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Distribution patterns and traits of weed communities along an urban–rural gradient under rapid urbanization in Shanghai, China

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In order to better understand the effects of urbanization on weed communities, the distribution of weed communities in Shanghai, China, was systematically investigated. The diversity of weed communities and four environmental factors, including the relative light intensity, soil moisture, soil compaction and soil pH, were measured in 1375 plots along an urban–rural gradient. The species diversity indices in each area along the urban–rural gradient were compared by using a one-way ANOVA. The weed communities were identified by using clustering methods that were based on relative dominance information. A canonical correspondence analysis was used to reveal the relationships between the species composition and the environmental factors at the community level and the Spearman's rank correlation test was used to test the relationship between the number of weed communities and each environmental factor. A total of 183 species, belonging to 41 families and 123 genera, was recorded. It was found that the species richness, Shannon–Wiener diversity index and Pielou evenness index followed a unimodal curve along the urban–rural gradient. The 1375 plots were divided into 133 weed community types. All four environmental factors significantly affected the species composition of the weed communities, but only soil compaction had significant effects on the number of weed communities. It was concluded that the diversification of habitat type and environmental change along the urban–rural gradient led to more weed communities in rural areas and fewer weed communities in urban areas. Based on the species' habitats and distribution patterns, the weeds were divided into "widespread", "urban" and "rural".

Keywords: diversity pattern, growth form, life form, weed management, weed types.

Rapid urbanization produces great changes in land utilization patterns (Currit & Easterling 2009). Rapid urbanization changes the distribution patterns of light, temperature, precipitation and soil conditions (Robert & George 2006) and makes these patterns more heterogeneous in urban areas (Zhao *et al.* 2006). These alterations cause significant changes in species diversity and the community structure, type and distribution patterns of urban vegetation (McKinney 2002; Kühn *et al.* 2004; Pyšek *et al.* 2004). The urban–rural gradient approach has been used effectively for several years to study the responses of flora, fauna and the environment to urbanization (McDonnell & Hahs 2008). Many studies that have been conducted on natural communities (Zhao *et al.* 2006), urban roadside vegetation (Cilliers & Bredenkamp 2000) and riparian-zone forest (Burton *et al.* 2009) have found that the species composition and community structure exhibit significant spatial differences along the urban–rural gradient. There are two viewpoints regarding the distribution pattern of

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biodiversity along the urban–rural gradient. One viewpoint is that the distribution pattern of species richness along the urban–rural gradient has no equilibrium of hump-shaped distributions; that is, the species richness of a suburban area is higher than that of urban and rural areas. The theoretical basis of this viewpoint is mainly the intermediate disturbance hypothesis, which states that a level of intermediate disturbance often leads to high biodiversity (Huston 1979). The alternate viewpoint considers the monotonically increasing species richness from urban to rural to be caused by human disturbance and the degree of landscape damage that is increasing monotonically along the urban–rural gradient (Li *et al.* 2005).

Urban vegetation can be divided into three categories: planted communities, natural communities and weed communities (Ohsawa *et al.* 1988). Planted communities have been introduced artificially into urban areas. Natural communities are primary or secondary communities that existed before human intervention and that were not cleared by the urbanization process. Weed communities are a specific feature of natural communities that have been subjected to human intervention but are not considered to be under control (Ohsawa *et al.* 1988; Nemoto 2006). These communities are highly sensitive to environmental changes and can rapidly alter their morphology, physiology and behaviors to adapt to these changes (Cilliers & Bredenkamp 2000; Benvenuti 2007; Zuo *et al.* 2008). Therefore, weeds offer an excellent opportunity to study the effects of urbanization on urban vegetation (Ohtsuka 1995). Many recent studies of urban vegetation, including studies of species diversity in urban habitats, cultivated flora in gardens and parks and wild flora of specific habitats (Marzluff *et al.* 2008), have addressed the topic of urban weeds. Likewise, a large number of studies on urban weeds has been carried out in many countries since the 1970s (Franceschi 1996; Benvenuti 2004; Alignier & Petit 2012; Wan *et al.* 2012). However, only a few studies have addressed the distribution pattern of weed communities along an urban–rural gradient or addressed the effects of rapid urbanization on weed communities along an urban–rural gradient.

Shanghai, one of the most urbanized cities in China, is located on a plain and its circular expansion pattern has produced an obvious urban–rural gradient. The urban environment of Shanghai has undergone great changes in the past 30 years and the surface water quality, air quality and urban heat islands exhibit different patterns along the urban–rural gradient (Wang *et al.* 2008; Zhang *et al.* 2010). These changes certainly have large effects on the vegetation of Shanghai. The objectives of this study were to: (i) survey the species diversity in different areas and clarify the distribution patterns of weed communities along the urban–rural gradient; (ii) explore the primary factors that determine community distribution patterns; and (iii) provide scientific support for the management of weeds, including weed control and weed utilization.

METHODS

Study site

This study was conducted in Shanghai, China, which is located on the eastern edge of the Yangtze River Delta (30°40′–31°53′N, 120°51′–122°12′E) (Fig. 1). This area lies in the transition zone between the subtropics and the warm temperate zone and has a subtropical monsoon climate. Its annual average temperature is 17.8°C and the annual rainfall is 1457.9 mm, with 60% of the rainfall being concentrated in the rainy season (May to September). Natural vegetation in the area has been seriously damaged because of the rapid urbanization of Shanghai in recent years. Most of the urban green space now consists of planted communities and only a few plots of secondary vegetation remain on Sheshan Mountain and Dajinshan Island. As the ecological environment of the islands and mountains is quite different than the environment of the urban areas, the study area does not include the islands or mountains.

Traffic management problems that resulted from the urban expansion of the city (Wang 2005) have been addressed by the construction of concentric ring roads. The inner ring road delimits the city center, while the outer ring road follows a 1–2 km zone around the outer city limit (Ministry of Housing and Urban–Rural Development of the People's Republic of China 1995). The area located within the inner ring road is the core area of Shanghai, whose history can be traced back to the 1840s. Since China's reform and the opening of its markets, rapid urban expansion has resulted in severe traffic congestion, which the ring road system was designed to alleviate.

The city was divided into five areas with differing degrees of urbanization, according to the circle structure of the city. The urban areas (designated by U) are located within the circle defined by the outer ring road and are subdivided into U1 (within the inner ring road), U2 (between the inner ring road and the central ring road) and U3 (between the central ring road and the outer ring road), according to the features of the urbanization process. The suburban areas (designated by S) are located between the outer ring road and the suburban ring road. The rural areas (designated by R) are located outside the suburban ring road (Fig. 1).

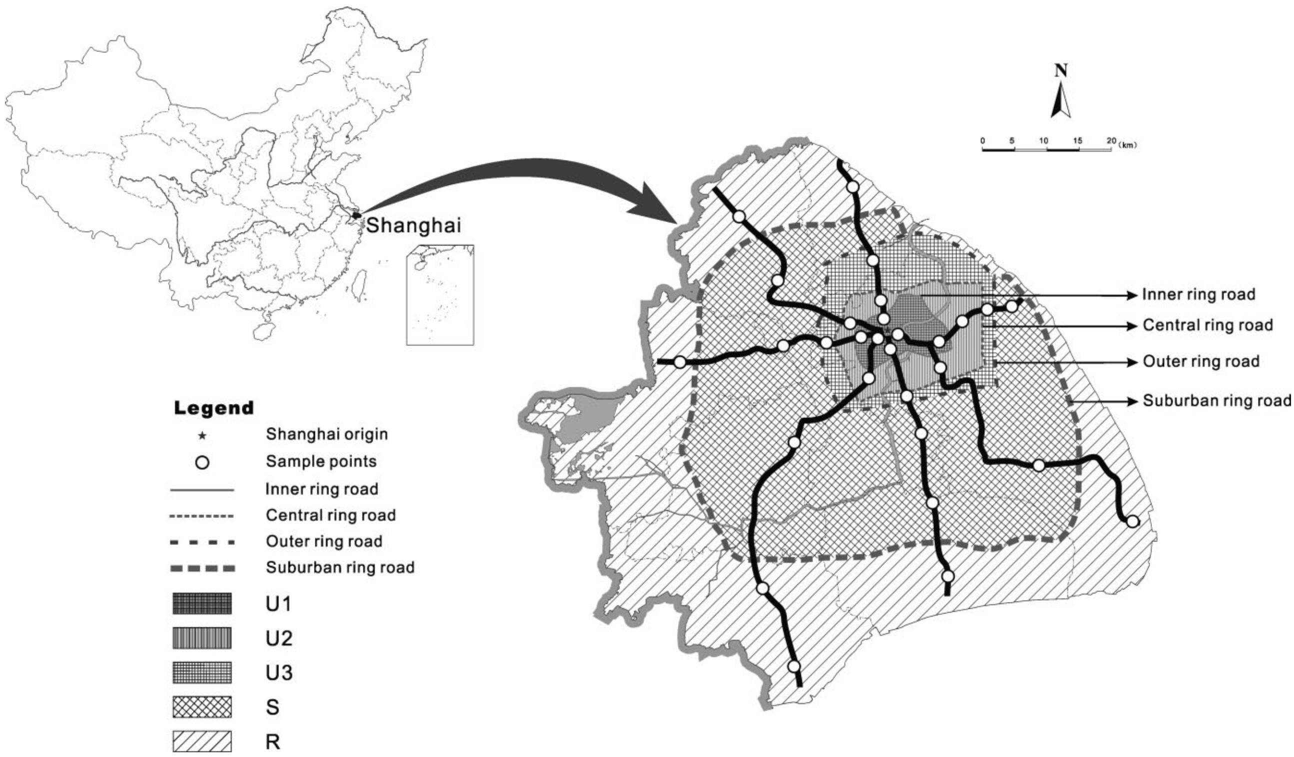


Fig. 1. Location of the study area and the sampling points. U1, Urban area within the inner ring road; U2, urban area between the inner ring road and the central ring road; U3, urban area between the central ring road and the outer ring road; S, suburban areas located between the outer ring road and the suburban ring road; R, rural areas located outside the suburban ring road.

Data collection

Field data on the weed communities were collected during field surveys in spring (from April to May in 2008 and 2009) and autumn (from September to October in 2008 and 2009). The field survey comprised two parts, the surface survey and the point survey. The surface survey was conducted in order to define all of the land-use types in the study areas that were surveyed and the point survey was conducted in order to define all of the weed communities in each sample point that was surveyed.

Based on the surface survey, seven land-use types were selected: road, street and transportation; residential areas; administration and public services buildings; non-development land; green space and square; industrial manufacturing; and agricultural land (Ministry of Housing and Urban–rural Development of the People's Republic of China 2011). The percentage of land-use type in each area of the urban–rural gradient is shown in Table 1. In addition, based on the point survey, using central Shanghai (People's Square) as the origin, 29 sample points were defined in a radial pattern along the urban–rural gradient (Fig. 1). Each sample point was used as the center of a circular sampling area with a radius of 1 km. In order to investigate the weed communities in all seven land-use types, plots were placed randomly but were stratified by land use in each circle. The size of each plot was determined in accordance with its community height (Ohtsuka 1999). The size of a plot was 1 m × 1 m when the height of the community was <1 m, while the size of the plot was 2 m × 2 m when the community height was between 1 m and 2 m. A plot size of 5 m × 5 m was used if the community height was >2 m. The length of a plot was 1 m or 2 m in some special habitats, such as a road crack or a road edge, with a width of <1 m.

In each plot, the species were identified and the maximum height of each species and community was measured. Furthermore, the coverage of each species and community was estimated. The geographic location of each plot was determined by using a global positioning system.

For each plot, the relative light intensity (%) was measured at the community height at five random points by using a light meter (Spectrum Technologies Inc.,

Table 1. Percentage of land-use type in each area of the urban–rural gradient

Area	Land-use type (T) (%)†								No. of survey points
	T1	T2	T3	T4	T5	T6	T7	Total	
U1	23.4	17.3	18.8	15.7	24.9	0.0	0.0	100.0	197
U2	15.8	18.1	33.0	5.9	24.9	2.3	0.0	100.0	221
U3	13.6	16.2	24.6	25.1	17.3	3.1	0.0	100.0	191
S	20.0	15.6	11.9	16.8	5.9	20.0	9.9	100.0	405
R	18.0	18.8	16.1	16.9	0.0	17.2	13.0	100.0	361

† T1, road, street and transportation; T2, residential areas; T3, administration and public services buildings; T4, non-development land; T5, green space and square; T6, industrial manufacturing; T7, agricultural land.

Aurora, IL, USA). The soil pH (pH meter; Spectrum Technologies Inc.), soil moisture (WET Sensor; Delta-T Devices Ltd, Cambridge, UK) and soil compaction (soil compaction meter; Spectrum Technologies Inc.) were measured in soil samples from five random points.

Data analysis

The data analysis used the pooled data of spring and fall.

Species' origin

The species' origin was determined according to Zhang and Lai (1993) and Shanghai Academy of Science and Technology (1999) and the species were divided into native species and alien species. The proportion of native species to alien species in each area along the urban–rural gradient was compared via a χ^2-test. Whether the species was cosmopolitan or not was determined by referring to the areal types of the Chinese genera of seed plants (Wu 1991).

Life form and growth form

The life form and growth form are the overall indicators of the functional traits that are related to adaptive ability, resource utilization and competitive strategy. All the species first were categorized into one of two life forms: perennial species or annual species. The latter category can be subdivided into winter annual species and summer annual species (Song 2002) (Table 2). The growth forms were categorized into eight groups (Numata & Yoshizawa 1988) and were classified further according to their height (Kitazawa & Ohsawa 2002) (Table 3). The classification of the growth forms in this study was based on Zhang and Hirota (2000). The proportions of the life form and growth form of the weed species in each area along the urban–rural gradient were compared via a χ^2-test.

Table 2. Classification of species life forms according to Song (2002)

Life form	Trait
Perennial	Lives for >2 years; grows and blooms over the spring and summer, dies every fall and winter and then returns in the spring from the root stock
Annual	
Winter annual	Completes its life cycle within 1 year and then dies; germinates during the fall and matures during the spring or summer of the following calendar year
Summer annual	Completes its life cycle within 1 year and then dies; germinates during spring or early summer and matures by the fall of the same year

Species diversity

Three indices were used to measure the diversity in each plot: species richness (S), the Shannon–Wiener index of diversity (H) and the Pielou evenness index of diversity (E) (Pielou 1969):

$$H = -\sum_{i=1}^{s} P_i \ln P_i \tag{1}$$

and $E = H/\ln S$, (2)

where P_i is the relative dominance of a species as a proportion between 0 and 1 and S is the total number of species.

All the diversity index calculations were carried out by using PC-ORD 5.0 (MjM Software Design,

Table 3. Classification of species growth forms according to Numata and Yoshizawa (1988) and Kitazawa and Ohsawa (2002)

Growth form	Trait	Representative species
Small growth form		
Procumbent	Extends creeping stems and root from various places	*Euphorbia humifusa* Willd.
Rosette	Has radial basal leaves and leafless flowering stems	*Taraxacum mongolicum* Hand.-Mazz.
Branched	The lower part of the stem has many branches and no obvious spindle	*Stellaria media* (L.) Vill.
Tussock	Forms the root first and then grows thickly	*Poa annua* L.
Climbing or liane	Has a stem that curls or clings to something	*Humulus scandens* (Lour.) Merr.
Large growth form		
Partial rosette	Shows a rosette in the early stage and becomes erect after the rosette withers	*Sonchus oleraceus* L.
Pseudo-rosette	Shows a residual rosette and has leaves on an erect stem	*Youngia japonica* (L.) DC.
Erect	The spindle of the aerial part of the plant has an obvious erect posture	*Chenopodium a1bum* L.

Gleneden Beach, OR, USA). The diversity average of all the plots was used to signify the diversity indices in each area. The diversity indices were compared among the areas by using a one-way ANOVA and a Least Significant Difference (LSD) test.

Dominant species

The relative dominance (D) of each weed species was calculated by using $D = h \times c$ of the species/the total sum of $h \times c$ of all the species in each plot, where h is the maximum height of the species and c is the coverage of the species. The number of dominant species within each plot was identified by using a dominance analysis, as follows. In a community dominated by a single species, D of that species is 100%. However, if two species share dominance, D = 50% ideally, while if three codominate, D = 33.3% and so on. The number of dominant species indicates the smallest deviation between the actual relative dominance and the expected percentage share of the corresponding codominant-number model. The deviation (d) was calculated by using the following equation (Ohtsuka 1999):

$$d = 1/N\left(\sum [x_i - x]^2 + \sum x_j{}^2\right), \quad (3)$$

where x_i is the actual percentage share of the top species (i.e. in the top dominant of the one-dominant model or the two top dominants in the two-dominants model and so on), x is the ideal percentage share, x_j is the percentage share of the remaining species and N is the total number of species.

Weed communities

The data from the plots were subjected to a cluster analysis (group linkage method: group average; distance measure: Bray–Curtis) using PC-ORD 5.0 for the relative dominance data for each species. The weed communities were divided based on the results of the cluster analysis and the communities were named according to their dominant species.

Environmental factors

A canonical correspondence analysis (CCA) ordination using CANOCO 4.5 (Microcomputer Power, Ithaca, NY, USA) was conducted in order to identify the relationship between the species composition of weed communities and the environmental factors. The significance of the CCA was tested by a Monte Carlo test with 1000 permutations. The arrow length in the CCA was used to show the size of such an effect across the environmental variables (Lepš & Šmilauer 2003). The mean values for the light conditions, soil moisture, soil compaction and soil pH along the urban–rural gradient were compared via a one-way ANOVA and a LSD test. The Spearman's rank correlation test was used to test the relationship between the number of weed communities and the mean values of the light conditions, soil moisture, soil compaction and soil pH in each area along the urban–rural gradient. Except for the CCA, all the other statistical analyses were carried out by using SPSS 13.0 for Windows (IBM SPSS Statistics, Chicago, IL, USA).

RESULTS

Species composition

In total, 183 weed species, belonging to 41 families and 123 genera, were observed in the 1375 plots. Among the 41 families, the largest was Gramineae (34 species) and the second-largest was Asteraceae (32 species), followed by Labiatae, Cyperaceae and Scrophulariaceae (nine species for each). For the 17 families (e.g. Primulaceae, Malvaceae and Acanthaceae), only one species was documented. Of the 183 species observed, 72 (39.3%) were perennial species and 111 (60.7%) were annual species. The annuals were further divided into 42 winter annual species and 69 summer annual species. Of the 183 species documented, 32 (17.5%) were alien species and 151 (82.5%) were native species. The number of weed species in the five areas, ranked from highest to lowest, was S (137) > R (126) > U2 (115) > U3 (101) > U1 (91). The number of weed species in the suburban and rural areas therefore was greater than the number in the urban areas. There was no significant difference in the proportion of alien species to native species in any of the areas along the urban–rural gradient (χ^2 = 0.884, d.f. = 4, P = 0.927) (Table 4).

Species diversity along the urban–rural gradient

The mean values of the species richness showed a unimodal trend along the urban–rural gradient. U1 exhibited the lowest species richness, which was significantly lower than the values found for U2, U3, S and R (F = 6.054, P = 0.000). The level of species richness peaked in U2 and then showed a trend of gradual decrease (Fig. 2a). According to the minimum and maximum values of species richness, it can be seen that at least one species occurred in each plot in each of the areas. The number of species that was found in a plot (11) was highest in U2 and U3, intermediate in S and R (10) and lowest in U1 (7) (Fig. 2a).

The mean values of the Shannon–Wiener index, similar to the species richness, exhibited a unimodal trend along the urban–rural gradient. The largest value occurred in U2 and the lowest value occurred in R (Fig. 2b). The Shannon–Wiener index of R was significantly lower than that of U2, U3 and S. U1 was significantly lower than U2 (F = 3.577, P = 0.007) (Fig. 2b). According to the minimum and maximum values of the Shannon–Wiener index, it can be seen that the largest value per area of the Shannon–Wiener index, ranked in order for the five areas, was S > U3 > U1 >R > U2 (Fig. 2b).

The mean values of the Pielou evenness index of diversity of the species in the five areas, ranked from highest to lowest, was U3 > U2 > U1 > S > R. The Pielou evenness index of diversity of R was significantly lower than that of U3, U2 and U1 (F = 3.219, P = 0.012) (Fig. 2c). According to the minimum and maximum values of the Pielou evenness index of diversity, it can be seen that the largest value per area of the Pielou evenness index of diversity, ranked over the five areas, was R > S > U3 > U1 > U2 (Fig. 2c).

Weed community diversity along the urban–rural gradient

The 1375 plots were divided into 133 weed community types, depending on the results of the cluster analysis (Fig. S1). Of the 133 dominant species, 26 (19.5%) were alien and 107 (80.5%) were native. The number of weed communities, ranked among the five areas, was S (91) > R (86) > U2 (81) > U3 (68) > U1 (58). The values for the suburban and rural areas were higher than those for the urban areas. The proportion of alien dominant species to native dominant species was not significantly different in any area along the urban–rural gradient (χ^2 = 0.992, d.f. = 4, P = 0.911) (Table 4). Few differences were found among the numbers of various life forms of the dominant species and no significant difference was

Table 4. Analysis of the origin of the weed species and dominant species in the different areas

Area	Weed species			Dominant species		
	Native species N (%)	Alien species N (%)	Total (N)	Native species N (%)	Alien species N (%)	Total (N)
U1	70 (76.9)	21 (23.1)	91	43 (74.1)	15 (25.9)	58
U2	94 (81.7)	21 (18.3)	115	62 (76.5)	19 (23.5)	81
U3	82 (81.2)	19 (18.8)	101	55 (80.9)	13 (19.1)	68
S	110 (80.3)	27 (19.7)	137	72 (79.1)	19 (20.9)	91
R	100 (79.4)	26 (20.6)	126	67 (77.9)	19 (22.1)	86

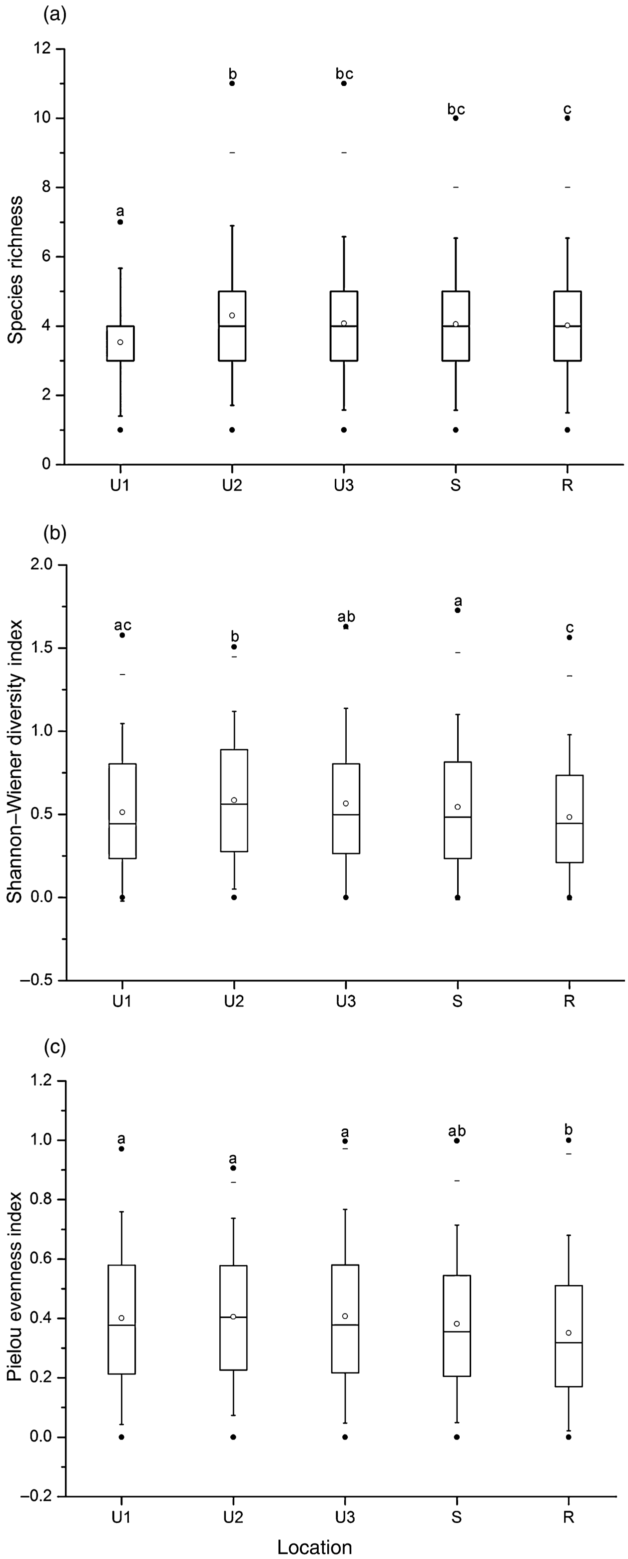


Fig. 2. Mean values (±standard deviation, SD) of the (a) species richness, (b) Shannon–Wiener index and (c) Pielou evenness index for weed species along the urban–rural gradient. U1, Urban area within the inner ring road; U2, urban area between the inner ring road and the central ring road; U3, urban area between the central ring road and the outer ring road; S, suburban areas located between the outer ring road and the suburban ring road; R, rural areas located outside the suburban ring road. Different letters indicate significant ($P < 0.05$) differences, based on the Least Significant Difference multiple comparison test. The whisker range shows the SD. (●), Minimum and maximum values; (○), mean values.

found in the proportions of the various life forms of the dominant species along the urban–rural gradient ($\chi^2 = 5.675$, d.f. = 8, $P = 0.684$). The number of dominant species with small growth forms (procumbent, rosette, branched, tussock, climbing or liane) was a little more than the number of dominant species with large growth forms (erect, partial rosette and pseudo-rosette) in the five areas (Fig. 3) and the proportions of dominant species with small growth forms and with large growth forms were not significantly different in the five areas ($\chi^2 = 0.984$, d.f. = 4, $P = 0.912$).

Of the 133 weed communities, 63 (47.4%) were distributed widely over the study areas. This type of weed was called a "widespread weed community" in this study (Fig. 4a). The life forms of the dominant species in these 63 communities varied slightly in their relative abundance. In 39 (61.9%) of these 63 communities, the dominant species had a small growth form. These species included *Taraxacum mongolicum* Hand., *Ixeris japonica* (Burm.) Nakai and *Sagina japonica* (Sw.) Ohwi. In 24 (38.1%) of these 63 communities, the dominant species had a large growth form and 15 (62.5%) of the 24 communities were pseudo-rosette or partial rosette (Fig. 5). They had a small growth form only in certain stages of their life cycle. Moreover, nearly half of the 63 communities had dominant species that were alien (16) or that were cosmopolitan (20).

In total, 18 (13.5%) communities were restricted to road cracks or road edges, lawns and urban glades in U1, U2 or U3. This type of weed was called an "urban weed community" in this study (Fig. 4b). For example, *Cardamine hirsuta* L. was predominant in the lawns and urban glades of U1, U2 or U3, *Duchesnea indica* (Andr.) Focke was predominant in the urban glades of U1, U2 or U3 and *Viola concordifolia* C.J. Wang was barely restricted to the urban glades in U1. The dominant species within these communities were perennial and

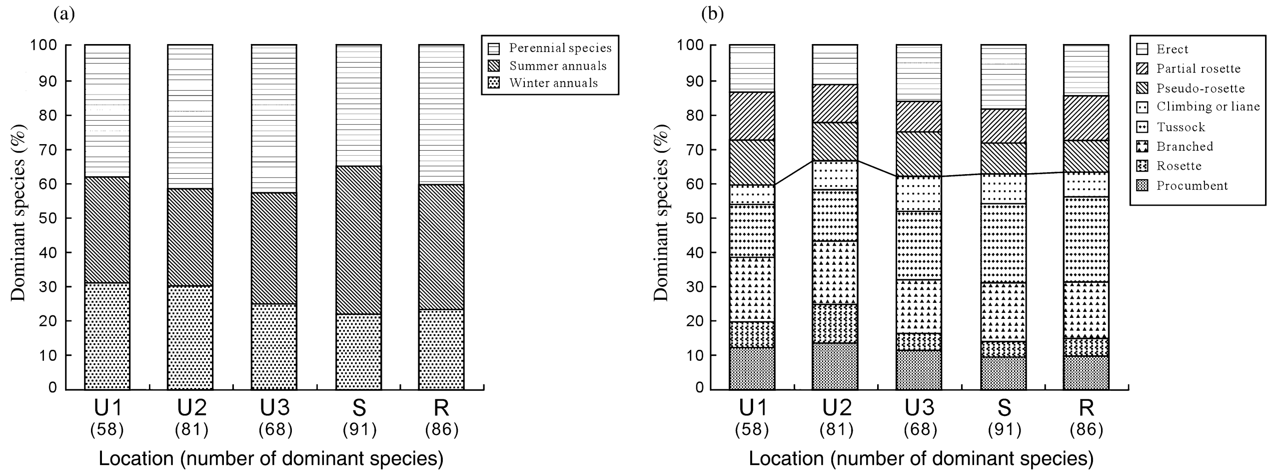


Fig. 3. (a) Life form composition and (b) growth form composition of the dominant species. The line connecting the bars in (b) represents the division between a small growth form and a large growth form. U1, Urban area within the inner ring road; U2, urban area between the inner ring road and the central ring road; U3, urban area between the central ring road and the outer ring road; S, suburban areas located between the outer ring road and the suburban ring road; R, rural areas located outside the suburban ring road.

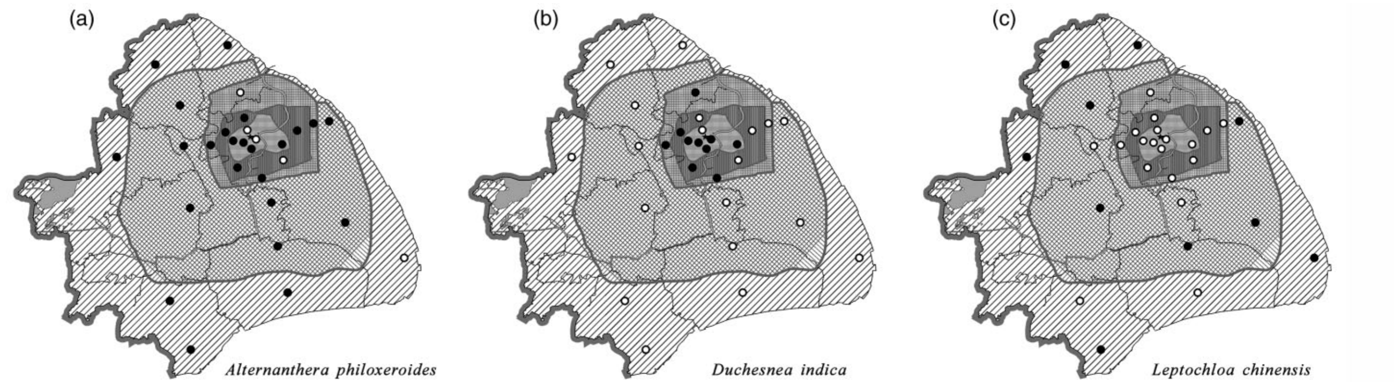
winter annuals (16 species in all) and primarily had small growth forms.

The other 52 (39.1%) communities tended to be restricted either to S or R (Fig. 4c) or to green spaces and administration and public services buildings in U1, U2 or U3 that were 50 or 60 years old. This type of weed was called a "rural weed community" in this study. Most of the dominant species in these 52 communities were perennials and summer annuals, such as *Dendranthema indicum* (L.) Des Moul., *Leptochloa chinensis* (L.) Nees and *Chenopodium album* L. Approximately 60% (30 species) of the dominant species had a small growth form and this value was greater than that found for the dominant species with a large growth form (22 species) (Fig. 5).

Pattern of environmental factors along the urban–rural gradient

The results of the Monte Carlo test showed that axis 1 and all the axes of the CCA were significantly different (P = 0.001). The results of the CCA showed that the correlation coefficients between the soil pH, soil moisture, soil compaction, light conditions and axis 1 were 0.187, −0.025, 0.237 and −0.504, respectively. The correlation coefficients between the soil pH, soil moisture, soil compaction, light conditions and axis 2 were 0.124, 0.393, −0.117 and −0.066, respectively. Axis 1 was closely related to the light conditions and axis 2 was related to the soil moisture. The CCA ordination revealed no marked separation among the species along the urban–rural gradient. The assemblage for the species of U1, U2 and U3 in the first and fourth quadrants showed a positive correlation with the soil pH and the soil compaction but a negative correlation with the light conditions. The species in R and S extended farther than those in U3, U2 and U1 and were dispersed into the second quadrant. They exhibited a positive correlation with the soil moisture. This finding indicated that the soil moisture was the most important environmental factor affecting the species composition of the weed communities in the rural areas that were studied (Fig. 6).

The mean values of the light conditions and soil moisture in R and S were higher than those in U1, U2 and U3. The light levels in R were significantly higher than in the other areas and the levels in S were significantly higher than those in U1 and U2 (F = 14.233, P = 0.000) (Fig. 7a). The soil moisture levels in R and S were significantly higher than those in U1, U2 and U3 (F = 23.146, P = 0.000) (Fig. 7b). The mean values of the soil compaction in U1, U2 and U3 were higher than those in R and S. The level of soil compaction in U1 was significantly higher than in R and S and the levels in U2 and U3 were higher than that in S (F = 9.028, P = 0.000) (Fig. 7c). The soil pH followed a unimodal trend along the urban–rural gradient, with the peak value occurring in U3 and the smallest value occurring in R. The ranking of these values from high to low was U3 > U2 > S > U1 > R and the pH value in U3 was significantly higher than in R (F = 3.002, P = 0.018)



Species number (%)		63 (47.4)	18 (13.5)	52 (39.1)
Life form	Perennial species	27 (42.8)	8 (44.4)	18 (34.6)
	Winter annual	18 (28.6)	8 (44.4)	6 (11.5)
	Summer annual	18 (28.6)	2 (11.2)	28 (53.9)
Growth form	Small growth form	39 (61.9)	12 (66.7)	30 (57.7)
	Large growth form	24 (38.1)	6 (33.3)	22 (42.3)
Origin	Native species	47 (74.6)	14 (77.8)	45 (86.5)
	Alien species	16 (25.4)	4 (22.2)	7 (13.5)
Areal type	Cosmopolitan	20 (31.7)	6 (33.3)	14 (26.9)
	Non-cosmopolitan	43 (68.3)	12 (66.7)	38 (73.1)

Fig. 4. Illustration of the distribution of the dominant species, specifically (a) a widespread weed community, (b) an urban weed community and (c) a rural weed community. (●), The distribution of the dominant species includes the sample point; (○), the distribution of the dominant species does not include the sample point.

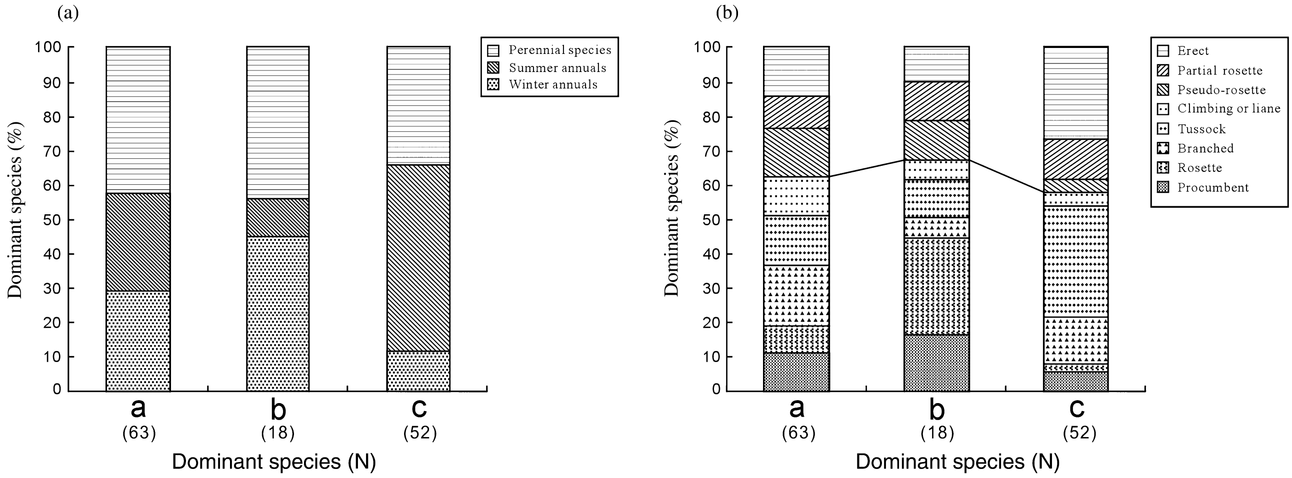


Fig. 5. (a) Life form composition and (b) growth form composition of the dominant species, where a = the dominant species that were widely distributed, b = the dominant species that were predominant in U1, U2 and U3 and c = the dominant species that were predominant in S and R. The line connecting the bars in (b) represents the division between a small growth form and a large growth form. U1, Urban area within the inner ring road; U2, urban area between the inner ring road and the central ring road; U3, urban area between the central ring road and the outer ring road; S, suburban areas located between the outer ring road and the suburban ring road; R, rural areas located outside the suburban ring road.

(Fig. 7d). In addition, the soil moisture, soil compaction and soil pH showed the largest ranges of values in S and R (Fig. 7). These large ranges might lead to more diverse habitat types in S and R.

The Spearman's rank correlation analysis of the number of weed communities and the mean values of the environmental factors in each area along the urban–rural gradient showed that soil compaction had a significant effect on the number of weed communities (P = 0.000) and that the light conditions, soil moisture and soil pH had no significant effect on the number of weed communities (P = 0.285, P = 0.104 and P = 0.747, respectively).

DISCUSSION

Pattern of weed communities along the urban–rural gradient

The patterns of biological diversity and the factors that influence them are core issues in biogeography and ecology (Gaston 2000). Biodiversity can follow different patterns, based on the integrative effects of the regional species pool, environmental conditions and ecological processes (Ricklefs 2006). This study showed that the number of weed communities in urban areas was less than the number found in suburban and rural areas. Many studies on plants, birds and insects have revealed similar trends (Blair & Launer 2002; Moffatt *et al*. 2004; Chace & Walsh 2006). According to Czech *et al*. (2000), these trends are caused primarily by increased human disturbance of the landscape as the urban population grows and high-density urban roads and buildings are constructed. There are two reasons for the greater number of weed communities in S and R, compared to U1, U2 and U3. First, there were more land-use types in S and R than in the other areas and S and R had more land-use types that were suitable for the growth of weeds (Table 1). Second, the environmental conditions were more varied in S and R because of large fluctuations in the soil moisture, soil compaction and soil pH (Fig. 7), thus providing more growth environments for plants with different ecological habits (Song *et al*. 2000). Meanwhile, the CCA showed that the species composition of the weed communities in these two areas was affected mainly by the light conditions and the soil moisture (Fig. 6). The light intensity and the soil moisture levels in S and R were higher because of lower impacts due to the building coverage and the drainage measures associated with urban construction. In addition, as a result of urban construction, large areas of abandoned land provided space that was suitable for species at different successional stages, such as the annual herb, perennial herb and even pioneer woody plants, including *Salix babylonica* L. and *Broussonetia papyrifera* L. (L'Hert. ex Vent.). Situations such as this might have

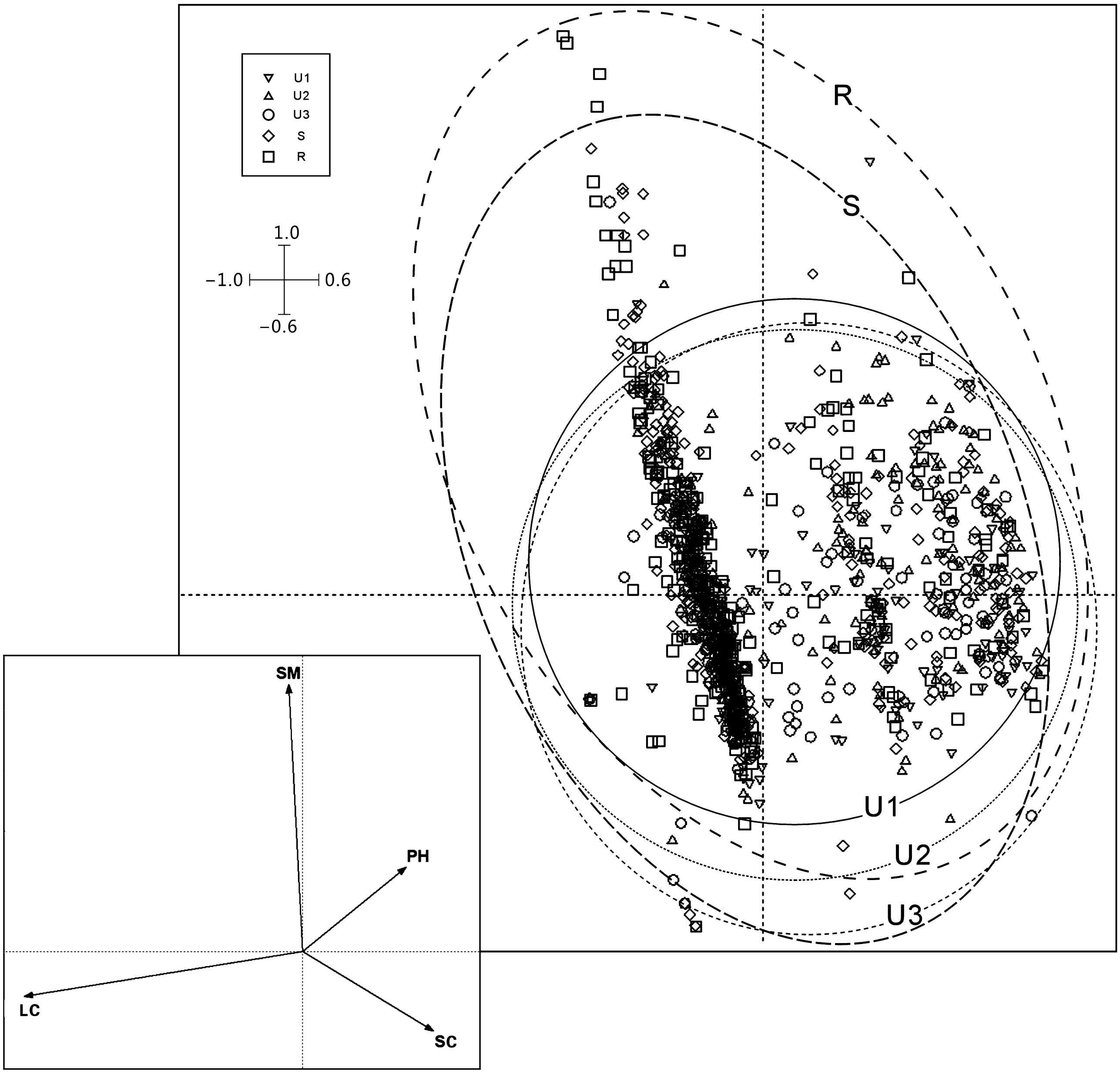


Fig. 6. Canonical correspondence analysis of species and environmental variables. U1, Urban area within the inner ring road; U2, urban area between the inner ring road and the central ring road; U3, urban area between the central ring road and the outer ring road; S, suburban areas located between the outer ring road and the suburban ring road; R, rural areas located outside the suburban ring road. LC, light condition; PH, soil pH; SC, soil compaction; SM, soil moisture.

caused the species richness and Shannon–Wiener index values for the weed communities to be higher in the urban–rural fringe.

Weed types and adaptation strategies

Many studies have addressed the distribution of plants and the classification of plant types in urban areas. For example, Wittig and Ruvkert (1985) used the levels of plant adaptation to urban environments to designate species as "highly urbanophobe", "moderately urbanophobe", "urban-neutral", "moderately urbanophile" or "highly urbanophile". In light of the significant spatial variation in species distribution and the unique effects of human activity on urban plants, McKinney (2002) categorized urban species as

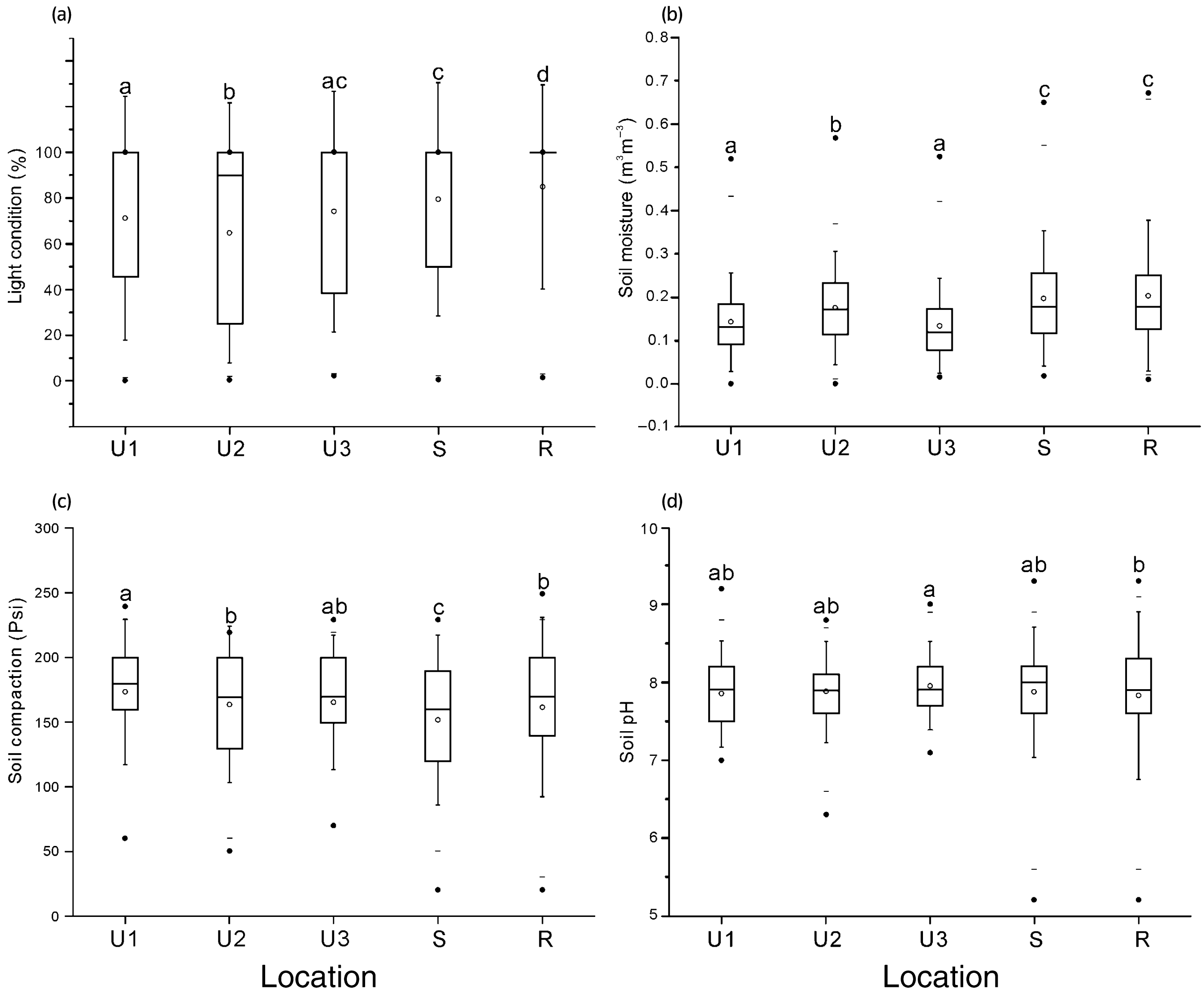


Fig. 7. Mean values (±standard deviation, SD) of the (a) light conditions, (b) soil moisture, (c) soil compaction and (d) soil pH along the urban–rural gradient. U1, Urban area within the inner ring road; U2, urban area between the inner ring road and the central ring road; U3, urban area between the central ring road and the outer ring road; S, suburban areas located between the outer ring road and the suburban ring road; R, rural areas located outside the suburban ring road. Different letters indicate significant ($P < 0.05$) differences, based on the Least Significant Difference multiple comparison test. The whisker range shows the SD. (●), Minimum and maximum values; (○), mean values.

"urban avoiders", "urban adapters" or "urban exploiters".

Based on the distribution and habitat of the 133 dominant species, this study divided the weed communities into three groups: "widespread", "urban" and "rural". The first group consisted of weed communities that were widely distributed over the study areas, such as land used for roads, streets and transportation, residential areas, administration and public services buildings, as well as non-development land along the urban–rural gradient (Table 1). This group included cosmopolitan and alien species with wide distributions. A study by Da *et al.* (2007) of the main exotic organisms in Shanghai found that most of the weed species that were widely distributed in the urban area were alien species, which is consistent with this study's results. As a consequence of the high proportion of alien species being widely distributed in communities over the study areas, the widespread weeds can be managed through the control of alien species by strengthening weed management practices.

The second group consisted of urban weeds that mainly occurred in the municipal areas, such as green spaces and the public square. These areas were characterized by the high frequency and intensity of human disturbance, such as trampling, mowing and manual weeding. This type of weed included two types of species, winter annual species and perennial species. The winter annual species blossom, bear fruit and complete their life cycle over a short time period, allowing them to avoid human disturbance. Studies on the species diversity of human-disturbed habitats in Central Europe and Chiba (Japan) also found that the species occurring in the areas with frequent human trampling primarily were winter annual weeds (Kitazawa & Ohsawa 2002; Lososová *et al*. 2006). The second type of weed that was found in the municipal area was perennial weed species with a small growth form that made them highly resistant to trampling. Therefore, they could adapt to or avoid high-intensity mechanical damage that was caused by frequent human activity within the urban areas and thus maintain their ability to reproduce and to disperse propagates (Tian *et al*. 2008). The urban weeds that occurred in only the municipal areas can be used in the following two ways: (i) choose the species with strong anti-interference ability and a more attractive landscape effect and convert them into ground-cover plants in order to increase the variety of species that is used in urban landscaping; and (ii) choose the strongly tolerant species for vegetation restoration and reconstruction in poor urban habitat conditions (such as abandoned land).

The third group that was identified consisted of rural weeds that occurred primarily in suburban or rural areas. These weed species mostly were distributed in farmland (Table 1) and were mostly perennial or summer annual weeds that are common in agroecosystems. Summer annual weeds have the same growing season as crops and therefore can avoid interference from crop harvesting or land management. Perennial weeds are able to grow because the cultivation depth is not sufficient to eliminate them (Nemoto 2006). For the rural weed communities, on the one hand, the distribution of weeds with special habits and adaptations can be an indicator of soil heavy metal pollution, soil nutrient conditions and the physical and chemical properties of the soil (Guo & Qiang 2002; Weidenhamer & Callaway 2010; Zhu & Wu 2012); this information can lay a foundation for the further control of soil heavy metal pollution or the adjustment of the soil fertilization strategy and management methods. On the other hand, the distribution and community succession of farmland weeds is closely related to the use of herbicides. As a result of the different weed-controlling spectrum of each herbicide, some originally dominant weeds become less dominant due to herbicidal control, but some herbicide-resistant weeds gradually develop from co-occurring weeds into dominant weeds after the long-term use of a particular type of herbicide in a certain area (Watanabe 2011). Therefore, according to the distribution of the weeds, a preliminary judgment can be made about the use of herbicides in the area. For example, if a rice field were dominated by grass species, such as *Echinochloa crus-galli* (L.) Beauv. and *L. chinensis* (L.) Nees, a preliminary judgment can be made that herbicides, such as bensulfuron-methyl, pyrazosulfuron-methyl, 2-methyl-4-chlorophenoxyacetic acid sodium salt and bentazon, might have been used continuously for field management. These herbicides can effectively control broad-leaved weeds and sedges. If the rice-field weeds were mainly perennial sedge weeds, herbicides that can effectively control annual weeds might have been used continuously, such as pretilachlor, butachlor and penoxsulam. According to the distribution of the weeds, the strategy of herbicide usage can be adjusted and a herbicide that is sensitive to these weeds can be chosen in order to improve the comprehensive technical system of weed control.

CONCLUSIONS

The present study focused on the distribution of weed communities along the urban–rural gradient and on the relationship between environmental factors and weed communities in Shanghai, China. The main factors influencing the species composition of the weed communities were the light conditions and the soil moisture in rural areas, the soil compaction in urban areas and the soil pH in suburban areas. Habitat variation led to diverse weed communities in the suburban and rural areas, but the loss and change of habitat led to fewer weed communities in the urban areas. Based on the results of this investigation of the distribution of the weed communities in Shanghai, the weed communities were divided into different groups according to their ability to adapt to the environment.

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SUPPORTING INFORMATION

Additional supporting information can be found in the online version of this article at the publisher's website:

Fig. S1. Cluster analysis dendrogram (group linkage method: group average; distance measure: Euclidean) of the 1375 plots, based on the relative dominance of each species.