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Original article

Plant taxonomic richness and phylogenetic diversity across different cities in China

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A B S T R A C T

Analyses of the phylogenetic relatedness of plant communities in urban areas have great potential to inform future diversity planning in expanding or new urban areas. The influences affecting the number of taxa found in urban areas and their phylogenetic diversity remains unclear. Both native and exotic (or imported) plant species can be found in urbanized areas: some grow spontaneously, and some are cultivated. These groups likely have different drivers: cultivated species diversity may be dependent on city wealth and the nature and extent of green space within those urban areas. In contrast, spontaneous species diversity may be more closely related to the constraints of climate. In this study, we analyzed the drivers of plant taxonomic richness and phylogenetic diversity of five groups (native-spontaneous, native-cultivated, exotic-spontaneous, exotic-cultivated and all) across 18 different cities in China that spanned different climate zones and socioeconomic status. We used both fieldwork and existing literature in our study. We constructed general linear models to assess whether the number of taxa and the phylogenetic diversity of plant life in each of the five studied groups could be related to any of two biophysical variable Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP as well as two socioeconomic variables, Gross Domestic Product (GDP) and Urban Greening Percentage (UGP). We identified 5163 plant species (229 families and 1730 genera) in the combined final plant species list from the 18 Chinese cities. The composition of all plant species was positively correlated ($p < 0.01$) with both MAP and MAT. Very few diversity metrics seemed to be related to the environmental factors tested, but the patterns were consistent with expectations. The Net Relatedness Index (NTI) of native cultivated species was negatively related to socioeconomic variable UGP (greater overdispersion with greater UGP), whereas the family richness and phylogenetic overdispersion of urban spontaneous plant species were positively related to the climate variable MAT. These findings might indicate long-term urban legacy effects over the course of centuries as have been observed in other world regions having a long history of urbanization.

1. Introduction

The number of studies regarding the causes of urban biodiversity within specific cities are increasing (Hope, 2003; Luck et al., 2009; Boone et al., 2010; Lowry et al., 2011; Wang et al., 2016). These studies indicate that socioeconomic variables, such as wealth, property values, education and active management regimes, drive plant diversity across different types of urban ecosystems (Hope, 2003; Kinzig, 2005; Escobedo et al., 2006; Luck et al., 2009; Wang et al., 2016).

Several previous studies were conducted to investigate the role of biotic and abiotic drivers of urban spontaneous plant species diversity (e.g., Knapp et al., 2012; Yang et al., 2015; Qian, 2013; Qian et al., 2016). However, few studies have been undertaken to determine if the causes of cultivated species diversity are different from those species that can reproduce and thrive spontaneously in urban environments. Urban plant taxa can be divided into two major groups, "native" and "exotic," each of which can be further subdivided into two categories. Native species can be considered either native-spontaneous or native-cultivated plant species; e.g., those that have been intentionally introduced for various purposes, such as ornamentals planted in parks and gardens. Exotic species can similarly be subdivided into exotic-spontaneous and exotic-cultivated plant species. Urban exotic species

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Table 1
Socioeconomic, biophysical and natural factors of the 18 cities of China.

City	Category	Regionalization	Climate zone	GDP (Billion Yuan)	Urban Greening percentage (%)	Mean Annual precipitation (mm)	Mean annual temperature (°C)	Latitude (N)	Longitude (E)	Altitude
Beijing	Municipality	North China	Temperate monsoon	1950	51	508	12.2	39.9	116.4	44
E'zhou	Prefecture level city	Central China	Subtropical monsoon	73	34	1282	17	30.4	114.8	17
Fuzhou	Prefecture level city	East China	Subtropical monsoon	467	43	1572	20.9	26.1	119.3	10
Guangzhou	Prefecture level city	South China	Subtropical monsoon	1542	41	1696	21.9	23.1	113.3	21
Haikou	Prefecture level city	South China	Tropical monsoon	90	42	1625	24.2	20.0	110.3	15
Hangzhou	Prefecture level city	East China	Subtropical monsoon	834	43	1378	18.4	30.3	120.2	19
Hong Kong	Special administrative region	South China	Subtropical monsoon	1790	70	2225	24.2	22.3	114.2	385
Huanggang	Prefecture level city	Central China	Subtropical monsoon	133	28	1352	16.4	30.5	114.8	49
Jiangmen	Prefecture level city	South China	Subtropical monsoon	200	43	2105	22	22.6	113.1	10
Lishui	Prefecture level city	East China	Subtropical monsoon	98	44	1755	17.8	28.5	119.9	74
Nanning	Prefecture level city	South China	Subtropical monsoon	280	42	1304	23	22.8	108.3	79
Qitaihe	Prefecture level city	Northeast	Temperate monsoon	24	40	549	4.8	45.8	131	204
Sanming	Prefecture level city	East China	Subtropical monsoon	147	41	1688	17.5	26.3	117.6	4
Shanghai	Municipality	East China	Subtropical monsoon	2160	37	1178	18	31.2	121.5	16
Shuangliu	County-level city	Central China	Subtropical monsoon	59	36	921	16.2	30.7	104.1	503
Urumqi	Prefecture level city	Northwest	Temperate continental	220	38	409	6.9	43.8	87.6	800
Wuhan	Prefecture level city	Central China	Subtropical monsoon	905	39	1284	16.5	30.6	11.3	15
Yiliang	County-level city	Southwest	Subtropical monsoon	17	43	1081	16.3	24.9	103.2	1539

are also able to grow spontaneously in urban environments and can spread by vegetative or seed propagation. While socioeconomic variables likely affect the diversity of cultivated plants in a city (Hope, 2003), climatic and soil factors may constrain which species can be planted. The diversity of cultivated plants depends mainly on human decisions, which in turn rely on socioeconomic indicators, historical factors, and local traditions and preferences (Hope, 2003; Luck et al., 2009; Boone et al., 2010; Lowry et al., 2011; Wang et al., 2016). Ornamentals add to the number of existing taxa and to the range of phylogenetic diversity of "urban flora," as they often are exotics from genera and families that are not represented in the local native flora (Pyšek et al., 2011; Jarosik et al., 2011). On the other hand, natural factors such as climatic variables may much more strongly determine the taxonomic richness and phylogenetic diversity of the spontaneous native and naturalized groups (Luck et al., 2009; Boone et al., 2010; Knapp et al., 2012; Lowry et al., 2011).

Some previous studies have used ground-level data to investigate the relationship between vegetation or plant diversity and its driving factors (Hope, 2003; Luck et al., 2009). However, two issues limit such urban greening studies. Firstly, studies concerning the causes of diversity among urban plants are mostly conducted at the intra-city level and rarely consider inter-city plant diversity variation. Secondly, urban plant species within specified regions and phylogenetic diversity across cities in different biomes and climate zones are rarely studied (Botzat et al., 2016). Analyses of the phylogenetic relatedness of plant communities across cities could inform future diversity planning in expanding or new urban areas, and phylogenetic diversity might become an easily measurable substitute for functional diversity. Phylogenies of existing urban plant communities of urban plants can also be used to assess the suitability of new or untested species palettes based on phylogenetic similarity (Pearse et al., 2013; Cook-Patton, 2015).

In this study, we analyzed the causes of plant taxonomic richness and phylogenetic diversity for five groups - native-spontaneous, native-cultivated, exotic-spontaneous, exotic-cultivated, and all species - across 18 cities in China that range across a large climatic space and that possess different socioeconomic characteristics. We selected two natural and two socioeconomic factors that may affect plant diversity of both cultivated and spontaneous species. Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP) were chosen for natural factors because they can constrain initial growth and ultimate survival of plants and may also affect the choice of cultivated species. Gross Domestic Product (GDP) and Urban Greening Percentage (UGP), which were scaled per capita, were chosen as socioeconomic factors, because the extent of green space in urban areas determines how much land is available for planting, and wealthier cities might have higher plant diversity because of their greater purchasing power (Hope, 2003). Using a compilation of urban plant species from these cities and ancillary socioeconomic factors from the literature and fieldwork (e.g., MAT MAP, GDP and UGP), we built statistical models to test whether the causes of diversity among the five plant groups differed. We anticipated that cultivated groups would be strongly driven by socioeconomic factors, whereas climatic factors would strongly drive the two spontaneous groups. Subsequently, we discuss how these findings can be used for urban greening planning in China's cities.

2. Materials and methods

2.1. Study design

The ability to sample vegetation in urban areas is subject to many restrictions and obstacles. Typically, the field investigations are time-consuming and costly, and access to a range of private grounds are often denied by the landowner. Furthermore, randomly-selected regions often have large water-covered areas or are otherwise information-poor, thus making sampling of plants impossible or meaningless. Such restrictions and obstacles were present in a case study of Beijing

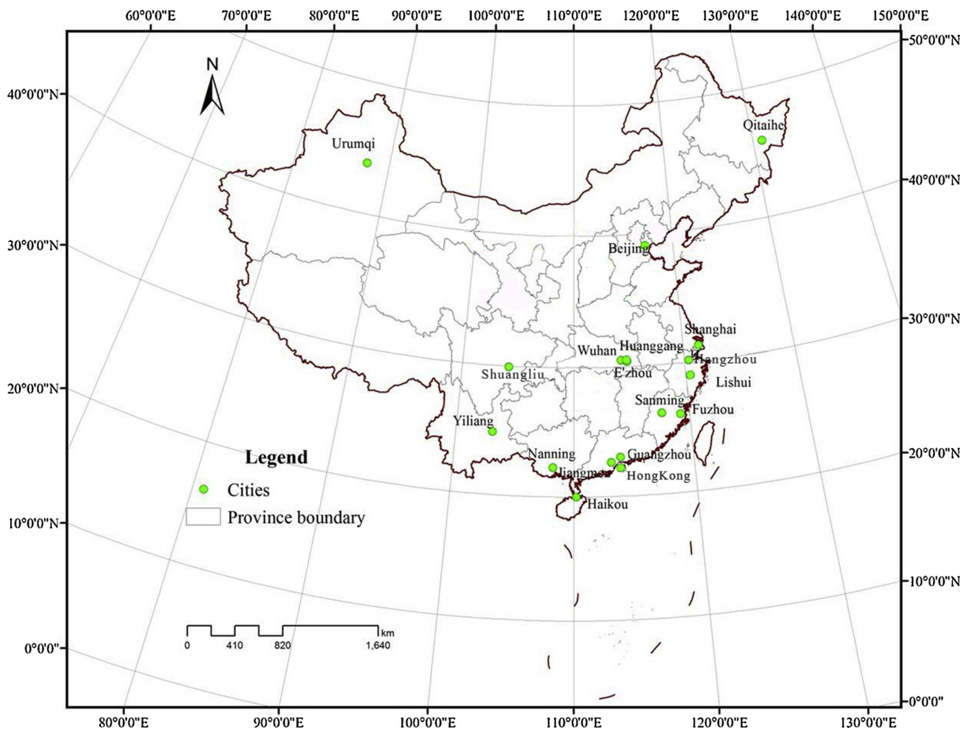

Fig. 1. The geographical spread of the 18 cities in China used in the analysis.

(Wang et al., 2015), and so we were unable to use the most desirable sampling technique: strictly-defined stratified random sampling. We, therefore, chose to adopt a unique sampling method for this study (see Wang et al., 2015) to identify sites that represent a meaningful distribution of socioeconomic variables in China by applying the following procedure, which had key elements of iterative random sampling:

We chose 18 Chinese cities satisfying the following four criteria: (1) each city selected has an extensive plant species list; (2) the cities are spread across different regions in China (i.e. east China, north China, central China, South China, Southwest, Northwest and Northeast), representing different climatic zones found in China (i.e., tropical monsoon, subtropical monsoon, temperate monsoon, temperate continental, plateau climate) (Table 1); and (3) the cities represent a spectrum of socio-administrative scales used in China (i.e. municipality, special administrative region, prefecture level city and County-level city). We endeavored to obtain the most diverse results possible. A map showing their distribution is provided in Fig. 1.

2.2. Data sources

Our urban plant species (native-spontaneous, native-cultivated, exotic-spontaneous, exotic-cultivated and all) for the 18 cities in the study were compiled using two methods. First, for the urban areas of Yiliang and Haikou in Yunnan and Hainan provinces, respectively, we set 117 and 96 "2×2 km" evenly spaced grids in the urbanized areas of both cities in 2015 and 2016. We identified 234 UFUs (Urban Functional Units; e.g., Schools, parks, etc.) in Yiliang and 191 UFUs in Haikou city covering the entire grid. For each plot, tree, shrub, and herbaceous plant species were identified using methods outlined in Wang et al. (2015) and Wang et al. (2016).

Second, we expanded our cities' dataset by systematically searching for the terms "urban plant", "urban vegetation", "urban biodiversity", "urban green space", and "urban diversity" in the China Knowledge website (www.cnki.cn) and the Science Direct website (http://www.sciencedirect.com) to find articles, books, and masters or doctoral theses with full plant species lists for their respective studied cities. Further, we checked all cities' plant species sampling methods (excluding aquatic and non-spermatophyte plant species), and we excluded studies with incomplete sampling methods (e.g., surveys only covering woody plants, or surveys not examining grasses, etc.). We excluded cities where there were obvious gaps in those cities' floral phylogenies. Using this approach, we found 16 additional cities with comprehensive plant species taxa lists.

We then combined and standardized the plant species lists and plant names using the following websites: 1) China natural history museum (www.cfh.ac.cn), 2), the plant list (www.theplantlist.org/), and 3) the species 2000 website (www.sp2000.org/). The final list was used to develop a presence-absence matrix across the different cities for all the identified plant species.

We divided all the plant species from the 18 urban floras into exotic-spontaneous, exotic-cultivated, native-spontaneous and native-cultivated groups. First, we separated native plant species from exotic plant species by checking Chinese Floras (e.g., Flora of China, Flora of Guangdong, Flora of Yunnan, etc). Second, while exotic-spontaneous species are listed by Jiang et al. (2011), it was hard to determine whether some exotic species (e.g., *Justicia adhatoda*) are spontaneous or cultivated in urbanized areas, so some species were assigned to both (e.g., exotic-spontaneous and exotic-cultivated). Third, we referred to Flora of China and other local floras for cultivated species in the 18 cities; i.e., we took the taxa recorded as cultivated in these floras as native-cultivated species in this study. The remaining native species were listed as native-spontaneous. Again, some species (e.g., *Amorphophallus konjac*) could be both native-cultivated and native-spontaneous; therefore, these species were listed under both groups.

We used the WorldClim database (version 1.4, available at www.worldclim.org) to obtain mean annual precipitation (MAP) annual sunshine duration (hrs) and mean annual temperature (MAT) data at a spatial resolution of 1 km (30 arc seconds). City-level data for Urban Greening Percentage (UGP), Gross Domestic Product (GDP),built-up areas (km^2), population (10 thousand), total output value of agriculture in 2013 (0.1 billion Yuan), total output value of industry in 2013 (Billion Yuan) and total retail sales of social consumer goods in 2013 (Billion Yuan) were obtained from the China Statistical Yearbook (People's Republic of China National Bureau of Statistics, 2014). After a first analysis, we abandoned most variables, as they were auto correlated. We kept mean annual precipitation (MAP) and mean annual temperature (MAT) as climate variables and Urban Greening Percentage (UGP), Gross Domestic Product (GDP) as socioeconomic variables, considering them as the most meaningful for our study questions.

2.3. Phylogenetic data

We created one single phylogenetic tree based on our entire species list for the 18 cities. We used *Phylomatic* of the Phylocom software to assemble a phylogenetic tree to estimate branch lengths and calculate phylogenetic metrics (Webb et al., 2008). We selected Zanne et al. (2014) as the mega tree. This phylogeny was developed from the most recent supertree available from the Angiosperm Phylogeny Website (mobot.org/MOBOT/research/apweb/).

The phylogenies produced by the Phylocom software often contain polytomies, (e.g., unresolved nodes). When these are numerous because of the presence of many genera with more species in genera, or families with many genera, etc., there is a considerable loss of information about relatedness among taxa. As mentioned, we excluded studies with incomplete sampling methods and cities with gaps in floral phylogeny (see Appendix 1 in supplementary material).

Based on the phylogenies of 18 cities' plant species (Appendix 1 in supplementary material), we endeavored to make the floras of 18 cities comparable at the city level, even though some of the urban floras are from the local floras (e.g., HKH and SCBGCAS (2011), Flora of Shanghai, etc.), while others are from limited sampling plots investigations (e.g., Haikou).

2.4. Statistical analysis

To measure each city's plant diversity, we used species richness as well as several phylogenetic indices calculated from the presence-absence matrices of "cities x species" for each plant group: we used Faith's phylogenetic diversity (PD) (Faith, 1992) package Picante to measure the total branch length spanned by the tree including all species in a local community (here meaning a city); we used Net Relatedness Index (NRI) and Net Taxon Index (NTI) (Pausas and Verdú, 2010) to measure whether species in a community are more closely related (clustered) or less related (overdispersed) phylogenetically than expected by chance by comparing the actual community against a randomized null community. NRI is based on the mean distance between all species in a community and thus is more sensitive to change at deep branches of the phylogeny, such as at plant family level. NTI is based on the mean distance between each species' closest relative in a community and thus is sensitive to changes at the tip of the phylogenies. We conducted the same analyses for the data subsets of native-spontaneous, native-cultivated, exotic-spontaneous, exotic-cultivated and all plant species. All metrics are sensitive to changes in phylogenetic tree topology and branch length and are often used as complementary descriptors (Kraft, 2007; Cadotte et al., 2010). A total of 999 permutations were performed to determine the metrics threshold. We used Picante packages (http://picante.r-forge.r-project.org/) to calculate PD, NRI, and NTI.

We used non-metric multidimensional scaling (NMDS) to reveal how cities in China were distinguished from one another based on their plant species composition and how these compositional changes correlated with socioeconomic and climatic factors (using the *envfit* function of the *vegan* package in R) for the native-spontaneous, native-cultivated, exotic-spontaneous, exotic-cultivated and all plant species data sets.

The number of species, genera, families, and phylogenetic diversity measures (PD, NRI, NTI), were each regressed with the climatic predictors MAT and MAP using a linear model in R (R Core Development Team, 2016), and the two socioeconomic predictors, GDP and UGP, against a full model. Firstly, we transformed the response and predictor variables as necessary to establish approximate normality. Secondly, we checked correlation among our predictor set to ensure that none of our four predictors were correlated. We tested all our six diversity measures (number of species, number of genera, number of families, PD, NRI, NTI) for each of the five plant categories (all, native-spontaneous, native-cultivated, exotic-spontaneous, exotic-cultivated) against a full model including GDP, UGP, and MAT.

As we had a very low number of sampling units (18), the use of ordinary model selection based on Akaike Information Criterion (AIC) values would be inappropriate, since that method assumes asymptotic properties that are valid only for large sample sizes (Austin and Tu, 2004; Dalposso et al., 2016). Therefore, thirdly, we evaluated R^2 values for full models and proceeded to model selection only for those response variables for which R^2 values exceeded 10%. Then, fourthly, we used bootstrapping via the *boot.stepAIC* functionof package *bootStepAIC* to generate statistics for which predictors were selected by the stepwise procedure across 1000 data re-samples (Rizopoulos, 2009). Predictors that are selected in 60% of samples can generate good predictive power for data (Austin and Tu, 2004), and we used this threshold as a cutoff to identify potential explanatory predictors. The *boot.stepAIC* function also provides the percentages for the signs of the parameter estimates across the sample runs, indicating the direction of effect as well as its consistency for all three data sets.

The Jaccard similarity index (J) was applied to measure species composition similarity across the different locations (McKinney, 2004). J was as: $J = c/(a+b+c)$, where a is the number of species unique to the first site, b is the number of species unique to the second site, and c is the number of species in common at both compared sites. J ranges between 0 and 1, where a result of 0 means that the two sites have no species in common, and a result of 1 means that the species composition of the two sites is identical. The similarity of the urban plant communities for the 18 cities was checked via calculating J in pairs of cities and then summarized J by the city. In order to see if the urban communities of a city were diverging from their natural communities, we calculated J for the similarities between urban and natural communities within each of the 18 cities. We examined the distance decay for the similarity relationships by plotting J against geographical distance for all pairs of cities. A matrix of pair-wise geographic distances was calculated using the coordinates of the 18 cities. To fit the relationships between J and geographical distance, we used generalized additive models (Wood, 2006). We conducted all analyses using the statistical software R, version 3.2.2 (R Core Team, 2016).

We used the statistical software R, version 3.2.2 (R Core Team, 2016) to perform a cluster analysis of the 18 urban flora based on the 18 cities' presence-absence matrices. Due to our limited number of cities' floras, we used all data in the clustering analyses. The clustering method divides flora data into different groups when the information about the composition is unknown (Fraley and Raftery, 1998). The basic procedure of conducting cluster analysis is to construct groups with homogeneous objects, which in our study are 18 different cities' flora from a well-defined proximity measure.

3. Results

3.1. Characteristics of China's urban flora

We recorded 2510 native-spontaneous plant species (178 families, 971 genera), 1367 native-cultivated species (159 families, 666 genera), 1430 exotic-spontaneous plant species (165 families, 796 genera), 404 exotic-cultivated plant species (84 families, 278 genera), and 5163 plant species ("all plant species" or simply "all") in total, excluding those characterized in more than one group (229 families and 1730 genera) in the final plant species list of the 18 cities (Table 2, Appendix 2 in supplementary material). The highest number of total plant species was recorded for Hong Kong, which also had the highest number of native-spontaneous, exotic-spontaneous and exotic-cultivated plant species. Lishui had the highest number of native-cultivated plant

Table 2
Number of native-spontaneous, native-cultivated, exotic-spontaneous, exotic-cultivated and all plant species families, genus and species across 18 different cities and the data sources of this study.

City	Native-spontaneous			Native-cultivated			Exotic-spontaneous			Exotic-cultivated			All species			Data source
	Families	Genera	Species	Families	Genera	Species	Families	Genera	Species	Families	Genera	Species	Families	Genera	Species	
Beijing	58	110	150	49	71	85	45	75	84	33	65	73	99	260	392	Wang et al. (2012)
E'zhou	77	127	169	57	90	110	45	75	84	34	63	69	116	306	431	Hou, (2009)
Fuzhou	43	54	63	30	41	52	46	76	82	21	26	28	90	182	225	Liu, (2011a)
Guangzhou	59	104	122	40	57	63	57	120	142	34	72	84	104	309	411	Cao, (2013)
Haikou	42	65	80	61	111	128	79	157	192	53	103	127	117	371	527	This study
Hangzhou	75	133	176	58	90	111	62	113	130	35	66	68	125	339	485	Xu, (2007)
Hong Kong	143	520	996	92	215	307	121	429	623	68	198	262	192	1035	2188	HKH and SCBGCAS (2011)
Huanggang	104	294	421	97	213	255	64	135	166	36	87	104	146	592	946	Liu, (2011b)
Jiangmen	36	51	63	21	27	29	38	57	62	21	28	30	71	148	184	Mo, (2014)
Lishui	124	412	805	112	272	408	71	173	240	41	94	111	166	729	1565	Yao, (2009a,b)
Nanning	60	99	116	30	41	52	50	96	112	34	53	60	117	273	341	Li, (2006)
Qitaihe	22	41	45	13	13	15	14	18	22	10	11	11	46	85	94	Yao, (2009a,b)
Sanming	103	232	353	76	126	171	73	134	160	39	67	75	152	453	759	Zhou, (2008)
Shanghai	109	349	558	91	217	292	108	386	552	64	187	252	158	869	1645	Xu, (2007)
Shuangliu	36	48	50	24	35	39	23	26	26	14	16	16	68	121	130	Xu, (2010)
Urumqi	61	200	374	49	124	199	61	145	230	33	68	83	99	392	886	Li, (2009)
Wuhan	75	152	207	74	117	149	46	71	78	32	57	63	124	329	497	Zhang, (2012)
Yiliang	82	186	243	83	159	204	91	211	266	49	100	116	142	525	829	Zhu et al. (2017)
Total	178	971	2510	159	666	1367	165	796	1430	84	278	404	229	1730	5163	

species. The lowest number of total plant species was found in Qitaihe, which also had the lowest number of native-spontaneous, native-cultivated, exotic-spontaneous and exotic-cultivated plant species (Table 2).

The first two most species-rich families of all five groups (native-spontaneous, native-cultivated, exotic-spontaneous, exotic-cultivated and all plant families) and the number of species per family for each city are listed in Table 3. For all five categories of plant species, Asteraceae, Poaceae, and Rosaceae were the three most species-rich families in most cities (Table 3). *Canna indica* (Cannaceae), *Juniperus chinensis* (Cupressaceae) and *Iris tectorum* (Iridaceae) were the most widely distributed plant species, present in 17 of the 18 cities. *Platycladus orientalis* (Cupressaceae), *Cynodon dactylon* (Poaceae), *Lagerstroemia indica* (Lythraceae), *Osmanthus fragrans* (Oleaceae), *Rosa chinensis* (Rosaceae) and *Salix babylonica* (Salicaceae) were the second most widely distributed plant species, found in 16 of the 18 cities.

Different cities have different dominant native-spontaneous, native-cultivated, exotic-spontaneous, exotic-cultivated and total plant species (Table 3). Rosaceae is the most common species-rich native-spontaneous family among the cities (10 of 18), while Poaceae is the most common species-rich native-cultivated family among the cities (11 of 18). Asteraceae is most common species-rich exotic-spontaneous family as well as the most common species-rich exotic-cultivated family among the cities (7 of 18, and 13 of 18, respectively). The most common species-rich plant families among the cities (9 of 18) are Poaceae and Rosaceae.

3.2. Phylogenetic diversity of China's urban plants

Phylogenetic diversity (PD) of all five species groups was greatest in Hong Kong and lowest in Qitaihe (Table 4). Native-spontaneous species communities were phylogenetically clustered in 7 cities for NRI (> 0, $p < 0.025$), and 10 cities for NTI (> 0, $p < 0.025$). Such indices examine significant departures from 0. Positive NRI and NTI values indicate phylogenetic or functional clustering (closely related species or functionally similar). Negative NRI and NTI represent phylogenetic or functional overdispersion (less or distantly or functionally dissimilar species). By and large, the NRI and NTI estimations of populace sources or species pools were near zero (i.e., NRI and NTI values were between -2 and $+2$). However, these values were interpreted as either "comparable" or "divergent" (i.e., positive or negative NRI or NTI, individually), since they indicated a significant temporal pattern ($P < 0.05$) reflecting effects on community PD (Cadotte and Davies, 2016). The greatest clustering was found in Urumqi and Beijing for both indices. Native-cultivated species communities had overdispersed communities in Beijing, Hangzhou and Yiliang (NRI < 0, $p > 0.975$) and clustering (NTI) in Haikou, Shanghai and Urumqi. NRI phylogenetically clustered exotic-spontaneous species communities in Huangang, and by NTI in Huangang, Shanghai, and Urumqi. Exotic-cultivated species communities were overdispersed in Fuzhou, Hangzhou, Lishui, Shuangliu, but clustered in Urumqi for NRI. NTI of the exotic-cultivated group was mainly clustered (8 cities). Plant communities including all species were overdispersed in Fuzhou, Hangzhou, Sanming, Shuangliu, Yiliang, but clustered in Urumqi and Huangang (NRI). NTI for these communities was positive for 11 cities (NTI > 0, $p < 0.025$), indicating phylogenetic clustering (Table 4).

3.3. Drivers of China's urban plant taxonomic richness and phylogenetic diversity

The species composition of all five groups were all significantly positively correlated with climate factors, but non-significantly correlated with socioeconomic factors (Fig. 2, Appendix 3). Few of the richness and phylogenetic diversity metrics for each plant category could be explained by the four predictors tested, and those relationships that were significant had low explanatory power (Appendix 3). For the variables that could be explained significantly by the predictors, the pattern was mostly consistent with our expectation (i.e., cultivated species diversity may be dependent on city wealth, and urban green space. Spontaneous species diversity may be more closely related to climate constraints). Climate drivers, represented by mean annual temperature (MAT), explained some patterns in the two spontaneous groups: NRI and NTI for native-spontaneous and number of families and NRI for exotic-spontaneous. The number of families in the total species group was also affected by MAT. In all significant cases, higher MAT had a positive effect on the number of families and increased overdispersion of the city plant species groups. Among the two cultivated groups, neither was overtly tied to climate, and only NTI could be associated with an urban green percentage (UGP): increased UGP caused

Table 3
Most diverse families in each category for each of 18 cities in China.

	Native-spontaneous		Native-cultivated		Exotic-spontaneous		Exotic-cultivated		All	
City	Family		Family		Family		Family		Family	
Beijing	Rosaceae	18	Rosaceae	13	Poaceae	6	Asteraceae	10	Rosaceae	34
	Leguminosae	7	Oleaceae	5	Asteraceae	5	Poaceae	9	Asteraceae	23
Guangzhou	Moraceae	7	Poaceae	4	Arecaceae	12	Poaceae	10	Euphorbiaceae	31
	Euphorbiaceae	15	Moraceae	4	Araceae	8	Leguminosae	10	Poaceae	22
Sanming	Rosaceae	25	Rosaceae	14	Liliaceae	7	Amaranthaceae	7	Rosaceae	44
	Lauraceae	19	Fagaceae	8	Ranunculaceae	7	Asteraceae	7	Lauraceae	27
Jiangmen	Rubiaceae	7	Myrsinaceae	1	Fabaceae	5	Apocynaceae	3	Moraceae	11
	Euphorbiaceae	6	Arecaceae	1	Myrtaceae	5	Myrtaceae	3	Euphorbiaceae	10
Yiliang	Rosaceae	21	Rosaceae	16	Arecaceae	11	Leguminosae	14	Leguminosae	42
	Fabaceae	10	Poaceae	13	Leguminosae	10	Asteraceae	10	Rosaceae	41
Haikou	Euphorbiaceae	7	Poaceae	10	Arecaceae	12	Asteraceae	11	Poaceae	27
	Poaceae	6	Leguminosae	7	Araceae	10	Euphorbiaceae	10	Euphorbiaceae	25
Urumqi	Amaranthaceae	31	Rosaceae	32	Asteraceae	37	Asteraceae	16	Asteraceae	62
	Poaceae	30	Cyperaceae	15	Asteraceae	22	Poaceae	10	Poaceae	54
Hong Kong	Cyperaceae	60	Poaceae	20	Scrophulariaceae	33	Leguminosae	32	Cyperaceae	110
	Fabaceae	60	Orchidaceae	38	Cyperaceae	29	Asteraceae	26	Poaceae	104
Shanghai	Cyperaceae	41	Rosaceae	22	Asteraceae	28	Asteraceae	30	Poaceae	88
	Rosaceae	36	Poaceae	15	Cactaceae	25	Poaceae	24	Asteraceae	77
Wuhan	Rosaceae	19	Rosaceae	14	Asteraceae	7	Leguminosae	9	Rosaceae	34
	Asteraceae	7	Leguminosae	8	Liliaceae	4	Asteraceae	7	Leguminosae	24
Shuangliu	Caprifoliaceae	3	Poaceae	5	Araliaceae	3	Poaceae	3	Poaceae	11
	Juglandaceae	3	Moraceae	3	Liliaceae	2	Labiatae	1	Rosaceae	7
E'zhou	Rosaceae	19	Leguminosae	8	Poaceae	6	Poaceae	8	Rosaceae	28
	Cyperaceae	10	Poaceae	8	Asteraceae	5	Leguminosae	8	Poaceae	27
Fuzhou	Malvaceae	4	Poaceae	5	Arecaceae	12	Myrtaceae	3	Arecaceae	17
	Moraceae	4	Moraceae	5	Apocynaceae	4	Agavaceae	3	Moraceae	11
Hangzhou	Rosaceae	13	Rosaceae	10	Asteraceae	8	Asteraceae	13	Rosaceae	27
	Poaceae	9	Oleaceae	6	Pinaceae	7	Poaceae	5	Asteraceae	25
Huanggang	Rosaceae	27	Rosaceae	14	Scrophulariaceae	16	Asteraceae	15	Asteraceae	48
	Liliaceae	17	Poaceae	11	Asteraceae	14	Poaceae	10	Rosaceae	44
Nanning	Moraceae	7	Poaceae	5	Arecaceae	13	Asteraceae	6	Arecaceae	18
	Fabaceae	6	Moraceae	5	Araceae	6	Amaranthaceae	5	Poaceae	16
Lishui	Rosaceae	48	Fagaceae	16	Scrophulariaceae	18	Asteraceae	16	Rosaceae	69
	Cyperaceae	38	Poaceae	16	Ranunculaceae	16	Leguminosae	11	Poaceae	58
Qitaihe	Rosaceae	6	Lauraceae	2	Ranunculaceae	2	Asteraceae	2	Asteraceae	10
	Asteraceae	4	Liliaceae	2	Ranunculaceae	1	Euphorbiaceae	1	Asteraceae	7

greater overdispersion in the native cultivated group. The exotic cultivated group could not be connected to any of the predictors. Finally, PD of the native spontaneous species was positively affected by GDP.

For all plant species in the 18 cities, J increased with MAT for all the plant species in 18 cities ($p < 0.0001$, adjusted $R^2 = 0.678$). No significant trends were observed for other variables (e.g., distance, latitude, GDP, UGP, Fig. 3).

The cluster analyses indicated that the18 cities' flora could be divided into three groups, the first group includes Qitaihe, Beijing and Urumqi, the three northern China cities. The second group includes

Table 4
Phylogenetic diversity of all species, exotic-spontaneous, exotic-cultivated, native-spontaneous and native-cultivated plant species from 18 different cities in China. PD = Phylogenetic Diversity, NRI = Net Relatedness Index, NTI = Nearest Taxon Index. Values of NTI and NRI which are $< < 0$ ($p > 0.975$ (bold)) indicate phylogenetic overdispersion, and values $> > 0$ ($p < 0.025$ (Italic)) indicate phylogenetic clustering.

	Native-spontaneous			Native-cultivated			Exotic-spontaneous			Exotic-cultivated			All		
	PD	NRI	NTI	PD	NRI	NTI	PD	NRI	NTI	PD	NRI	NTI	PD	NRI	NTI
Beijing	18444.5	*4.2*	*4.1*	7446	**−2.3**	1.2	4076.1	0.4	1.2	6423.5	0.3	*3.4*	16203.1	−0.9	*4.9*
E'zhou	21056.4	*2.7*	*3.8*	8470.2	0.7	1.3	4146	0.2	0.6	7027	−1.3	*2.1*	18921.9	0.3	*3.6*
Fuzhou	10677.3	−1.4	0.7	4759.6	−0.6	1.7	2751.5	0.1	−0.7	7765.3	**−2.9**	−0.6	14890.7	**−5.4**	−1
Guangzhou	16664.4	*2.3*	*1.7*	5795.7	−1.2	1.5	4794.4	−0.4	0.2	10621.3	−1.4	1.4	18475.7	−1.6	*3.3*
Haikou	11324.4	1.3	*3.5*	9669.3	−0.3	*2.6*	6624.9	0.3	0.5	13717.4	−1	1.4	20349.1	−0.2	*5.7*
Hangzhou	23042.9	−0.3	1.5	9386.6	**−2.2**	1.4	4519.4	−1.7	−0.1	10737	**−4.9**	0.3	22303.4	**−5.9**	1.7
Hong Kong	83073.1	−1.4	0.7	20,703.2	−0.5	−0.2	10630.9	1.2	0.9	32011.9	0.9	*3.6*	60447.2	−0.3	*4.7*
Huanggang	44180.1	1.0	*2.2*	17,281.9	1.7	1	4841.6	*2.5*	*3.2*	10844.6	0.6	*3.9*	33988.8	*2*	*2.8*
Jiangmen	9441.4	*2.5*	*2.6*	3500.2	−1	−0.3	2454.2	−0.8	1.2	5446.6	1.4	1	11109	0.2	1.5
Lishui	71165.5	1.4	−0.3	25,383.7	1.3	0.4	6126.7	0.1	0.1	15105.9	**−2.2**	*3.8*	49776.3	−0.7	1
Nanning	17050.8	0.0	0.4	5484.5	−1.1	−0.6	3948.4	−0.6	0.3	9025.1	−1.3	1.9	17520.3	−2	1.5
Qitaihe	7136.2	*3.0*	*2.7*	2102.1	−0.1	−0.5	1549.9	0.6	−0.6	2375.2	−0.2	*2.3*	7417	−0.4	0.6
Sanming	38714.0	0.0	1.8	12,975.6	−0.7	1.6	4836.1	−0.9	−0.4	12578.7	−1.2	−0.1	31243.8	**−2.5**	*2.1*
Shanghai	52382.5	1.5	*2.5*	17,619.1	−0.4	*4.3*	9554.3	1.3	*2.5*	26853.1	−3.3	*7.5*	44435.4	−1.6	*10.3*
Shuangliu	8982.7	−0.4	0.1	3680.9	−0.2	2	1796.5	−1.2	−0.6	3579.8	**−2.4**	−1.9	9243.7	**−2.4**	0.1
Urumqi	30471.6	*4.3*	*9.6*	11,396.5	1.7	*5.5*	4268.5	1.7	*2*	14213.5	*2.4*	*3.5*	23708	*4.2*	*9.7*
Wuhan	25161.0	*2.2*	*2.8*	10,897.8	0.6	1.8	3985.7	1	0.2	6961.3	−1.4	1.7	21084.3	0.7	*3.4*
Yiliang	2898.9	−0.3	1.4	14,829.1	**−3.7**	1.4	6017.9	0	1	17728.9	−4.2	1.9	31570.6	**−6.6**	*3.1*

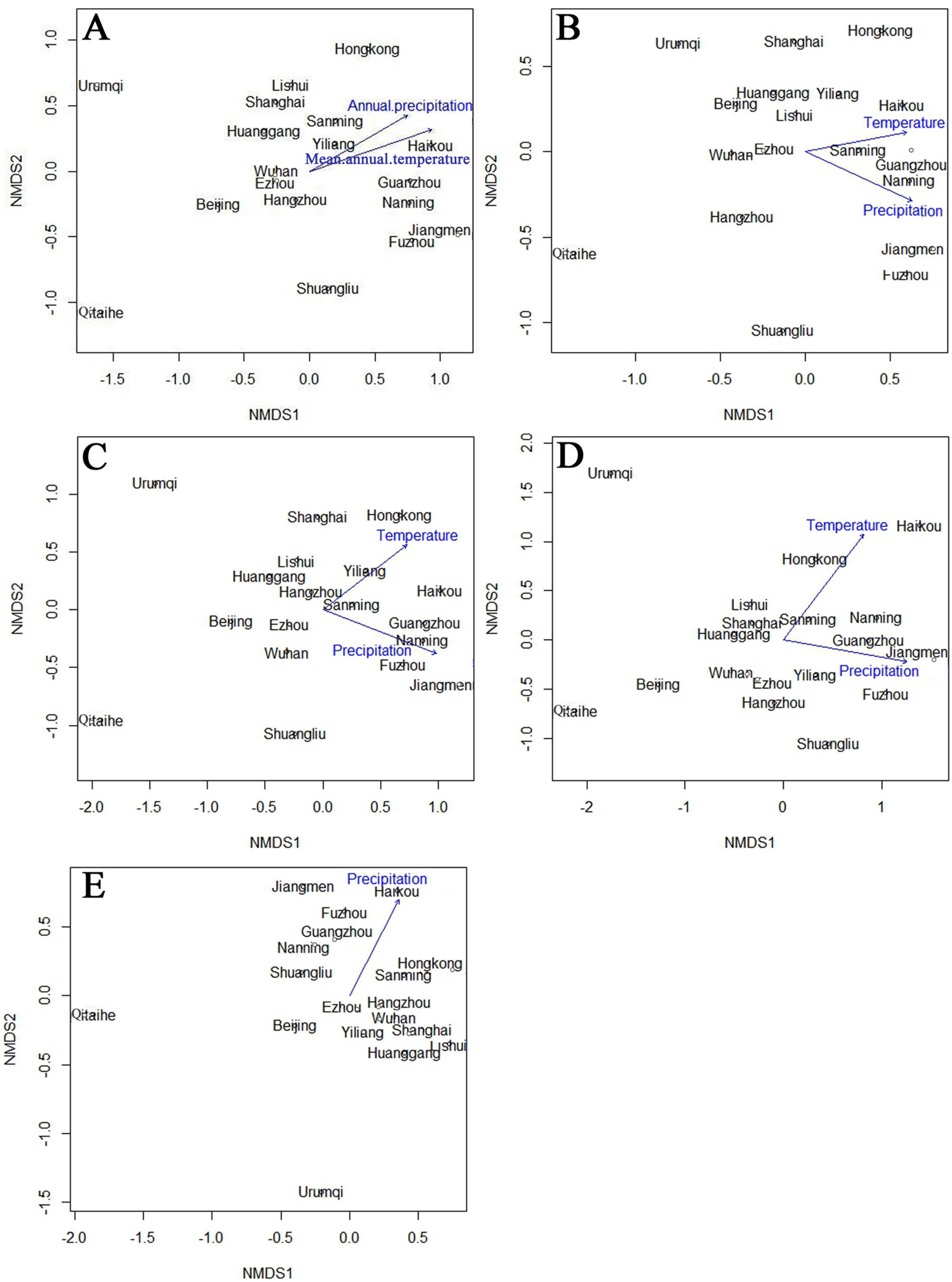

Fig. 2. Non-metric multidimensional scaling (NMDS) for all species, exotic-spontaneous, exotic-cultivated, native-spontaneous and native-cultivated species across 18 cities in China. A = All species, B = Exotic-spontaneous, C = exotic-cultivated, D = native-spontaneous and E = native-cultivated. Plot-level environment variables (GDP: gross domestic product; UGP: urban green percentage; MAP: mean annual precipitation; and MAT: mean annual temperature) that were significantly related to each ordination ($P < 0.05$) are indicated on each panel (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

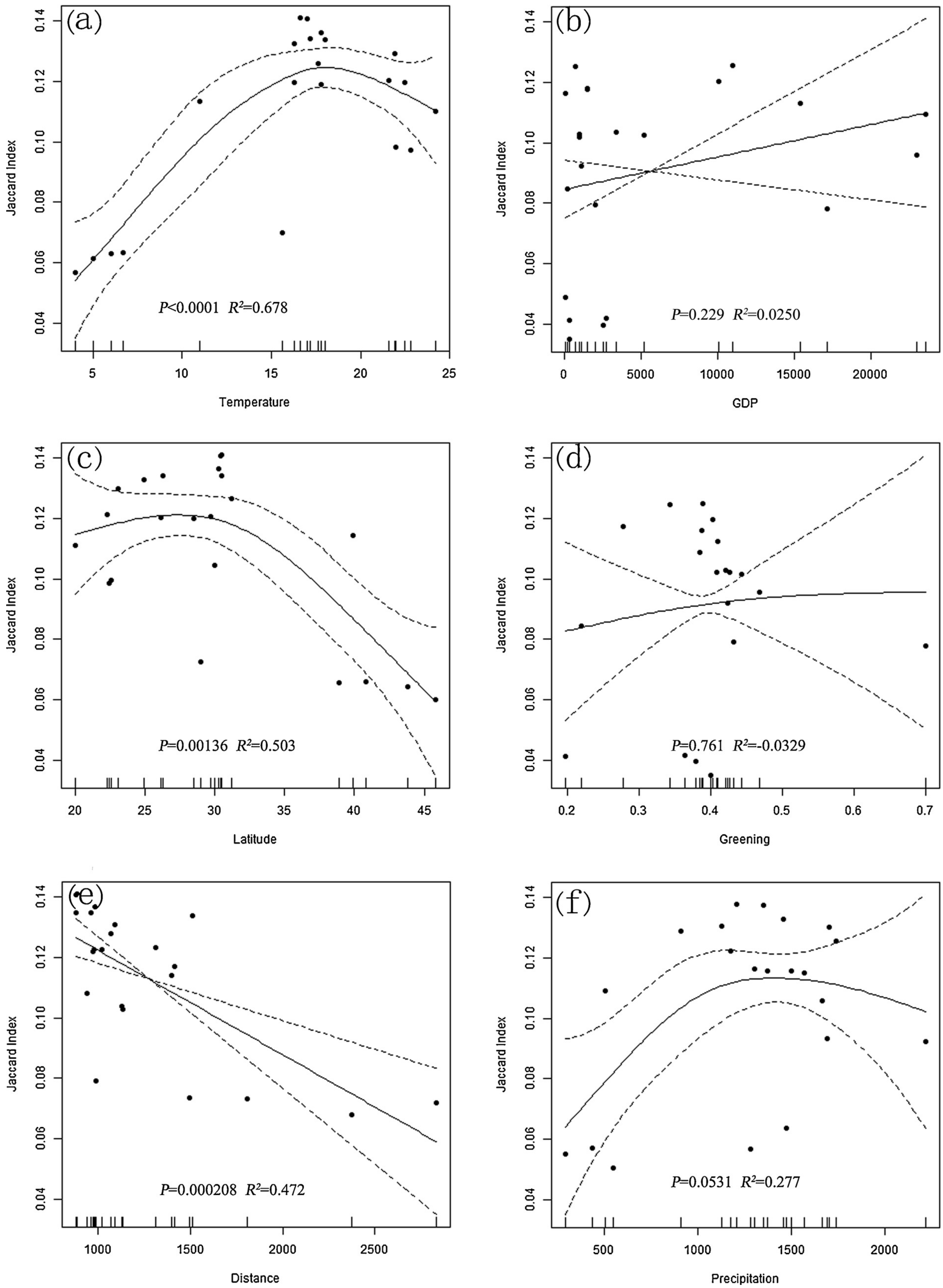

Fig. 3. Jaccard similarity index values expressing similarity in the composition of: (a) Mean Annual Temperature (MAT), (b) Gross Domestic Product (GDP), (c) Latitude, (d) Urban Greening Percentage (UGP), (e) Distance and (f) Mean Annual Precipitation (MAP). Lines suggest significant trends fit by the generalized additive models.

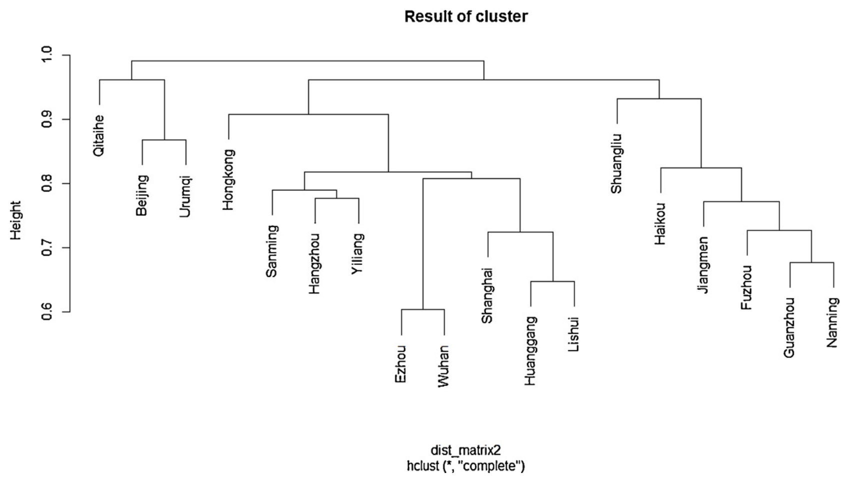

Fig. 4. Cluster analysis of the 18 urban flora in China based on the 18 cities' absent and present matrix of all plant species.

Shuangliu, Haikou, Jiangmen, Fuzhou, Guangzhou and Nanning, six southern to central cities. The third group includes Hong Kong on one branch and the remaining 8 cities – central and eastern cities – on a sister branch, (Fig. 4).

4. Discussion

4.1. Patterns of urban plant taxonomic richness and phylogenetic diversity

The most species-rich family for native-spontaneous species is Rosaceae, also appearing as the most species-rich family in five cities (Sanming, Yiliang, Urumqi, Shanghai, and Wuhan). Rosaceae comprises native plants from tropical to temperate China and are widely used horticulturally in China's cities. The most species-rich families for exotic-spontaneous species are Asteraceae and Poaceae, which appeared in all cities except for Fuzhou and Jiangmen (Table 3). There are many medicinal, ornamental, and economic plants in Asteraceae. While members of Asteraceae are insect-pollinated, most Poaceae are wind-pollinated and propagate rapidly, with sexual reproduction occurring in less than a year (Jiang et al., 2011). The most species-rich family for native-cultivated species is also Rosaceae (Table 3). Rosaceae are commonly cultivated for urban parks, roads, and squares as ornamentals, ground cover, hedgerows or protective materials. However, in Haikou, Yiliang, Fuzhou, and Nanning (all southern cities), the most species-rich exotic-spontaneous family is Arecaceae, which is a plant family widely distributed in tropical and subtropical areas (Table 2). As reported by Qian et al. (2016) real estate developers and urban planners in cities tend to favor greening plants that have ornamental traits. Furthermore, these southern cities, found relatively close to each other, share a similar climate (subtropical or tropical monsoon climate) (Fig. 1), and have high intercity commercial activity (Qian et al., 2016), possibly indicating higher intercity homogenization than in the other studied cities.

Among the cities we analyzed, Hong Kong had the highest PD value as well as the greatest native and exotic-spontaneous species richness. We calculated NTI or NRI to judge if the phylogenetic pattern was random or not. In this study, we found that Yiliang had the lowest NRI value for native-cultivated plant species, meaning species were less related than they would be by chance alone, and also a low NRI value for exotic-cultivated species (even though non-significant). Yiliang is a flower-trading city that is very active in the horticultural industry and can easily harbor many plant families and species. Urumqi had consistently clustered plant communities for all plant groups, which is likely due to the harsh climate and growing conditions found there. The overdispersion of exotic-cultivated plants in Fuzhou, Hangzhou, and Shuangliu (within Chengdu) might indicate these cities have a higher GDP.

4.2. Driving forces of urban plant taxonomic richness and phylogenetic diversity

We found that diversity in the "spontaneous" categories was mostly related to climate factors. MAT had a positive effect, so cities with warmer mean temperatures had higher family richness and overdispersion. Temperature is important in limiting the dispersal of species from humid and warm regions to drier and colder areas (Lu et al., 2018). While the spontaneous groups were mostly unrelated with socioeconomic factors, the cultivated groups were related to socioeconomic factors only (Appendix 3), in agreement with our expectations. However, very few diversity measures of any group were found to be statistically related to the predictors we used here. It is plausible that these relationships do not exist; however, we think it is more likely that our sample size was too small to provide robust results, even with bootstrapping. Although we do not report the results here for variables that were selected in less than 60% of bootstrapped datasets (see Methods for a description of the statistical approach), it was clear that those variables have consistent effects in the models where they were selected. That suggests that a larger sample of cities might confirm the general difference in drivers of urban spontaneous and cultivated plant diversity.

We also observed that species composition was related only to climate drivers and not to socioeconomic drivers in our data (Fig. 2). This result could either be an artifact of the differences in richness between the northern cool and dry cities versus the southern warm and wet cities, or it could indicate species-level differences in climate tolerance that cause further differences in species composition, regardless of whether the species are spontaneous or cultivated. This observation warrants further investigation. As reported by Lososová (2012), climatic controls on plant species assemblages lead to significant spatial patterning and the large-scale distribution of urban plant species.

The cluster analyses indicated that the floras generally follow the distribution pattern of the climatic zones: the three northern cities' flora cluster together, and belong to the warm temperate climate zone. Five southern cities' flora cluster together; these cities fall into the tropical or subtropical climate zone, some of them being geographically located next to each other (Haikou, Guangzhou, and Nanning). Wuhan and E'zhou, two closely located cities of central China, occur as sister branches in the phylogeny. However some cities do not follow the geographic pattern: Shuangliu is a central city, but clusters with southern cities, and Hong Kong is on its own branch in the phylogeny, neighboring a cluster of central Chinese cities. The distribution patterns could not be attributed to climate alone, but also very likely to anthropological factors (e.g., urban greening percentage) or perhaps the varied sampling methods themselves.

4.3. Biotic homogenization

The selection of urban greening species in China depends on the national greening policy as well as on special requirements for major events (e.g., Beijing Olympics). As the policy is not necessarily borne out of local needs and urban citizens' requests, biotic homogenization for China's cities occurs (Qian et al., 2016). In another words, the selection of suitable greening species and urban planning is decided by urban greening bureau, rather than choosing from the existing local options (Miller, 1997; Jim, 1999; Niemelä, 1999; Nagendra and Gopal, 2010; Qian et al., 2016). Therefore, in order to avoid urban biotic homogenization, more flexible urban greening policies suitable to local climate and socioeconomic variables should be used.

Most studies indicate that urbanization reduces the phylogenetic diversity of urban plants. By calculating the overall phylogenetic characteristics of German flora, Knapp et al. (2008) found that cities are a hot spot of plant species richness, and may have more species than the surrounding rural environment. However, the phylogenetic diversity of urban areas does not reflect this high species richness, because the richness likely results from the presence of closely related species having similar functions, and that have adapted to the special urban habitat. This reduction in phylogenetic divrsity may reduce the ability of plants to respond to changes in the environment. Čeplová et al (2015) studied spontaneous urban plant communities of 32 cities in Central Europe, finding that the phylogenetic diversity of all urban plant communities was lower than that of the null models. The introduction of alien species, number of archaeophytes, and degree of disturbance reduced the phylogenetic diversity of urban plant communities in their study. Disturbance in urban habitats may be a strong environmental filter, limiting the number of lineages that can survive in the urban habitat.

4.4. Data completeness

Hong Kong has the highest PD, NRI, and NTI than any of the other cities examined. However, the very comprehensive and complete flora list of Hong Kong (i.e.,HKH and SCBGCAS (2011)) relative to that for other cities in our list (where data completeness is less certain) may have played an important role in generating that result. After plotting the data on the phylogeny, we found that some of the subtropical cities have huge differences in native-cultivated plants. A coarse flora list will exclude many clades or branches in the city-wide phylogenetic tree, which will result in lower PD, NRI or NTI. Therefore, it is urgent to generate comprehensive and complete urban flora lists for future urban plant diversity estimation and planning.

In this study, the diversity of tropical Haikou was unexpectedly lower than that of subtropical Hong Kong (Table 2). The species richness of the "native-spontaneous" groups in Fuzhou (26 N), Haikou (20 N), Jiangmen (22 N) are 63, 80, and 63 respectively. Again, though, we used the Flora of Hong Kong as the data source of Hong Kong, while we only used 191 sampling sites to obtain the number of plant species in tropical Haikou due to limited time and energy in the field investigation. As such, plant diversity is likely underestimated in tropical Haikou.

4.5. Final comments

Overall, we found that mean annual temperature (MAT) drives urban spontaneous diversity, with greater family richness and overdispersion in warmer cities. NTI of native cultivated species negative effected by UGP (Table 5). The approach adopted in this study could be used to prescriptively design appropriate urban plant community assemblages as part of green infrastructure practices. Developing phylogenies of existing urban plants could even be used to assess the suitability of proposed urban spontaneous plant species as part of landscape designs. Future comparative research using our approach with other disparate cities and the use of standardized field data protocols could also be adapted to shed light on questions of plant homogenization, invasiveness and phylogenetic adaptations to urban environments.

The top priority is to select appropriate plant species when considering the urban planning, rather than to maximize the commercial benefits and human demands (Miller, 1997; Jim, 1999; Niemelä, 1999; Nagendra and Gopal, 2010). Also, to ensure both that plant communities are well suited to the specific local conditions in which they are developed and that planners should explore ways of increasing the proportion of native species (Da and Song, 2008; Nagendra and Gopal, 2010; Bürgi, 2015; Guo et al., 2015). Unfortunately, only a few cities in China have recognized this need; however, one exception is found in Shanghai, where there are plans to construct 'near-natural' species spaces (e.g., Da and Song, 2008; Da et al., 2009; Guo et al., 2015). This failure to encourage native plant species has eventually led to the current situation within the 18 Chinese cities studied here, where the artificial landscaping has diverged greatly from the remnant natural communities. Future urban planning strategies need to be carefully designed to emphasize native species and their importance in order to avoid the recent tendency toward uniformity in urban greening practice.

By providing some initial observations on plant diversity, this study can enable countries and regions to formulate urban planning strategies. Our investigation here lays the groundwork for future work that may fortify and extend our understanding of urban landscapes. Financial and biogeographic elements are largely perceived as great indicators of plant invasions on the planet (Taylor and Irwin, 2004; Stohlgren et al., 2005), but the characteristics of species that enhance "invasiveness" have also been emphasized in many studies (Gosper and Vivian-Smith, 2009). Similarly, our results lead us to suggest that the relative significance of financial and biogeographic factors may rely upon the species themselves. On a wide scale, the mechanisms by which urban species may spread have not been fully examined, especially with respect to the exotic plant trade or other human-driven activities. We had more than 30 cities in the beginning of our study, but because some of the cities' floras had been constructed via biased sampling or had incomplete plant species lists, we could only keep the final18. Therefore, we call for unbiased and comprehensive sampling to be conducted in more cities. Such fulsome studies will generate more complete plant species lists, which in turn will be more useful and precise for local and national urban greening planning in the future. Furthermore, studies have often concluded that regions sustaining native plants are similarly favored by exotics (Stohlgren et al., 2005; Fridley et al., 2007). Be that as it may, exotic-invasive species are often quite phylogenetically distinct from native plants, and have different biological characteristics (Long et al., 2009; Ricotta et al., 2009). Further examination of less well-studied or obvious factors leading to "plant trespassers", such as we attempted in this study, can aid in our understanding of exotic as well as natural intrusions. Continued studies of phylogenetic relationships among species in urban native and exotic flora will elaborate the evolutionary history, from which better management strategies for urban native species and recent "intruders" can be derived.

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Table 5
Minimum significant models predicting diversity indices for the different plant categories. Minimum models selected using stepwise selection based on AIC. Minimum models were selected using stepwise selection of the full model for 4000 bootstrapped samples of the data. All response variables except NRI were $\log_e(x + c)$ transformed to normalize data and avoid NANs. R^2 values taken from the maximal model with original data.

	R^2	GDP*			UGP			MAT		
Native spontaneous		%	pct +	pct-	%	pct +	pct-	%	pct +	pct-
Species	0.12	–			–			–		
Genera	0.11	–			–			–		
Families	0.16	–			–			–		
PD	0.29	80.4	98.9	1.09	–			–		
NRI	0.43	–			–			88.9	1.4	98.6
NTI	0.29	–			–			72.8	2.1	97.9
Native cultivated										
Species	0.06	–			–			–		
Genera	0.07	–			–			–		
Families	0.09	–			–			–		
PD	0.07	–			–			–		
NRI	0.15	–			–			–		
NTI	0.25	–			66.6	0.3	99.7	–		
Exotic spontaneous										
Species	0.24	–			–			–		
Genera	0.29	–			–			–		
Families	0.32	–			–			61.9	96.4	3.6
PD	0.30	–			–			–		
NRI	0.14	–			–			61.6	0.5	99.5
NTI	0.07	–			–			–		
Exotic cultivated										
Species	0.26	–			–			–		
Genera	0.26	–			–			–		
Families	0.30	–			–			–		
PD	0.26	–			–			–		
sNRI	0.11	–			–			–		
NTI	0.10	–			–			–		
All										
Species	0.14	–			–			–		
Genera	0.17	–			–			–		
Families	0.25	–			–			61.4	94.8	5.2
PD	0.16	–			–			–		
NRI	0.13	–			–			–		
NTI	0.14	–			–			–		

* GDP are $\log_e$-transformed.

this great Canadian biologist for her patience and help in the past ten years.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ufug.2019.02.004.

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