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RESEARCH ARTICLE

Plant phylogenetic diversity along the urban–rural gradient and its association with urbanization degree in Shanghai, China

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Abstract

Context The spatial distribution of plant diversity in urban areas is fundamental to understanding the relationship between urbanization and biodiversity. Previous research has primarily focused on taxonomic levels to assess species richness. In contrast, investigations into the spatial patterns of phylogenetic diversity in urban plants remain limited.

Objectives This study aims to investigate the spatial patterns of plant phylogenetic diversity along an urban–rural gradient and quantify how phylogenetic diversity and the degree of urbanization are related.

Methods A survey of vascular plants was conducted at 134 randomly selected sample plots along four urban–rural transects in Shanghai, China. Three phylogenetic diversity metrics were calculated: Faith's phylogenetic diversity (PD), net relatedness index (NRI), and net nearest taxon index (NTI), along with the urbanization degree index (UDI). Regression analysis was employed to quantify the spatial patterns of plant phylogenetic diversity across different taxa along the urban–rural gradients and their relationships with UDI.

Results The study observed seven distinct patterns of plant phylogenetic diversity along the urban–rural gradients in different taxa, which support the previous hypotheses that biological distribution patterns at the species level also hold true at the phylogenetic level. Faith's phylogenetic diversity (PD) showed a linear increase with increasing UDI for total, woody, perennial, and cultivated plant assemblages. The UDI explained 3–36% of the variation in PD for these taxa. In contrast, PD for annual and spontaneous plants exhibited a linear decrease with increasing

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UDI, which explained 25% and 3% variation in PD for annual and spontaneous plants, respectively. The net relatedness index (NRI) for woody, perennial, and cultivated plants, as well as the net nearest taxon index (NTI) for perennial and cultivated plants, linearly increases with UDI, whereas the NRI for total, annual, and spontaneous plants, as well as NTI for total, woody, annual, and spontaneous plants linearly decrease with UDI. However, some of these trends were only marginally significant.

Conclusions The spatial patterns of plant phylogenetic diversity varied along the urban-to-rural gradients, indicating that urban environmental filtering has an impact on plant phylogenetic diversity. Urbanization increased the phylogenetic richness of different plant taxa in Shanghai but resulted in more clustering and relatedness of species within plant assemblages. Phylogenetic richness exhibited a linear increase with UDI, while the phylogenetic divergence decreased with UDI. The UDI is a useful predictor for examining variations in plant phylogeny due to urbanization. Our findings provide insights into how urbanization impacts plant phylogenetic diversity, helping urban plant diversity conservation.

Keywords Spatial pattern · Gradient analysis · Phylogenetic diversity · Phylogeny · Urbanization · Shanghai

Introduction

More than half of the world's eight billion people are now residing in urban areas as a result of rapid urbanization around the globe (United Nations 2022). Urban vegetation (or greenspace) is a primary provider of ecosystem services. Plant species diversity is vital for urban vegetation for maintaining the stability and functioning of urban ecosystems, thereby essential to the health and well-being of urban residents (Sandifer et al. 2015; De Carvalho and Szlafsztein 2019). However, the recent rapid urbanization and the continued trend projected worldwide have led to significant habitat and biodiversity loss surrounding urban areas (Simkin et al. 2022). Concurrently, urbanization and landscape fragmentation have already led to biotic homogenization (Kuhn and Klotz 2006; McKinney 2006; Schwartz et al. 2006; Zeeman et al. 2017), genetic diversity reduction, (Johnson and Munshi-South 2017), and non-native species promotion and invasion (Aronson et al. 2015; Cadotte et al. 2017), ultimately affecting urban ecosystem functions and human well-being. Therefore, maintaining the taxonomic and phylogenetic diversity of urban plants is critical to the sustainability of urban ecosystem services and urban resident well-being.

The urban area is characterized by a high proportion of impervious surfaces, and its residents are primarily engaged in industrial and commercial businesses or services (Li et al. 2013). The rural area primarily consists of agricultural and natural land, with its residents predominantly involved in agriculture management and production (Seto et al. 2002). The urban–rural gradient refers to the changes in environmental settings along transects extending the central urban areas to the rural locations (McDonnell and Stiles 1983; McDonnell and Pickett 1990). The urban–rural gradient concept has been widely used to analyze the variations of physical environmental variables, urbanization processes, landscape and biodiversity patterns, etc. (Luck and Wu 2002; Williams et al. 2005; Hope et al. 2006; Briber et al. 2013; Seress et al. 2014; Wang et al. 2020). For biodiversity distribution patterns, previous studies have identified at least six distinct responses of species richness along the urbanization gradient: no response, negative, intermittent, intermediate, positive, and bimodal responses, respectively (McDonnell and Hahs 2008). These patterns, especially for urban plants, reflect floristic responses/adaptations to urbanization through environmental filters, i.e., habitat fragmentation, habitat transformation, urban environmental conditions, and human preference, which usually operate simultaneously on urban flora. These influences can be quantitatively assessed using taxonomic, phylogenetic, trait, and structural metrics of plant communities or assemblages (Williams et al. 2009). For example, six response patterns of plant species diversity in different taxa have been detected along the urban–rural gradients in Shanghai, China (Wang et al. 2020). Additionally, studies have observed no response, negative and positive responses of plants to urbanization along the urbanization gradient in Melbourne, Australia (Hahs and McDonnell 2007; McDonnell and Hahs 2008). However, the majority of these studies have primarily focused on plant taxonomic diversity, leaving phylogenetic aspects less explored.

Phylogenetic diversity, a critical component of plant diversity, is a comprehensive indicator that encompasses both species richness and evolutionary relationships within a community (Faith 1992; Kraft et al. 2007; Donoghue 2008). Phylogenetic diversity accounts for the length of all branches linking a set of species on the evolutionary tree. Therefore, given the same number of species, the phylogenetic diversity can be highly different depending on how closely the species are related evolutionarily. Evidence suggests that closely related species exhibited greater trait similarity, potentially compromising ecosystem stability and resilience (Loreau 2000; MacIvor et al. 2016). Furthermore, phylogenetic patterns within a community can also be used to infer the dominant factors driving its assembly, assuming ecological traits are conserved across species (Kembel 2009; Kraft et al. 2014). Therefore, phylogenetic diversity offers a more comprehensive understanding of how urbanization impacts the structure and composition of plant communities, offering insights into the underlying community assembly (Knapp et al. 2012, 2008; Zhu et al. 2021, 2019).

Phylogenetic diversity has been utilized to investigate plant responses to environmental change along various gradients, including edaphic factors, climate, drought, and solar radiation, particularly along elevational gradients in natural conditions (Kluge and Kessler 2011; Qian et al. 2014; López-Angulo et al. 2018). Recently, phylogenetic methods have been increasingly used to investigate urbanization impacts on plant communities. These studies, which often compare urban and natural areas or among sample sites with different urbanization degrees (Knapp et al. 2008, 2017; Cui et al. 2019; Cheng et al. 2022; Yang et al. 2022; Zhu et al. 2021), revealed diverse response patterns. For instance, the phylogenetic diversity of cultivated species linearly declined with increasing urbanization degree (indicated by human population density), whereas the phylogenetic relatedness of spontaneous species linearly increased with urbanization degree in Zhanjiang City, Guangdong, China (Cheng et al. 2022). In Germany, urban species richness increased, but phylogenetic diversity decreased (Knapp et al. 2017). These findings highlight the complex and varied impacts of urbanization on plant communities, underscoring the need for further investigation into the patterns of plant phylogenetic diversity along the urban–rural gradient.

Previous studies demonstrated that urbanization degree could serve as a significant predictor of plant diversity in urban environments. For example, in Shanghai, woody and perennial urban plant species richness increased with urbanization degree in a non-linear and linear way, respectively, while annual plants decreased linearly (Wang et al. 2020). Tree and shrub diversity increased with increasing urbanization in Melbourne, Australia (McDonnell and Hahs 2008). Plant phylogenetic diversity showed varied responses to urbanization. A study conducted in European cities revealed that urban plant phylogenetic diversity declined with urbanization degree during the past 320 years (Knapp et al. 2017). The phylogenetic diversity of woody plants increased with urbanization at a regional scale in northeastern China (Yang et al. 2022). However, the phylogenetic diversity of annual plant species grown in the courtyard along the urban–rural gradient in Minneapolis, Minnesota, USA, showed no significant change with urbanization degree (Knapp et al. 2012). These varied findings underscore the complexity of the relationship between plant phylogenetic diversity and urbanization degree, highlighting the need for further exploration to elucidate this relationship.

As the economic engine city of the Yangtze River Delta urban agglomeration, Shanghai has experienced extensive urban expansion over the past decades. The urban area increased more than threefold from 847.9 km^2 in 1985 to 2796.5 km^2 in 2015 (Wu et al. 2023). Rapid urbanization resulted in diverse land uses and high landscape heterogeneity, creating pronounced urban–rural gradients (Li et al. 2013). Therefore, it is an ideal place to study the impacts of urbanization on plant biodiversity. This study aims to explore the spatial distribution patterns of plant phylogenetic diversity along the urban–rural gradient and its relationship with urbanization degree. The specific questions we address are: (1) What are the spatial patterns of plant phylogenetic diversity along the urban–rural gradient? (2) How do phylogenetic patterns vary among different plant taxonomic groups? and (3) How is plant phylogenetic diversity influenced by the degree of urbanization? The findings are expected to enhance our understanding of how urbanization affects phylogenetic diversity in megacities and can provide insights into the conservation of urban plant diversity.

Method

Study sites

Shanghai (120° 52′-122°12′ E, 30° 40′-31° 53′ N) is located in the eastern part of the Yangtze River Delta region, China, with an area of 6340.5 km^2 and an average elevation of 2.9 m above sea level. The city borders the East China Sea in the east and Jiangsu and Zhejiang provinces in the west, and the estuary of the Yangtze River in the north (Fig. 1). It has a northern subtropical monsoon climate with precipitation of 1028.6 mm and an annual average temperature of 16.6 °C (calculated from the data recorded by the Xujiahui meteorological station from 1951 to 2020). The total population was 24.89 million, and the GDP reached 4.32 trillion Yuan (nearly US $ 614.20 billion) by the end of 2021 (Shanghai Bureau of Statistics 2022). The native vegetation types mainly consist of evergreen broadleaf forests and mixed evergreen and deciduous broadleaved forests (Zhou 1984). However, due to long-term intense human activities and disturbances, the natural vegetation can only be found as remnant forest stands on low hills such as Sheshan, Tianma, etc., and offshore islands like Dajinshan (Shanghai Academy of Sciences 1999). The predominant contemporary vegetation consists of artificial urban green spaces and cultivated

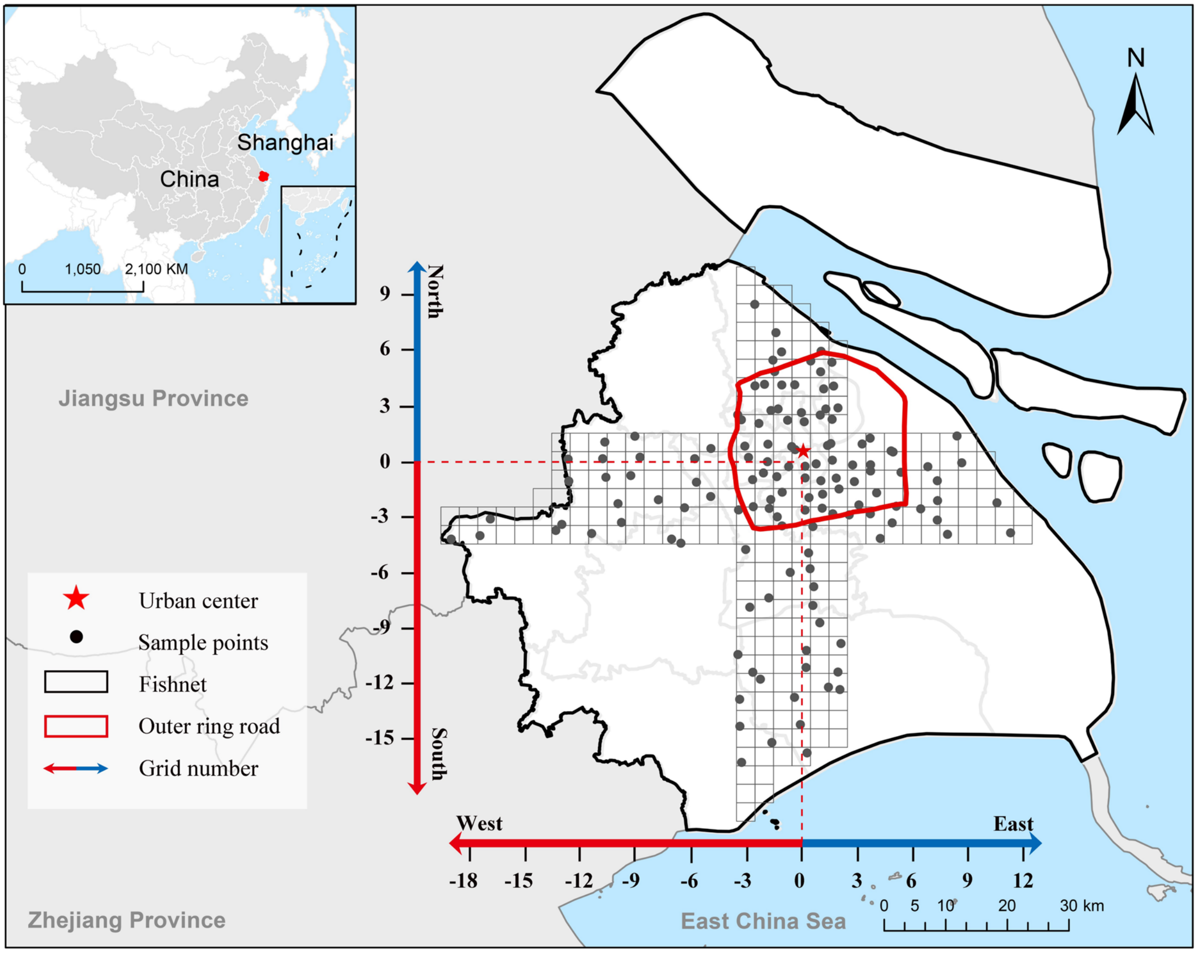


Fig. 1 Location of the study, urban–rural transects, and sampling plots distribution. The east–west and north–south transects run through the central urban area of Shanghai

crops. A previous investigation in Shanghai recorded 2991 vascular plant species belonging to 1100 genera and 202 families, among which 1199 species are wild plants belonging to 601 genera and 150 families, and the remaining 1792 species are cultivated plants (Ma 2013). Rapid urbanization and associated human activities in the past decades has led to considerable loss of native species and increase of alien species in Shanghai (Zhao et al. 2006; Wang et al. 2020).

Urbanization gradient, sampling design, and plant field investigation

To investigate the spatial pattern of plant phylogenetic diversity along the urbanization gradient, we used the previously set two 18 km-width transects, which run across the urban center to rural areas along the east–west and south-north directions, respectively (Wang et al. 2020). The grids on urban–rural transects were numbered in sequence of 0 from the urban central to the rural grids, respectively. Grid numbers to the northern and eastern directions were assigned positive values, while those grids to the southern and western directions were assigned negative values (Fig. 1).

In this study, we employed the previously designed sampling method, namely, the dual-density, randomized, tessellation-stratified sampling adapted from Hope et al. (2003) to obtain the sample sites in Shanghai (Wang et al. 2020). The sampling area consists of 3 km × 3 km grids along the two 18 km-width transects. To get representative and spatially unbiased samples, we separated the study area into two parts: inside and outside the urban core area, using the Outer Ring Road as the dividing line. Sampling density was set to 3:1, i.e., one sampling site was randomly selected within each grid inside the urban core area, while one sampling site within every three grids outside. Eventually, we surveyed 134 sample plots, with 68 plots located in the urban core area and 66 samples outside the core area (Fig. 1).

A plant field survey was conducted between July and September from 2014 to 2017 using the modified Whittaker sample plot (20 m × 50 m) at each sampling point, considering the high heterogeneity of urban landscape and urban green spaces (Stohlgren et al. 1995). All vascular plant species and their abundance within each sampling plot were recorded. Plant species were identified according toFlora of China" (Wu and Hong 2013).

The recorded plants were classified into woody and herbaceous plants, and the herbaceous were further classified into annual and perennial herbs according to their life form. Plant species were also classified into spontaneous and cultivated plants according to their growth status using "The Checklist of Shanghai Vascular Plants" as a reference (Ma 2013). For details of the sampling design and species identification, please refer to Wang et al. (2020).

Plant phylogenetic diversity measurement

The measurement of phylogenetic diversity typically encompasses three dimensions: richness, divergence, and regularity (Tucker et al. 2017). Among these measures, richness and divergence are commonly assessed using single-dimensional indices (Vamosi et al. 2009). In this study, three phylogenetic metrics, namely, Faith's phylogenetic diversity, net relatedness index, and net nearest taxon index, were employed to measure plant phylogenetic diversity. Initially, a phylogenetic tree was constructed based on the Angiosperm Phylogeny Group IV (APG IV) (Jin and Qian 2022). Faith's phylogenetic diversity (PD) of a sample was defined as the sum of branch lengths of all internodes traversed between the root and all sampled species on a phylogeny tree (Faith 1992). PD, therefore, will increase with the number of species increasing (Vamosi et al. 2009). PD is a kind of richness metric that sums up the phylogenetic differences in an assemblage and can capture the differences in phylogenetic composition between assemblages (Tucker et al. 2017). It was calculated using Eq. (1):

$$PD = \sum_{i=1}^{n} length_i \tag{1}$$

where n is the number of species within the plot, and $length_i$ denotes the branch length of species i in the phylogenetic tree.

The net relatedness index (NRI) and net nearest taxon index (NTI) are standardized effect sizes of mean pairwise distance (MPD) and mean nearest taxon distance (MNTD), respectively. Therefore, we first calculate the MPD and MNTD. The MPD refers to the mean evolutionary distance between all species pairs in the community or assemblage, while the mean nearest taxon distance (MNTD) refers to the average evolutionary distance between any species and its nearest phylogenetic neighbor in the community or assemblage (Webb et al. 2002, 2008). They were calculated using the following equations:

$$MPD = \frac{\sum_i^n \sum_j^n \delta_{i,j}}{n}, i \neq j \tag{2}$$

$$MNTD = \frac{\sum_i^n min\delta_{i,j}}{n}, i \neq j \tag{3}$$

where n is the number of species in the community. The phylogenetic distance matrix, denoted as δ, is composed of branch lengths representing the phylogenetic distances between species. Specifically, $\delta_{i,j}$ indicates the phylogenetic distance between species i and j. The $min\delta_{i,j}$ represents the minimum phylogenetic distance between species i and all other species within the community. MPD and MNTD are metrics used to measure the divergence of phylogenetics among taxa or individuals in an assemblage (Tucker et al. 2017); they describe the phylogenetic structure of a community or assemblage. MPD describes the overall structure, including both basal and terminal evolutionary branches, while MNTD describes structures closer to the phylogenetic tip (terminal evolutionary branches). The smaller the MPD and MNTD values, the closer the phylogenetic relationship between assemblage species (Vamosi et al. 2009; Silva-Junior et al. 2018).

To calculate the NRI and NTI, we used the observed MPD and MNTD in a community or assemblage relative to the random values (MPD_{null} and $MNTD_{null}$) generated by a null model (Webb et al. 2002; Kraft et al. 2007). NRI and NTI are standardized phylogenetic diversity indexes, which are usually employed to characterize the phylogenetic structure. They were calculated using the following equations (Webb et al. 2002):

$$NRI = -1 \times \frac{MPD_{obs} - mean(MPD_{null})}{SD(MPD_{null})} \tag{4}$$

$$NTI = -1 \times \frac{MTND_{obs} - mean(MTND_{null})}{SD(MTND_{null})} \tag{5}$$

where MPD_{obs} and $MNTD_{obs}$ are the observed values of MPD and MNTD, respectively; $mean(MPD_{null})$ and $mean(MNTD_{null})$ are the average of MPD and MNTD obtained from the null model (999 randomizations), respectively. SD is the standard deviation. Positive values of NRI or NTI indicate phylogenetic clustering, which means that species tend to be closely related in the community or assemblage. Negative NRI or NTI indicates phylogenetic overdispersion, implying that species are more distantly related. If NRI (or NTI) equals zero, it means that the community's phylogenetic structure is random (Kraft et al. 2007; Kembel 2009).

The "Picante" package was utilized to calculate all the phylogenetic diversity indices (Kembel et al. 2010). All computation was conducted in the R (v4.2.2).

Urbanization degree calculation

Urbanization degree can be measured through various metrics, such as urban population proportion, percent urbanized land, and economic urbanization (Wu et al. 2023), as well as urbanized land in percentage, road density, and distance to the city center (Wang et al. 2020; Liu et al. 2022). Among these, the proportion of urban land has been shown to be a significant predictor of plant diversity (Wang et al. 2020). Hence, the percentage of urbanized land was used to measure the urbanization degree of each sample site. We employed the urban land use land cover data which was produced by Wang et al. (2020) from one m-resolution aerial images of Shanghai in 2013 based on the land use and land cover classification system proposed by Li et al. (2013). Here, the urbanized land, including the land use types of residential, transportation, industrial, and public facilities within a one km-radius circle centered on each sampling point, was used to calculate the degree of urbanization:

$$UDI = \frac{S_{urbanland}}{S} \tag{6}$$

where UDI is the urbanization degree index, $S_{urban\ land}$ is the area of urbanized land, and S is the total area of all land use types within the circle.

Statistic analysis

Polynomial regression was employed to profile the spatial distribution patterns of plant phylogenetic diversity along urban-to-rural gradients across different taxa. To conduct the regression fitting, a sequential grid number ranging from the urban center to rural areas was used as a surrogate to represent the independent variable of urbanization degree. The average value of each phylogenetic index within the corresponding grid number was calculated as the dependent variable. In cases where multiple fitting models existed, the Akaike Information Criterion (AIC) was utilized to identify the optimal model. Regression analysis was employed to explore the relationships between urbanization degree and phylogenetic diversity indexes. We employed Akaike Information Criterion (AIC) to determind the optimal fitting among multiple regression models. Generally, a lower AIC value indicates a better fit for the model. In this study, several polynomial regression models exhibited slightly lower AIC values compared to the linear regression model. For instance, the maximum difference in AIC values between the polunomial and linear regression models was only 6.46. However, we ultimately chose the linear regression model due to its ability to straightforwardly capture variations in phylogenetic diversity with UDI. All calculations were performed using R and SPSS packages, while figures were generated using OriginPro 2021.

Result

Spatial patterns of phylogenetic diversity along the urban–rural gradients

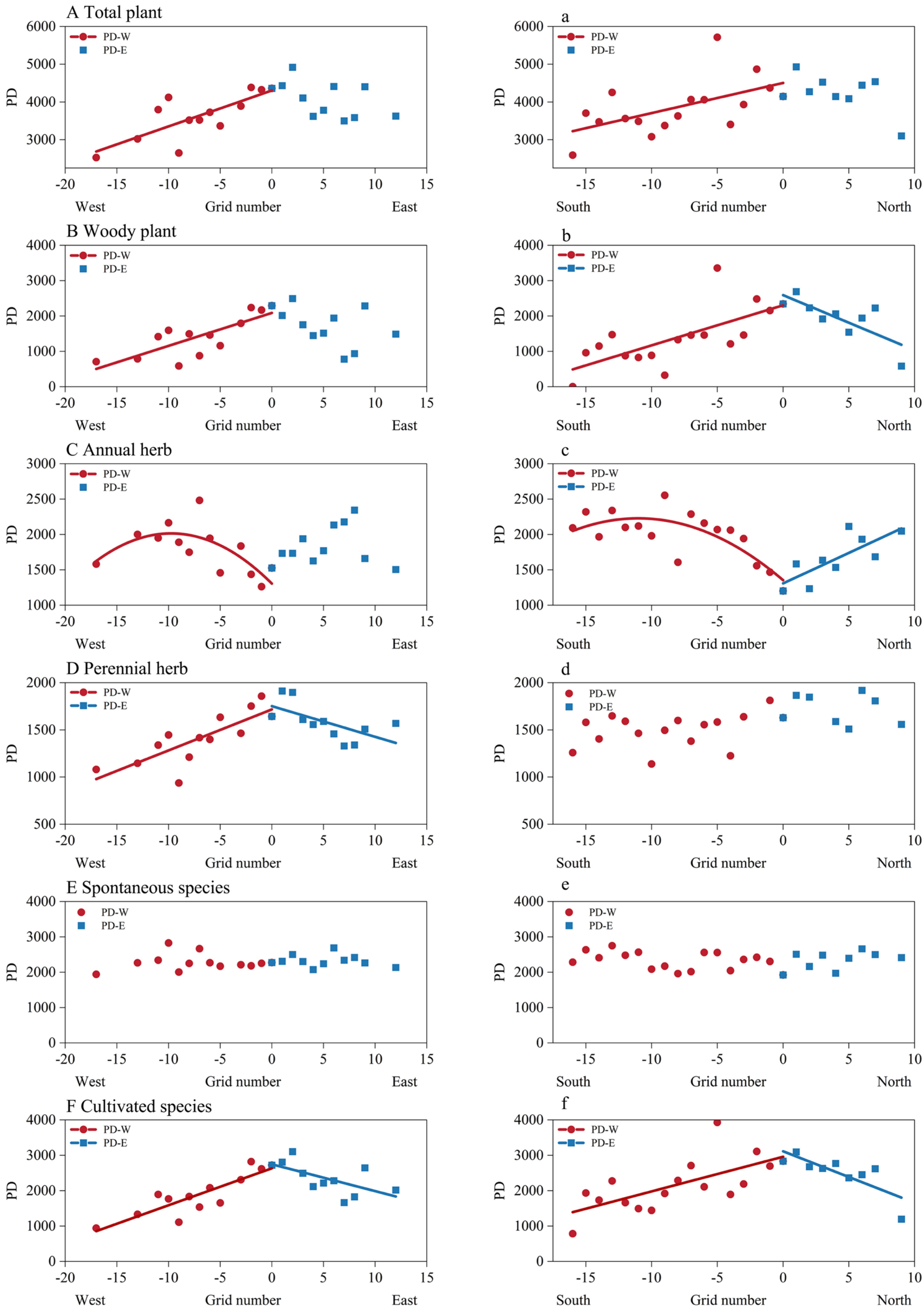
The Faith’s Phylogenetic Diversity (PD) of plant species across various taxa exhibited three distinct spatial patterns along the four urban–rural gradients. First, we see a clear linear decreasing pattern along the urban-to-rural gradients for total plant species (Fig. 2A, a), the woody plants (Fig. 2B, b), perennial herbs (Fig. 2D), and the cultivated species (Fig. 2F, f). Second, we found an unimodal pattern for annual herbs along the western and southern gradients (Fig. 2C, c). Third, we witnessed a linear increasing trend along the northern urban-to-rural gradient for annual herb plants (Fig. 2c). However, the PD of the spontaneous species did not show any significant pattern along the four gradients (Fig. 2E, e). The fitting equations and their significance for spatial patterns are presented in Table S2.

The net relatedness index (NRI) of plants along the urban-to-rural gradient also exhibited complex spatial patterns. NRI displayed a consistent linear increase from the urban-to-rural area for total plants in the eastern, northern, and southern transacts (Fig. 3A and a), for the annual herbs in the northern (Fig. 3c), and for the spontaneous plants in the western, northern and southern gradient (Fig. 3E and e). A linear decrease in NRI was observed for the woody species in the eastern gradient (Fig. 3B). The perennial herbs exhibited an unimodal pattern (quadratic polynomial fitting) (Fig. 3d) and cubic polynomial fitting (Fig. 3D) in the southern and eastern gradients, respectively. In addition, most NRI values along the urban–rural gradients are positive except for the woody plant taxon and a few other taxa, denoting a general trend of phylogenetic clustering.

The net nearest taxon index (NTI) also presents four patterns along the urban-to-rural gradients: A linear increase in NTI was observed for total plants in the southern gradient (Fig. 4a), for the annual herb plants in the northern gradient (Fig. 4c), and for the spontaneous in the western, northern and southern gradients (Fig. 4E and e). A linear increase was observed for the perennial herbs in the western gradient (Fig. 4D), while a bimodal pattern was found in the northern and cubic polynomial pattern in the southern gradients for the perennial herbs (Fig. 4d). Similar to NRI, most of the NTI values among the taxa along the urban–rural gradients are positive except for the woody plant taxon and a few other taxa, indicating a prevalent phylogenetic clustering pattern.

The relationship between plant phylogeny and urbanization degree

Two types of linear relationships were revealed between UDI and plant PD in all taxa (Fig. 5). The PD for the taxa of overall plants, woody plants, perennial herbs, and cultivated plants linearly increases with rising UDI. Although the PD exhibited large variations among sample plots within the same urbanization degree segments, the UDI could explain the variation of PD by 20%, 34%, 23%, and 36% for total plants, woody plants, perennial herbs,


A Total plant
a
B Woody plant
b
C Annual herb
c
D Perennial herb
d
E Spontaneous species
e
F Cultivated species
f
PD-W
PD-E
PD
Grid number
West
East
South
North
-20
-15
-10
-5
0
5
10
15
6000
5000
4000
3000
2000
1000
2500
1500
500

◂**Fig. 2** Spatial patterns of Faith's PD of different plant taxa along the two urban–rural gradients in Shanghai

and cultivated plants, respectively. Conversely, the PD of annual herbs and spontaneous plants linearly decreases as UDI increases. The UDI could explain the variation of PD of annual herbs and spontaneous plants by 25% and 3%, respectively.

The NRI of woody, perennial, and cultivated plant taxa displayed significant linear increasing trends with the urbanization degree index (UDI) (Fig. 6b, d, f). The UDI can explain their variations of NRI changes with 8%, 4%, and 9%, respectively. Conversely, the NRI of total, annual, and spontaneous plant taxa exhibited linear decreasing trends with UDI rising, but only the spontaneous and annual herb taxon displayed a significant decrease ($R^2=0.10$ and $R^2=0.07$ respectively) (Fig. 6a, c, e).

The NTI trends of perennial and cultivated plant taxa exhibited a similar pattern to that observed for NRI, showing a linear increase with UDI (Fig. 7d and f). In contrast, the NTI of both total and spontaneous plant taxa showed a consistent linear decline with increasing UDI (Fig. 7a and e). The UDI accounts for 12%, 21%, 14%, and 7% of the variation in NTI for total, perennial, spontaneous, and cultivated plant taxa, respectively. However, there were no statistically significant decreases observed in the NTI of woody and annual plant taxa despite a slight linear decreasing trend with UDI (Fig. 7 b and c).

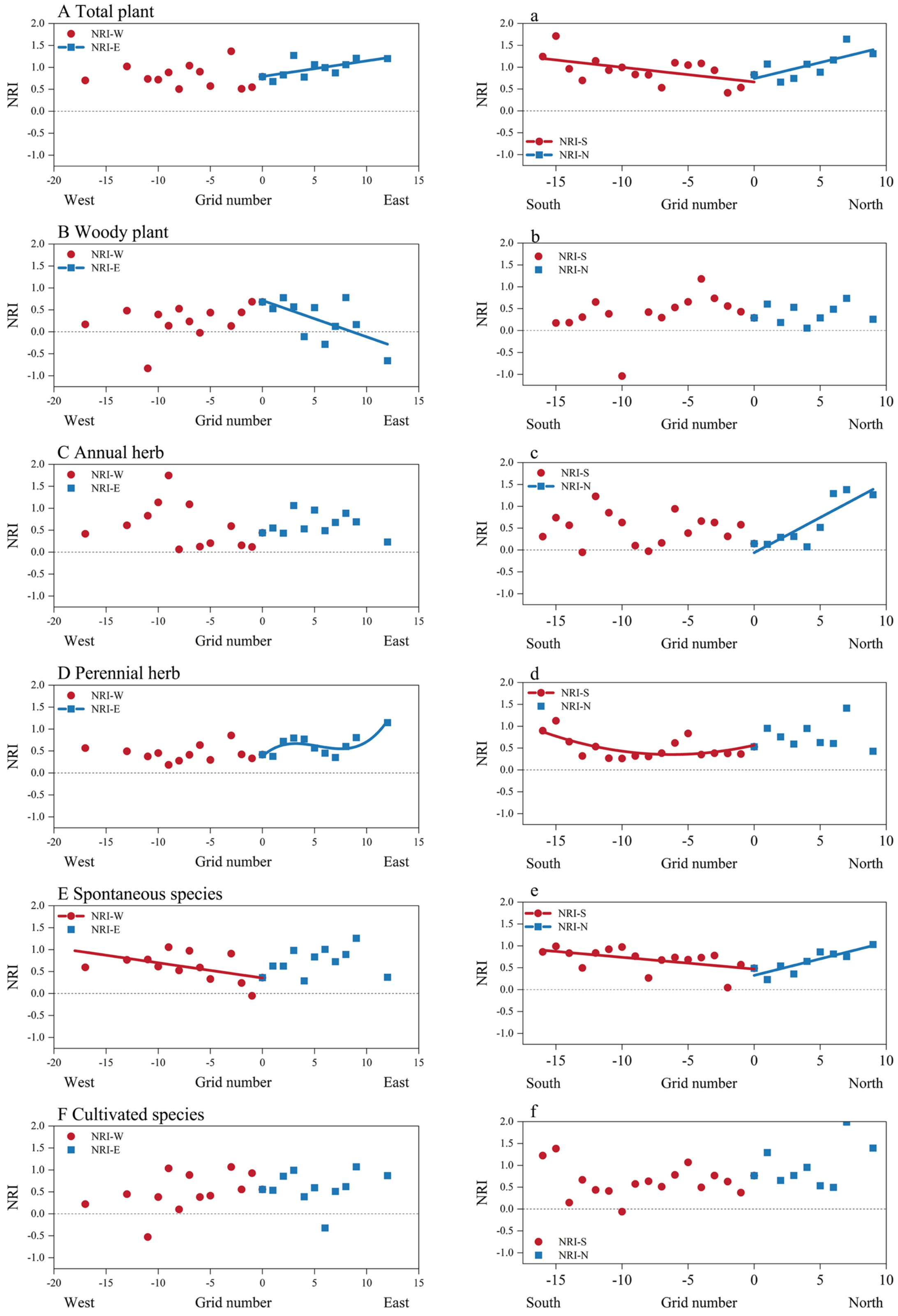
Discussion

Multiple patterns of plant phylogenetic diversity along the urban–rural gradient

To the best of our knowledge, multiple patterns of plant phylogenetic diversity were observed for the first time along the urbanization gradient. A total of seven distinct spatial distribution patterns of plant phylogenetic diversity were identified (Fig. 8), including linear increase, linear decrease, negative quadratic decrease, unimodal response, intermittent response, bimodal response, and no response. In comparison to the patterns summarized by McDonnell and Hahs (2008), four novel patterns were discovered. The previous study has documented six patterns in various taxa at the level of plant species along urban–rural gradients (Wang et al. 2020).

The phylogenetic metrics utilized in this study, such as PD for richness and MPD, MNTD, NRI, and NTI for divergence/structure (Vamosi et al. 2009; Tucker et al. 2017), enable us to comprehensively capture the phylogenetic responses of plant communities or assemblages to diverse environments and human disturbances in urban areas characterized by various landscape types and heterogeneous patterns. Furthermore, the application of an urban–rural gradient analysis provides valuable insights into how plant phylogenetic diversity is influenced by degrees of urbanization.

The phylogenetic metrics of different plant taxa exhibited distinct spatial patterns that reflect variations in richness and structure along the urban–rural gradient. Faith's Phylogenetic Diversity (PD), whether for total plant species or woody, perennial, and cultivated plants, showed a generally linear decreasing trend for species assemblages across most taxa from urban to rural areas. This indicates an decrease in phylogenetic richness from urban to rural areas. This may be due to the higher heterogeneity of habitats in cities, providing more ecological niches for various lineages (Ricotta et al. 2008). Additionally, Shanghai has introduced a significant number of cultivated species in the past 40 years (Du et al. 2023). This artificial increase in plant species richness has resulted in an enhanced branching length within the phylogenetic tree. The introduction of distantly related species also contributes to closer proximity among nearest phylogenetic relationships. A study conducted in Germany found a higher richness of plant species in urban areas. However, this increase in species richness did not correspond to an increase in phylogenetic diversity, which was mainly due to the fact that these groups with high species richness were composed of closely related species that share similar functional traits and are able to adapt to urbanization (Knapp et al. 2008). The disparities between the findings of the German study and our own may be due to differences in taxonomic and spatial scales, which have been shown to influence community phylogenetic diversity (Cavender-Bares et al. 2006; Swenson et al. 2006, 2007). Notably, the sampling grid used in the German study covered the entire country, making it 15 times larger than ours. At larger scales and under different


A Total plant
B Woody plant
C Annual herb
D Perennial herb
E Spontaneous species
F Cultivated species
a
b
c
d
e
f
NRI-W
NRI-E
NRI-S
NRI-N
NRI
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-20
-15
-10
-5
0
5
10
15
West
Grid number
East
South
North

◂**Fig. 3** Spatial patterns of NRI along the urban–rural gradients in different plant taxa

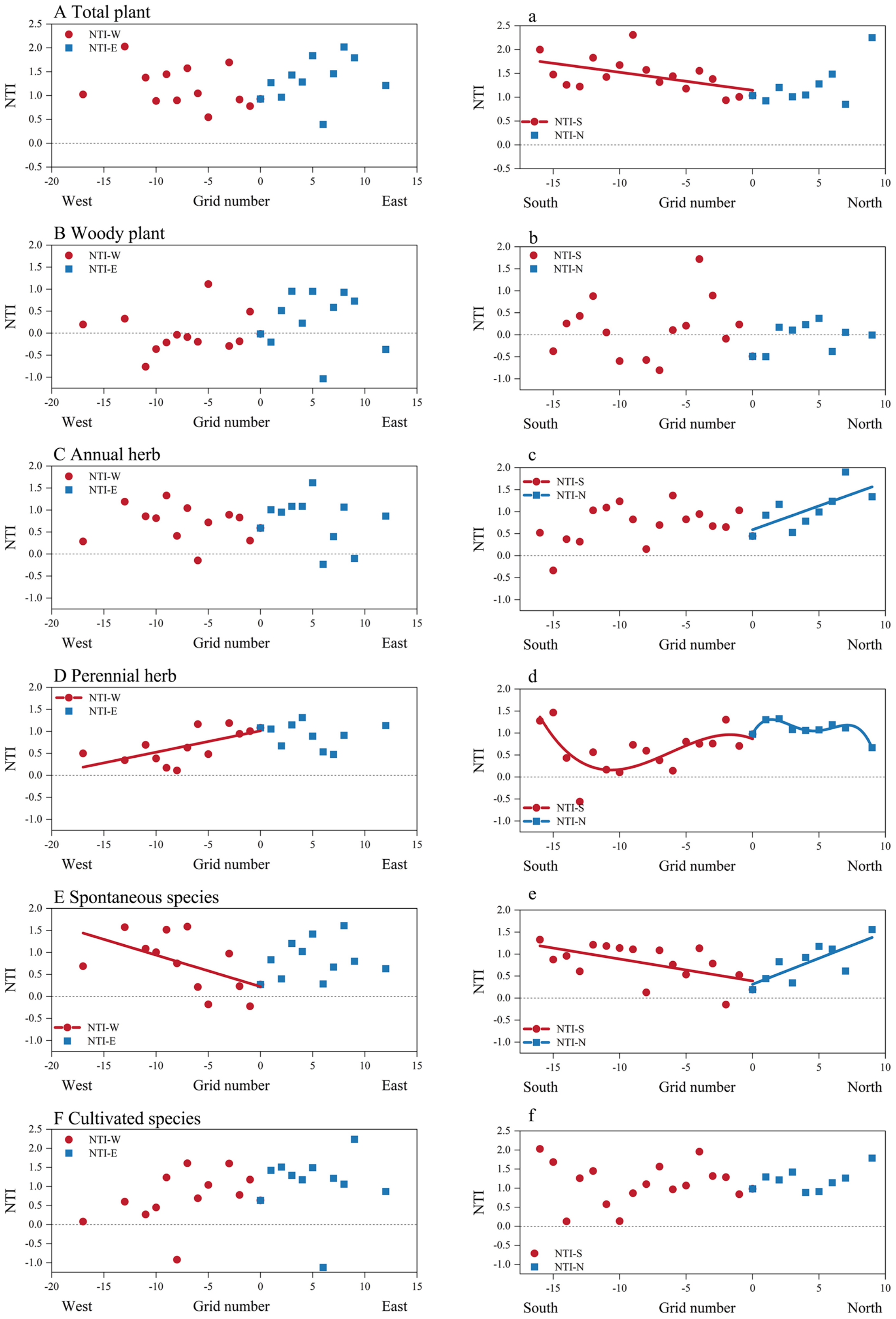
urban histories, patterns of plant phylogenetic development may exhibit varying gradient patterns. Therefore, when studying phylogenetic diversity, it is crucial to consider scale and environmental context dependency more attentively (Knapp et al. 2012).

The PD of annual plants displayed unimodal patterns along the western and southern transects while showing linear decrease and non-quantitative response along the northern and eastern gradient. The highest values of PD were observed in the transitional zones of urban and rural areas (Fig. 2C and c). Similar patterns were also identified for winter annuals (i.e., biennial plants) in semi-natural environments within the Minneapolis–Saint Paul metropolis, Minnesota, USA (Knapp et al. 2012). These findings may be attributed to the dispersal strategy of annual plants, which are primarily wind-dispersed and well-adapted to urban–rural ecotones where moderate disturbance usually occurs and highly heterogeneous landscapes exist to provide diverse habitats that facilitate their growth (Williams et al. 2005; Knapp et al. 2012; Li et al. 2013; Giehl and Jarenkow 2015; Fornal-Pieniak et al. 2022). The decrease in phylogenetic diversity of annual plants in the central urban area may be attributed to intensive artificial disturbances, such as frequent mowing during green space management (Chollet et al. 2018), extinction of ruderal species (Cui et al. 2019), and introduction of non-native species (Padullés Cubino et al. 2019). For example, commonly occurring annual herbs, such as *Galinsoga parviflora*, *Polygonum aviculare*, and *Setaria viridis* (Table S1), are frequently eradicated from urban green spaces like lawns and gardens in Shanghai due to being considered weeds. The spontaneous species exhibited non-responsive patterns (Fig. 2E and e). This may be due to the fact that spontaneous plants consist of native and/or alien species that can randomly distribute themselves across various habitats (Qian et al. 2020). In comparison to the spontaneous species, the PD of cultivated species linearly decreased from urban to rural areas. This suggests that the phylogenetic diversity of cultivated species could effectively reflect the changes in human preference for plant species along the urban–rural gradient, thus serving as an index of human preference in selecting urban plant species.

The phylogenetic structural metrics, namely, net relatedness index (NRI) and net nearest taxon index (NTI), did not consistently exhibit significant patterns along the urban-to-rural gradients compared to those of PD. On the one hand, there was a consistent linear increase in NRI for both total and spontaneous plant species along the gradients from urban to rural areas, indicating an decreased clustering of phylogenetic structure for these taxa as they transitioned from urban to rural environments. NRI for woody plants exhibited a linear decrease trend in the eastern transect (Fig. 3B), while NTI and NRI for annual herbs increased along the northern gradient (Figs. 3c and 4c). No significant response patterns were observed along the other gradients. In contrast, perennial plants displayed different patterns along four gradients from urban to rural areas. NTI and NRI for cultivated plant taxa did not exhibit any significant patterns, indicating that the phylogenetic structure demonstrated diverse responzses along the urban-to-rural gradients. On the other hand, the vast majority of the assemblages exhibited positive values for NRI and NTI, indicating a clustering phylogenetic structure and closer relatedness among species. However, a woody taxon in several assemblages shows negative values, suggesting the species are distantly related. The positive NRI and NTI values observed along the urban-to-rurual gradients suggest the presence of environmental filtering, which significantly influences plant composition in both urban and rural areas (Webb 2000; Webb et al. 2002). The diverse patterns of plant phylogenetic diversity along the urban-to-rural gradients may be attributed to individual and/or collective impacts of habitat transitions, landscape fragmentation, human interference, and urban environment (Williams et al. 2009), as well as urban morphology and history (Aronson et al. 2016; Huang et al. 2019). These influencing factors can exhibit higher spatial heterogeneity along the urban–rural gradients, thereby differentiating the intensities of various environmental filters such as pollution load and urban heat islands (Williams et al. 2009).

The Impacts of Urbanization on Plant Phylogenetic Diversity

A significant relationship was observed between plant phylogenetic diversity metrics and urbanization degree. However, plant taxa displayed different


A Total plant
B Woody plant
C Annual herb
D Perennial herb
E Spontaneous species
F Cultivated species
a
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NTI-E
NTI-S
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◂**Fig. 4** Spatial patterns of NTI along the urban–rural gradients in different plant taxa

response patterns of phylogenetic diversity in relation to urbanization. Faith's phylogenetic diversity (PD) exhibited a significant linear increase with increasing urbanization degree for total, woody, perennial, and cultivated plants (Fig. 6a, b, d, f). The variations in PD could be explained by the urbanization degree index (UDI) ranging from 3 to 36%. On the other hand, the NRI and NTI metrics for the overall plant presented a declining trend as UDI increased; however, the trend of NRI was not statistically significant. In contrast, NRI for woody plants and both NRI and NTI for perennial and cultivated plants demonstrated a linear increasing trend with UDI. This indicates an increase in plant phylogenetic richness, along with a closer phylogenetic structure and closer relatedness among the species as the urbanization degree rose in Shanghai. It should be noted that there are some outliers in Figs. 5, 6, and 7. This is because the high heterogeneity of urban landscapes and intense human interference can significantly influence local phylogenetic diversity, leading to substantial variations. For example, The PD within grid number -5 exhibits higher values (Fig. 2a) due to the location of the sample plot (No. 339) in a villa area where a large number of cultivated ornamental plants have been introduced, resulting in an elevated level of phylogenetic diversity. Although there are some individual outliers depicted in these figures, they present genuine local situations that cannot be disregarded.

Our findings demonstrated a significant increase in phylogenetic richness of the total, woody, perennial, and cultivated plants (Fig. 5a, b, d, f), while a decrease in annual and spontaneous plants (Fig. 5c, e) with increasing urbanization degree. A previous study at species level also reported similar results (Wang et al. 2020). These results highlight that urbanization can enhance both species and phylogenetic richness of total, woody, perennial, and cultivated plant assemblages. The increase in phylogenetic richness could be attributed to the widespread introduction of ornamental tree species during urban greening in the process of urbanization over the past decades in Shanghai (Qian et al. 2016). Similar findings have been observed along the urban–rural gradient in northeastern China (Yang et al. 2022) and Minneapolis-St. Paul, Minnesota, USA (Knapp et al. 2012). However, as urbanization degree increases, there is a decline in phylogenetic divergence among species within woody, perennial, and cultivated plant assemblages. These species exhibited more phylogenetic clustering and relatedness (Figs. 6b, d, f, and 7d, f). A slight declining trend was observed for the overall phylogenetic distance of plant assemblages (Figs. 6a and 7a), suggesting that urbanization has a minor impact on the overall phylogenetic distance but significantly influences the closest phylogenetic relationships represented by the tips of the evolutionary tree (NTI in this study, Fig. 7a) (Kraft et al. 2007, 2015). The phylogenetic divergence of the annual and spontaneous plants exhibited an increasing trend, while their clustering and relatedness showed a decreasing pattern (Fig. 6c and e). However, both of the NTI and NRI of annual herbaceous plants decreased (Figs. 6 c and 7c). Several factors contribute to this phenomenon: (1) habitat transformation and fragmentation, such as urban heat islands and pollution, which favor species adapted to high environmental pressures but disadvantage annual herbaceous and spontaneous species (Knapp et al. 2012; Pandey et al. 2015; Čeplová et al. 2017) (2) the introduction of exotic species enhances competitive exclusion within plant communities, leading to an expansion in phylogenetic structure (Čeplová et al. 2015); (3) human maintenance of green space acts as an environmental filter for spontaneously occurring herbaceous species (Kendal et al. 2012;Cavender-Bares et al. 2020; Blanchette et al. 2021; Cheng et al. 2022).

limitations and future research directions

There are several limitations in this study. Firstly, we did not take into account the individual plant abundance when calculating phylogenetic metrics. Previous studies have shown that the abundance could influence MPD and lead to overestimating the overall phylogenetic diversity of a community or assemblage (Xu et al. 2016). Therefore, future investigations on urban plant phylogenetic diversity should consider utilizing abundance-weighted structure indices such as abundance-weighted MNTD and AW-MNTD (Miller et al. 2017). Secondly, the lack of simultaneously investigated functional trait data prevented us from integrating

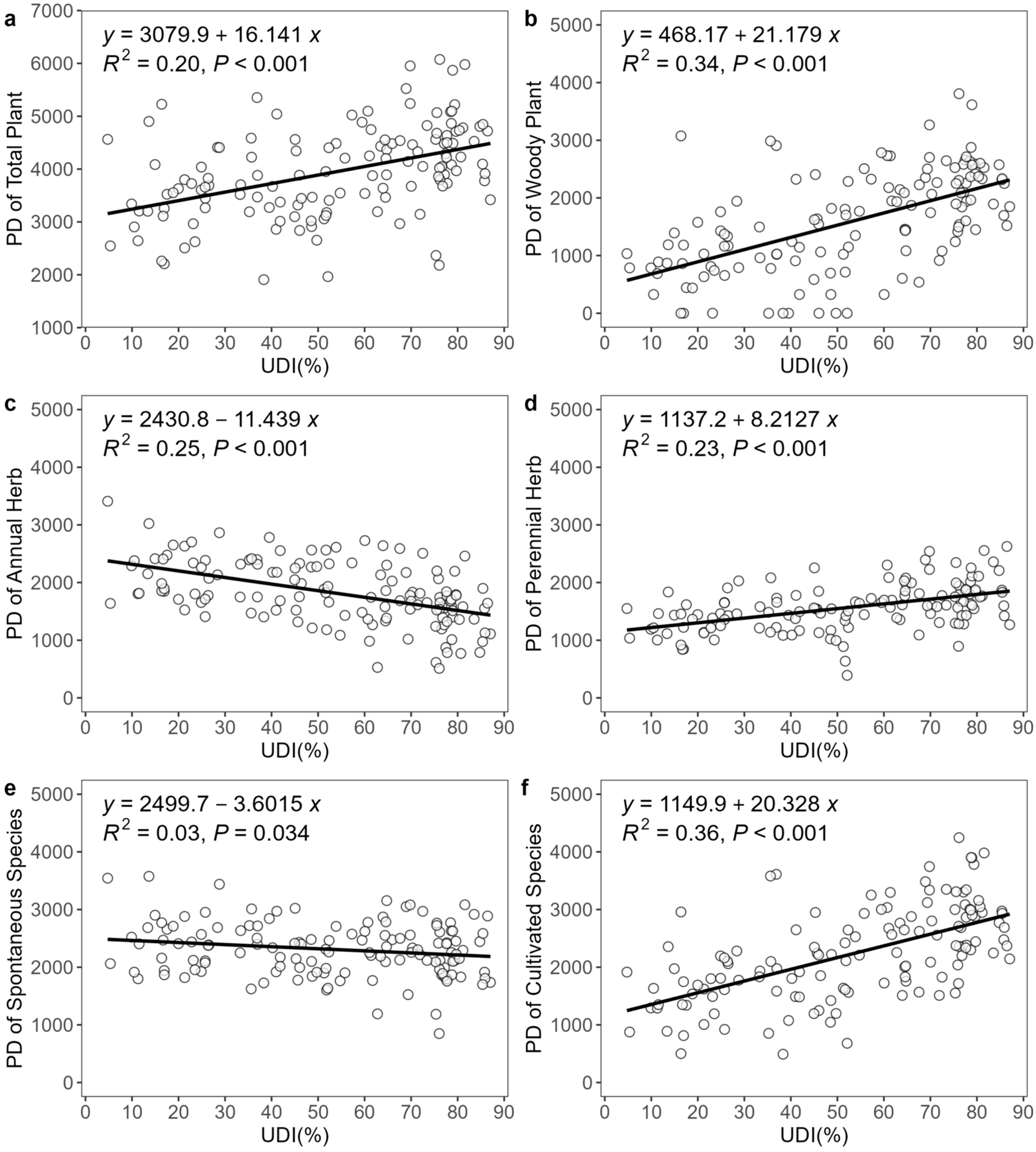

Fig. 5 The relationship between PD and urbanization degree (UDI) for different plant taxa

plant functional traits into our analysis. Previous studies have shown that incorporating functional trait variables significantly enhances the analysis of plant phylogenetic diversity (Knapp et al. 2012, 2008; Yang et al. 2014; Chollet et al. 2018; Cui et al. 2019). Thirdly, this study only used a single index to quantify the relationship between urbanization degree and plant phylogenetic diversity, although our results, along with those of a previous study (Wang et al. 2020),

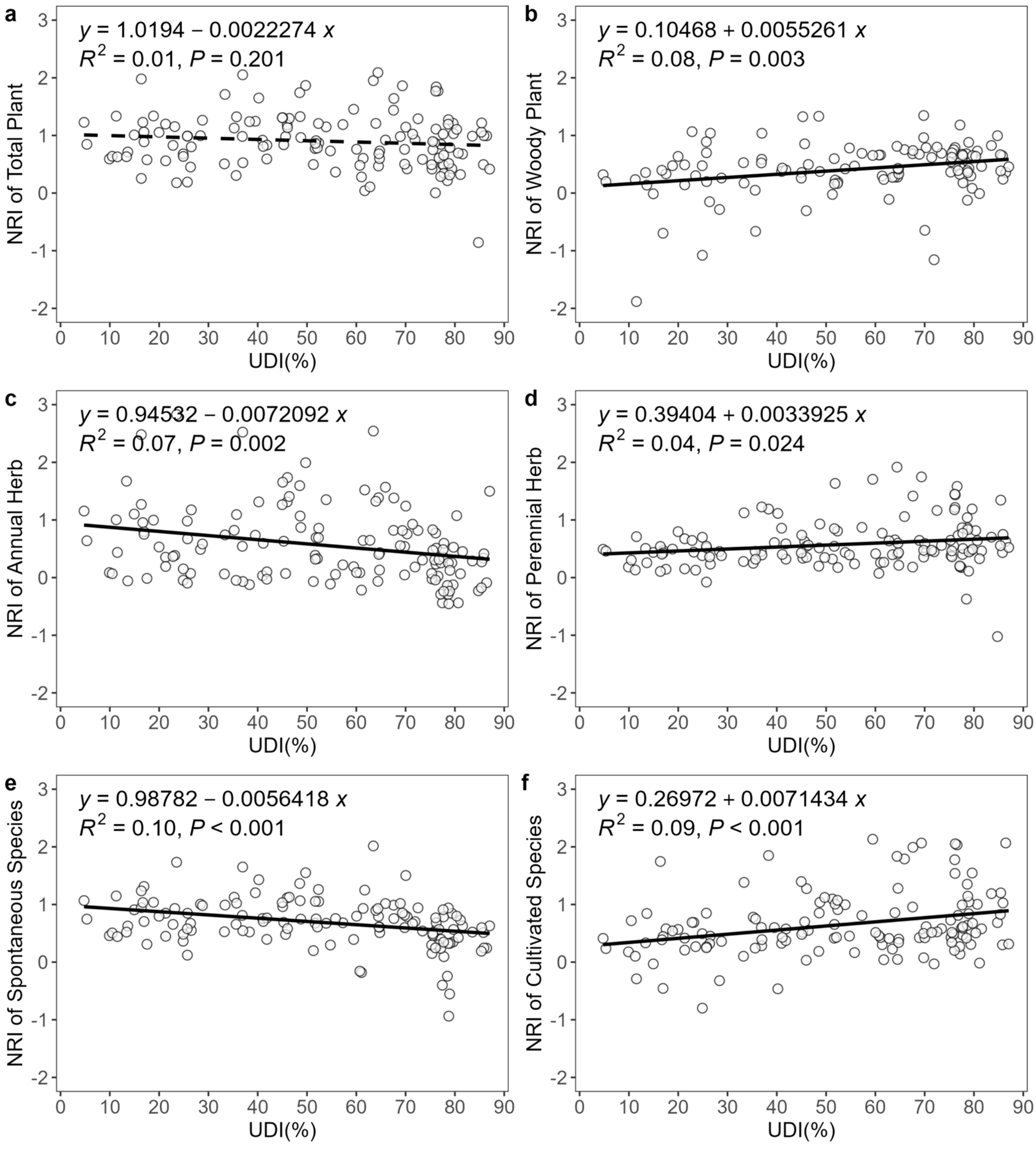

Fig. 6 The relationship between NRI and urbanization degree (UDI) for different plant taxa

demonstrated that utilizing urban land proportion as an indicator of urbanization degree is a robust predictor. Nevertheless, it is worth noting that previous studies have utilized alternative indices such as house density (Knapp et al. 2012), the combined index integrating the ratio of urban land cover to population, landscape shape index, and dominant land cover (Hahs and McDonnell 2006), or urban socio-economic factors including land use or cover, population density, house prices,

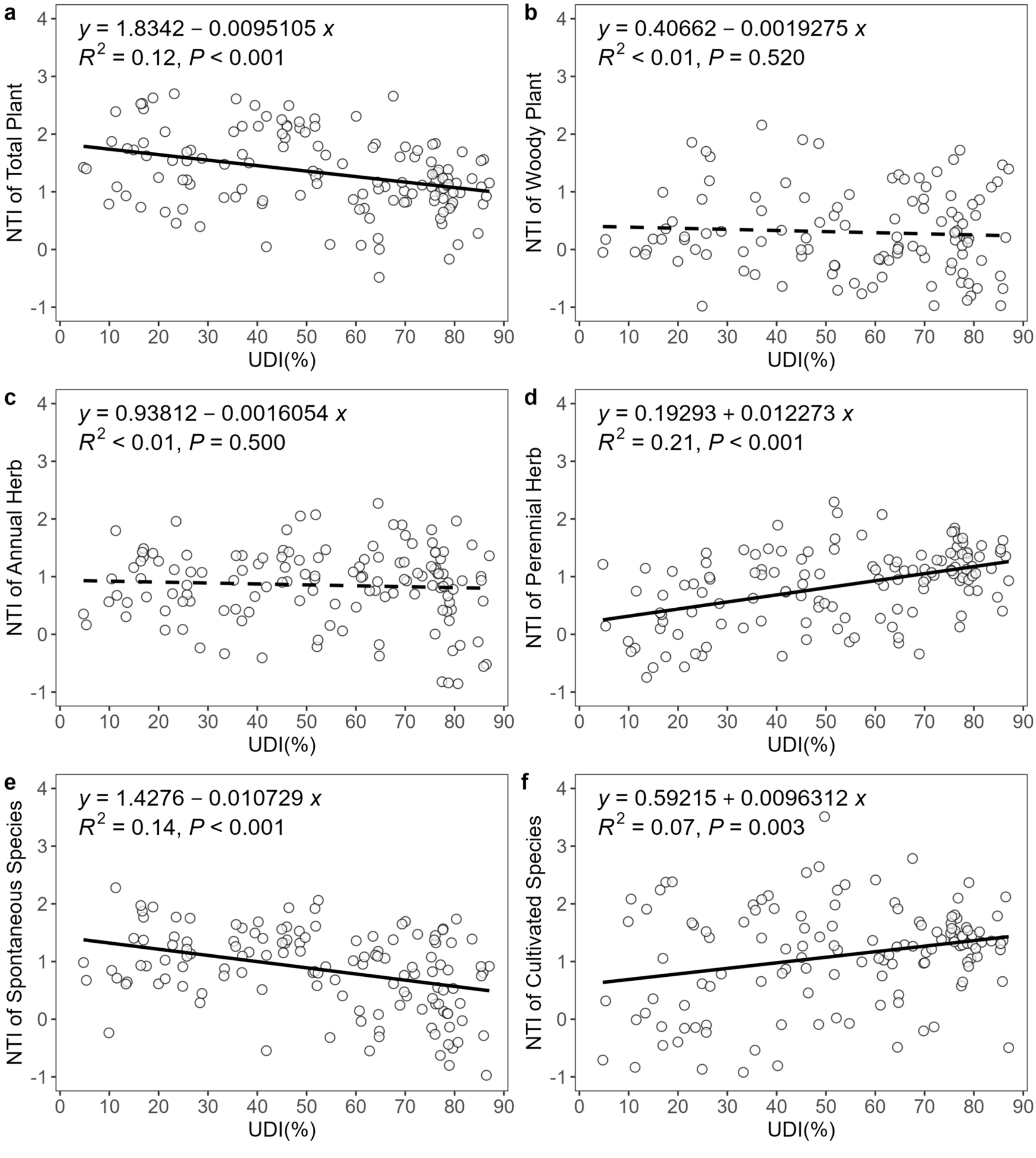

Fig. 7 The relationship between NTI and urbanization degree (UDI) for different plant taxa

and building age (Zhu et al. 2021). Additionally, some studies have considered the percentage of artificial surface area (Yang et al. 2022), which closely resembles the index employed in our analysis. Future investigations should encompass more measures of urbanization, especially when exploring urbanization impacts on phylogenetic diversity utilizing approaches such as the structural equation model. Lastly, it is worth noting that the urbanization degree could account for the variation

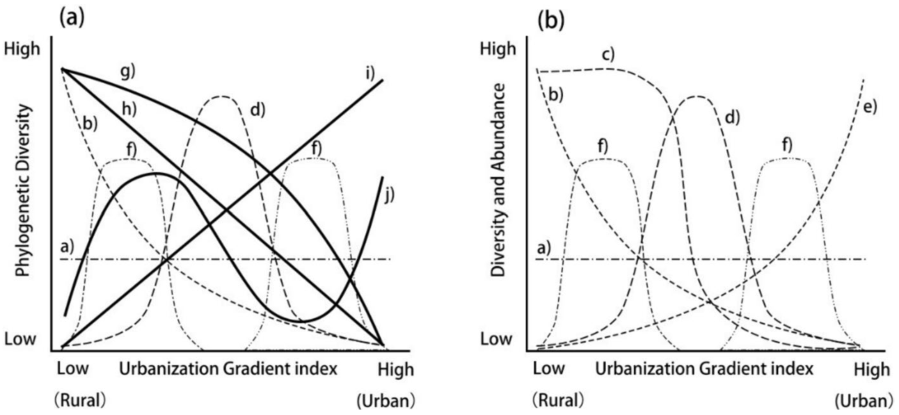

Fig. 8 The distribution patterns of plant phylogenetic diversity identified along the urban–rural gradient in Shanghai. In sub-figure (**a**), solid lines represent newly observed patterns in this study, while dashed lines represent patterns similar to those previously identified by McDonnell and Hahs (2008). The sub-figure (**b**) presents the summarized responses of species richness along the urbanization gradient for comparision (redrawn from McDonnell and Hahs 2008). **a** no response, **b** concave decrease, **c** punctuated response, **d** unimodal, **e** convex increase, **f** bimodal response, **g** convex decrease, **h** linear decrease, **i** linear increase, and **j** intermittent

in plant phylogenetic diversity across different taxa, ranging from 3% (PD of the perennial) to 36% (PD of the cultivated), suggesting that apart from the impact of urbanization, other factors such as landscape patterns, physical environment, socio-cultural elements, and human activities may also serve as potential or even direct drivers that should be taken into consideration. Therefore, future studies should consider exploring the underlying mechanisms through which urbanization influences plant phylogeny by adopting a multi-factor and multi-pathway approach like the structural equation model (Laliberté et al. 2014; Lopez et al. 2018).

Conclusions

This study revealed six distinct spatial distribution patterns of plant phylogenetic diversity along the urban–rural gradients in Shanghai, demonstrating the feasibility of quantifying plant responses to urbanization at the phylogenetic level. The diverse phylogenetic spatial patterns observed reflect the variations in urban environmental filtering along the urban–rural gradients. Furthermore, significant linear relationships were found between the degree of urbanization and both richness and structural metrics of plant phylogeny. Specifically, there was an increase in phylogenetic richness for total, woody, and perennial plant assemblages with increasing levels of urbanization, while annual and spontaneous plants exhibited a decreasing trend. The phylogenetic diversity of woody, perennial, and cultivated plant assemblages significantly decreased with urbanization. However, the annual and spontaneous plant assemblages exhibited either significant or marginally significant increasing trends. Urbanization degree, measured by the proportion of urban land cover, serves as a reliable indicator to predict plant phylogenetic variations along the urban–rural urbanization gradient.

Author Contribution Conceptualization: Junxiang Li, Yutong Gao. Methodology: Yutong Gao, Meng Wang, Junxiang Li. Software: Yutong Gao. Investigation: Meng Wang, Xing Bi, Yuhan Liu, Guojian Chen, Shengjian Kuang, Junxiang Li. Data Curation: Yutong Gao, Meng Wang. Data analysis: Yutong Gao, Junxiang Li. Writing—Original Draft: Yutong Gao, Junxiang Li. Writing—Review & Editing: Junxiang Li, Caiyan Wu, Shaopeng Li, Conghe Song. Visualization: Yutong Gao. Supervision: Junxiang Li, Caiyan Wu. Project administration: Junxiang Li, Meng Wang. Funding acquisition: Junxiang Li, Caiyan Wu. Resources: Junxiang Li.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interest The authors declare no competing interests.

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