RESEARCH ARTICLE

Phylogenetic and functional structures of plant communities along a spatiotemporal urbanization gradient: Effects of colonization and extinction

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Abstract

Question: Urbanization has remarkable impacts on the phylogenetic and functional structures of plant communities. Both temporal and spatial comparisons along urbanization gradients are widely used in related studies, but there has been a lack of consistency in the results. Moreover, there is a need for studies that determine species assembly mechanisms through immigration and extinction. Therefore, two questions were addressed: (a) How do the phylogenetic and functional structures of ruderal species respond to urbanization, and do their shifts follow a similar pattern along temporal and spatial urbanization gradients? (b) What are the key underlying processes, i.e., either extinction- or colonization-caused clustering, that determine the phylogenetic and functional structures of ruderal species under urbanization?

Study site: Two metropoles (Shanghai and Harbin) experiencing rapid urbanization in China.

Methods: We collected occurrence data on ruderal species from 1955 and the present in two cities. Standardized effect sizes of mean pairwise phylogenetic distance and of mean pairwise functional distance values (MPD_{SES} and MFD_{SES}, resp.) were calculated to test whether there was phylogenetic and/or functional structure clustering along spatial or temporal urbanization gradients. $\beta\text{-}MPD_{SES}$ and $\beta\text{-}MFD_{SES}$ values were used to quantify the similarities among colonists, extinct species, and residents.

Results: Along both the spatial and temporal gradients, the MPD_{SES} values in each city decreased from significantly positive to significantly negative with increasing urbanization. Inconsistently, along the temporal gradients, the $\beta\text{-}MPD_{SES}$ values of the colonists/extinct species to the residents were significantly negative; along the spatial gradients, the $\beta\text{-}MPD_{SES}$ values of extinct species to residents were significantly positive with increasing urbanization.

Conclusions: We found there was a clear phylogenetic clustering of ruderal species with increasing spatial and temporal urbanization gradients. Our analysis showed that the changes across the urban–rural gradient are mainly driven by species going extinct that are phylogenetically dissimilar to the resident species. The temporal

dynamics are, however, primarily driven by colonist species that are phylogenetically similar to the resident species.

KEYWORDS

colonists, extinction, invasive species, ruderal species, space-for-time substitution, urban plant community

1 | INTRODUCTION

Changes in human-influenced landscape structure and in species migration have a remarkable impact on natural species composition worldwide (Collingham & Huntley, 2000; HilleRisLambers, 2015; Keshtkar & Voigt, 2016; Vitousek, Mooney, Lubchenko, & Melillo, 1997). One of the core anthropogenic activities responsible for these changes is urbanization (Hautier et al., 2015; Ives et al., 2016; McKinney, 2002, 2008), heavily modifying the local environment to suit human needs and desires (Palma et al., 2017). Fifty-four percent of the world population lived in urban areas in 2015, and this will increase continually and rapidly to 60% by 2030 (World Health Organization & UN-Habitat, 2016).

The dense population and intensive industrial and transportation activities in urban areas have caused habitat loss and fragmented landscape structures in local ecosystems (Currit & Easterling, 2009; Mack & Lonsdale, 2001; McDonnell et al., 1997; Price, Dorcas, Gallant, Klaver, & Willson, 2006). Moreover, numerous exotic plant species have colonized urban regions through global trade and gardening practices (Boivin et al., 2016; Hope et al., 2003). Such transitions may affect not only the taxonomic composition but also the phylogenetic and functional patterns of plant communities (Čeplová et al., 2015; Johnson, Tauzer, & Swan, 2015; Knapp, Kühn, Schweiger, & Klotz, 2008; Knapp, Kühn, Stolle, & Klotz, 2010; Knapp, Winter, & Klotz, 2017; Piano et al., 2016).

The effects of urbanization on plant community patterns have generally been studied using temporal comparison approaches (before–after urbanization gradients) and spatial comparison approaches (urban–rural gradients). The latter can be considered to be a space-for-time substitution method. So far, empirical studies have used spatial comparison because of the difficulty in obtaining historical plant data and indicate that the phylogenetic diversity of plant species decreases with increasing spatial urbanization (Breza, 2015; Johnson et al., 2015; Knapp et al., 2012). Furthermore, it has been reported that urbanization favors native and non-native spontaneous species with disturbance-tolerant traits, i.e., ruderal species (including weeds and grasses), in urban ecosystems and also leads to a change in the phylogenetic and functional structures of species, as well (Duncan et al., 2011; Palma et al., 2017; Ricotta, Godefroid, Heathfield, & Mazzoleni, 2015; Ricotta, Heathfield, Godefroid, & Mazzoleni, 2012). However, few studies have explicitly addressed the dynamic effects of temporal urbanization on plant communities. Due to the limited growth rates or resilience of species, the responses

of plant species to the habitat changes are time-lagged as the result of dynamic processes over long periods, and the spatial patterns of plant species under urbanization could be biased (Bonthoux, Barnagaud, Goulard, & Balent, 2013). It has been suggested that space-for-time substitutions might ignore the actual dynamic effects of urban development and landscape changes over time but overestimate the variation due to spatial heterogeneity (Adler & Lauenroth, 2003; Bonthoux et al., 2013; Fukami & Wardle, 2005). Thus, there is a need for studies simultaneously applying time series and spatial comparison approaches to analyze the induced biases.

Phylogenetic and functional structures depict species' evolutionary histories and mechanisms of species assembly mediated through environmental stressors and species interactions (Chave, Chust, & Thébaud, 2007; Díaz & Cabido, 2001; McGill, Enquist, Weiher, & Westoby, 2006). Greater phylogenetic/functional diversity and healthier structures lead to a higher ecosystem stability (Knapp et al., 2017). Studying the responses of phylogenetic and functional structure to urbanization will not only guide us to conserve our urban nature, but will also offer deep insights into the mechanisms underlying how urbanization affects plant biodiversity. For instance, environmental filters could cluster the phylogenetic structure of species and select similar functional traits by preventing the persistence of unsuitable species in a particular habitat. As an abiotic-environmental filter, disturbance regimes tend to cause phylogenetic and functional clustering in plant communities (Brunbjerg, Borchsenius, Eiserhardt, Ejrnæs, & Svenning, 2012; Čeplová et al., 2015). In contrast, competitive exclusion can disperse species' phylogenetic and functional structures by limiting the coexistence of closely related species through intense competition, just as Darwin's naturalization hypothesis claims (Yannelli, Koch, Jeschke, & Kollmann, 2017). Meanwhile, current studies indicate that competitive exclusion might also lead to phylogenetic and/or functional clustering by excluding groups of ecologically similar species with low competitive abilities (Mayfield & Levine, 2010). In this case, species with lower competitive abilities are excluded by the stronger ones, which should cause dissimilarity in functional traits among the species that become extinct and residents.

Recently, in order to distinguish the effects of immigration and local extinction processes on plant communities, a new analytical strategy was proposed in a study on phylogenetic and functional changes over community succession by comparing the phylogenetic and functional similarities among colonists and extinct and resident species (Li et al., 2015). If phylogenetic clustering occurs,
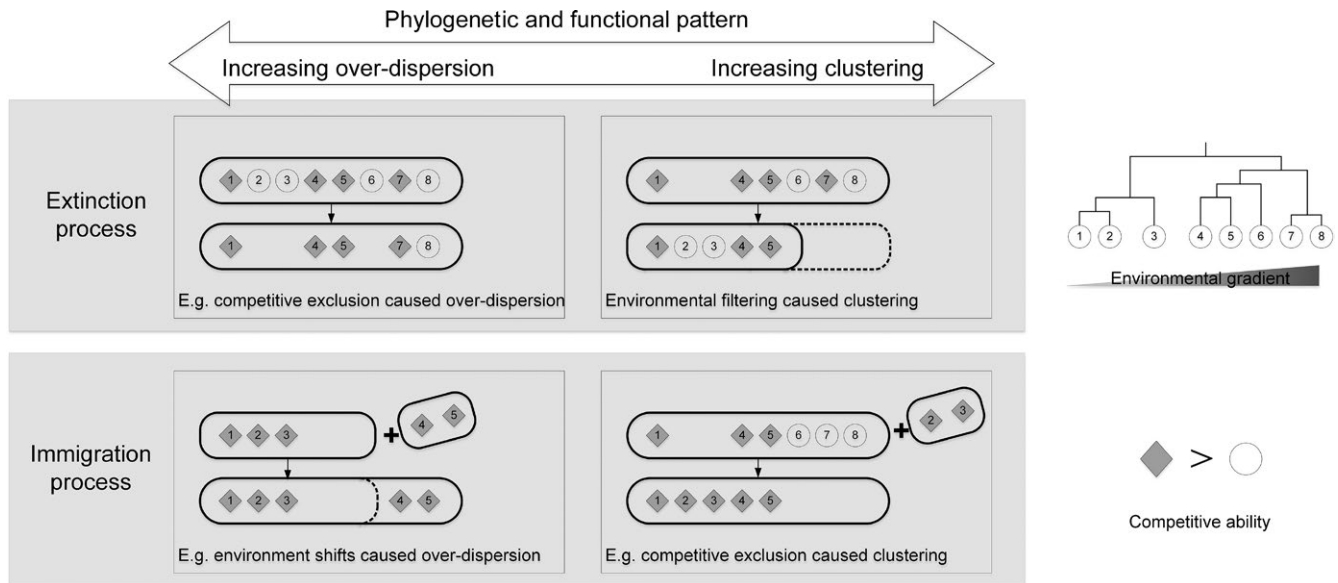
FIGURE 1 Environmental filters and competitive exclusion influence the phylogenetic pattern of species assembly processes through colonization and extinction. Competitive exclusion may also cause phylogenetic/functional clustering by excluding groups of ecologically similar species with low competitive abilities (Mayfield & Levine, 2010). Colonizers might also be less related to residents and thus cause overdispersion, just as Darwin proposed in his naturalization hypothesis. The white circle represents species with similar niche requirements, and the gray rhombus represents species with similar competitive abilities

this may be due to the local extinction of species that are phylogenetically and functionally dissimilar to the residents or due to the colonization of species that are phylogenetically and functionally similar to the residents (Li et al., 2015). Likewise, overdispersion could be driven by the extinction of species that are phylogenetically and functionally similar to the residents or by the colonization of species that are phylogenetically and functionally dissimilar to the residents (Figure 1). Hence, distinguishing the contributions of colonization and extinction to the changes in phylogenetic and functional structures in urbanization could reveal the key underlying mechanism that rules species assembly in urban areas.

As spontaneous plants in urban area, ruderal plant species have high sensitivity and a short lifecycle, and thus can respond to the urban habitat heterogeneity and rapidly adapt to the habitats by changing their morphology, physiology and behavior. Thus, ruderal species are the optimally indicators for urbanization (Chen, Wang, Liang, Liu, & Da, 2014; Tian, Song, & Da, 2015). In this study, we analyzed the phylogenetic and functional structures of ruderal plant species in two Chinese cities and evaluated the differences among colonists/extinct species and residents using time series (before–after urbanization) and spatial comparison approaches (urban–rural urbanization gradients). We aimed to reveal the responses of ruderal phylogenetic and functional structures to urbanization and to specifically answer the following two questions:

1. How do the phylogenetic and functional structures of ruderal species respond to urbanization, and do their shifts follow a similar pattern along temporal and spatial urbanization gradients?

2. What are the key underlying processes, i.e., either extinction- or colonization-caused clustering, that determine the phylogenetic and functional structures of ruderal species under urbanization?

2 | MATERIALS AND METHODS

2.1 | Ruderal occurrence data

To identify the floristic changes of ruderal plant species along spatial and temporal urbanization gradients, occurrence data were obtained from two of our previous studies in Shanghai city and Harbin city (Chen et al., 2014; Tian et al., 2015), two metropoles experiencing rapid urbanization in China. Both studies indicated that the ruderal species composition changed significantly along urban–rural gradients. The study in Harbin also illustrated that the phenotypic plasticity had decreased in perennial species but increased in annual species in the past half century.

Shanghai is located at the edge of the Yangtze River Delta (6,340 km[2] in size; 31°13′50″ N, 121°28′25″ E), where the climate is subtropical monsoon with a mean annual temperature of 17.8°C and an average annual rainfall of 1,457.9 mm. Harbin (10,198 km[2] in size; 45°45′48.08″ N, 126°38′56.03″ E) is located on the southeastern edge of the Songnen Plain, which has a typical continental monsoon climate with a mean annual temperature of 5.2°C and an average annual precipitation of 569.1 mm. Both cities have been constructed from a central point and extend radially outwards following a concentric circle pattern, with characteristic inner, mid and outer circles.

Our two studies used an identical survey approach along urban–rural gradients. Each study took the central point of the city as the origin and established sampling sites in a radial pattern, which was

partitioned by the central-suburban ring road. At equal radial distances of 1 km at each site, plots of 1 m² were placed randomly in all typical habitat types (road gaps, lawns, abandoned land with developed soils, abandoned land with gravel, arable land, shrub–grassland gaps, forest gaps, wetlands, and secondary forest). Each investigation was conducted during the growing season (April–May in spring and August–September in autumn). In each plot, species were identified following the *Flora Reipublicae Popularis Sinicae* (Flora of China Editorial Committee, 2013). Meanwhile, their origins were identified following *The Checklist of the Chinese Invasive Plants* (Ma, 2013). In total, 1,375 plots in Shanghai and 1,763 plots in Harbin were investigated.

Furthermore, we included the historical ruderal occurrence data of Harbin city recorded in 1955 (Baranov, Gordeev, & Kuzmin, 1955) to analyze dynamic shifts across temporal urbanization gradients. Baranov et al. (1955) investigated the same area as we did in 2011, which contained nearly all the ruderal habitat types at that time (see details in Chen et al., 2014). The data contained a large amount of information with, for most species, the scientific name, the Chinese name of that time and the habitat. Because the plant classification systems differed between the historical and recent data, we redefined the family, genus and species of the ruderal vegetation and transformed all species names into APGIII (Angiosperm Phylogeny Group, 2009).

2.2 | Phylogenies and functional traits

We constructed phylogenetic trees using the online tool Phylomatic (Webb & Donoghue, 2005) and used the stored phylogenetic tree by Zanne et al. (2014) to assemble a phylogenetic tree and estimate branch lengths. Then, we removed all single-daughter nodes using the function *multi2di* in the package *ape* in R (Paradis, Claude, & Strimmer, 2004). The final trees were accurate to the genus and species level and provided a realistic approximation of the real seed plant phylogeny (Webb & Donoghue, 2005).

For each species that occurred in the urban–rural gradients of the two cities, we collected five traits that have been commonly used in studies of plant communities to represent resource partitioning differences and resource competition differences (Adler, Hillerislambers, & Levine, 2007; Duncan et al., 2011; Vallet, Daniel, Beaujouan, Rozé, & Pavoine, 2010). Specifically, the maximum plant height was used to represent access to light, carbon acquisition and reproductive strategies of species and is directly associated with the light-competitive ability (Bazzaz, Ackerly, & Reekie, 2000; Westoby, Falster, Moles, Vesk, & Wright, 2002). Life forms are used to reflect plants' adaptive strategies during seasons with adverse conditions (Ellenberg & Mueller Dombois, 1967). The vegetation form pertains to the plants' subterranean organs, which are associated with the ability to compete for water and nutrients (Hayasaka, Fujiwara, & Box, 2009). Fruiting time is commonly associated with the vegetative and reproductive selection pressures on the timing of the different phases (Cornelissen et al., 2003). All traits were recorded from the *Flora Reipublicae Popularis Sinicae* (Flora of China Editorial Committee, 2013) and

Chinese Colored Weed Illustrated Book (Zhang & Hirota, 2000). Life forms were categorized into three levels (summer-annual, winter-annual, perennial). The growth forms were categorized into eight levels (procumbent, rosette, branched, tussock, climbing/liana, partial rosette, pseudorosette, erect). The fruiting time was categorized into four levels (spring, summer, autumn and winter). The vegetation forms were categorized into five levels (widest extent of rhizomatous growth, moderate extent, narrowest extent, clonal growth by stolons and struck roots, non-clonal growth).

To explore the evolutionary lability of the traits, we used Blomberg's *K* statistic (Blomberg, Garland, & Ives, 2003) to test the phylogenetic signal of continuous traits and used the "*phylo.signal. disc*" function (Rezende, Lavabre, Guimarães, Jordano, & Bascompte, 2007) to quantify the phylogenetic signal of other categorical traits. The significance of the phylogenetic signals was determined by the rank of the observed relative to the null distribution for 999 replications.

Furthermore, a functional distance matrix was created using the Gower dissimilarity method (Gower, 1971), which allows for missing data and categorical data, to represent the dissimilarity of species in a multiple-trait space. The Gower distance matrix and the unweighted pair-group clustering method using arithmetic averages were used to construct a trait dendrogram in order to apply identical analytical methods to the phylogenetic and trait data (Petchey & Gaston, 2002). The *gowdis* and *hclust* functions in FD package (version1.0-12) were used in these analyses (Laliberté et al. 2014). All analyses were conducted in R version 3.4.1 (RCore Team 2017).

2.3 | Phylogenetic and functional structure measures

Three spatial subsets (urban, suburban and rural areas) in both cities and two temporal subsets (the years 1955 & 2011) in Harbin were extracted based on the historical and survey data in order to examine how the phylogenetic structure varies along spatiotemporal urbanization gradients. For each subset, the mean pairwise phylogenetic distance (MPD) of all possible species pairs was calculated to determine the phylogenetic diversity (Webb, Ackerly, McPeek, & Donoghue, 2002). The mean pairwise functional distance (MFD) was determined using the dendrogram mentioned above to assess the variation in the competitive ability of ruderal species with urbanization. Subsequently, the observed MPD and MFD values were compared to their respective expected values under a null model of random community assembly using standardized effect sizes (SES) of MPD and MFD for each subset, i.e.,

$$\text{MPD}_{\text{SES}} = \frac{(\text{observed MPD} - \text{mean of random MPD})}{\text{SD of random MPD}}$$

Values significantly more negative than random suggest a phylogenetically clustered tendency, while those significantly more positive than random indicate an overdispersed structure (Webb, 2000). Because both phylogenetic and functional structures are sensitive

to the statistical properties of different null models (Hardy, 2008), we used three different null models. The taxa null model was obtained by shuffling distance matrix labels across all taxa included in the distance matrix. The phylogeny null model was created by drawing species from the pool of species occurring in the phylogeny pool with equal probability. The independent null model was established by randomizing the community matrix with the independent swap algorithm and was the strictest null model (Norden, Letcher, Boukili, Swenson, & Chazdon, 2012). These metrics were calculated using the package *picante* in R version 3.4.1. (Kembel et al., 2010).

2.4 | Phylogenetic and functional patterns of species colonization and local extinction

Across the temporal urbanization gradients, we defined the extinct species as those that were recorded only in 1955, while colonist species were those that were recorded only in 2011. Resident species were those that were recorded in both 1955 and 2011. Across the urban–rural gradients, we defined the extinct species as those that were recorded only in the rural area, while the colonist species were those that were recorded only in the suburban/urban area, and resident species were those that were recorded in both the rural and suburban/urban areas. We followed a similar approach as that proposed by Li et al. (2015), with two metrics, β-MPD (mean pairwise phylogenetic distance between colonists/extinct species and residents) and β-MFD (mean pairwise functional distance between colonists/extinct species and residents), to determine the mean pairwise phylogenetic and functional distance between colonists/extinct species and residents in order to quantify the similarities between the colonists/extinct species and residents of each subset. Negative SES values indicate that colonists/extinct species are more closely related or similar to the residents than expected by chance, while positive values indicate the opposite. We performed these analyses

for each subset using the *comdist* and *comdistnt* functions in the R package *picante*.

The shifts in phylogenetic and functional structures along urbanization gradients do not only depend on the relatedness of the colonists and locally extinct species to residents but also on the phylogenetic and functional structures of the colonists and locally extinct species. Thus, we calculated the MPD_{SES} and MFD_{SES} for colonists and locally extinct species in each subset using identical null models for β-MPD_{SES} (standardized effect size of MPD between colonists/extinct species and residents) and β-MFD_{SES} (standardized effect size of MFD between colonists/extinct species and residents) as those mentioned above.

3 | RESULTS

3.1 | Changes in phylogenetic and functional structures

Overall, the phylogenetic structures of ruderal species exhibited clear clustering trends with increasing urbanization both spatially and temporally. The maximum plant height (K value: 0.4947, $p < 0.01$; lambda value: 0.9717, $p < 0.01$) and other categorical traits revealed significant phylogenetic signal (see details in Table 1).

In Harbin city, the standardized effect size of mean pairwise phylogenetic distance (MPD_{SES}) values decreased from significantly positive ($p < 0.01$) in 1955 to significantly negative ($p < 0.01$, Table 2) in 2011 under all three null models, which indicates that the phylogenetic structures of ruderal species clustered with increasing urbanization over time.

Along the urban–rural gradients of both cities, the MPD_{SES} values were negative (Figure 2, $p < 0.05$) and were increasingly negative when going from rural to urban systems via suburban areas under all three models. The MPD_{SES} value was significantly

TABLE 1 Traits used in the analyses and phylogenetic signals were tested based on the "*phylo.signal.disc*" function for four categorical traits (Rezende et al., 2007)

Functional traits	Data source	% Missing data	Observed number of changes	Mean null number of changes	*p*	Categories
Height	FRPS[a]	8	–	–	–	Continuous traits
Life forms	FRPS[a], CCW[b]	0	66	90	0.001	Summer-annual, Winter-annual, Perennial
Fruiting time	FRPS[a]	4	53	65	0.001	Spring, Summer, Autumn, Winter
Vegetation forms	CCW[b]	14	45	56	0.001	Widest extent of rhizomatous growth, Moderate extent, Narrowest extent, Clonal growth by stolons and struck roots, Non-clonal growth
Growth forms	CCW[b]	6	68	124	0.001	Procumbent, Rosette, Branched, Tussock, Climbing or liana, Partial rosette, Pseudorosette, Erect

To check phylogenetic signal of four categorical traits, minimum number of trait state changes across the phylogenetic tree was compared to a null model generated by randomizing the trait states across the tips of the tree 999 times (Maddison & Slatkin, 1991). If the observed minimum number of changes significantly lower than expected mean null values, we considered that related species have similar trait states (presence of phylogenetic signal).
[a] Flora Reipublicae Popularis Sinicae. [b] Flora of China and Chinese Colored Weed Illustrated Book.

TABLE 2 The temporal comparison of phylogenetic structures in Harbin were measured using the standardized effect sizes of mean pairwise phylogenetic distance (MPD$_{SES}$) with three null models

Null models	Observed MPD	Mean of random MPD	SD of random MPD	MPD$_{SES}$	*p* value
Richness					
1955	295.590	291.421	1.491	2.632**	1.000
2011	257.007	291.358	7.222	−4.597**	0.001
Phylogeny					
1955	295.590	291.465	1.496	2.778**	1
2011	257.007	291.492	7.342	−4.532**	0.001
Independent					
1955	295.590	290.973	1.548	3.041**	1
2011	257.007	279.636	5.532	−4.086**	0.001

The taxa null model was obtained by shuffling distance matrix labels across all taxa included in the distance matrix. The phylogeny null model was created by drawing species from the pool of species occurring in the phylogeny pool with equal probability. The independent null model was established by randomizing the community matrix with the independent swap algorithm. Positive MPD$_{SES}$ values indicate overdispersion, and negative MPD$_{SES}$ values indicate clustering. MPD = Mean pairwise phylogenetic distance; MPD$_{SES}$ = standardized effect size of MPD; ** means very significant (*p* < 0.01).
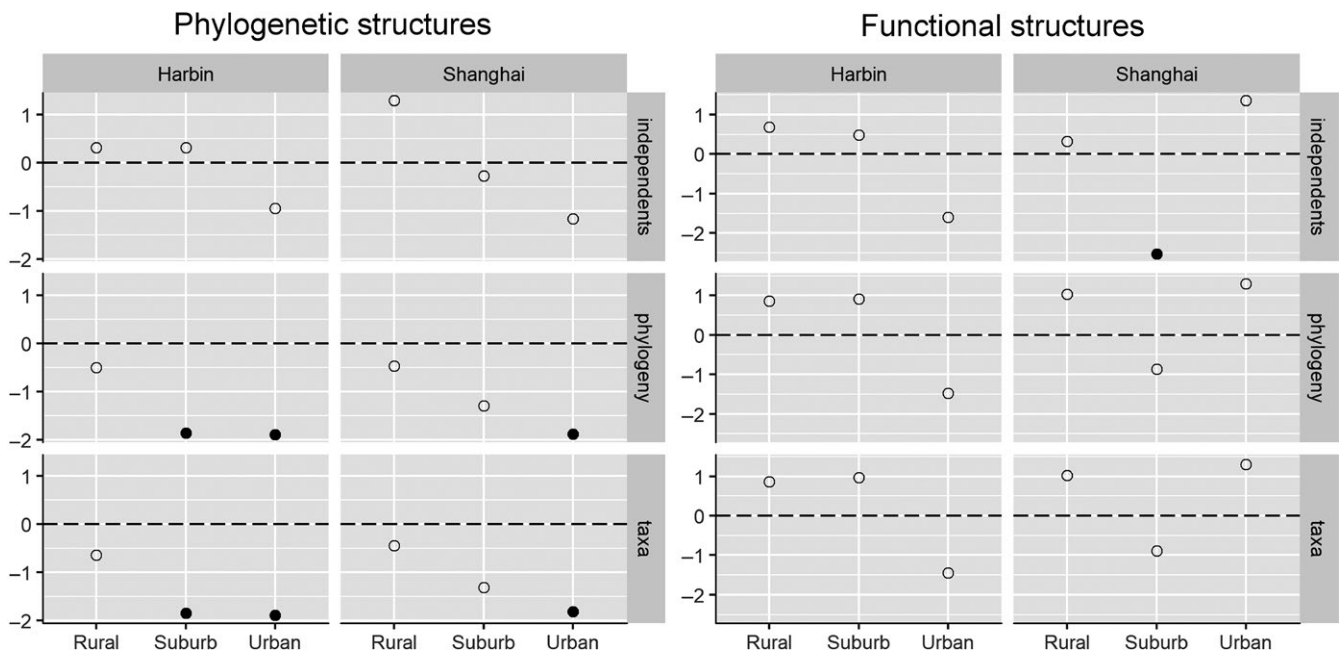

FIGURE 2 Ruderal phylogenetic (left) and functional (right) structures along urban–rural gradients. The spatial changes in phylogenetic and functional structures in Shanghai and Harbin were measured using the standardized effect sizes of the mean pairwise phylogenetic/functional distance (MPD$_{SES}$/MFD$_{SES}$) using three null models. The x-axis indicates the urban–rural gradients, and the y-axis indicates the results under the three null models. The black circle indicates a significant difference from that expected by chance (*p* < 0.05); the white circle indicates a non-significant difference from that expected by chance (*p* > 0.05)

negative in the urban areas of both cities (except under the independent null model) and in the Harbin suburban area. These results demonstrate that the phylogenetic structures also clustered with increasing spatial urbanization. Meanwhile, there were no significant functional shifts along the spatial urbanization gradients (Figure 2), showing that the observations of mean pairwise functional distance (MFD$_{SES}$) were similar to the expectations by chance. The only exception was in the Shanghai suburban area, where the MFD$_{SES}$ was significantly negative under the independent null model (*p* < 0.05).

3.2 | Phylogenetic and functional patterns of species colonization and extinction

In Harbin city, the β-MPD$_{SES}$ of colonists to residents for the temporal gradient was significantly negative, and the MPD$_{SES}$ of colonists was significantly negative, indicating that colonists of closely related species were more similar to the residents than expected by chance. In addition, the β-MPD$_{SES}$ of extinct species to residents was significantly negative for the temporal gradient, which indicates that extinct species were more similar to residents than expected by

TABLE 3 Phylogenetic distances and functional dissimilarities of colonists/extinct species and residents along temporal and urban–rural gradients

City	Gradients	Groups	Species No.	Phylogenetic structure		Functional structure	
				MPD_{SES}	$\beta\text{-}MPD_{SES}$ to residents	MFD_{SES}	$\beta\text{-}MFD_{SES}$ to residents
Harbin	1955→2011	Colonists	110	−4.3493**	−3.7079**	–	–
		Extinct species	65	2.7035**	−1.5481*	–	–
Shanghai	R→S	Colonists	30	−0.006	−0.2354	0.062	−2.710**
		Extinct species	19	0.9904	2.3084*	0.0510	0.3602
	R→U	Colonists	41	−0.5073	−0.8088	−0.0308	0.4918
		Extinct species	24	0.2654	3.1197**	−0.9094	−0.8545
Harbin	R→S	Colonists	13	0.0611	0.0091	0.0611	0.4581
		Extinct species	54	0.3057	2.3868*	0.3057	−0.3825
	R→U	Colonists	6	−1.0150	−1.0301	−2.4224*	−1.2642*
		Extinct species	77	−0.1270	1.8476*	0.8170	1.5256

The phylogenetic distances and functional dissimilarities between colonists/extinct species and residents were measured using the $\beta\text{-}MPD_{SES}$ and $\beta\text{-}MFD_{SES}$ based on Li's approach (Li et al., 2015). Negative values indicate colonists/extinct species are more similar to the residents than random draws from the species pool, while positive values suggest the opposite. MPD_{SES} = standardized effect size of MPD; MFD_{SES} = standardized effect size of MFD; $\beta\text{-}MPD_{SES}$ = standardized effect size of MPD between colonists/extinct species and residents; $\beta\text{-}MFD_{SES}$ = standardized effect size of MFD between colonists/extinct species and residents.* means significant ($p < 0.05$); ** means very significant ($p < 0.01$).

chance, while the MPD_{SES} of extinct species was significantly positive, i.e., indicating overdispersion.

Along the spatial urbanization gradient of both cities, the $\beta\text{-}MPD_{SES}$ of colonists to residents was not significantly different from zero for any paired gradient. However, the $\beta\text{-}MPD_{SES}$ of extinct species to residents was significantly positive between all paired gradients (Table 3), which indicates that the phylogenetic structures of extinct species were more dissimilar to those of residents than expected by chance. On the other hand, the functional structure of ruderal species showed no significant shift towards clustering or overdispersion along the urban–rural gradients. The $\beta\text{-}MFD_{SES}$ of colonists to residents was significantly negative for the rural to suburban area in Shanghai city and from the rural to urban area in Harbin city (Table 3), which indicates that the functional structures of colonist species were more similar to those of residents than expected by chance. Extinct species had no significant functional relationship with residents.

4 | DISCUSSION

The urbanization process is expected to cause large-scale global biotic homogenization (McKinney, 2006), with biodiversity becoming more similar over a specified time interval due to species colonization and extinction (Early et al., 2016). This homogenization phenomenon caused by urbanization has also led to a dramatic decline in phylogenetic richness and divergence in urban floras (Knapp et al., 2012). Based on these global patterns and in light of the rapid urbanization process in China over the past half century, we hypothesized that not only did the phylogenetic diversity of ruderal species decline in Chinese cities, but their structures also clustered with increasing urbanization intensity.

By combining the spatiotemporal phylogenetic data of ruderal species, our results demonstrate that there was a clear phylogenetic transition from early overdispersion to later clustering under the temporal urbanization process in Harbin city. Meanwhile, phylogenetic clustering from rural to urban areas also occurred in both cities. Several studies have shown similar results when exploring the phylogenetic or functional patterns of different taxa (i.e., birds, insects, bats, and fish) under urbanization. For instance, Riedinger et al. (2013) reported that on the considered scale (36 km[2] in their study), bat species were more similar than expected from null models with an increase in anthropogenic habitats, although the species richness decreased. Ricotta et al. (2015) documented that significant clustering also occurred across the phylogeny of the urban flora of Belgium.

Our analyses indicated for the first time that both temporal comparison and spatial comparison approaches could show similar clustering patterns with increasing urbanization but that the underlying drivers of this clustering were different. At the temporal scale, the holistic clustering patterns suggest that the similarity between the colonists and residents drove phylogenetic clustering as their predominant role, even though the similarity between the extinct species and the residents simultaneously drove phylogenetic overdispersion. Across the spatial gradients, however, the phylogenetic clustering was primarily driven by the dissimilarity between the extinct species and the residents, while the colonists had no significant effect. These results suggest that the spatial comparison does not always reflect the actual processes of temporal dynamics. Moreover, an important question that arises is why the drivers along the temporal versus spatial urbanization gradients were so different. To answer these questions, the underlying mechanisms maintaining plant diversity across spatial and temporal urbanization gradients should be examined.
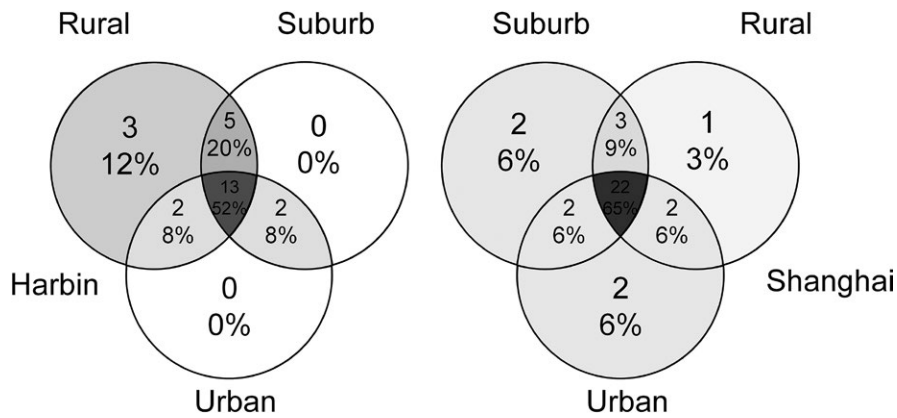
FIGURE 3 Venn diagram illustrating the distribution pattern of invasive species in each region (urban, suburban and rural) of Harbin (left) and Shanghai (right); the gray intensity is proportional to the percentage. More than 85% of the invasive species are distributed in at least two regions along the urban–rural gradients

At the temporal scale, urbanization causes various habitat changes, e.g., during the last half century in Harbin city, the annual temperature showed a significant increasing trend, with a rate of 0.4°C/10 years. Of the total arable land, 54.7% was converted to urban land from 1976 to 2010 (Chen et al., 2014). Moreover, the population increased from 1 million in the 1950s to more than 9 million in 2010s, which significantly intensified the frequency and intensity of disturbance in urban areas. Combining our results, we concluded that with rapid urbanization over time, the ruderal species were suffering from exposure to highly stressful environments, which acted as a multifilter, selecting ruderal species with suitable tolerance traits. Specifically, multiple species with similarly suitable traits were selected for in the immigration and extinction processes, which caused colonists to become more phylogenetically similar to the residents than by chance. Meanwhile, the colonist species also strengthened the intercompetitive relationships among closely related species, and the weaker competitors were eliminated by stronger ones in the neighboring ecological niches, which caused the similarity between the extinct species and the residents. For instance, because of the similar ecological niches of *Solidago canadensis* and *Solidago decurrens* but stronger competitive ability of *S. canadensis*, *S. canadensis*, as an invasive species, colonized local ecosystems and eliminated the indigenous species *S. decurrens* (Dong, Lu, Zhang, Chen, & Li, 2006).

Differently, at the spatial scale, even though the phylogenetic structures also shifted towards clustering with increasing urbanization, only the phylogenetic structure of extinct species was significantly dissimilar to that of the residents, and we could not detect any phylogenetic signature between the colonists and the residents. These results demonstrate that phylogenetic clustering across spatial urbanization gradients mainly occurred through species elimination processes instead of immigration processes. It thus seems that a set of species with unsuitable traits was filtered out by abiotic environmental changes, i.e., environmental filtering or that species groups with lower competitive abilities were excluded by the stronger ones, i.e., competitive exclusion. However, in two of these cases, the colonist species should also be significantly more similar to residents than by chance, which was not consistent with our results. After analyzing the species composition and the origin of

each spatial subset (Figure 3), we inferred that the reason for this result was that colonists in the immigration processes include many invasive species that lack natural enemies in the local urban ecosystem and can spread quickly to every spatial urbanization gradient. Therefore, the spatial comparison substitution would cause bias in terms of reflecting the real effect of invasive species as the colonists on the phylogenetic patterns of the community. The temporal-based approaches were free from this problem because the time at which the species immigrated had been determined.

Moreover, in order to distinguish between the possible mechanisms of the extinction processes, environmental filtering and competitive exclusion, functional traits were used in an attempt to determine the relative importance of abiotic and biotic processes in driving the community assembly (Mason & de Bello, 2013). A meta-analysis of the functional traits of annual plants showed that differences in resource competition could be well correlated with maximum height, phenology, seed mass and several other traits (Kraft, Godoy, & Levine, 2015). This hypothesis provides an understanding of the pathways through which community assembly processes affect functional traits (Mayfield & Levine, 2010). Therefore, we evaluated the differences in competition based on the five correlated functional traits we selected. The results did not correspond with the expectation that competitive exclusion drove the phylogenetic and functional clustering through the exclusion of groups of ecologically similar species with low competitive abilities but demonstrated that the urbanization process did not have significant effects on the competitive abilities of ruderal species at the regional scale (Table 3). Therefore, based on the assumption that the phylogenetic distances among species are conservative in terms of their functional traits and environmental preferences over evolutionary time, there was not sufficient evidence to demonstrate in our study that competitive exclusion was the primary mechanism for species clustering through spatial extinction processes.

Hence, we suggest that immigration processes in urban areas are the dominant forces across temporal urbanization gradients in clustering the phylogenetic structure of ruderal species, in line with predictions from other studies (Ricotta et al., 2009; Ricotta et al. 2012; Čeplová et al., 2015). In contrast, extinction instead of the immigration process is the primary driver of phylogenetic
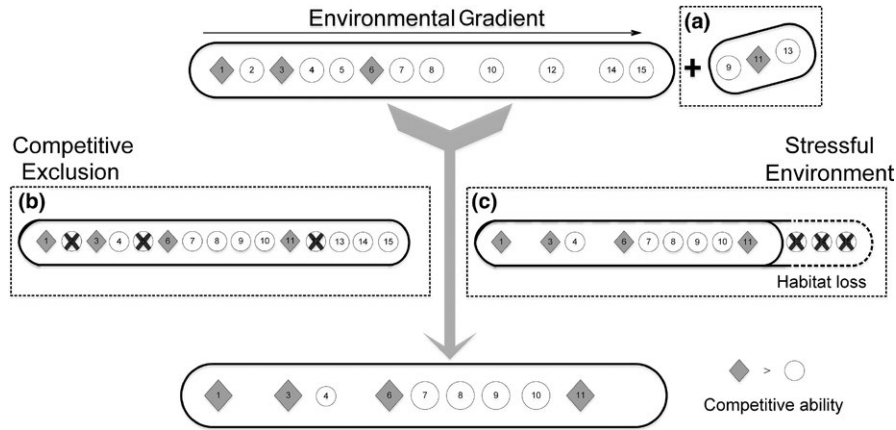
FIGURE 4 The ruderal sorting process under urbanization at the regional scale. (a) Colonist species with suitable competitive ability that immigrated into the urban area through global trade and gardening practice. (b) These species strengthened the intensity of competition among closely related species, thereby eliminating local species with lower competitive ability. (c) Environmental modification increases the strength of abiotic filtering (e.g., disturbance and drought stress), thereby preventing colonization by and the persistence of unsuitable species. White circles represent species with similar niche requirements, and gray rhombi represent species with similar competitive abilities

clustering across spatial urbanization gradients. Abiotic/environmental filters represented by stressful environments and disturbances in urban areas are the possible mechanisms underlying such clustering by preventing the establishment or persistence of species in particular habitats. Additionally, competitive exclusion may also play an opposite role in the temporal clustering processes, which dispersed the phylogenetic structure of ruderal species by limiting coexistence among closely related species but not by excluding groups of ecologically similar species with low competitive ability (Figure 4).

5 | CONCLUSIONS

Urbanization has profoundly affected facets of diversity in local ecosystems and has caused biotic homogenization among different urban areas through species immigration and extinction processes. By using ruderal species as our selected species group, our study found that the drivers obtained using the spatial comparison substitution approach differed from those found with the temporal comparison approach. Hence, we suggest that the deficiencies of spatial comparison substitutions should be seriously considered in related studies. Further, we speculate that biotic homogenization will continue to intensify with accelerated species invasions and expanding urbanization in the future.

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