Urban Ecosystems (2026) 29:142
https://doi.org/10.1007/s11252-026-02000-9

RESEARCH

Species–park networks reflect the spatial structure of urban green infrastructure

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Received: 28 November 2025 / Accepted: 27 April 2026

Abstract

As cities expand, natural and semi-natural habitats are increasingly restricted in extent and connectivity, posing major challenges for biodiversity conservation. Urban parks, as nodes of green infrastructure, improve ecological connectivity in the urban landscape, yet their functional role in supporting urban plant communities remains challenging to quantify. This study aimed to investigate whether differences in the functional role of urban parks are reflected by their spatial location within the green infrastructure. We applied a bipartite species-park network approach to assess the role of urban parks in supporting plant species in three historic cities in north-eastern Italy. In 2024, we surveyed 57 parks, recorded vascular plant species in nested plots and measured park attributes including area, distance to the city centre, distance to other parks and tree canopy cover. Species–park networks were used to quantify the functional role of each park through park specialisation, importance, compositional representativeness, and colonisation potential. Statistical models showed that parks further from the city centre supported richer plant communities and hosted species more dependent on individual parks, while parks at intermediate distances from the centre acted as compositional links between parks closer and further from the city centre. Parks with greater tree canopy cover tended to host species that achieved comparatively higher local cover but showed reduced compositional representativeness to other parks. Our results revealed that the functional role of parks in supporting plant communities was strongly associated with their spatial location within the green infrastructure, providing insights for urban biodiversity conservation and landscape planning.

Keywords Bipartite network · Green infrastructure · Habitat connectivity · Urban biodiversity · Urban park

Introduction

Urban expansion is increasingly replacing natural and semi-natural habitats with buildings and impervious surfaces, reducing habitat availability and ecological connectivity (Della Bella et al. 2021; Li et al. 2022). According to McDonald et al. (2018), urban expansion between 1992 and 2000 led to the loss of approximately 190,000 km² of habitats. In addition, global assessments indicate that urbanisation has reduced local species richness by nearly 50% and species abundance by 38% in intensively developed urban areas compared to pristine baseline environments (Newbold et al. 2015). Urban areas are projected to continue to expand, with global urban expansion expected to be 1.8–5.9 times greater in 2100 than in 2000 (Chen et al. 2020). Such trends emphasise the urgent need for biodiversity conservation strategies that improve the ecological permeability of the urban matrix and maintain connectivity between remnant habitat fragments (Hostetler et al. 2011).

Urban green spaces are essential elements to mitigate the loss of biodiversity in the urban landscape (Castelli et al. 2021), and their attributes (in terms of e.g., composition and spatial configuration) have a strong influence on the ecological permeability of the urban matrix (Paudel and States

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Published online: 08 May 2026

2023). The movement of organisms through the urban matrix underpins the ecological functions that sustain populations and communities, which in turn support the provision of ecosystem services to urban dwellers (Stanworth et al. 2024). The urban landscape itself represents the spatial context in which the demand for ecosystem services reaches its highest intensity, due to the high population density and concentration of socio-economic activities. Consequently, ensuring the supply of ecosystem services is not only ecologically desirable, but also socially imperative.

The dependence of ecosystem services on the maintenance of dispersal processes in the urban matrix (e.g., Mendes et al. 2025) has led to planning approaches that prioritise urban green space connectivity. In the urban landscape, these efforts have evolved into the framework of green infrastructure (Li et al. 2017). Green infrastructure can be defined as a strategically planned network of green spaces designed and managed to provide a wide range of ecosystem services, while promoting biodiversity conservation (EC 2013). Green infrastructure consists of nodes that provide core habitats where species can survive, and corridors or stepping stones that facilitate movement between them. The green infrastructure framework emphasises that the value of individual green spaces depends not only on their intrinsic attributes (e.g., composition), but also on the extent to which they are integrated into and connected to the wider green infrastructure network. In this view, the ecological and functional contribution of a single green element is amplified or constrained by its location, connectivity, and interaction with surrounding green spaces, underscoring that it is the network as a whole, rather than isolated components, that ultimately shapes its overall value.

Within the urban landscape, the nodes of the green infrastructure are mostly urban parks, which are often the largest and most structurally complex green spaces (Nielsen et al. 2014; Huang et al. 2021). Empirical studies have shown that urban parks may have relatively high levels of biodiversity, including threatened species, emphasising their role as refugia in the urban landscape (Rummo et al. 2025). The recognised importance of urban parks for biodiversity has led to extensive research into the attributes that determine their conservation value. Empirical evidence suggests that both park-level attributes (e.g., size, age, isolation, distance to the city centre, structural heterogeneity, management regime) and urban matrix attributes interact to determine biodiversity patterns (Chang et al. 2021; Ren et al. 2022; Liu et al. 2023, 2025; Lorenzato et al. 2024). Nevertheless, a major limitation of previous work on urban park contribution to supporting biodiversity is the tendency to evaluate parks as separate entities rather than components of a network (but see Torabi et al. 2020). Comparative studies (e.g., La Sorte et al. 2023) represent steps towards a systemic perspective but are often limited to comparing species richness without capturing the interdependencies between urban parks within an integrated network. Network analysis can fill this gap by mapping the relationships between urban parks and species, with parks linked by species to form a functional ecological network. The approach of linking spatially distinct landscape elements through the species they host was first proposed by Marini et al. (2019) as the species-habitat network approach, in which habitat can refer to any spatially distinct landscape element. It was conceived to assess the relative importance of species and habitat types within a landscape and to quantify emergent properties of habitat networks. Since then, the species-habitat network approach has been applied to issues related to biodiversity conservation, including the assessment of colonisation potential, the effects of habitat fragmentation, and habitat responses to alien plant invasion in various non-urban landscapes (Lami et al. 2021; Palmeirim et al. 2022; Fantinato et al. 2023). However, although the species–habitat network approach has the potential to enhance understanding of how landscapes function as networks of interconnected elements, its application to the analysis and planning of urban green infrastructure remains largely unexplored.

Building on these insights, the present study aimed to assess the functional role of urban parks in supporting urban plant communities as part of a functional ecological network and to assess whether differences in their functional role are reflected by an explicit spatial location within the green infrastructure. Spontaneous plants were selected as the taxonomic focus because they reflect local ecological assembly processes rather than intentional planting decisions, while providing the primary resource base for animal communities (Del Tredici 2010; Li et al. 2023). The analyses were carried out in three cities in north-eastern Italy that are comparable in terms of cultural, socio-economic and landscape context, and population density: Treviso, Venice (mainland) and Vicenza. To achieve these objectives, we determined both the species richness and the functional role of each park in supporting urban plant communities using a bipartite species-park network in which the parks are indirectly linked by the species they harbour. In addition, we investigated how spatial and structural attributes of parks such as size, connectivity, distance to the city centre and tree canopy cover influence both species richness and the functional role of each urban park.

Materials and methods

Study site and data collection

The study investigated urban parks in three historic cities in north-eastern Italy: Treviso (45°40’03.0"N 12°14’42.8"E), the part of Venice on the mainland commonly referred to as Mestre (45°29’23.3"N 12°14’18.0"E; hereafter Venice), and Vicenza (45°32’52.2"N 11°32’43.4"E). The cities are located in the eastern Po Valley in the alluvial plains of the rivers Brenta and Piave and are relatively near each other: The distance between Vicenza and Treviso and between Vicenza and Venice is approximately 55 km, while Treviso and Venice are 19 km apart. The three cities show a dense, compact urban centre that gradually transitions into a spatially diffuse periphery, with an average population density of 1,424 ± 97 inhabitants per km^2. Their green infrastructure mostly consists of public parks and historic gardens, which represent the ecological nodes of the network. While a few historic parks are of Renaissance origin, most of them were established more recently, with an age gradient from the city centre towards the periphery: the further from the city centre, the more recent the establishment of the parks, generally dating from the 1970 s in the city centres to the early 2000 s in the periphery. Regardless of the city, management of the urban parks involves regular mowing (once a month on average), with more frequent management in spring and summer and slower management in autumn and winter. Although few in number, the corridors consist mainly of tree-lined streets, while the stepping stones include smaller planted elements such as flowerbeds, individual trees, balconies, and courtyards.

In this study, we selected freely accessible urban parks with a minimum area of 1,000 m^2. This threshold was chosen to distinguish urban parks from smaller green spaces, such as flowerbeds (Iraegui et al. 2020). To ensure that only parks embedded within the dense urban matrix were included, we restricted the selection to parks located within a 4 km radius of the city hall in each city. The 4 km radius was adopted as an empirical criterion to address the difficulty of identifying urban boundaries in landscapes characterised by pronounced urban sprawl, where the transition between the dense, compact urban centre and the spatially diffuse periphery is not distinct. In addition, as urban sprawl may occur at relatively short distances from the city hall due to irregular urban expansion patterns, park inclusion was further based on the surrounding spatial context, retaining only sites embedded within the dense, compact urban matrix and excluding parks located in the spatially disperse urban matrix. All parks meeting these criteria were included in the study, resulting in a total of 57 urban parks surveyed, 14 in Treviso, 22 in Venice and 21 in Vicenza. In each urban park, we collected vegetation plots at the park centroid. If the centroid was occupied by a facility, the plot was established at the nearest point with vegetation. In spring and summer 2024 (from April to June), we established two nested vegetation plots per park: a smaller plot measuring 3.16 × 3.16 m (hereafter, small plots) was centrally nested within a larger 10 × 10 m plot (hereafter, large plots). The smaller plot was used to characterise species composition based on plot dimensions typically used to sample herbaceous and synanthropic plant communities (Chytrý and Otýpková 2003), while the larger plot provided a broader representation of species occurrence within each park, allowing to limit the over-representation of local microhabitats and reduce the underestimation of rare or patchily distributed species. Within each plot, we identified all vascular plants in the herbaceous layer and estimated their relative abundance by recording their percentage cover. Shrub and tree species were not recorded, as they are usually planted intentionally and therefore do not reflect the contribution of urban parks to spontaneous plant communities.

Furthermore, for each urban park, we recorded spatial attributes known to influence plant species richness and composition in the urban landscape (Li et al. 2024). Using high-resolution orthophotos (0.2 m; Regione del Veneto 2018), we measured the park area, the mean inter-park distance among centroids, and the distance to the city centre, defined as the location of the city hall. Mean inter-park distance was calculated using only parks within the 4 km radius of the city hall in each city. To assess potential redundancy with distance to the city centre, we quantified their correlation, which was weak (Pearson’s $r = -0.35$; see Data Analysis for collinearity assessment). To capture the structural heterogeneity of the vegetation, we estimated the percentage of the park area covered by tree canopy. All spatial analyses were performed in QGIS 3.22.13 (QGIS Development Team 2022).

Data analysis

For each city, we created two plant species × urban park matrices: one based on data collected from the small plots and one based on data from the large plots. In both matrices, the entries corresponded to the percentage cover of each plant species in each park. The plant species × urban park matrices were then used to create bipartite species-park networks (Memmott 1999). As a result, six species–park networks were constructed, comprising two networks (small-plot and large-plot based) for each of the three cities. Networks were created separately for each city and plot size to avoid artificially linking parks that are not part of the same green infrastructure and to prevent mixing species covers from different plot sizes. Traditionally, bipartite networks have been applied to interactions between two trophic levels, such as interactions between plants and pollinators or plants and herbivores (e.g., Fantinato et al. 2021; Swain et al. 2022). The framework has been extended to species-habitat networks, where the nodes correspond to species and habitats and the links represent the occurrence or abundance of species within habitats (Marini et al. 2019). In this study, habitats correspond to individual urban parks; therefore, we constructed bipartite species–park networks in which nodes represent plant species and parks, and links indicate species percentage cover in each park. By creating bipartite species-park networks, we aimed at capturing the functional role of urban parks as interconnected nodes in supporting urban plant communities.

For each species-park network, we calculated four park-level metrics to characterise the functional role of each urban park in supporting urban plant communities. Specifically, we quantified urban park specialisation using the normalised Kullback–Leibler distance (d′; Blüthgen et al. 2006) with the 'dfun' function of the bipartite package (Dormann et al. 2008); urban park importance using node strength S (Bascompte et al. 2006) with the 'strength' function of the bipartite package (type = "Bascompte"); compositional representativeness using weighted closeness centrality (wCC; Ballantyne et al. 2017) with the 'closeness_w' function of the bipartite package; and colonisation potential using potential for apparent competition (PAC; Holt 1977; Müller et al. 1999) with the 'PAC' function of the bipartite package. All metrics were derived from quantitative species cover matrices, and only values corresponding to park nodes were retained for subsequent analyses. For clarity, d′, S, wCC, and PAC are hereafter referred to as urban park specialisation, urban park importance, compositional representativeness, and colonisation potential, respectively. The ecological interpretation of each metric and the meaning of low and high values are summarised in Table 1.

To assess the influence of urban park attributes (i.e., park area, mean inter-park distance, distance to the city centre, and tree canopy cover) on plant species richness and network metrics (i.e., urban park specialisation, importance, compositional representativeness, and colonisation potential) quantified on small and large plots, we fitted Generalised Linear Mixed Models (GLMMs) and Linear Mixed Models (LMMs) using the lme4 package (Bates et al. 2015). Models were fitted separately for small-plot and large-plot datasets, each combining parks from the three cities. The unit of analysis was the park; therefore, network metrics were treated as park-level variables. Prior to analysis, we assessed multicollinearity between fixed effects using the Variation Inflation Factor (VIF; Zuur et al. 2009). All VIF values were <3, indicating negligible collinearity, so all fixed effects were retained. To facilitate comparison between variables and improve model convergence, all park attributes were standardised to z-scores (mean = 0,

Table 1 Interpretation of network metrics used to characterise urban parks

Metric	Symbol	Ecological interpretation	Explanation of low values	Explanation of high values	References
Urban park specialisation	d′	How unique a park's species composition and/or percentage covers is compared to other parks in the city	Park hosts species and percentage covers similar to those found in many other parks	Park hosts species and/or percentage covers that are uneven across the city park network	Blüthgen et al. 2006
Urban park importance	S	How important a park is for the persistence of species across the city	The park hosts several species occurring in many other parks with similar percentage coverage	The park disproportionately supports one or more species, as most of their total cover across the city is concentrated there	Bascompte et al. 2006
Compositional representativeness	wCC	How representative a park is of the overall species composition of the urban park network	Park occupies a peripheral position in the compositional space of the urban park network	Park occupies a central position in the compositional space of the urban park network	Ballantyne et al. 2017
Colonisation potential	PAC	Potential for species exchange between parks, reflecting source–recipient dynamics within the network	Park has low potential to act as a source or recipient of species relative to other parks	Park has high potential to act as a source or recipient of species relative to other parks	Holt 1977; Müller et al. 1999; Lami et al. 2021

SD = 1). For plant species richness, we used GLMMs. On small plots, counts were underdispersed (assessed using the 'dispersiontest' function; package AER; Kleiber and Zeileis 2008), so a Poisson error distribution with a log-link function was used. On large plots, richness was overdispersed, so models were fitted with a negative binomial distribution. Urban park attributes were entered as fixed effects, species richness as the response variable, and city identity as a random factor. For the relationship between park attributes and network metrics, we fitted LMMs with park attributes as fixed effects, each network metrics (log10-transformed to improve normality and homoscedasticity) as a response variable, and city identity as a random factor. Moreover, we included the quadratic term of the urban park attributes in both GLMMs and LMMs to account for possible nonlinear relationships (without removing the linear term). Interactions among fixed effects were not considered in order to maintain model interpretability, given the relatively small sample size and the complexity of the network metrics. In addition, neither park age nor management frequency was included, as age consistently varied with distance to the city centre and management frequency showed little variation among urban parks. Models were simplified by backward elimination of non-significant fixed effects, and the significance of the fixed effects was tested using likelihood ratio tests (LRTs). For all models, we calculated the conditional and marginal coefficients of determination (R^2c and R^2m, respectively) using the 'r.squared' function of the MuMIn package (Barton 2015). R^2c represents the variance jointly explained by fixed and random factors, while R^2m captures the variance explained by fixed factors alone. All statistical analyses were performed in R version 4.4.0 (R Core Team 2024).

Results

Sampled urban parks varied in size, spatial configuration and structural heterogeneity of vegetation (i.e., percentage of the urban park area covered by tree canopy). Across all 57 parks, the mean park area was 15,850 ± 22,465 m^2 (mean ± SD). At city level, the mean park area was 10,378 ± 6,702 m^2 in Treviso, 10,452 ± 9,726 m^2 in Venice, and 25,153 ± 33,775 m^2 in Vicenza. The mean inter-park distance was 1,509 ± 248 m in Treviso, 1,836 ± 273 m in Venice, and 1,353 ± 363 m in Vicenza, with an overall mean park distance of 1,578 ± 369 m. The mean distances from the city centre were 1,567 ± 545 m in Treviso, 2,281 ± 1,077 m in Venice, and 2,168 ± 1,003 m in Vicenza, with an overall mean distance to the city centre of 2,064 ± 974 m. Tree canopy cover ranged from 43.9 ± 28.1% in Treviso to 62.4 ± 28.1% in Venice and 51.7 ± 29.3% in Vicenza, with an overall mean tree canopy cover of 53.9 ± 29.0%.

Overall, we recorded 92 plant species in the small plots and 126 species in the large plots. Mean species richness across all parks was 12.4 ± 3.7 in the small plots and 17.0 ± 5.6 in the large plots. In the small plots, seven species occurred in more than half of the plots, most of which were a subset of the most common species in the larger plots (*Cynodon dactylon* (L.) Pers., *Taraxacum officinale* F.H.Wigg., *Plantago lanceolata* L., *Potentilla reptans* L., *Trifolium repens* L., *Bellis perennis* L., *Trifolium pratense* L.). In the large plots, eleven species occurred in more than half of the plots, including *C. dactylon*, *T. officinale*, *P. lanceolata*, *P. reptans*, *T. repens*, *B. perennis*, *Plantago major* L., *Prunella vulgaris* L., *Trifolium pratense* L., *Lolium perenne* L., and *Centaurea nigrescens* Willd. On small plots, the mean species richness varied between cities and was the highest in Treviso (13.6 ± 4.0), intermediate in Venice (12.3 ± 3.9), and the lowest in Vicenza (11.7 ± 3.3). On large plots, richness followed a similar pattern (Treviso: 20.2 ± 5.4; Venice: 16.4 ± 6.3; Vicenza: 15.6 ± 4.3; Table 2). Overall, a small group of widespread species dominated across the urban parks, while most species were subordinate, highlighting the diversity in plant composition of the sampled parks.

When the small plots were assessed, the urban parks generally showed moderate specialisation, suggesting that a few species achieved higher cover in specific parks compared to others, while most species displayed broadly comparable cover values across the parks (Table 2). Urban park importance was relatively high, reflecting the presence of species whose total cover within the network was associated with specific parks (Table 2). Compositional representativeness and colonisation potential were both low, suggesting

Table 2 Park-level network metrics for urban green spaces in Treviso, Venice, and Vicenza calculated on small and large plots. The values are presented as mean ± SD

City	Plot size	d′ (± SD)	S (± SD)	wCC (± SD)	PAC (± SD)
Treviso	3.16 × 3.16 m	0.38 ± 0.08	3.50 ± 2.58	(5.95 ± 1.53) × 10^{-3}	0.07 ± 0.01
Venice	3.16 × 3.16 m	0.45 ± 0.13	3.00 ± 2.10	(2.07 ± 0.52) × 10^{-3}	0.05 ± 0.01
Vicenza	3.16 × 3.16 m	0.39 ± 0.13	2.24 ± 1.48	(2.16 ± 0.65) × 10^{-3}	0.05 ± 0.01
Overall	3.16 × 3.16 m	0.41 ± 0.12	2.84 ± 2.06	(3.06 ± 1.89) × 10^{-3}	0.05 ± 0.02
Treviso	10 × 10 m	0.30 ± 0.08	4.64 ± 2.83	(5.66 ± 1.36) × 10^{-3}	0.07 ± 0.02
Venice	10 × 10 m	0.44 ± 0.15	4.00 ± 2.86	(1.89 ± 0.59) × 10^{-3}	0.05 ± 0.01
Vicenza	10 × 10 m	0.36 ± 0.12	3.24 ± 2.67	(1.99 ± 0.50) × 10^{-3}	0.05 ± 0.01
Overall	10 × 10 m	0.38 ± 0.14	3.88 ± 2.79	(2.85 ± 1.80) × 10^{-3}	0.05 ± 0.02

Table 3 Model results testing the effects of spatial and structural attributes of urban parks on plant species richness and network metrics in the small plots

Response variable	Fixed effect	Estimated coefficient	SE	χ2	p	R^2m	R^2c
Species richness	Distance to the city centre (z-score)	0.159	0.041	14.843	< 0.001	0.222	0.291
d' (log10-transformed)	Mean inter-park distance (z-score)^2	0.031	0.015	4.356	0.036	0.205	0.205
	Tree canopy cover (z-score)	0.031	0.015	4.167	0.041		
S (log10-transformed)	Distance to the city centre (z-score)	0.149	0.044	8.703	0.003	0.154	0.264
wCC (log10-transformed)	Mean inter-park distance (z-score)	−0.043	0.020	4.592	0.032	0.066	0.811
	Tree canopy cover (z-score)	−0.052	0.016	9.309	0.002		
PAC (log10-transformed)	Distance to the city centre (z-score)^2	−0.036	0.016	5.541	0.018	0.104	0.495
	Tree canopy cover (z-score)	−0.031	0.013	5.699	0.016		

limited compositional links and a weak species exchange of urban parks within the network (Table 2). Comparisons at the city level revealed different within-city patterns (Table 2). In Venice, urban parks exhibited the highest levels of specialisation, indicating that several species reached high cover in specific parks while occurring at much lower cover, or were absent, in others. In Treviso, urban parks had the highest values for park importance, compositional representativeness, and colonisation potential, suggesting that parks tended to hold a large share of some species' total cover, shared their species composition more extensively, and consequently being potentially entailed in species exchange. In Vicenza, the network metrics consistently showed intermediate values, indicating moderate compositional differences and moderate levels of species exchange among parks.

When the large plots were assessed, urban park specialisation decreased, indicating that differences in the relative cover of species among urban parks became less pronounced (Table 2). Urban park importance increased, as more species had a substantial proportion of their total cover concentrated in specific parks (Table 2). In contrast, urban park compositional representativeness and colonisation potential remained relatively low, indicating limited species sharing among urban parks and limited directional influence on one another (Table 2). The city-level patterns were consistent with those observed for the small plots: Treviso showed the highest values of compositional representativeness and colonisation potential, Venice exhibited the highest levels of specialisation, and Vicenza occupied an intermediate position (Table 2). Overall, the network results showed that urban parks varied in their functional role in supporting urban plant communities within each green infrastructure.

In both the small and large plots, urban park attributes significantly influenced species richness of plants and network metrics. Species richness in both small and large plots increased with distance to the city centre, suggesting that parks far from the city centre harboured more plant species (Tables 3 and 4; Fig. 1). Urban park specialisation showed a U-shaped relationship with mean inter-park distance and was positively related to tree canopy cover in both the small and large plots (Tables 3 and 4; Figs. 2 and 3). Parks located either very close to or relatively far from other parks tended to host species that reached much higher cover locally than in the other parks. The positive association with canopy cover indicates that parks with higher cover of tree canopies are more likely to host species that show high cover while being subordinate or absent in the other parks. Urban park importance, which reflects species dependence on individual parks, also increased with distance to the city centre in both small and large plots, suggesting that urban parks further from the city centre host species that are more dependent on specific urban parks (Tables 3 and 4; Figs. 2 and 3). In the small plots, compositional representativeness decreased significantly with mean inter-park distance and tree canopy cover (Table 3; Fig. 2). In contrast, in the large plots, compositional representativeness showed a hump-shaped relationship with both mean inter-park distance and distance to the city centre, while it showed a negative relationship with

Table 4 Model results testing the effects of spatial and structural attributes of urban parks on plant species richness and network metrics in the large plots

Response variable	Fixed effect	Estimated coefficient	SE	χ2	p	R2m	R2c
Species richness	Distance to the city centre (z-score)	0.155	0.042	13.861	< 0.001	0.188	0.358
d' (log10-transformed)	Mean inter-park distance (z-score)^2	0.046	0.020	5.479	0.019	0.187	0.228
	Tree canopy cover (z-score)	0.043	0.019	5.525	0.018		
S (log10-transformed)	Distance to the city centre (z-score)	0.174	0.048	10.099	0.001	0.168	0.310
wCC (log10-transformed)	Mean inter-park distance (z-score)^2	−0.037	0.017	4.698	0.030	0.088	0.806
	Distance to the city centre (z-score)^2	−0.068	0.019	11.867	< 0.001		
	Tree canopy cover (z-score)	−0.035	0.016	4.887	0.027		
PAC (log10-transformed)	Distance to the city centre (z-score)^2	−0.047	0.014	10.347	0.001	0.151	0.454
	Tree canopy cover (z-score)	−0.032	0.012	6.994	0.008		

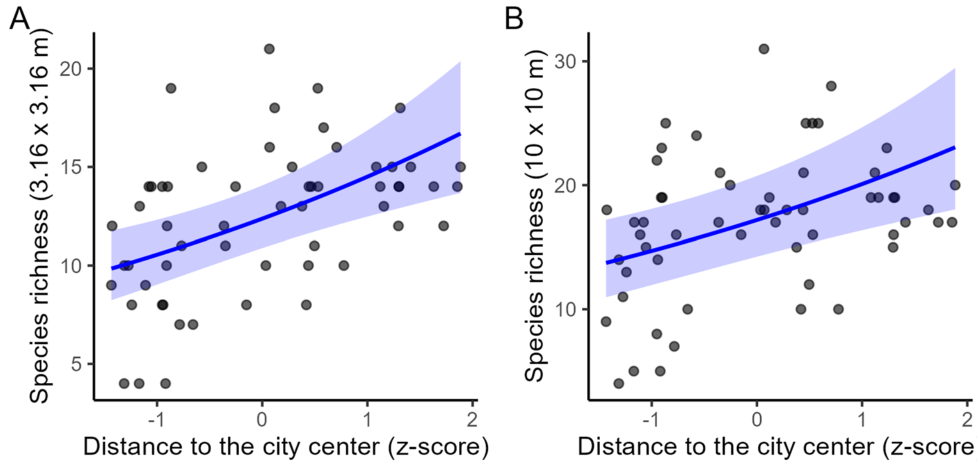

Fig. 1 Relationship between the species richness of plants and distance to the city centre (z-score) when considering small (i.e., 3.16 × 3.16 m) (A) and large (i.e., 10 × 10 m) plots (B). Grey circles represent individual data points, the blue line indicates the linear mixed model estimates, and the shaded blue area denotes the 95% confidence interval

tree canopy cover (Table 4; Fig. 3). Consistently for both plot size, colonisation potential, which captures the potential for species exchange among parks within the network, showed a hump-shaped relationship with distance to the city centre and a negative relationship with tree canopy cover. In other words, parks at intermediate distances to the city centre were more strongly connected (i.e., had greater potential for species exchange) than parks both close of further from the city centre, and increasing tree canopy cover was associated with reduced potential for species exchange (Tables 3 and 4; Figs. 2 and 3). No significant relationships were found between plant species richness and network metrics with urban park area in either the small or the large plots.

Overall, the network metrics showed that both spatial configuration and structural heterogeneity of vegetation influence the functional role of urban parks in supporting urban plant communities. Parks located further from the city centre harboured greater species richness, which was reflected in higher values for urban park importance. In contrast, mean inter-park distance and tree canopy cover influenced urban park specialisation and compositional representativeness. Patterns of colonisation potential also suggest that parks at intermediate distances from the city centre play a key role in species exchange within the network, thereby enhancing compositional connectivity across the urban landscape.

Discussion

When examining species richness at the level of individual parks, distance to the city centre proved to be the only significant predictor. Many studies have investigated how distance to the city centre affects species richness in the urban landscape (e.g., Matthies et al. 2015). Our results have shown that plant species richness is higher in parks further from the city centre, a pattern consistent with previous findings for both plants (Ranta and Viljanen 2011; Von Der Lippe and Kowarik 2008) and other taxonomic groups, including birds (MacGregor-Fors and Ortega-Álvarez 2011; Yang et al. 2020). Distance to the city centre is generally considered as an indicator of human pressure, with sites closer to the city centre being more exposed to anthropogenic disturbance (Chen et al. 2000; Wang et al. 2004). Consequently, parks further from the city centre are likely to be less exposed to disturbance, which may favour the maintenance of richer plant communities. In addition, the observed pattern may reflect an effect of park age, as parks located further from the city centre are generally more recently established and may therefore exhibit higher levels of extinction debt (Kuussaari et al. 2009).

Remarkably, network-based metrics revealed additional aspects of the functional role of urban parks within the green infrastructure that were not captured by addressing species richness of plants alone. Parks further from the city centre had higher importance values than those closer to the city centre, suggesting that plant species are disproportionately dependent on them, thus complementing the observed relationship between plant species richness and distance to the city centre. In addition, urban park specialisation, which reflects the extent to which species are concentrated in particular parks, either because they reach comparatively higher cover there or are absent from most other parks, was unrelated to distance from the city centre but was instead associated with mean inter-park distance. Specifically, we observed a U-shaped relationship, with urban parks in clusters or highly isolated showing the highest specialisation, while urban parks at intermediate distances showed lower specialisation. The high specialisation of clustered parks may occur because spatially close parks can support species that achieve high cover within the cluster while remaining absent or present at much lower cover in more distant parks. In these cases, species may become locally abundant only within the cluster, creating pronounced differences in

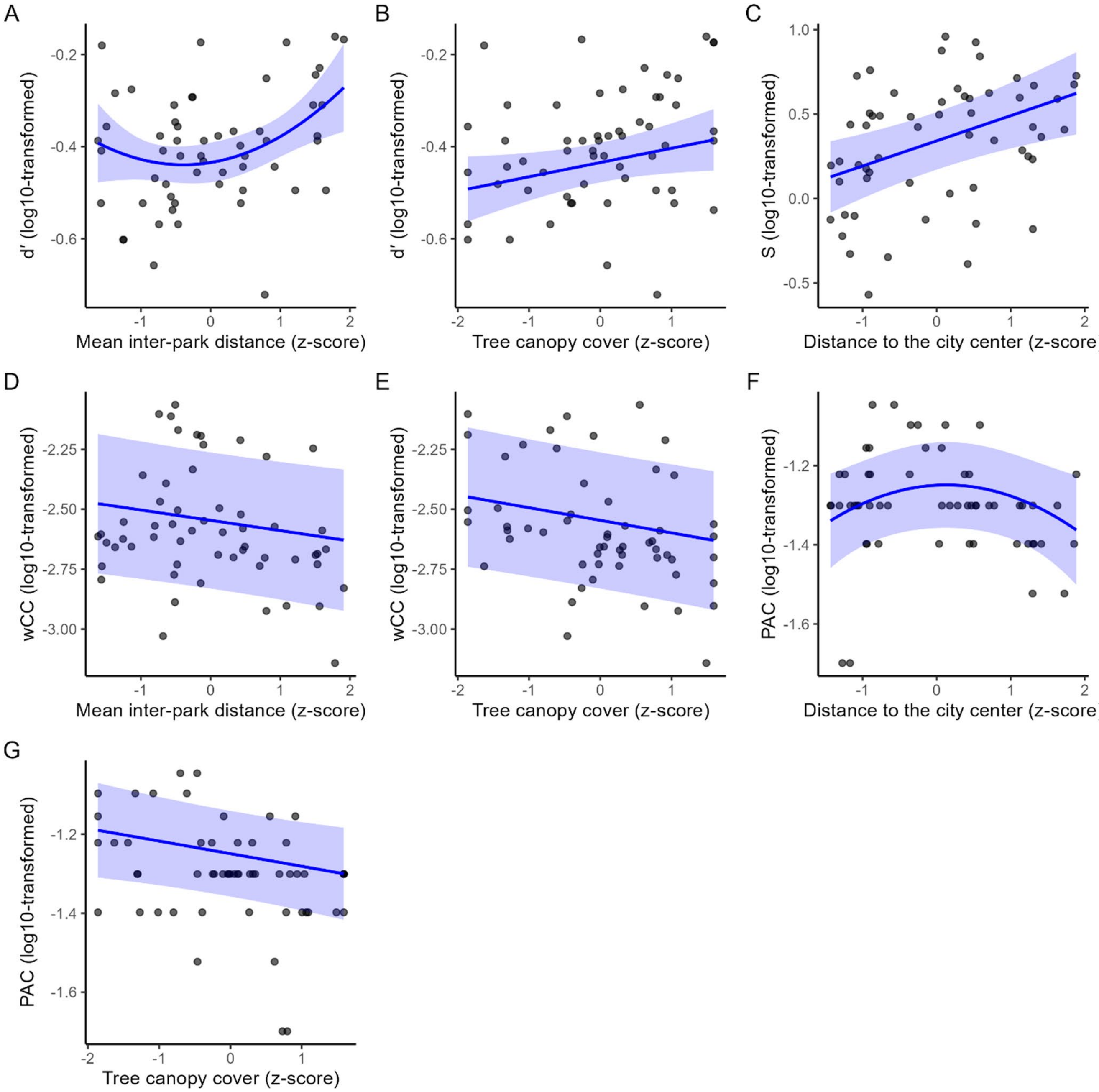

Fig. 2 Relationships between species–park network indices and urban park attributes based on the small plots (i.e., 3.16 × 3.16 m plots). Only statistically significant relationships are shown: (**A**) urban park specialisation (log10-transformed) vs. mean inter-park distance (z-score); (**B**) urban park specialisation (log10-transformed) vs. tree canopy cover (z-score); (**C**) urban park importance (log10-transformed) vs. distance to the city centre (z-score); (**D**) compositional representativeness (log10-transformed) vs. mean inter-park distance (z-score); (**E**) compositional representativeness (log10-transformed) vs. tree canopy cover (z-score); (**F**) colonisation potential (log10-transformed) vs. distance to the city centre (z-score); and (**G**) colonisation potential (log10-transformed) vs. tree canopy cover (z-score). Grey circles represent individual data points, the blue line indicates the linear mixed model estimates, and the shaded blue area denotes the 95% confidence interval

relative cover among parks and consequently higher specialisation values. The observed spatially structured specialisation is consistent with the 'SLOSS principle' originally proposed by Diamond (1975) and with the SS > SL (i.e., several small > single large) pattern commonly reported for urban parks, whereby parks tend to share species more strongly with nearby sites than with more distant ones, reflecting the limited dispersal capacities of many urban taxa (La Sorte et al. 2023). Isolated parks may also exhibit high specialisation, as their limited proximity to other parks

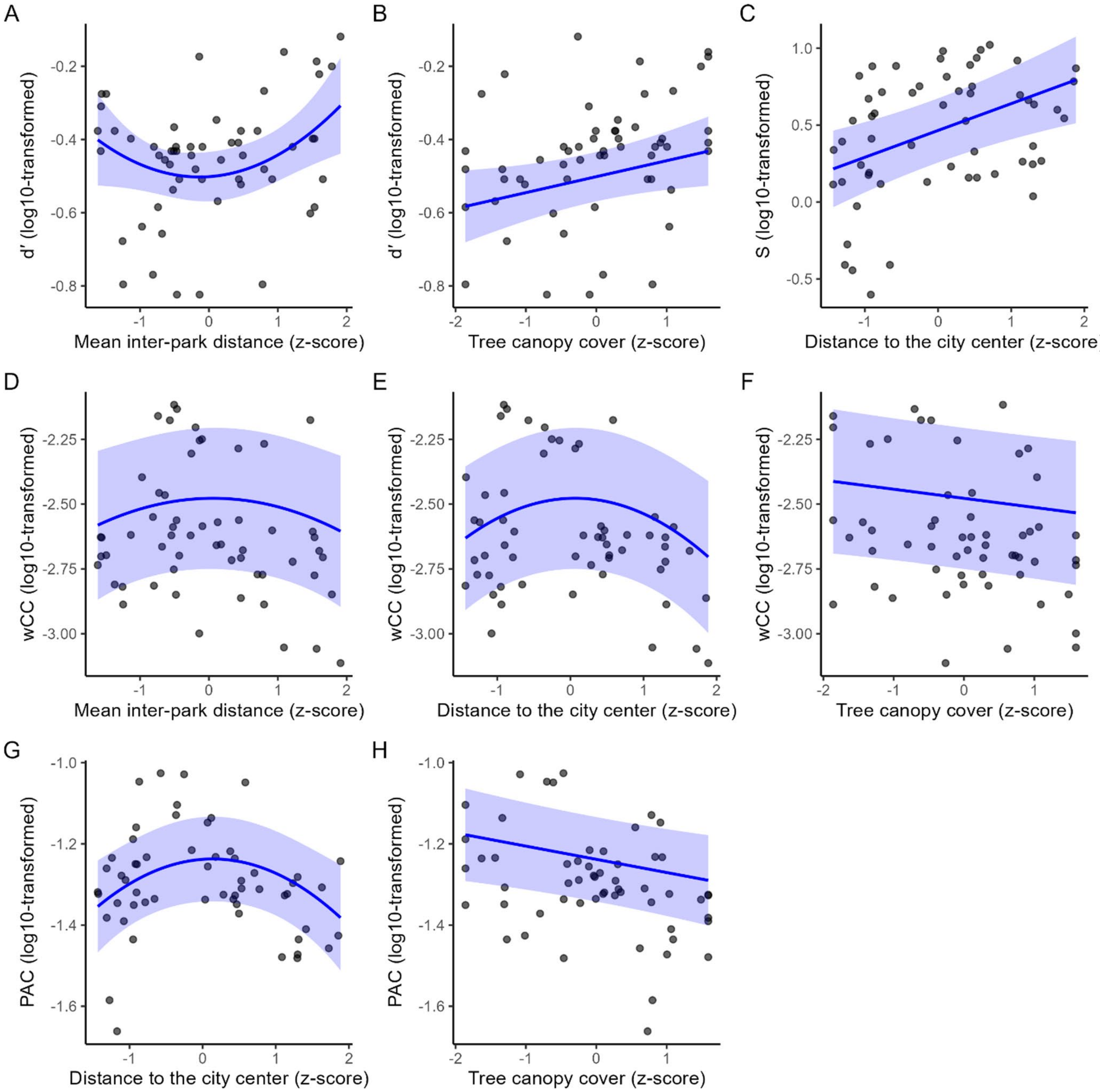

Fig. 3 Relationships between species–park network indices and urban park attributes based on the large plots (i.e., 10 × 10 m plots). Only statistically significant relationships are shown: (**A**) urban park specialisation (log10-transformed) vs. mean inter-park distance (z-score); (**B**) urban park specialisation (log10-transformed) vs. tree canopy cover (z-score); (**C**) urban park importance (log10-transformed) vs. distance to the city centre (z-score); (**D**) compositional representativeness (log10-transformed) vs. mean inter-park distance (z-score); (**E**) compositional representativeness (log10-transformed) vs. distance to the city centre; (**F**) compositional representativeness (log10-transformed) vs. tree canopy cover (z-score); (**G**) colonisation potential (log10-transformed) vs. distance to the city centre (z-score); and (**H**) colonisation potential (log10-transformed) vs. tree canopy cover (z-score). Grey circles represent individual data points, the blue line indicates the linear mixed model estimates, and the shaded blue area denotes the 95% confidence interval

can allow certain species to reach high local cover without spreading to the wider urban green infrastructure. By contrast, parks located at intermediate distances tend to display more balanced patterns of relative cover across parks, resulting in lower specialisation values.

Compositional representativeness, which indicates how representative a park is of the overall species composition of the urban park network, provided complementary information and was consistent with the overall patterns identified by urban park specialisation. When large plots were analysed, compositional representativeness peaked at intermediate mean inter-park distances, suggesting that parks located at intermediate distances serve as important connectors between different species pools within the urban landscape. In contrast, compositional representativeness declined with increasing inter-park distance when small plots were examined. This difference likely reflects the effect of plot size on the number and identity of species recorded: larger plots capture a greater proportion of subordinate species (Hill et al. 1994; Gotelli and Colwell 2001; Dengler et al. 2020), which in our study enabled parks at intermediate distances to display stronger compositional links, whereas subordinate species are underrepresented in small plots, causing parks at short distances to appear more compositionally representative. Interestingly, the relationship with distance from the city centre clarified where urban parks with high compositional representativeness are located within the urban landscape. Urban parks with high compositional representativeness tended to be located at intermediate distances from the city centre, highlighting their functional role in connecting parks in the city centre with those further away by sharing a broader range of plant species. The same pattern was observed for colonisation potential, which also peaked at intermediate distances from the city centre, indicating a stronger exchange of species. Overall, urban parks situated at intermediate distances contributed disproportionately to maintaining compositional connectivity within the urban green infrastructure.

Structural attributes of urban parks also influenced their functional role in supporting urban plant communities. Tree canopy cover was positively related to urban park specialisation, indicating that parks with greater tree cover tended to host species that achieved comparatively higher local cover than in other parks. The observed pattern may be linked to the presence of shade-tolerant species, which have become increasingly rare in urban landscapes characterised by the heat-island effect and limited water availability (de Barros Ruas et al. 2022). Shade-tolerant species tend to perform poorly in open, highly illuminated areas and therefore occur at low cover, or are entirely absent, in parks lacking tree canopies. Under suitable microclimatic conditions, such as the cooler and moister environments created by tree canopy cover, shade-tolerant species can attain substantially higher local cover, thereby increasing the specialisation values of urban parks. The negative relationship between tree canopy cover and colonisation potential may indicate that shade-tolerant species have limited capacity to establish beyond favourable microhabitats. Consequently, urban parks with higher tree canopy cover exhibited lower compositional representativeness, reflecting a reduced ability to represent the overall species composition of the urban park network; nevertheless, compositional differentiation among parks may contribute to higher city-wide species richness.

Conclusions

By integrating the spatial configuration and structural attributes of urban parks into the species–park network, this study shows that the contribution of parks to urban plant communities extends beyond patterns of local species richness. Parks further from the city centre were particularly important for supporting the richness and abundance of plant species, while parks at intermediate distances from the city centre served as compositional bridges between urban areas closer or further to the centre. Tree canopy cover influenced both the specialisation and compositional representativeness of parks, shaping how distinct each park was in its species composition. Overall, the findings highlight that the role of urban parks within green infrastructure is determined by their spatial location and structural attributes. They also demonstrate that network-based approaches offer an effective framework for assessing urban green infrastructure as an integrated system and for identifying functionally important landscape elements to support targeted planning and management interventions.

Author contributions E. F. conceived the study, designed the methodology, conducted the analyses, and led the writing of the manuscript. E. F. and F. F. collected the field data. E. Z., R. R., P. G., G. A., (A) D. B., S. M. P., and G. (B) contributed to interpreting the results, provided critical feedback, and assisted in revising and improving the manuscript. All authors read and approved the final version of the manuscript.

Funding Fantinato Edy was funded by the project ATLAS: Studying symbiotic scenarios linking heritage assets and green areas to prepare historic cities to face climate change (PCI2024-153441; Joint Programming Initiatives Cultural Heritage and Global Change – JPI CH) and by the IRIDE Fund of the Department of Environmental Sciences, Informatics and Statistics, Ca' Foscari University of Venice. Zendri Elisabetta was supported by the project ATLAS (PCI2024-153441; JPI CH) and by the Italian Ministry of University and Research. Rummo Rosario was funded under the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4 – Call for tender No. 3138 of 16 December 2021, rectified by Decree No. 3175 of 18 December 2021 of the Italian Ministry of University and Research, funded by the European Union – NextGenerationEU. Glasnović Peter was funded by the IRIDE Fund of the Department of Environmental Sciences, Informatics and Statistics, Ca' Foscari University of Venice. Della Bella Andrea was funded by Comune di Cartigliano and by the Italian Ministry of University and Research. Simone Marino Preo was funded by the project ATLAS (PCI2024-153441; JPI CH). Aronne Giovanna and Buffa Gabriella were supported by the Italian Ministry of University and Research.

Data availability Data will be stored in Datarepository Unive (https://datarepository.unive.it/) upon article acceptance.

Declarations

Competing interests The authors declare no competing interests.

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