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DYNAMICS OF DIVERSITY, DISTRIBUTION PATTERNS AND INTERSPECIFIC ASSOCIATIONS OF UNDERSTORY HERBS IN THE CITY-SUBURB-EXURB CONTEXT OF WUHAN CITY, CHINA

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Abstract – The dynamics of herb diversity, distribution patterns and interspecific associations of dominant herbs in natural forests at three growing stages in a city-suburb-exurb context in Wuhan City were studied using a fixed plot. The results show that the composition, diversity indices, mean and total richness gradually increased with the city-suburb-exurb gradient. Codominant species across temporal dynamics in Qinglong Mountain were stable, however, there were remarkable changes in the city-suburb context. Qinglong Mountain (exurb context) had the densest codominant herbs, *Woodwardia japonica*, *Spider brake* and *Parathelypteris glanduligera*, throughout the growing season. However, Shizi Mountain (suburb context) and Hongshan Mountain (urban context) had low-density and monodominant herbs at three stages. The overall strength of associations among herbs increased with the city-suburb-exurb context, and pairs of positive associations and significant associations (r>0.5 or r<-0.5) were more frequent on Qinglong Mountain. Therefore, the exurb-suburb-city landscape context in response to urbanization had a notable effect on the features of the understory herb layer.

Key words: Disturbance, habitat changes, herb dynamics, landscape context, urbanization

INTRODUCTION

Urbanization, the process of a large expanse of impervious surface (Blair et al., 1997) and simplification of vegetation structure (McKinney, 2008), has been identified as a major environmental threat (Wang et al., 2012). Urbanization and land-use changes are occurring at extraordinary rates that lead to a decrease in environmental quality and the fragmentation of natural habitats (Burton et al., 2009; Vallet et al., 2010). In addition, environmental changes along a city-suburb-exurb gradient in response to urbanization, such as road density, air pollution and human frequentation, produce a gradient of natural habitat loss and fragmentation that steepens from rural areas toward the urban center (McKinney, 2002). It is intuitive that the increasing fragmentation of natural habitats by human disturbances in the direction toward urban centers will tend to have an influence on biodiversity (McKinney, 2002) and the process of interspecific associations (Haila, 2002).

Investigation of the factors that bring about changes in the biodiversity and processes of fragmentation of the city-suburb-exurb forests in Wuhan is essential to the development of conservation strategies. Biodiversity encompasses not only species diversity but also the structure and function of the ecosystem (Ledo et al., 2009). Thus, it may be possible to detect changes in biodiversity by analyzing the dynamics of diversity, patterns and associations of dominant species. Furthermore, changes in the diversity indices and patterns and associations of dominant species over time have served to assess the effect of anthropogenic disturbances in forests (Battles et al., 2001; Polyakov et al., 2008). As the basic component of an ecosystem, the herbaceous layer in forests provides the majority of species diversity in most forest ecosystems, is an important player in a wide range of ecosystem functions, such as nutrient cycling and energy flow, and directly responds to habitat changes (Roberts, 2004). Vegetation in urban areas can also be used as a general indicator of environmental conditions and ecological processes, because urban vegetation reflects the interaction between human impact and natural development (Cilliers et al., 2000). Most previous studies on anthropogenic disturbances in forest have focused on the dominant tree canopy and woody understory, with little or no consideration of the herbaceous layer (Roberts, 2004). Understanding how this species-rich and ecologically important layer responds to urbanization is needed as a guide for conservation. Moreover, the gradient paradigm introduced to study urban ecology has proven to be a useful tool for describing human-induced disturbances in urban areas (McDonnell et al., 2008; Burton et al., 2005; Niemelä et al., 2009; Zipperer et al., 2000 and Pickett et al., 2009). Thus, the gradient paradigm will be used in this study to investigate and discuss the dynamics of species diversity and distribution pattern of herbal dominant species in the city-suburb-exurb context.

The overall goal of this study was to identify changes in the understory herbaceous layer that may influence forest function and processes, along a city-suburb-exurb gradient in Wuhan. The following two questions will be addressed: (1) how does the species diversity (dynamics of family, genera, species of forests, within-habitat diversity and the important value of dominant herbs) of the herbaceous layer vary with a city-suburb-exurb gradient; (2) how do the distribution patterns and interspecific associations of dominant species of the herbaceous layer change with the city-suburb-exurb gradient.

MATERIALS AND METHODS

Study area

The study was conducted in Wuhan, a city of rapid urbanization, at the confluence of the Yangtze River and its longest tributary, the Han River, central China (113°41'—115°05'E, 29°58'—31°22'N). It has a subtropical monsoon climate, with an average annual temperature of 16.6°C and annual average rainfall of 1 269 mm, most of which occurs during April and October. The vegetation type is from central subtropical evergreen broad-leaved forest to northern subtropical evergreen broadleaf forest. Due to land-use changes and industrialization in the process of urbanization, the type of native vegetation has mainly changed into coniferous broadleaved mixed forests.

Based on the criteria of urbanization level (McKinney, 2002), the urban core (city) has an impervious surface of more than 50%, the impervious surface of a suburb is from 20% to 50%, and the impervious surface of an exurb is less than 20%. According to the differences of urbanization in Wuhan, Hongshan Mountain was selected as the city site (C) (adjacent land types are commercial land and traffic land), Shizi Mountain as the suburb site (S) (adjacent land is for educational and scientific research), and Qinglong Mountain as the exurb site (E) (adjacent land type is agricultural land) (Fig. 1). Site situations were listed in Table 1.

Study design

In June 2011, an 8 m × 8 m fixed plot, which included 16 small 2 m × 2 m quadrates, was established within each site. The edge of each plot was marked for later measurement. The species, height, coverage and location (X, Y) of each herbaceous individual in each fixed plot were investigated and marked respectively in July 2011 (LGS – late stage in growing season), the beginning of March 2012 (EGS – early stage in growing season) and the end of May 2012 (MGS – middle stage in growing season). The prolate axis and minor axis of the shadow of the plants were measured by ruler, and then the coverage was calculated. To avoid the subjective error of estimation, the herbs were first classified according to the characteristics of each species on the China plant network and the number of each herb was recorded.

Data analysis

The importance values (IV) of species were calculated using the following formula (Wang et al., 2009): IV herb = (relative height + relative coverage + relative frequency) × 100/3

Species diversity indices (Wang et al., 2012) were the Shannon-Wiener index $H = -\sum P_i \ln P_i$, Simpson's diversity index: $D = 1 - \sum P_i^{\,2}$, Pielou's evenness index: $J = (-\sum P_i / \ln P_i) / \ln S$, and the Richness index S. P_i is the relative IV of the species, and S is the total species.

Spatial patterns and the interspecific associations of plant species in forests are important for revealing how species interact with each other and with the environment, and hence have important implications for optimal forest management (Zhang et al., 2010). In order to research the dynamics of interspecific association of herbaceous species in a city-suburb-exurb context, we constructed Pearson correlation networks of interspecific relationship.

Pattern analysis and dynamics of pattern figures of dominant species were from the position (X, Y) of each herb individual in pattern inventories. Interspecific associations of herbs were calculated using Pearson's correlation in 16 small 2 m × 2 m quadrates.

Passage 1.0 software was employed in pattern analysis, and Pearson's correlation analysis was carried out using SPSS (SPSS 11 Copyright: SPSS Inc.). Pattern figures of dominant species were drawn with Origin 7.0, and Pearson's correlation networks were drawn with R software (SPAA package).

RESULTS

Dynamics of herb diversity in forests along a city-suburb-exurb context

Dynamics of species composition of understory herbs

The number of family, genera and species of understory increased with the gradient of city-suburb-exurb at the early stage of the growing season (EGS), middle stage (MGS) and late stage (LGS), respectively (Table 2). Family, genera and species was highest in EGS on Shizi Mountain and Qinglong Mountain, while it was highest in MGS on Hongshan Mountain.

Woodwardia japonica was the monodominant understory herb on Hongshan Mountain (city context) at three stages. *Parathelypteris glanduligera*, *Commelina communis* and *Lygodium japonicum* were each the monodominant understory herb in LGS, EGS and MGS on Shizi Mountain (suburb context), respectively. Codominant species *W. japonica, Spider brake* and *P. glanduligera* existed on Qinglong Mountain (exurb context) at three stages, with a decreasing dominance of *S. brake* in EGS (Table 3).

Dynamics of species diversity of understory herbs

The Simpson-Wiener index (H), the Simpson index (D), mean richness and total richness of the three growth stages increased with the city-suburb-exurb gradient at EGS, MGS and LGS, respectively (Table 4). The diversity indices H and D, and evenness index (J) increased on Hongshan Mountain and decreased on Shizi Mountain with the temporal gradient of EGS-MGS-LGS, whereas these indices indicated a unimodal change on Qinglong Mountain (Table 4).

Dynamics of distribution pattern of dominant herbs in city-suburb-exurb context

Consistent with dynamics of important value, *W. japonica* exhibited a specific spatial distribution at three stages. *Saxifraga stolonifera* emerged in LGS on Hongshan Mountain (city context) (Fig. 2A). The monodominant understory herbs, *P. glanduligera*,

Table 1. Stand characteristics at different sites.

Site	Altitude (m)	Slope (°)	Canopy cover (%)	Forest types	Dominant Tree	Landscape context	Distance to city center (km)
Hongshan mountain	80	27.5	73.5	CBF	*Cc*, *Pm*, *Qs*	City	0
Shizi mountain	55	16.8	74.1	CBF	*Cc*, *Pm*, *Qs*	Suburb	7.6
Qinglong mountain	180	2	75.2	CBF	*Cc*, *Pm*, *Mg*	Exburb	20.8

CBF: coniferous broadleaved mixed forest. *Cc*: *Cinnamomum camphora*; *Pm*: *Pinus massoniana*; *Qs*: *Quercus spp.*; *Mg*: *Metasequoia glyptostroboides*.

Table 2. Dynamics of species composition of understory herbs in the city-suburb-exurb context.

Sites	Context	LGS			EGS			MGS		
		Family	Genera	Species	Family	Genera	Species	Family	Genera	Species
Hongshan mountain	City	4	4	4	4	4	4	6	6	6
Shizi mountain	Suburb	6	7	7	8	8	8	7	7	7
Qinglong mountain	Exurb	8	9	9	12	12	12	8	8	8

EGS, early stage in the growing season; LGS, late stage in the growing season; MGS, middle stage in the growing season.

Table 3. Dynamics of important value of dominant herbs in the city-suburb-exurb context.

Species	LGS			EGS			MGS		
	Hongshan Mt.	Shizi Mt.	Qinglong Mt.	Hongshan Mt.	Shizi Mt.	Qinglong Mt.	Hongshan Mt.	Shizi Mt.	Qinglong Mt.
Rosa multiflora	/	/	/	/	/	/	/	27.26	/
Stellaria media	/	/	/	/	/	16.24	/	/	/
Malachium aquaticum	/	/	/	/	/	< 3	/	/	/
Woodwardia japonica	52.39	3.52	8.54	69.3	20.1	36.11	79.33	< 3	30.61
Spider brake	13.41	/	11.15	4.31	< 3	< 3	/	/	11.42
Parathelypteris glanduligera	/	55.21	9.89	/	/	30.46	13.31	/	4.73
Smilax china	/	< 3	< 3	/	/	/	/	/	< 3
Dioscorea opposita	/	5.39	/	/	/	/	3.65	/	/
Saxifraga stolonifera	16.24	/	< 3	/	/	< 3	/	/	/
Lygodium japonicum	/	/	/	/	/	< 3	< 3	36.85	< 3
Fallopia multiflora	/	/	/	/	/	/	/	6.97	/
Commelina communis	/	/	< 3	/	60.4	< 3	/	< 3	< 3
Vitis amurensis	/	/	/	/	/	/	/	/	/
Radix ophiopogonis	/	/	/	6.25	5.78	< 3	< 3	/	< 3

EGS, early stage in the growing season; LGS, late stage in the growing season; MGS, middle stage in the growing season.

Carex rigescens and *L. japonicum* had absolute dominance, respectively in LGS, EGS and MGS on Shizi Mountain (suburb context). However, they scarcely appeared in other growing seasons (Fig. 2B). Compared with Hongshan Mountain and Shizi Mountain, the number of dominant species on Qinglong Mountain (exurb context) increased significantly. Codominant *W. japonica, S. brake* and *P. glanduliger*

Table 4. Dynamics of diversity index statistics at different months in a city-suburb-exurb context.

Sites	LGS			EGS			MGS			Mean richness	Total richness (no repeated)
	H	*D*	*J*	*H*	*D*	*J*	*H*	*D*	*J*		
Hongshan mountain	1.337	0.726	0.964	1.114	0.544	0.692	1.196	0.711	0.716	4.7	8
Shizi mountain	1.716	0.783	0.882	1.968	0.833	0.896	1.837	0.82	0.944	7.7	12
Qinglong mountain	2.062	0.856	0.939	2.214	0.863	0.891	1.898	0.826	0.895	9.7	17

EGS, early stage in the growing season; LGS, late stage the growing season; MGS, middle stage in the growing season.

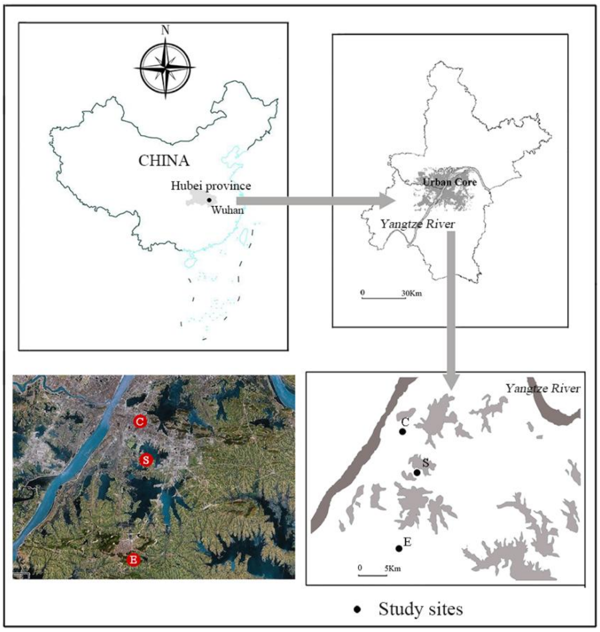

Fig. 1. The location of study sites (C, city site; S, suburb site; E, exurb site) along a city-suburb-exurb gradient in Wuhan city, central China.

existed at three stages on Qinglong Mountain, however, *W. japonica* was in absolute advantage and *P. glanduliger* tended to decrease in LGS. In addition, *Stellaria media* only emerged in EGS and then disappeared (Fig. 2C).

Dynamics of interspecific association of understory herbs in the city-suburb-exurb context

The overall association strength among herbaceous species gradually increased in the city-suburb-exurb context (gradient of Hongshan Mountain-Shizi Mountain-Qinglong Mountain).

Pairs of positive association were less than that of negative association at three stages on Hongshan Mountain (2 via 4 in LGS and EGS, and 6 via 15 in MGS) and Shizi mountain (8 via 13 in LGS, 9 via 19 in EGS, and 7 via 14 in MGS). However, pairs of positive association were more in the three stages on Qinglong Mountain (20 via 16 in LGS, 46 via 20 in EGS, and 16 via 12 in MGS). Pairs of significantly positive or negative association (r >0.5 or r <-0.5) were more on Qinglong Mountain (6, 8 and 2) than on Hongshan mountain (1, 0 and 0) and Shizi mountain (1, 3 and 0). Only one pair of significant positive association can be found between *S. brake* and *S. stolonifera* in LGS on Hongshan Mountain. However, there was no significant association between any two species in EGS and MGS (Fig. 3A). The density and association of herbs on Shizi Mountain was higher than that on Hongshan Mountain, with an especially highly significant positive correlation among *Humulus scandens, S. brake* and *Rhizoma Cyperi* in EGS (Fig. 3B). Interspecific association on Qinglong Mountain was much more complex, which indicated not only an extremely significant positive association but also a remarkable negative association, especially many pairs between dominant herbs *W. japonica, S. brake* and *P. glanduligera* and other common herbs. Moreover, a significant positive association can be found at three stages (Fig. 3C).

DISCUSSION

An approach-based gradient paradigm was used to examine relationships between a city-suburb-exurb

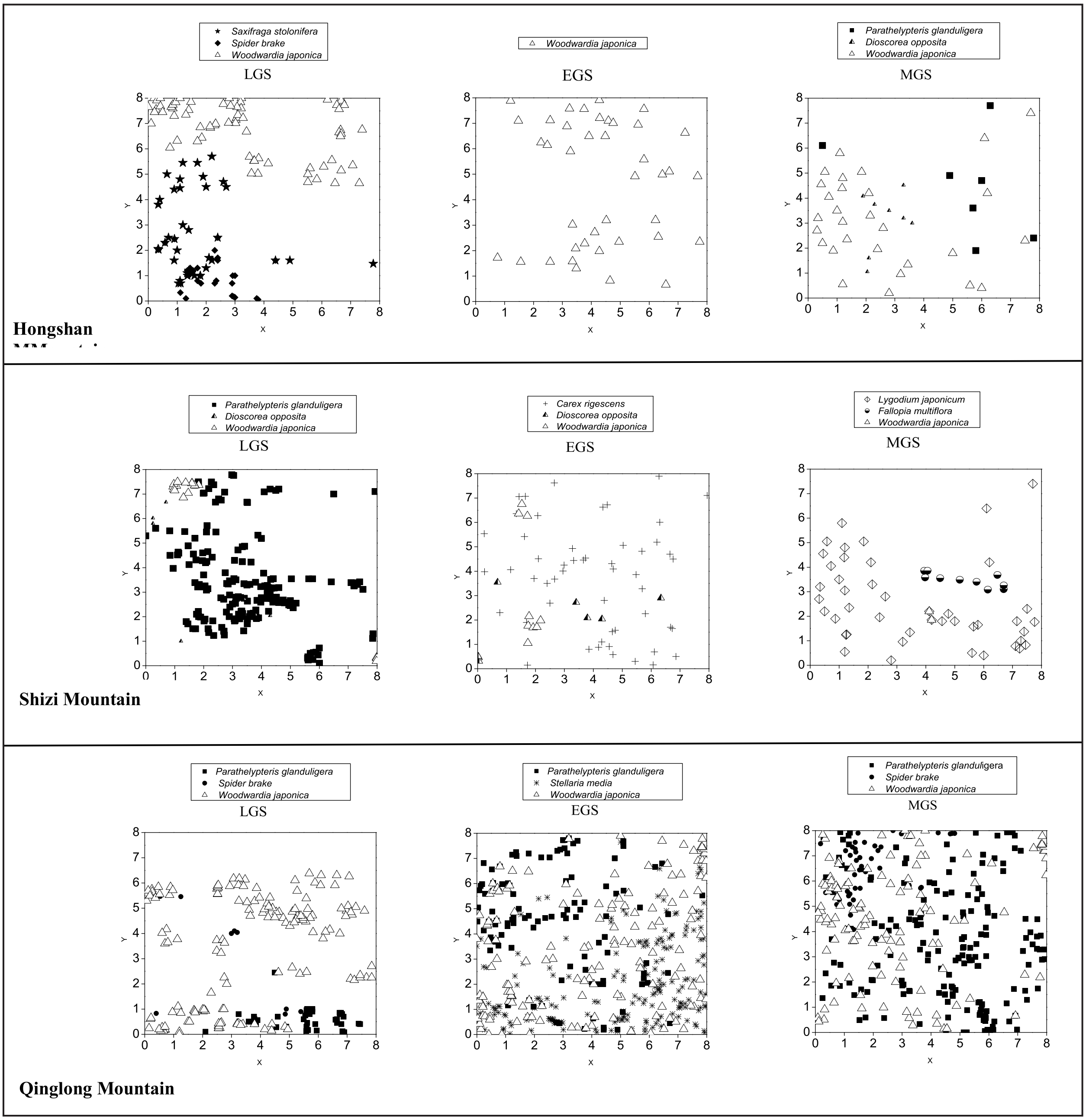

Fig. 2. Dynamics of distribution pattern of understory dominant herbs in a city-suburb-exurb context. EGS, early stage in the growing season; LGS, late stage in the growing season; MGS, middle stage in the growing season.

context and understory herb layer characteristics in three growing stages to understand better the potential consequences of urbanization on forest ecology. Urbanization produced an anthropogenic disturbances gradient (McKinney, 2002), such as disturbances from the adjacent land. In a previous study, the intensity of disturbance, including coverage (rubbish and tiles), trampling (paths, visitors com-

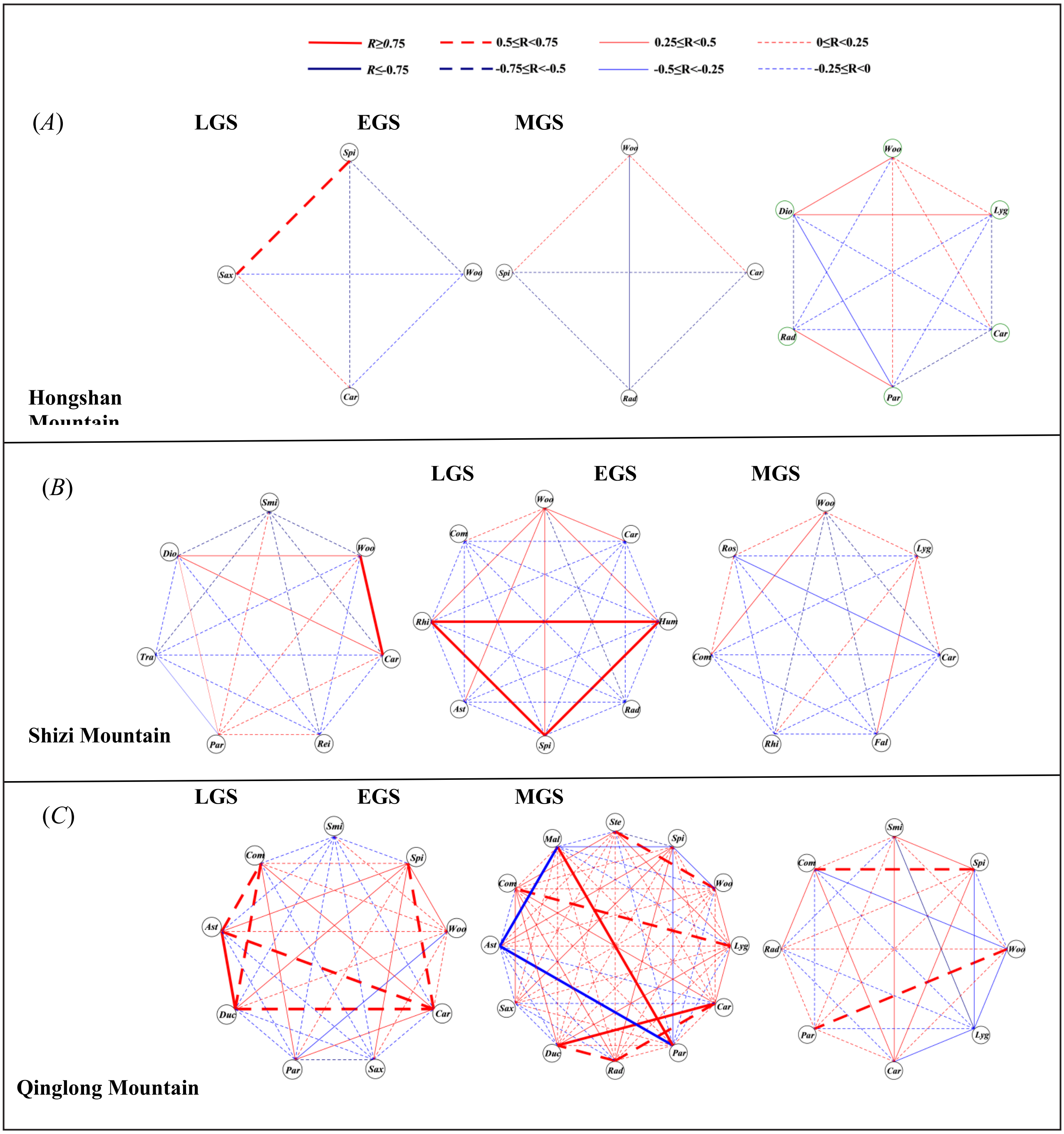

Fig. 3. Dynamics of Pearson correlation networks of understory herb species in a city-suburb-exurb context. Species represented by a polygonal vertex. The red line between the two vertices shows positive association; the blue line shows negative association. The strength of interspecific association changes with line width and solidity. EGS, early stage in the growing season; LGS, late stage in the growing season; MGS, middle stage in the growing season. *Ast – Aster ageratoides; Car – Carex rigescens; Com – Commelina communis; Dio – Dioscorea opposite; Duc – Duchesnea indica; Fal – Fallopia multiflora; Hum – Humulus scandens; Imp – Imperata cylindrical; Lyg – Lygodium japonicum; Mal – Malachium aquaticum; Par – Parathelypteris glanduligera; Rad – Radix ophiopogonis; Rei – Reineckia carnea; Rhi – Rhizoma Cyperi; Ros – Rosa multiflora.*

ing from different adjacent lands and the distance to edge) and deforestation (anthropogenic caves and stumps) increased with the gradient of exurb-suburb-city, which is similar to many studies (Pickett et al., 2008; Vallet et al., 2010; Li et al., 2012). Thus, different forms, intensities, the structure and composition of land use and the surrounding landscape context resulting from disturbances were important factors affecting species composition and richness in the forest (Bennett et al., 2004).

As the basic component of a forest community, the herb layer could directly respond to changes in habitats (Roberts, 2004). Therefore, it made sense to investigate the effect of urbanization gradient on the characteristics of understory herbs layer. In our study, we found landscape context to have a marked impact on the number of family, genera and species in the understory (Table 2) and species composition (Table 3). In addition, codominant species across temporal dynamics on Qinglong Mountain were in a relatively stable state, which indicated that the composition of herbaceous species on Qinglong Mountain was much steadier, but there were remarkable changes in the city-suburb context. The change of herb species could be the response that sharply decreased with the increase of disturbances in the gradient of exurb-suburb-city. This was similar to other previous studies (McKinney, 2002; Burton et al., 2008). Intense disturbances could affect the performance and abundance of herbs greatly. Forests suffered a higher intensity of disturbance (human activity and destroyed (disturbed cover)) in the city than those in the suburb and exurb. One example is a disturbance that leaves the forest canopy intact but disrupts the forest floor and soil, such as high recreational use around campgrounds (Roberts, 2004). Thus, high fragmentation resulting from disturbances, such as trampling, compacting soil and creating gaps in urban areas, might drive down herb species by reducing local population size and gene flow from other populations (Vallet et al., 2010; Rosas et al., 2011).

The results also indicated that the Simpson-Wiener index (H), Simpson index (D), mean richness and total richness of herb species of natural forests increased with the gradient of city-suburb-exurb (Table 4). This was in accord with previous studies showing that habitat changes, such as fragmentation of natural habitats in response to urbanization, will reduce the species diversity and increase the similarity of urban forests (McKinney, 2002; Burton et al., 2008, 2009). This may be related to the degree of fragmentation and habitat changes caused by human disturbance. Urbanization produces comprehensive physical changes that strongly affect the natural habitats of herbs, such as road density, air pollution, frequency of human activities and other indicators of anthropogenic disturbance (McKinney, 2002). Severe disturbance of the forest floor and soil, along with the complete removal of understory vegetation, especially in a city context, have the greatest potential impacts on the herbaceous layer. Under these conditions, only species that are capable of regenerating from widely dispersed seeds may reappear, resulting in reduced species diversity (Roberts, 2004).

The density of dominant herbs was clearly highest on Qinglong Mountain (exurb context) and it had codominant *W. japonica, S. brake and P. glanduliger* throughout the growing season. However, Shizi Mountain (suburb context) had monodominant herbs and Hongshan Mountain (urban context) had low-density and single dominant species at three stages (Fig. 2). The violent encroachment of urbanization destroyed the diversity and growth rhythm of herbaceous plants, which affected the succession of community and ecological balance. A disturbance generates a new environment, which triggers ecological succession (Azeria et al., 2011), and the species themselves may influence the dynamics of succession, particularly in later stages, through complex interspecific interaction (inhibition/competition and facilitation) (Callaway et al., 1997; Bruno et al., 2003; Yamada et al., 2006). It was suggested that Qinglong Mountain, whose adjacent land type is agricultural land, was scarcely disturbed by human activities, which helped community to reach stability through natural succession.

Associations of species can affect species coexistence and be used to point to mechanisms and dynamic processes that facilitate coexistence (Zhang et al., 2010). Interspecific differences in habitat association contribute to species diversity because direct competition is reduced or eliminated (Yamada et al., 2006). Regardless of positive association or negative association, it is propitious to ecological stability. The overall association strength among herbaceous species gradually increased in the city-suburb-exurb context, and pairs of positive association and significant association ($r>0.5$ or $r<-0.5$) were more in three stages on Qinglong Mountain (Fig. 3). Positive association in a particular species pair indicates similar resource usage and niche overlapping (Zhang et al., 2010). Conversely, negative association in a species pair indicates repellency between the two species, which may be the result of long-term adaptation to different environments, different resource usage, and explain the niche separation (Bunyavejchewin et al., 2003; He et al., 1997). Each species was restricted to a more or less wide range of habitats (Zhang et al., 2010). Specific association on Qinglong Mountain was much more complex, which indicated not only extremely significant positive association but also remarkable negative association, while there were seldom significant associations in the city-suburb context, especially on Hongshan Mountain. This might be the result of intense disturbances changing the forest floor and soil in natural habitats. Conservation efforts should be directed toward avoiding combinations of severe disturbance to the understory vegetation and forest floor and soil (Roberts, 2004).

Dynamics of growing stages had little effect on understory herb layer characteristics. However, habitat changes along the exurb-suburb-city gradient in response to urbanization had notable effect, showing a decrease of species diversity and community stability. Therefore, effective measures for herb diversity conservation should be implemented. Further studies on the effects of soil and air quality in the city-suburb-exurb context on herb diversity are needed to understand the deep effect of adjacent land use on natural forests in favor of protection of plant diversity in Wuhan city.

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