer dry, base-rich, fertile habitats (Thompson and McCarthy 2008). However, most recent findings of PFTs studies have examined the impact of urbanization on plant communities in Central Europe and North America (Vallet et al. 2010). Further studies are needed to detect which PFTs in subtropical forests are associated with plant survival under potential urbanization stress. PFTs between urban and rural forests may reflect the changes linking to the regeneration and persistence of species (Kühner and Kleyer 2008; Knapp et al. 2008a, b; Williams et al. 2005). Human activities change plant composition in part by favoring exotic species or pioneer species (Günter et al. 2009). The native species that survive in the urban environment are usually those that tolerate barren environments or that regenerate aggressively following disturbances (Sagar et al. 2003; Zhu et al. 2007).

Plant composition and species diversity in urban remnant forests have been shown to be associated with landscape context (Reitalu et al. 2009) and with the intensity of present management (Aavik et al. 2008) and have been expected to differ in their response to soil chemical and physical properties (Ma 2005). The relationships between urbanization-related factors (e.g., different types of built area, socioeconomic factors, geological diversity, sample scale, habitat loss) and plant species richness have been investigated in Rome, Brussels, Phoenix (AZ), Central Germany, and Plzeň (Celesti-Grapow et al. 2006; Godefroid and Koedam 2007; Hope et al. 2003; Knapp et al. 2008a, b; Kühn et al. 2004; Pautasso 2007; Pyšek et al. 2004). Although changes in the structural patch isolation and connectivity in urban and surrounding landscape could determine the availability of seed resource and restrict the distribution of species assemblage in remnant forests (Cunningham 2000), environmental pollution and deterioration caused by urbanization could prevent the local plant diversity in the understory layer from returning to its original status (Forey et al. 2008; García-Mora et al. 1999). Some ecologists insisted that species richness is predominantly controlled by local ecological factors and only secondarily by factors operating at the landscape level (Marini et al. 2007; Wright et al. 2003). Tait et al. (2005) suggested that the effects of shifts in environmental factors driven by urbanization may have a long-term significant effect on the plant communities. It is necessary to identify the cause-and-effect relationship between urbanization impact and plant characteristics, which will be helpful in current and future management of the remnant forests in the urban environment.

There is abundant literature on plant characteristics of temperate and boreal forests in urban areas (see above), but there is indeed not much literature on the effect of urbanization on the plant species diversity and PFTs in subtropical forests. The subtropical evergreen broad-leaved forest is one of the main subtropical forest types in South and East Asia, but has experienced significant pressure from rapid urbanization (Ohsawa 1990; Wang et al. 2006). South China is a major location of evergreen broad-leaved forests (Kira 1991), which has experienced large-scale land-use changes during the last decades. Although governmental policies have helped increase the coverage and volume of forests, the regenerated forests mainly consist of young, simple, and single-layer vegetation (Guo et al. 2006). The remnant evergreen broad-leaved forests in South China are scattered in patches of varying sizes and have experienced acid rain, nitrogen deposition, and heavy metal pollution. Although some of these remnant forest patches have been widely studied at local scales (Yin et al. 2002; Cai et al. 1998), they have not been investigated with respect to the mechanisms acting between the impact of urbanization-related factors and plant characteristics to guide their management, conservation, and restoration. For this reason, we investigated the remnant subtropical evergreen broad-leaved forests in urban and rural areas in South China and attempted to answer the following specific questions: (1) How does urbanization affect the species diversity and PFTs in the subtropical evergreen broad-leaved forests? and (2) What are the dominant environmental drivers associated with the urbanization effects (i.e., along the urban–rural gradients)?

Methods

Site selection and description

The study area is located at Guangzhou (112°57′–114°3′ E, 22°26′–23°56′ N), the capital and the political and economical center of Guangdong Province in South China. The area is characterized by a typical subtropical monsoon climate with southwest prevailing wind in summer and north prevailing wind in winter. The average annual temperature is about 21.5 °C. The annual precipitation ranges from 1,370 to 1,965 mm, with a distinct wet season from April to September and the dry season from October to March. The potential zonal climax vegetation of the region is subtropical evergreen monsoon broad-leaved forests (Editorial Committee of Forests of Guangdong 2005). The soil type is lateritic red soil developed from granite and sand shales. Guangzhou has a total area of 7,434 km^2 and had a population of about 10,000,000 in 2008. Since the late 1970s, it has undergone a rapid transition from traditional agriculture-based economy to industry-based and technology-based economy. Moreover, increasing urbanization has caused serious environmental degradation to the remnant urban forests. As one of the most densely populated areas on Earth, Guangzhou accurately has an area of only 290 km^2 of natural secondary forests, in the form of natural reserves, fengshui (sacred) forests, and scenic forests. The 290-km^2 area contains 9.4 % of the total forest area and 3.9 % of the greater Guangzhou area (Zhang et al. 2004).

To minimize sampling error, we selected sample forests by the following three criteria: first, the forests contained late successional stage vegetation typical of the Pearl River Delta; second, the forest patch areas were >1 ha and at least 1 km away from a major highway; and third, the forests are in protected areas and had not directly experienced natural and anthropogenic disturbances for at least 50 years. Thirty plots of forests (each 20×20 m) of about 12,000 m^2 were surveyed according to these criteria: five in Baiyun Mountain (BYu) of Baiyun District (resident population density of 2,057 individuals km^{-2}), five in Pugang (PGu) of Tianhe District (resident population density of 11,930 individuals km^{-2}), five in Luogang (LGu) of Luogang District (resident population density of 563 individuals km^{-2}), and five in each of Shizao (SZr), Shimen (SMr), and Baimangtang (BMr) of Conghua District (resident population density of 262 individuals km^{-2}) (Guangzhou Yearbook Editorial Committee 2010) (Fig. 1). BYu, PGu, and LGu represent the urban area where most industry factories and residential buildings are situated, respectively. SZr, SMr, and BMr are located in natural reserves, about 70–78 km away from the center of Guangzhou, and considered as the rural area. The sample plots in urban and rural areas were selected based on satellite images and field reconnaissance to represent the entire range of conditions presenting in these remnant forests.

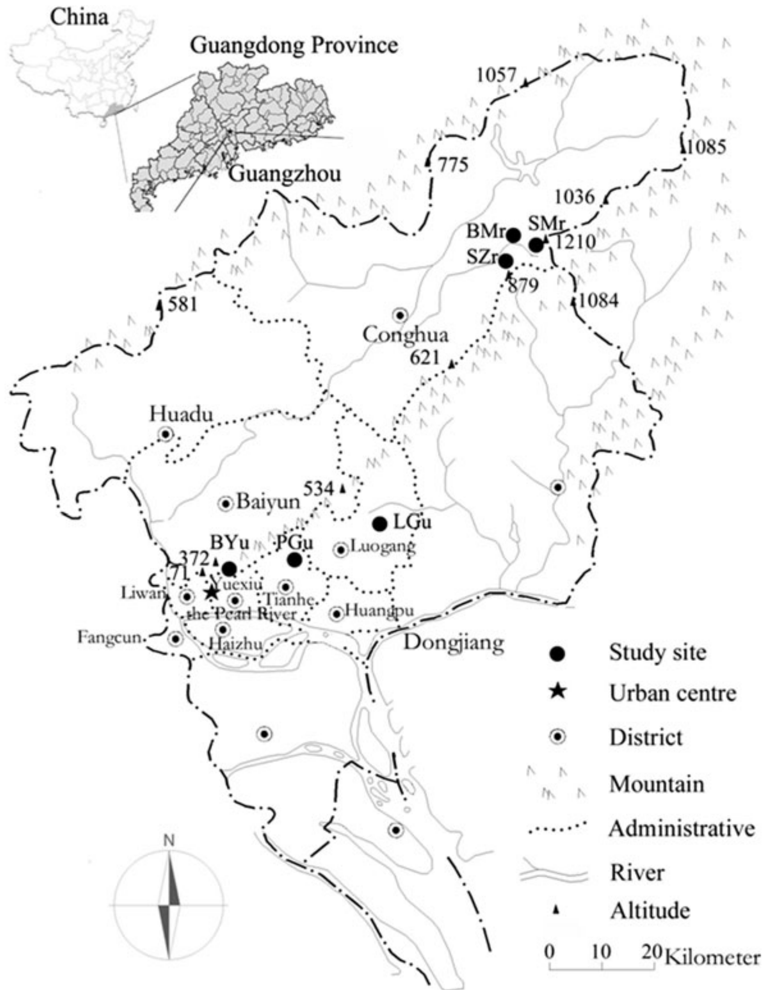

Fig. 1 The location of the six study sites (*BYu*, *PGu*, *LGu*, *SZr*, *SMr*, and *BMr*) in Guangzhou, indicated by the *solid circles*

Plant species sampling and functional trait classification

This research was carried out from March 2009 to March 2010. Five plots, each of 400-m^2, were selected and divided into four 100-m^2 (10×10-m) quadrats at each study site. Woody species, i.e., trees with diameter at breast height (1.3 m height) >2 cm, were counted and identified in each quadrat. Shrubs and herbs were counted and identified in a 5×5-m subquadrat and a 1×1-m subquadrat that were randomly located within each quadrat, respectively. We identified species and noted their characteristics according to the Flora of China (Liu 1996). We chose PFTs which could be easily determined based on available published data and field data for each plant species in the study and then could be classified according to their known or assumed relationship to disturbance (Cornelissen et al. 2003). The PFTs classified into groups concerned the capacity of dispersal, establishment, and persistence (for a listing of trait groups, PFTs, and function, see Table 3).

Environmental factors analysis

Topographical factors such as altitude and slope were recorded using the Global Positioning System. Light intensity in the understory was measured at 1.3 m height with an LI-250 light meter (LI-COR, Lincoln, NE, USA) at 12:00 of the day with no visual cloud cover and corrections for open sky light readings.

Soil sample collection and analysis

Approximately six soil cores (5 cm diameter, 0–20 cm depth) were collected and mixed from each quadrat.

We collected a total of 120 soil samples in all sites, which were pooled, air-dried, passed through sieves, and then subjected to chemical analysis. For the determination of soil physical properties, three soil cores were randomly collected with a cutting ring (100 cm^3, 10 cm depth) from each quadrat (Table 1).

Data analysis

CANOCO 4.5 for Windows was conducted to analyze the data set (30 sample plots, 308 species) to describe the variances of species composition at different land-use sites with canonical correspondence analysis (CCA) species–samples biplot. R Language 2.11.0 was conducted to calculate the three biodiversity indices (Magurran 1988): (1) Shannon–Wiener index $H=-\sum P_i \ln P_i$, where P_i is the relative abundance of i species at each quadrat and H describes the species richness and the equitability of individual distribution within species; (2) Simpson's index $D=1-\sum P_i^2$, where P_i is the proportion of the individuals in species i and D reflects the dominance in the community; and (3) Pielou's index $J=H/\ln S$, where S is the number of species and J reflects the evenness in the community. Species diversity indices and environmental factors were compared among the six study sites using one-way analysis of variance (ANOVA). We used chi-square tests to assess the heterogeneity of PFTs among the six study sites. According to the chi-square test, traits were significantly different among the six study sites when $P<0.05$.

In order to analyze the relationships between environmental factors and plant distribution, we first selected the weighted averaging method (detrended correspondence analysis) with detrending for indirect gradient analysis for a constrained analysis. Since the largest gradient value was larger than 4.00 (4.89 in our results), we then employed unimodal methods (CCA) for further analysis. CCA is an effective ordination method to analyze the relationships between plant distribution and environmental factors (Ter Braak et al. 2004). In our analysis, the data matrix consisted of

Table 1 Standard test methods for laboratory determination of soil physical and chemical properties

Soil properties	Measurement	References
pH	Extracted in 1 M KCl with a soil-to-solution ratio of 1:2.5 with a pH meter	Rowell (1994)
Moisture content	Weighed for moisture content by the mass method before being dried to constant temperature (105 °C)	Liu et al. (1996)
Bulk density	Weighed after being dried to constant temperature (105 °C) and calculated the dried soil quality in unit volume	Liu et al. (1996)
TP	Determined by the HF–$HClO_3$ digestion method followed by Mo–Sb colorimetric method	Liu et al. (1996)
Available phosphorus (Olsen-P)	Extracted in a solution of 0.025 M HCl and 0.03 M NH_4F and determined by Mo–Sb colorimetric method	Liu et al. (1996)
TN	Determined with K-06 full automatic azotometer	Liu et al. (1996)
Ammonium nitrogen (NH_4^+)	Determined by the indophenols blue method followed by colorimetry	Liu et al. (1996)
Nitrate nitrogen (NO_3^-)	Determined after cadmium reduction to NO_2^-, followed by the sulfanilamide–NAD reaction	Liu et al. (1996)
Organic carbon (SOC)	Determined by potassium dichromate oxidation titration and outside heating method	Liu et al. (1996)
Cu	Extracted by HF–$HClO_4$–HNO_3 digestion method and determined with flame atomic absorption spectrophotometer	Nieuwenhuize et al. (1991)
Cd		Nieuwenhuize et al. (1991)
Pb		Nieuwenhuize et al. (1991)
Zn		Nieuwenhuize et al. (1991)
Ca		Nieuwenhuize et al. (1991)
Mg		Nieuwenhuize et al. (1991)
K		Nieuwenhuize et al. (1991)
Na		Nieuwenhuize et al. (1991)

30 samples, and 20 environmental factors were used to examine the species–environment relationships. Pearson correlation analysis was used to determine the relationships between the 20 environmental factors and 3 plant diversity indices of tree, shrub, and herb layers, respectively. We also use stepwise forward selection to select variables which have significant impacts on species composition by CANOCO 4.5 for Windows. Linear regression was used to create the response curves between significant variables and Shannon–Wiener index in the herb layer.

Results

The characteristics of plant composition, species diversity, and PFTs between urban and rural forests

The species with higher weight (i.e., dominant species) of the total number of species and their relationships with plots were shown in Fig. 2. We observed distinct characteristic species in urban sites such as BYu and PGu, i.e., *Lophatherum gracile* and *Ixora chinensis* (species preferred forest edges and roadside) and *Acronychia pedunculata* (a common shrub species of secondary forests). As typical mesophilic species,

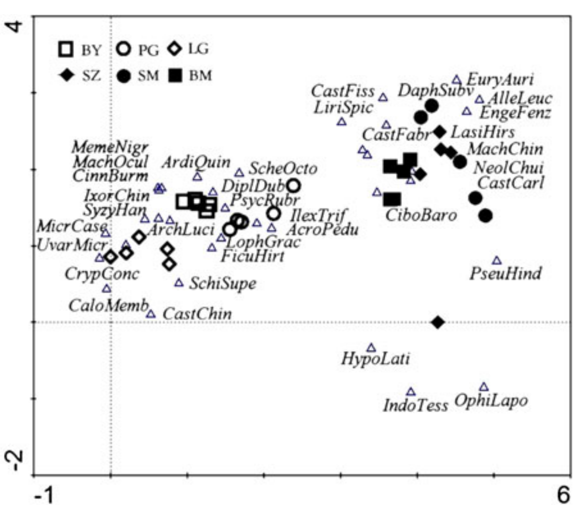

Fig. 2 Two-dimensional CCA ordination diagram of the first two axes showing the distribution of 30 sampling plots and species with the weight >3 % in total layer (*triangles and abbreviated Latin names*, with the *first four letters* stand for genus name and the *last four letters* stand for species name, respectively)

Cryptocarya concinna, *Calophyllum membranaceum*, and *Microdesmis casearifolia* completely dominated the tree, shrub, and herb layers at the LGu site (Fig. 2). While in rural areas, multiple dominant species consisted of *Machilus chinensis*, *Pseudosasa hindsii*, *Indocalamus tessellatus*, *Cibotium barometz*, *Alleizettilla leucocarpa*, and *Eurya auriformis*, all shade-tolerant and hygrophilous herbaceous species (Fig. 2).

Values for the Shannon–Wiener index (H), Simpson's index (D), and Pielou index (J) were shown in Table 2. In the tree layer, H, D, and J values tended to be higher in rural areas than in urban sites, and medium in the LGu site. In the shrub layer, there was no difference between urban and rural areas. In the herb layer, H, D, and J values were significantly higher in rural forests than in urban sites.

The number of species with PFTs favoring persistence, dispersal, and establishment varied among different study sites. Three traits (i.e., Mesophanerophyte life form, gravity/clonal growth dispersal mode, and drupe fruit types) were significantly different among the six sites. In urban areas, the percentages of species with those PFTs were similar at PGu and LGu but different from BYu. In rural areas, the percentages of species with those PFTs were similar at SZr, SMr, and LGu. The differences in the percentage of species with PFTs among the six sites indicated two opposite trends of PFTs in urban and rural forests. For instance, species with the followings traits were more likely to colonize rural than urban sites: the Chamaephyte and Nanophanerophyte life form, gravity/clonal growth dispersal mode, and capsule fruit types (Table 3). In contrast, species with the Mesophanerophyte life form and drupe fruit types tended to have the abilities to survive and take over the population dominance in the urban environment (Table 3).

Relationships between environmental stress and plant characteristics

Soil conditions were more acidified in urban areas compared to rural areas (Table 4). Compared to the background value of surface soil in Guangdong Province (Soil Survey Office of Guangdong Province 1993), Pb, Cd, and Zn concentrations in both urban and rural forest exceeded the background value of 35.87, 0.094, and 49.71 mg kg^{-1}, respectively. The soil heavy metal concentrations (Cu and Pb) and soil bulk

Table 2 Species diversity indices at the six study sites

Diversity indices		Values of diversity indices (mean ± SE)					
		Urban			Rural		
		BYu	PGu	LGu	SZr	SMr	BMr
Shannon–Weiner index (*H*)	Tree layer	2.08±0.10b	2.23±0.13b	2.63±0.11a	2.82±0.17a	2.75±0.19a	2.83±0.19a
	Shrub layer	3.05±0.03a	2.03±0.12b	2.16±0.12b	2.51±0.27ab	2.22±0.29b	2.79±0.13a
	Herb layer	1.46±0.31b	0.73±0.23c	0.73±0.25c	2.51±0.14a	2.00±0.11ab	2.13±0.24a
Simpson's index (*D*)	Tree layer	0.81±0.02b	0.84±0.01b	0.88±0.01a	0.92±0.01a	0.92±0.01a	0.92±0.01a
	Shrub layer	0.94±0.00a	0.80±0.04b	0.77±0.03b	0.81±0.06ab	0.78±0.08b	0.88±0.03ab
	Herb layer	0.55±0.03bc	0.39±0.02c	0.32±0.02c	0.87±0.01a	0.80±0.02ab	0.81±0.02ab
Pielou index (*J*)	Tree layer	0.80±0.03bc	0.77±0.02c	0.84±0.02ab	0.89±0.01a	0.89±0.02a	0.90±0.02a
	Shrub layer	0.88±0.01a	0.74±0.03ab	0.68±0.04b	0.69±0.07b	0.66±0.08b	0.78±0.03ab
	Herb layer	0.54±0.11ab	0.56±0.15ab	0.37±0.14b	0.81±0.05a	0.79±0.04a	0.74±0.03a

Means in a row followed by different letters are significantly different ($P<0.05$) according to the one-way ANOVA and least significant difference test

density were higher in urban areas than in rural areas. Soil Cu concentrations in urban forests reached or even exceeded the background value of 17.0 $mgkg^{-1}$. However, the concentrations of soil basic elements (K and Na) and nutrients (total nitrogen [TN] and ammonia [NH_4^+]) were higher in rural areas than in other sites.

All canonical axes of CCA were significant ($F=0.87$, $P=0.002$ and $F=2.57$, $P=0.002$, respectively). The CCA results indicated that the first axis and the second axis (which explained 17.8 and 33.6 % of the variance in species data and 20.9 and 39.4 % of the variance in the relationship between species and environment, respectively) were sufficient to explain the species–environment relationships in the data (Fig. 3). From Fig. 3, we found a very clear separation of plots between urban and rural areas associated with different environmental factors (i.e., topography, light, and soil properties). Specifically, plots within urban areas were related to soil Cu and total phosphorus (TP) concentrations, soil bulk density, and light intensity, while plots in rural areas were tied to altitude, slope, soil pH, and soil Na and K concentrations.

In order to further identify the effect of each environmental factor on plant distribution, we used the automatic forward selection to inspect the marginal effects of all environmental factors with the Monte Carlo tests by using CANOCO. Table 5 showed that the marginal effects of altitude, soil Na and K concentrations, soil pH, and light intensity on plant species were higher than other factors (Lambda1> 0.60). Monte Carlo test showed that these variables significantly affected plant composition ($P=0.002$). In addition, slope, soil organic carbon (SOC), and soil Zn, nitrate (NO_3^-), and TN concentrations had significant impacts on plant composition ($P<0.05$) (Table 6).

Since the patterns of the Shannon–Wiener index between urban and rural forests were similar with Simpson's index and Pielou's index (Table 2), we used the linear regression model to analyze the correlation between Shannon–Wiener index in herb layer and significant environmental factors (Fig. 4). Soil pH and soil K, Na, and TN concentrations showed positive correlations with herbaceous diversity, which indicated that herbaceous diversity was negatively related to soil acidification and positively correlated with soil nutrients (Fig. 4a–d). Specifically, herbaceous diversity showed negative correlations with soil heavy metals including Cu concentrations (Fig. 4e).

Discussion

The difference of plant composition, species diversity, and PFTs between urban and rural forests

The CCA diagrams showed that the distribution of shade-intolerant pioneer species in urban areas was

Table 3 The percentages of plant species and the number of species (in parentheses) possessing functional traits at the six study sites

Trait group	Trait	Functions related to urbanization pressure	P value	Species with indicated trait % (number) for each site					
				Urban			Rural		
				BYu (93)	PGu (54)	LGu (66)	SZr (176)	SMr (159)	BMr (108)
Leaf life span	Deciduous	Establishment, persistence	0.77	5.38 (5)	7.41 (4)	3.03 (2)	3.41 (6)	4.4 (7)	4.63 (5)
	Evergreen		1.00	92.5 (86)	90.7 (49)	95.5 (63)	94.9 (167)	93.7 (149)	94.4 (102)
	Deciduous/ evergreen		0.99	2.15 (2)	1.85 (1)	1.52 (1)	1.7 (3)	1.89 (3)	0.93 (1)
Leaf hairiness	Pubescent	Persistence (response to stress)	1.00	25.8 (24)	27.8 (15)	28.8 (19)	26.1 (46)	27 (43)	26.9 (29)
	Hairless		0.89	66.7 (62)	68.5 (37)	60.6 (40)	59.1 (104)	56.6 (90)	62 (67)
	Pubescent/hairless		0.10	7.53 (7)	3.7 (2)	10.6 (7)	14.8 (26)	16.4 (26)	11.1 (12)
Leaf texture	Herbaceous	Persistence (plasticity/response to stress)	0.97	7.53 (7)	7.41 (4)	4.55 (3)	6.25 (11)	5.66 (9)	6.48 (7)
	Herbaceous to membranous		1.00	0 (0)	0 (0)	0 (0)	1.14 (2)	1.26 (2)	0.93 (1)
	Membranous		0.93	2.15 (2)	1.85 (1)	0 (0)	1.14 (2)	1.26 (2)	0.93 (1)
	Membranous to papyraceous		0.57	3.23 (3)	5.56 (3)	4.55 (3)	2.27 (4)	1.89 (3)	4.63 (5)
	Papyraceous		0.20	34.4 (32)	20.4 (11)	16.7 (11)	28.4 (50)	27 (43)	26.9 (29)
	Papyraceous to coriaceous		0.12	8.6 (8)	14.8 (8)	19.7 (13)	10.2 (18)	10.1 (16)	8.33 (9)
	Coriaceous		0.93	44.1 (41)	50 (27)	54.5 (36)	50.6 (89)	52.8 (84)	51.9 (56)
Life form	Chamaephyte	Persistence (competitive ability, longevity)	0.20	20.4 (19)	11.1 (6)	9.09 (6)	19.9 (35)	15.7 (25)	19.4 (21)
	Geophyte		0.97	2.15 (2)	1.85 (1)	0 (0)	2.84 (5)	2.52 (4)	1.85 (2)
	Nanophanerophyte		0.16	26.9 (25)	16.7 (9)	18.2 (12)	27.8 (49)	33.3 (53)	27.8 (30)
	Microphanerophyte		0.72	37.6 (35)	40.7 (22)	42.4 (28)	31.8 (56)	34.6 (55)	31.5 (34)
	Mesophanerophyte		0.02	12.9 (12)	29.6 (16)	28.8 (19)	17.6 (31)	13.8 (22)	18.5 (20)
	Therophyre		0.74	3.23 (3)	0 (0)	1.52 (1)	1.14 (2)	1.26 (2)	0.93 (1)
Dispersal mode	Wind	Dispersal, establishment	0.73	12.9 (12)	11.1 (6)	10.6 (7)	7.39 (13)	8.18 (13)	8.33 (9)
	Gravity/clonal growth		0.05	35 (33)	22.2 (12)	15.2 (10)	33 (58)	29.6 (47)	32.4 (35)
	Animal		0.48	51.6 (48)	66.7 (36)	74.2 (49)	59.7 (105)	62.3 (99)	59.3 (64)
Fruit type	Capsule	Dispersal (in time/space)	0.19	16.1 (15)	11.1 (6)	7.58 (5)	18.8 (33)	17.6 (28)	20.4 (22)
	Follicle		0.64	5.38 (5)	1.85 (1)	1.52 (1)	3.98 (7)	5.03 (8)	1.85 (2)
	Nut		0.42	7.53 (7)	3.7 (2)	7.58 (5)	8.52 (15)	8.18 (13)	13 (14)
	Drupe	Establishment (seedling growth)	0.05	18.3 (17)	37 (20)	42.4 (28)	29 (51)	30.2 (48)	30.6 (33)
	Berry		0.84	21.5 (20)	24.1 (13)	22.7 (15)	19.3 (34)	20.8 (33)	15.7 (17)
	Pome		1.00	0 (0)	0 (0)	0 (0)	0.57 (1)	0.63 (1)	0 (0)
	Collective		1.00	1.08 (1)	0 (0)	0 (0)	0.57 (1)	0.63 (1)	0 (0)
	Syconus		0.99	3.23 (3)	1.85 (1)	1.52 (1)	1.7 (3)	1.89 (3)	0 (0)
	Achene		0.98	1.08 (1)	0 (0)	1.52 (1)	2.27 (5)	1.89 (4)	1.85 (2)
	Legume		0.28	4.3 (4)	9.26 (5)	6.06 (4)	2.84 (6)	3.14 (6)	2.78 (4)
	Caryopsis		0.08	7.53 (7)	1.85 (1)	3.03 (2)	1.14 (2)	1.89 (3)	2.78 (3)
	Sproangia		0.56	14 (13)	9.26 (5)	6.06 (4)	11.4 (18)	8.18 (11)	11.1 (11)
Sexual pattern of flowers	Bisexual	Establishment	0.94	55.9 (52)	64.8 (35)	66.7 (44)	62.5 (110)	63.5 (101)	60.2 (65)
	Unisexual		0.99	30.1 (28)	25.9 (14)	27.3 (18)	27.3 (48)	29.6 (47)	29.6 (32)
	Sproangia		0.52	14 (13)	9.26 (5)	6.06 (4)	10.2 (18)	6.92 (11)	10.2 (11)

Traits are significantly different among the six study sites ($P<0.05$) according to the chi-square text

Table 4 Environmental factors at the six study sites (N=30)

Variables	Urban			Rural		
	BYu	PGu	LGu	SZr	SMr	BMr
Altitude (m)	292±4.30d	29.8±0.71e	52.7±0.60e	822±1.31b	978±26.5a	413±17.6c
Slope (°)	48±1.22a	3.00±0.15d	14.2±1.72c	46±4.00a	42±2.00a	34±3.67b
Light intensity	1,071±95.7a	500±78.1b	147±34.4d	346±31.7c	329±15.7c	343±20.1c
Soil pH	3.83±0.01bc	3.88±0.02b	3.71±0.01c	4.27±0.09a	4.24±0.06a	4.26±0.06a
Soil bulk density (gcm^{-3})	1.17±0.07ab	1.26±0.02a	1.30±0.07a	1.28±0.12a	1.11±0.08b	1.06±0.06b
Soil moisture content (%)	11.1±0.68c	11.7±0.27b	14.1±0.47ab	14.9±1.91a	12.2±0.44bc	10.1±0.39c
Soil TP (gkg^{-1})	0.03±0.00b	0.04±0.00a	0.03±0.00b	0.02±0.00c	0.020.00cd	0.01±0.00d
Olsen-P (gkg^{-1})	1.07±0.01bc	3.20±0.24a	1.42±0.08b	0.58±0.08cd	0.89±0.04c	1.31±0.21b
Soil TN (gkg^{-1})	0.19±0.01c	0.24±0.01b	0.22±0.01bc	0.28±0.00a	0.24±0.02b	0.31±0.02a
Soil NH_4^+ ($mgkg^{-1}$)	5.31±0.41b	5.36±0.34b	5.73±0.48b	5.61±0.55b	6.27±0.67b	12.4±2.24a
Soil NO_3^- ($mgkg^{-1}$)	3.81±0.54d	7.13±0.55cd	21.4±0.92a	23.1±1.36a	13.5±2.06b	7.61±0.54c
SOC (gkg^{-1})	4.76±0.20c	12.3±0.94a	5.82±0.36bc	5.37±0.34c	5.98±0.27bc	7.19±0.68b
Soil Cu (μgml^{-1})	0.08±0.01b	0.12±0.01a	0.09±0.01b	0.05±0.01c	0.04±0.00cd	0.03±0.00d
Soil Cd (μgml^{-1})	0.02±0.00a	0.02±0.00a	0.02±0.00a	0.03±0.00a	0.02±0.00a	0.01±0.00b
Soil Pb (μgml^{-1})	0.52±0.02ab	0.59±0.06a	0.63±0.05a	0.28±0.04c	0.45±0.03b	0.62±0.03a
Soil Zn (μgml^{-1})	0.31±0.01d	0.48±0.01c	0.51±0.02c	0.59±0.02b	0.64±0.00a	0.68±0.01a
Soil Ca (μgml^{-1})	0.27±0.03b	0.23±0.03b	0.19±0.02b	0.29±0.01b	0.19±0.04b	0.54±0.09a
Soil Mg (μgml^{-1})	1.53±0.09a	0.55±0.02cd	0.51±0.02d	0.68±0.02bc	0.56±0.00cd	0.71±0.04b
Soil K (μgml^{-1})	116±2.65c	50.2±3.85d	26.7±0.47e	182±6.15ab	184±2.90a	170±6.57b
Soil Na (μgml^{-1})	11.6±1.13d	11.3±0.95d	11.1±0.78d	82.6±8.33c	101±5.37b	133±5.69a

Values of environmental factors (mean ± SE) within rows sharing the same letter are not significantly different (one-way ANOVA with Tukey's HSD; P<0.05)

positively related to the light intensity (Fig. 2), which is common for urban habitats (Lososová et al. 2006), while most of the shade and hygrophilous herbaceous species in rural areas were positively correlated with the soil pH and soil nutrients. The characteristic species in urban forests were those that preferred forest edges, roadside, or a wide range of environments. In addition, the dominant species such as *Castanopsis fissa* and *Uvaria microcarpa* can survive in barren and drought soils and establish their population dominance in the urban environment, which indicated that the native species which reproduced vigorously in the urban environment might have had the ability to endure barren and drought environments (Knapp et al. 2008c). McKinney (2002) and Günter et al. (2009) also found that pioneer and barren-tolerable and drought-tolerable species tend to colonize disturbed sites. Our results are consistent with the findings of previous studies that forests under continuing disturbance would remain at early successional stages and contain few barren-tolerable species (Webb and Fa'aumu 1999). Dominant and subdominant species such as *I. tessellatus*, *P. hindsii*, *A. leucocarpa*, *E. auriformis*, and *Liparis delicatula* share similar ecological niches in rural areas and some of them such as *Pellionia scabra*, *Scleria herbecarpa*, and *C. barometz* widely grow in moist and shady environments. This indicates that rural environments are more suitable than urban environments for species, especially those that prefer moist habitats to reproduce. Chocholoušková and Pyšek (2003) concluded that the flora of the city differed from that of the surroundings in higher demands for light, nitrogen and soil reaction, and lower demands for moisture.

In our study, herbaceous diversity was higher in rural forests compared to urban forest sites, which might contribute to the presence of multidominant

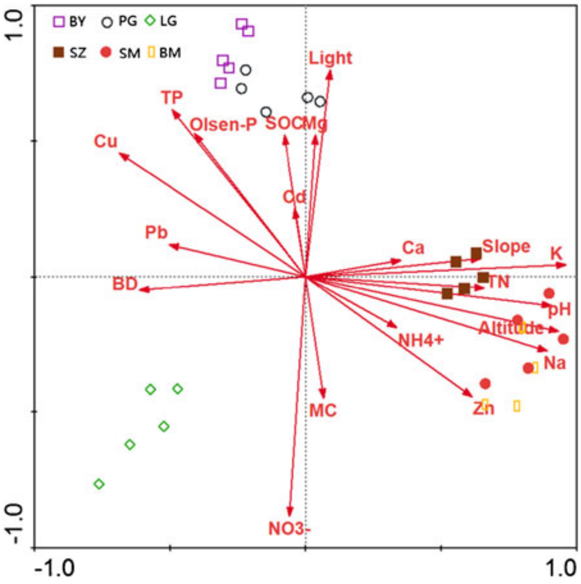

Fig. 3 Two-dimensional CCA ordination diagram of the first two axes showing the distribution of 30 sampling plots and environmental factors (vectors): *Light* light intensity, *BD* soil bulk density, *MC* soil moisture content, *TN* total nitrogen, *SOC* soil organic carbon, *TP* total phosphorus, *Olsen-P* available phosphorus

species in rural forests. Most studies have reported that urban forest sites have higher plant species diversity than rural forests, but those species consist of a higher proportion of exotic species (Moffatt et al. 2004). Kühn et al. (2004) have also shown that native species are more abundant in urban than rural areas. Our results indicated that the remnant forests in urban forest sites which served as local species pools had significantly lower native understory species diversity than those in rural forest sites. As environmental degradation continues, the plant community could regress toward the medium or even early successional stage with low plant diversity, simple structure, and a lack of native species resource. Fortunately, previous studies also demonstrated that the herbaceous diversity can recover quickly after disturbance (Roberts 2004; Selmants and Knight 2003), but not if the disturbance is continual (Zhu et al. 2007). Based on succession theory in subtropical monsoon evergreen broad-leaved forests (Wang et al. 2006), we presumed that forests in urban areas would progressively succeed toward the zonal climax vegetation if there are no further drastic disturbances.

Our study showed that PFTs indicating plant performance such as dispersal, establishment, and persistence varied among different study sites. Our results indicated that urban forests tend to prefer the species with Mesophanerophyte life form and drupe fruit types. In contrast, species in rural forests possessed Chamaephyte and Nanophanerophyte life forms which were composed mainly of understory species, gravity/clonal growth dispersal mode, and capsule fruit types. Duffy and Meier (1992) described a similar tendency in life forms between urban and rural forests. We also know that geophytes have a high risk of extinction in urban areas (Williams et al. 2005). In studies somewhat similar to ours, Burton and Samuelson (2008) and Burton et al. (2009) also indicated that understory species were more vulnerable to urbanization effects than overstory species in riparian forests; this is different from several studies which have shown that urbanization preferably selects short-lived species (Jacquemyn et al. 2003; Kühner and Kleyer 2008; Kleyer 1999). These differences perhaps can be attributed to the longer life spans and the greater structural durability of overstory species than understory species (Esler and Rundel 1999). In our study, species dispersed by gravity or clonal growth were abundant in rural forests, probably because they often travel only a few centimeters per year (Dzwonko and Loster 1992; Moffatt et al. 2004). Previous studies also found that plants with potential for long-range dispersal were abundant at sites with high disturbance, while those with small-range dispersal were abundant at sites with medium disturbance (Burton et al. 2009; Kleyer 1999; Knapp et al. 2008c). That urbanization favors plants with high dispersal capacities has been reported in many locations (Kühner and Kleyer 2008; Moffatt et al. 2004). Although understanding the relationships between PFTs and specific urbanization pressure will require additional research, it is no doubt that management of species functional diversity at the regional scale requires more attention to the understory species and especially those with small-range dispersal capacities.

Impacts of environmental stress on plant distribution

CCA analysis clearly showed the relative positions of species and plots along the most important ecological gradients, indicating that topography, soil nutrients, soil pH, and light played the most important roles in the distribution of vegetation. Previous studies suggested that plant distribution was mainly determined

Table 5 Marginal and conditional effects of environmental factors on vegetation obtained from the summary of forward selection

Marginal effects			Conditional effects			*P* value	*F*
Variable	Var. *N*	Lambda1	Variable	Var. *N*	Lambda A		
Altitude	20	0.79	Altitude	20	0.79	0.002	11.85
Soil Na	18	0.76	Light intensity	26	0.61	0.002	10.10
Soil K	17	0.74	Soil K	17	0.33	0.002	5.82
Soil pH	1	0.67	Soil SOC	6	0.29	0.002	5.34
Light intensity	26	0.60	Slope	19	0.14	0.002	2.57
Slope	19	0.56	Soil pH	1	0.12	0.002	2.32
Soil Zn	14	0.48	Soil Zn	14	0.11	0.002	2.14
Soil NO_3^-	4	0.45	Soil NO_3^-	4	0.12	0.012	1.86
Soil Mg	16	0.42	Soil TN	5	0.09	0.008	1.80
Soil Cu	11	0.39	Soil Cd	12	0.08	0.084	1.64
Soil TN	5	0.33	Soil Mg	16	0.06	0.072	1.33
Soil SOC	6	0.30	Soil Pb	13	0.07	0.122	1.26
Soil moisture content	10	0.21	Soil Cu	11	0.06	0.114	1.26
Soil TP	7	0.20	Soil Na	18	0.06	0.120	1.26
Soil Ca	15	0.18	Soil moisture content	10	0.05	0.378	1.04
Soil bulk density	9	0.15	Soil NH_4^+	3	0.05	0.376	1.04
Soil Pb	13	0.14	Soil Ca	15	0.05	0.434	1.01
Soil Cd	12	0.10	Soil AP	2	0.04	0.722	0.80
Soil AP	2	0.07	Soil bulk density	9	0.04	0.816	0.79
Soil NH_4^+	3	0.06	Soil TP	7	0.03	0.726	0.73
Soil Olsen-P	3	0.06	Soil Olsen-P	6	0.03	0.722	0.77

by environmental factors such as climate, topography, and soil at the regional scale (Jafari et al. 2004). There was little difference in terms of climate among our sample plots, plant distribution may be potentially influenced by topographical factors and soil properties. Topography partly influenced the redistribution of soil resources such as soil moisture content and the accumulation and export of K, Na, Ca, and Mg, and therefore, it indirectly influenced plant distribution (Burke et al. 1999; Sebasti 2004). Previous studies showed that topography and soil properties interacted in plant distribution, indicating that they were both important factors for determining plant distribution (Webb and Fa'aumu 1999).

Although topographical factors dominated the spatial heterogeneity of plant composition, the impacts associated with urbanization-related environmental stress could affect remnant forests in urban settings. Our results identified the significant negative relationships between herbaceous diversity and urbanization-related factors (i.e., soil pH, soil nutrients leaching, and Cu concentrations). With the rapid urbanization expansion, acid rain has become one of the most important environmental issues in Guangzhou, where the value of rain pH had decreased from 4.78 to 4.34, and the frequency of acid rain had increased from 62.3 to 82.6 % from 1999 to 2008 (Huang et al. 2009). SO_4^{2-} and NO_3^- are the basic ions which affect the acidity of precipitation in Guangzhou. The concentrations of sulfur dioxide and nitrogen oxide in precipitation were 0.034 and 0.055 mgm^{-3} in urban areas and 0.055 and 0.021 mgm^{-3} in rural areas in Guangzhou, respectively (Guangzhou Environmental Protection Agency 1999–2009). It might be due to the occurrences of industrial enterprises and motor vehicles which produce emissions of sulfur dioxide and nitrogen oxide, polluting the urban areas of Guangzhou (Guangzhou Environmental Protection Agency 1999–2009). Our results were consistent

Table 6 Pearson's correlations among the 3 plant diversity indices and 20 environmental factors (N=30)

Impact factor	Tree layer			Shrub layer			Herb layer		
	H	D	J	H	D	J	H	D	J
Altitude	0.517**	0.536**	0.562**	ns	ns	ns	0.714**	0.674**	0.545**
Slope	ns	ns	0.378*	0.560**	0.362*	ns	0.639**	0.559**	0.370*
Light intensity	−0.691**	−0.715**	−0.414*	0.464**	0.443*	−0.508**	ns	ns	ns
Soil pH	0.551**	0.558**	0.531**	ns	ns	ns	0.717**	0.663**	0.522**
Soil bulk density	ns	ns	ns	−0.397*	−0.392*	−0.365*	ns	ns	ns
Soil moisture content	ns	ns	ns	−0.467**	−0.512**	−0.583**	ns	ns	ns
Soil TP	−0.688**	−0.653**	−0.662**	ns	ns	ns	−0.557**	−0.478**	ns
Soil Olsen-P	ns	ns	ns	ns	ns	ns	ns	ns	ns
Soil TN	0.535**	0.540**	0.435*	ns	ns	ns	0.576**	0.568**	0.543**
Soil NH_4^+	0.364*	0.369*	ns	ns	ns	ns	ns	ns	ns
Soil NO_3^-	0.515**	0.471**	0.374*	ns	−0.442*	−0.541**	ns	ns	ns
SOC	ns	ns	−0.418*	−0.373*	ns	ns	−0.371*	ns	ns
Soil Cu	−0.635**	−0.635*	−0.642**	ns	ns	ns	−0.682**	−0.597**	−0.415*
Soil Cd	ns	ns	ns	ns	ns	ns	ns	ns	ns
Soil Pb	ns	ns	ns	ns	ns	ns	−0.367*	ns	ns
Soil Zn	0.769**	0.744**	0.579*	ns	ns	ns	0.482**	0.483**	0.419*
Soil Ca	ns	ns	ns	0.364*	ns	ns	ns	ns	ns
Soil Mg	−0.532**	−0.557**	ns	0.569**	0.466**	0.515**	ns	ns	ns
Soil K	0.452*	0.460*	0.527**	ns	ns	ns	0.820**	0.769**	0.613**
Soil Na	0.688**	0.684**	0.645**	ns	ns	ns	0.667**	0.642**	0.494**

ns not significant

*P<0.05, **P<0.01 (two-tailed P values)

with the findings of previous studies that urbanization pressure was positively correlated with soil acidification in North America and northwestern France (Moffatt et al. 2004; Vallet et al. 2008). Soil acidification may imbalance cations over anions uptake in the rhizosphere of plants via either actively fixing N_2 gas or taking up NH_4^+ ions as the major source. The excess cations over anions by plants results in the acidification of rhizosphere, which may make conditions unfavorable for some species (Bolan et al. 1991). Moreover, soil acidification is closely related to soil nutrient concentrations, which will impact the availability and accumulation of these elements. While soil pH value decreases, the order of cation adsorption was as follows: H^+>exchangeable cations of Ca^{2+}, Mg^{2+}, and K^+. In order to buffer H^+, exchangeable cations were exchanged during the process, which lead to the loss of nutrients in soil. Some studies have reported that acid deposition and soil acidification may lead to the leaching of soil basic elements, especially Ca^{2+} and Mg^{2+} (Augustin et al. 2005). Hutchinson et al. (1998) also found that soil basic elements remain vulnerable to acid deposition. Moreover, the heavy metal pollution in urban areas caused by industrial, traffic, and solid waste pollution have severely affected the remnant forests. It may contribute to the heavy metal hyperaccumulation in soil which influence the growth of plant by accumulating in roots, stems, leaves, and grain or even lead to the nutrients stress of plant and reduce plant species diversity (Farago 1994; Kabata-Pendias 2004; Singh 2005; Zheng et al. 2007). Further studies should be developed for explaining the toxic pathology between plant characteristics and specific heavy metal pollution. Consistent with other study (Guntenspergen and Levenson 1997), our results also suggested that soil-mediated effects

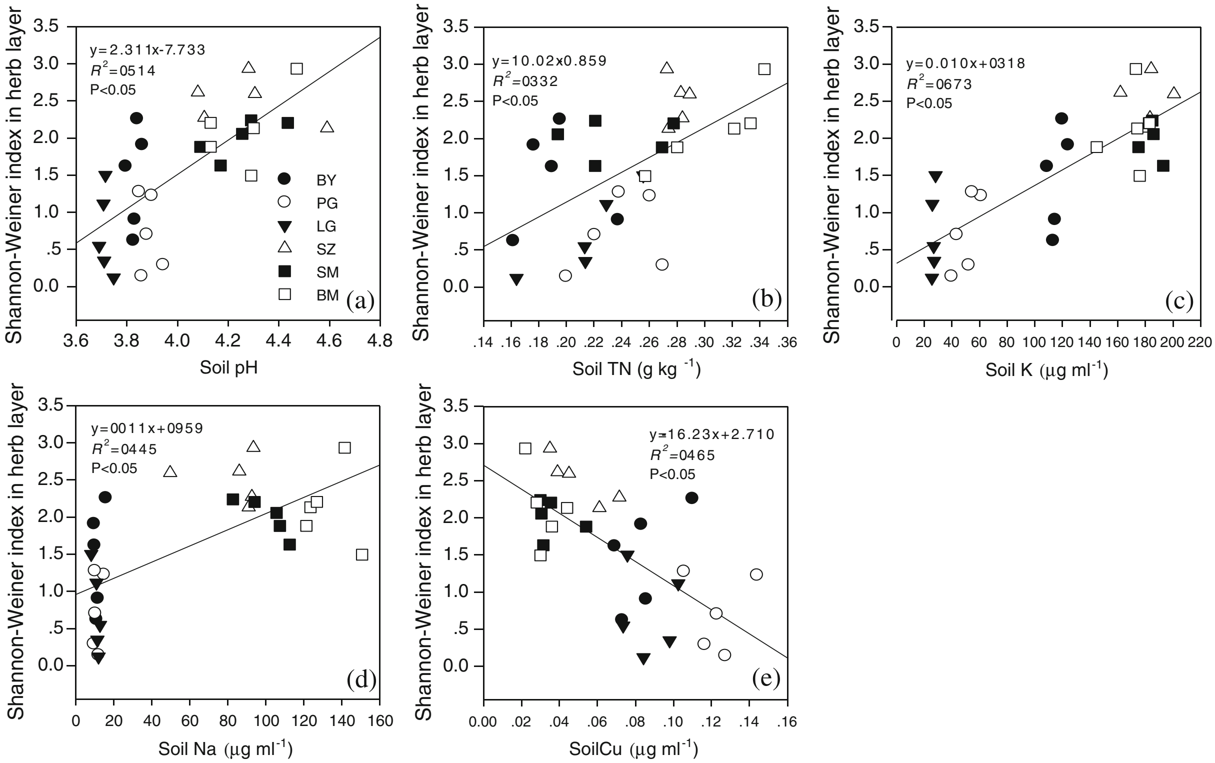

Fig. 4 Linear regression model showing the relationships between Shannon–Weiner index in herb layer and soil pH (**a**) and soil TN (**b**), K (**c**), Na (**d**), and Cu (**e**) concentrations

of acidification and soil heavy metal pollution mainly caused by industrial pollution were important indicators of urbanization for determining plant distribution across different land-use sites, which drive the competitive interactions that lead to plant composition change and make conditions unfavorable for some species.

Conclusions

Our results show that herb plant species diversity declined and species in the remnant forests differed from that of rural areas in higher demands for light and lower demands for moisture, which are typical for forests in general. Subtropical forest species react in a specific way to urbanization with overstory life form and animal dispersal capacity. The vulnerable herb species and those with low dispersal capacity are facing a high risk of extinction in urban areas. Although landscape structure and dynamics directly influence forests in urban settings, soil acidification, nutrients leaching, and heavy metal pollution are likely to have long-term effects and will present significant challenges for ecological restoration. Findings from these inventories could help researchers determine the threshold level of urbanization for maintaining maximum biodiversity and be incorporated into monitoring assessments to protect the remnant forests in urban areas of South China. Future efforts should focus on the environmental stresses which influence vegetation and biogeochemistry cycles in urban ecosystems.

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