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RESEARCH

Invasive alien plants and the city: distribution patterns in response to urban elements and urbanization in three of the largest cities in Italy

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Abstract

Cities are extensively colonised by invasive alien plants, and their spread can negatively impact urban ecosystems including remaining natural habitats. It is therefore crucial to understand how invasive alien plants spread across urban landscapes and which anthropogenic drivers favour their persistence. Accordingly, in three of the largest Italian cities (Milan, Rome and Turin), a pool of alien species highly invasive in Europe was selected and their distribution was studied. Using a stratified sampling design defined along a gradient of urbanization, we analysed the distribution and abundance of 26 target species in relation to urban elements (e.g. linear infrastructures, gardens and buildings). With almost 20,000 occurrences, the analysis highlighted that, within the species' pool, the most widespread spontaneous alien plants were *Ailanthus altissima* (Mill.) Swingle, *Parthenocissus* agg., *Phytolacca americana* L., *Robinia pseudoacacia* L. and *Sorghum halepense* (L.) Pers. Notably, *Ulmus pumila* L. was widespread in Milan and Turin. In response to the gradient of urbanization, a clear distinction emerged between species adapted to highly disturbed central areas, i.e. *A. altissima*, and those more suited to suburban contexts, i.e. *R. pseudoacacia*. Along the entire gradient, physical constraints limited the occurrence of species on buildings and other sealed areas, whereas gardens and road sides were the most receptive urban elements in terms of taxa richness and frequency. This comparative study of urban alien flora in three large Italian cities contributes to the understanding of distribution patterns and secondary spread of alien species in highly urbanised contexts of Southern Europe. Our study suggests that strategies for preventing and managing the colonisation of invasive alien plants in cities should be tailored to certain species, depending on levels of urbanisation and fine-scale land use.

Keywords *Ailanthus altissima* · Biological invasion · Bioreceptivity · Imperviousness · *Robinia pseudoacacia* · Urban habitat

Introduction

Urban ecosystems are a hotspot of invasive alien plants (Potgieter et al. 2024), whose presence can be detrimental to biodiversity (Montaldi et al. 2024) and to the ecosystem services provided by remnant urban flora and vegetation (Potgieter et al. 2017) and by green, blue and grey infrastructures (Potgieter et al. 2022; Stroud et al. 2022). Invasive alien species can exacerbate many negative impacts in cities, affecting both citizens' health (e.g. allergies) and activities, increasing fire risk and damaging infrastructure and historical heritage (Celesti-Grapow and Ricotta 2021; Montagnani et al. 2023). As these urban ecosystems develop into a source of invasive alien species, their negative effects can spread to peri-urban, rural and natural surrounding areas (Pyšek 1998; Cadotte et al. 2017; Campagnaro et al. 2022).

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Urban ecosystems represent a unique combination of environmental conditions that do not exist in unmodified landscapes (Cadotte et al. 2017). In part due to a constant human interference, cities provide a wide variety of microhabitats, refugia and niches (Cervelli et al. 2013) where alien plants can thrive (Gentili et al. 2024). Moreover, urban areas are a hub for the intentional and accidental introduction and spread of alien species due to the large availability of propagules (e.g. widely planted for ornamental purposes in public and private properties) and a dense network of pathways and vectors of dispersal which facilitate their proliferation (Potgieter et al. 2020).

As a result of the interplay of all these factors, invasive alien species usually succeed in cities more than in other contexts (Cadotte et al. 2017). Typically, successful invaders are generalist taxa that cope with transformed edaphic (e.g. technosoils, altered water supply), climatic (micro- and meso-scaled) and ecological (e.g. transformed competition levels) conditions which change rapidly and repeatedly (Lososová et al. 2012; Tranquillo et al. 2024). They can take advantage of altered circumstances that can be more suitable than those found outside the urban context (i.e. rural or natural environments; Salinitro et al. 2019). Furthermore, the diversity of the urban environment promotes the persistence of phylogenetically distant species with different ecological requirements, both aliens and natives (Dylewski et al. 2023).

However, it is evident that not all invasive alien plants possess the same capacity to thrive in urban environments (Alessandrini et al. 2025). Because they have undergone different adaptations in response to the stress and disturbance regimes of urban environments, the magnitude of their impacts in urban areas varies in relation to species and urban characteristics. Accordingly, identifying the most widespread species and their urban distribution patterns is pivotal to effectively managing biological invasions and reducing their impact in both public and private places (Štajerová et al. 2017; Potgieter and Cadotte 2020). Understanding how invasive alien species interact with and respond to urbanisation can provide insights into biological invasions under the expansion of human-dominated landscapes and global change (Lahr et al. 2018).

With respect to these considerations, we aimed to investigate how a pool of highly invasive alien plants is distributed across the urban matrix taking into account two physical properties of cities that facilitate spread of alien plants: the level of urbanization (i.e. the proportion of impervious or artificial areas) and habitats (Potgieter et al. 2024). Analysing these two factors allowed us to investigate the degree of spread of species and, indirectly, the 'bio-receptivity' of habitats (hereinafter 'urban elements'), i.e. how prone the urban elements are to colonization by invasive alien species. To this end, we carried out an extensive survey in Milan, Rome and Turin, three of the largest Italian cities representative of many European metropolitan areas falling in the Continental (Milan and Turin) and Mediterranean (Rome) biogeographical regions (EEA 2002; Cervellini et al. 2020). Target species were known from the literature to be invasive in a variety of environments in Italy, Europe, and or globally (Galasso et al. 2024; Nentwig et al. 2018), and that have severe impacts on the environment, economy and/or human health.

Methods

Urban study areas

Surveys were carried out in the metropolitan areas of Milan, Rome and Turin (Fig. 1b). For Milan and Turin, surveys were performed inside or immediately outside the borders of municipalities. For Rome, the area considered was circumscribed by a ring road around the city that includes the most inhabited areas of the city (Grande Raccordo Anulare, GRA).

Rome is the largest and most populated city in Italy (2,754,719 inhabitants), Milan the second (1,371,850 inhabitants), and Turin the fourth (846,926 inhabitants) (https://demo.istat.it/app/?i=D7B&l=it*)*. Based on biogeographic regions, Milan and Turin fall in the Continental region, while Rome in the Mediterranean one. Both Milan and Turin are in the Po plain at an average elevation of 120 m and 239 m a.s.l. respectively, while Rome has a highly varied topography, ranging from about 20 to 139 m a.s.l.

In the decade 2010–2020, the mean annual temperature and rainfall were respectively 15.9 °C and 828 mm for Milan, 15.1 °C and 1002 mm for Turin, 17.7 °C and 786 mm for Rome (ISTAT 2024). Both Rome and Turin are crossed by major rivers, the Tiber and the Po, respectively.

Selection of target taxa

The pool of analysed species comprised 26 taxa as reported in Table 1. The presence of the taxa in the cities was obtained from databases and the literature. The selection was based on the following criteria:

(1) Invasive status: all selected taxa are invasive in at least one region in Italy (Galasso et al. 2024);

(2) Occurrence as established in at least two of the target cities;

(3) Ascertained impacts on ecosystem structures (e.g. suppression of other species), urban components (e.g. buildings, infrastructures) or citizen health (e.g. allergies) based on bibliography (Table 1).

Table 1 – List of the target taxa and the abbreviations of their names used in the study. For each taxon, examples of references supporting its invasiveness and the type of impact are reported

Family	Taxon	Abbreviation	References to negative impacts
Sapindaceae	*Acer negundo* L.	Ace_neg	Campagnaro et al. (2018)
Simaroubaceae	*Ailanthus altissima* (Mill.) Swingle	Ail_alt	Campagnaro et al. (2018)
Asteraceae	*Ambrosia artemisiifolia* L.	Amb_art	Montagnani et al. (2017)
Fabaceae	*Amorpha fruticosa* L.	Amo_fru	Boscutti et al. (2020)
Asteraceae	*Artemisia annua* L.	Art_ann	Cristofori et al. (2020)
Moraceae	*Broussonetia papyrifera* (L.) Vent.	Bro_pap	Kudrnovsky et al. (2022)
Scrophulariaceae	*Buddleja davidii* Franch.	Bud_dav	Tallent-Halsell and Watt (2009)
Asteraceae	*Helianthus tuberosus* L.	Hel_tub	Popay (2025)
Cannabaceae	*Humulus japonicus* Siebold & Zucc.	Hum_jap	EPPO (2018)
Oleaceae	*Ligustrum lucidum* W.T.Aiton	Lig_luc	Fernandez et al. (2020)
Oleaceae	*Ligustrum sinense* Lour.	Lig_sin	Cash et al. (2020)
Caprifoliaceae	*Lonicera japonica* Thunb.	Lon_jap	Larson et al. (2007)
Vitaceae	*Parthenocissus* agg. (*P. inserta* [A.Kern.] Fritsch, *P. quinquefolia* [L.] Planch.)	Par_sp	Rojas-Sandoval (2025)
Paulowniaceae	*Paulownia tomentosa* (Thunb.) Steud.	Pau_tom	Dehnen-Schmutz (2021)
Phytolaccaceae	*Phytolacca americana* L.	Phy_ame	Tanner and Fried (2020)
Rosaceae	*Prunus laurocerasus* L.	Pru_lau	Rusterholz et al. (2018)
Fagaceae	*Quercus rubra* L.	Que_rub	Campagnaro et al. (2018)
Polygonaceae	*Reynoutria japonica* Houtt.	Rey_jap	Lavoie (2017)
Fabaceae	*Robinia pseudoacacia* L.	Rob_pse	Campagnaro et al. (2018)
Asteraceae	*Senecio inaequidens* DC.	Sen_ina	Eller and Chizzola (2016)
Cucurbitaceae	*Sicyos angulatus* L.	Sic_ang	Kurokawa (2025)
Asteraceae	*Solidago* spp. (*S. canadensis* L., *S. gigantea* Aiton)	Sol_sp	Pal et al. (2015), Fenesi et al. (2015)
Rosaceae	*Spiraea japonica* L.f.	Spi_jap	Global Invasive Species Database (2025)
Poaceae	*Sorghum halepense* (L.) Pers.	Sor_hal	Peerzada et al. (2023)
Arecaceae	*Trachycarpus fortunei* (Hook.) H.Wendl.	Tra_for	Fehr et al. (2024)
Ulmaceae	*Ulmus pumila* L.	Ulm_pum	Brunet et al. (2013)

Two taxa were considered at the generic level due to issues in identification and technical constraints: *Parthenocissus quinquefolia* (L.) Planch. and *P. inserta* (A.Kern.) Fritsch were considered as an aggregate because they can often be hard to distinguish due to the variability of distinctive morphological traits (e.g. adhesive disks) (Pignatti et al. 2017); *Solidago canadensis* L. and *S. gigantea* Aiton (*Solidago* spp.) because they are highly variable and late-flowering species (floral stem emerges in late summer and its hairiness is one of the main distinctive traits), consequently the distinction between the two can sometimes be challenging during a single vegetative season survey.

Again due to identification issues, a third taxon, *U. pumila*, was expanded in our treatment to include its hybrids (*U. pumila* × *U. minor*), which show mixed or intermediate morphological traits between the alien elm and the native one, *U. minor* Mill. (Cogolludo-Agustín et al. 2000; Bertolasi et al. 2015).

Field sampling design

A 500 m × 500 m cell grid was superimposed over each city. The grid was a subsample of the 10 km × 10 km grid used by the European Commission for defining the distribution of alien species of Union concern ex Regulation EU n. 1143/2014 (see documentation available at: https://easin.jrc.ec.europa.eu/easin/Documentation/Baseline*)*. In each city, 40 cells of the grid were sampled along a gradient of urbanization. Cells were selected based on the percentage of cover and degree of fragmentation of ‘artificial surfaces’; class ‘1’ according to the Urban Atlas dataset 2018 (updated 2021, code: https://doi.org/10.2909/fb4dffa1-6ceb-4cc0-8372-1ed354c285e6) (Fig. 1a). For each cell, the percentage of cover and degree of fragmentation of artificial surfaces were calculated according to *landscapemetrics* R package (‘cover area’ and ‘patch density’ functions, respectively; Hesselbarth et al. 2019).

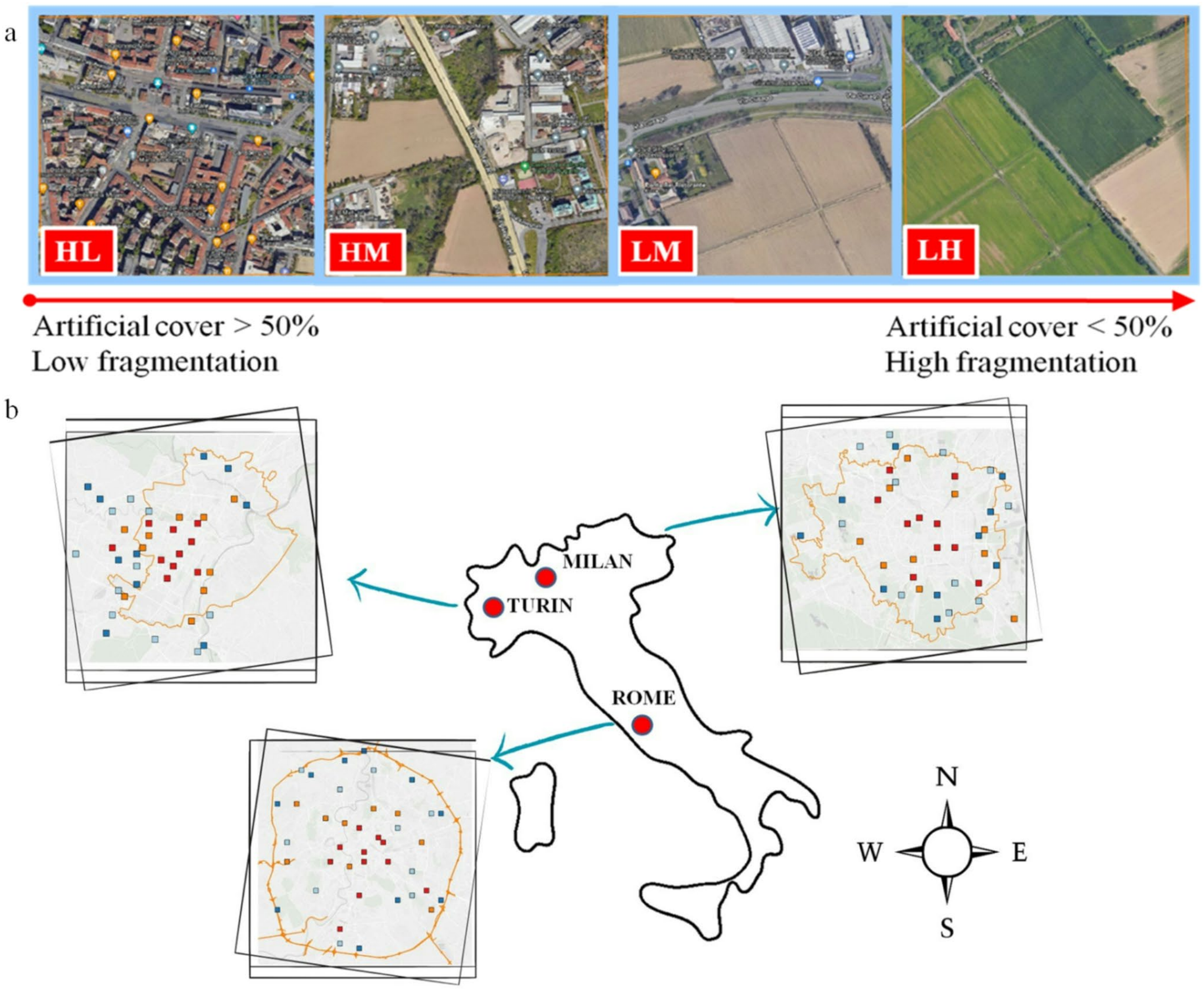


Fig. 1 Visual example of the gradient of urbanization used for cell selection (1a) and distribution of surveyed cells in Milan, Rome and Turin classified based on urban categories (1b - red cells: HL; orange cells: HM; blue cells: LM; light blue cells: LH)

To classify cells following a gradient of urbanization, the two metrics were combined resulting in four 'urban categories' (Table 2). We adopted a stratified and spatially balanced sampling design. For each urban category ten cells were chosen following two criteria: (1) cells had to be equally dispersed in the whole considered city area, in order to obtain a set of representative samples; (2) in each cell, there should be no clear predominance (<40% of cell surface based on zonal statistics applied to the Urban Atlas and performed using the *landscapemetrics* R package) of certain urban elements, such as roads, railways, green areas, watercourses or wastelands. Lastly, the selection also took into account the overall accessibility of the cell. Sampled cells and their urban category are shown in Fig. 1b.

Table 2 – Codification of urbanization cover through urban categories based on the coverage and patch density of artificial surfaces within the entire cell area

Code	Urban category	Cover area (% of cell surface)	Patch density
HL	High cover and low fragmentation	≥50%	≤5
HM	High cover and medium fragmentation	≥50%	5<x<20
LM	Low cover and medium fragmentation	<50%	5<x<20
LH	Low cover and high fragmentation	<50%	≥20

Field survey

Field surveys were carried out from spring to autumn 2023. Due to the timing of the project, each cell was surveyed once. Target taxa were selected that could be easily identified throughout the entire survey period. In each cell of each city, a team of botanists surveyed all accessible areas and recorded every occurrence of target species. For each record of occurrence, we collected the following information: (1) geographic coordinates (GPS); (2) status as occurring in cultivation or as a spontaneous individual or population; (3) urban element where the taxon was recorded (see the following paragraph '*Urban elements*'); and (4) area occupied (m^2) by the taxon.

Urban elements

The term 'urban element' was taken from the urban design glossary and it typically refers to the physical building blocks of the city (von Richthofen et al. 2018). In our case, we indicate as urban elements the components of the urban landscape of the target cities, those indicated by Potgieter et al. (2024) as 'habitats'. The two-tiered list of all urban elements considered in the study is provided in detail in Table S1, where for each macro-scaled element all associated lower-scale elements are listed (=meso-scaled elements). The list is specific for the target cities, not universal (e.g. harbours are not listed). Macro-scaled elements were 'abandoned areas', 'agricultural areas', areas for services and activities ('service areas'), 'buildings', 'green areas', 'infrastructures', 'natural areas' and watercourses ('water').

During field surveys, to prevent oversampling, we evaluated distinct occurrences based on distances between cores of presence (dependent on species dispersal and propagation strategy) and the different type of colonized environment, e.g. if two occurrences of the same species were close but falling in two different meso-scaled urban elements, they were recorded as different occurrences.

Data analysis

Overview of the most widespread and frequent target taxa

First, a general overview of those taxa that are more widespread and frequent in our surveys was compiled. Subsequently, cultivation status was used to separate the records (total and for each city) into two groups: those sites where species were recorded as cultivated and those where they were spontaneous. The following statisticalanalyses were based only on occurrences of taxa with spontaneous status. Then, to identify the most frequent taxa across the whole dataset and explore how the occurrence of target taxa varied across cities, we used network and multivariate analyses (detailed in *Distribution patterns of taxa across urban elements and urban categories*).

Taxa richness, frequency and mean occupied surface across urban elements and categories

Univariate parametric analysis of variance (ANOVA) was performed to analyse differences in taxa richness (number of taxa per cell), taxa frequency (number of records per cell) and mean occupied surface across two factors: urban elements (eight levels as previously listed macro-scaled urban elements) and urban categories (four levels: HL, HM, LM, LH) and effects of their interactions (two-way ANOVA). For the univariate analysis, we performed one-way ANOVA using the aov() function in R (R Core Team 2024). In case of unbalanced datasets (e.g. urban elements), univariate PERMANOVA was applied and the Euclidean distance was used for calculating the distance matrix (Anderson 2001). PERMANOVA was performed with PRIMER statistical package version 7 (Anderson et al. 2008). Further details on univariate analysis can be found in the supplementary material (S1).

Distribution patterns of taxa across urban elements and urban categories

We used network analysis to explore how the occurrence of target taxa varied across urban elements and urban categories. For each urban element and urban category, a separate co-occurrence network was built. In each network, nodes represented taxa, and edges (i.e. links between nodes) indicated how frequently two taxa co-occurred within the same cell per urban element or category. Networks were undirected and weighted, with edge weight reflecting co-occurrence frequency.

The centrality of taxa within each network – measured using eigenvector centrality – was calculated based on the structure of co-occurrences: that is, how often a taxon co-occurred with others across sampling cells, and how central its co-occurring taxa were within the network (Vignery and Laurier 2020). This allowed us to identify the most central taxa for each city, urban element and urban category, i.e. those that are both widespread and closely associated with other widespread taxa.

Node size and colour were scaled according to eigenvector centrality values. Edge thickness and colour reflected the strength of the connection between taxa (i.e. co-occurrence frequency). To improve the readability of the graphs, outliers (i.e. marginal taxa with minimal connections as *Spiraea japonica*) were excluded. All network analyses were carried out in R (v4.4.1) using the igraph package (Csardi and Nepusz 2006) and visualised in Gephi (v0.10.1; Bastian et al. 2009) using the Fruchterman-Reingold algorithm

(Fruchterman and Reingold 1991). Further details on network analysis can be found in the supplementary material (S1).

Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) highlighted dissimilarities in taxa composition across urban elements and categories, strengthening the results from network analysis. PERMANOVA was performed with PRIMER statistical package version 7 (Anderson et al. 2008). Pair-wise comparisons were used as *a posteriori* tests to identify significant dissimilarities and taxa contributing the most to dissimilarities were identified by dissimilarity percentages (cut-off 70%) using SIMPER test. Only for the most central taxa, the mean occupied surface per species was compared considering urban elements and categories, at the cell level, with univariate parametric analysis of variance (ANOVA) (see previous paragraph).

Overview of meso-scaled urban elements

We retained meso-scaled elements (subcategories of the (macro) urban elements) for a more detailed analysis of preferential colonization by target taxa. Differences in taxa frequency in each of the meso-scaled elements were represented in a pie chart for each macro-scaled element. Then, each taxon identified as relevant based on the network analysis (high values of centrality) was examined in detail and its frequency in each meso-scaled element was represented with circular barplots. Graphics were elaborated with *ggplot2* package in R (Wickham 2016).

Results

Overview of the most widespread and frequent target taxa

In total, we surveyed approximately 30 km^2 of urban environments and gathered 23,776 occurrence records, 19,351 of which referred to spontaneously growing taxa. The most frequent taxa were mostly found as spontaneous, with few cases of cultivation (Fig. 2).

Considering the pool of target taxa common to all cities, the most widespread and frequent spontaneous species were *Ailanthus altissima*, *Sorghum halepense*, *Phytolacca americana* and *Robinia pseudoacacia* (eigen centrality≥0.75) (Fig. 3, Table S2.1). *A altissima* and *S. halepense* were the most widespread and frequent species according to their centrality and degree of closeness (Table S2.1), followed by *Ulmus pumila* and *Parthenocissus* agg. (eigen centrality≥0.5). Marginal species, i.e. those taxa with a very low number of records of occurrence and occupied cells were *Quercus rubra*, *Humulus japonicus*, *Ambrosia artemisiifolia*, *Senecio inaequidens*, *Paulownia tomentosa*, *Helianthus tuberosus* and *Reynoutria japonica; Spiraea japonica* was found spontaneously growing in a single site in Milan (see Fig. S2).

The centrality of taxa varied by city: *A. altissima* and *R. pseudoacacia* were tied as the most central species in Rome, while *P. americana* and *S. halepense* were most central in Milan and Turin (Fig. 3). Moreover, *A. altissima* was central in Milan but not in Turin, where *U. pumila* dominated.

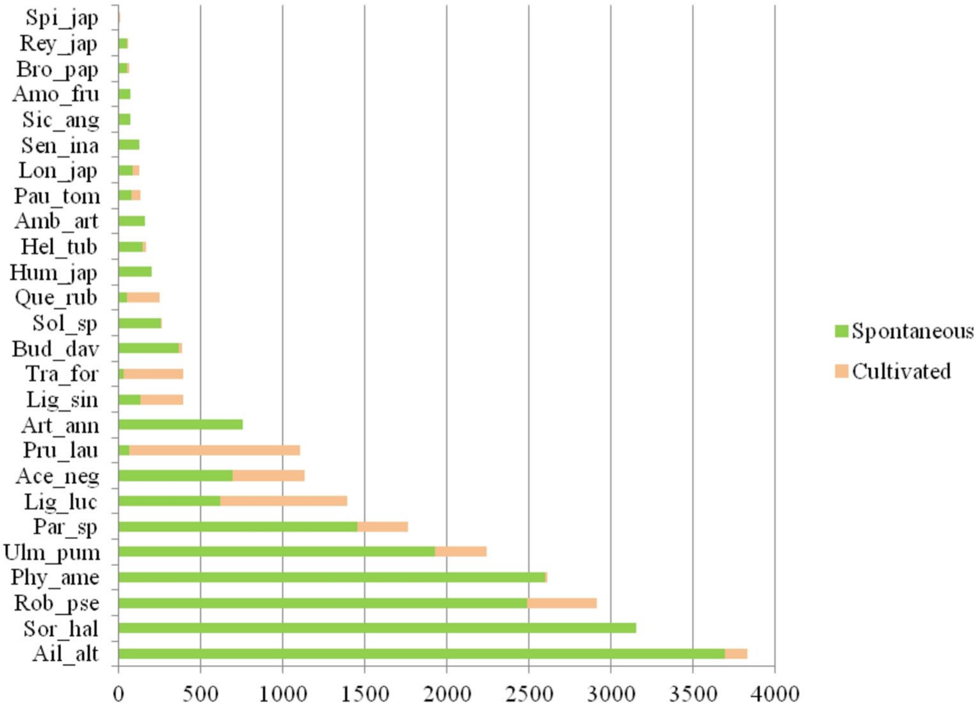


Fig. 2 General overview of the total number of records collected for each taxon and divided between number of sites where taxa were found as spontaneous and cultivated. The full names of the taxa and their corresponding abbreviations are reported in Table 1

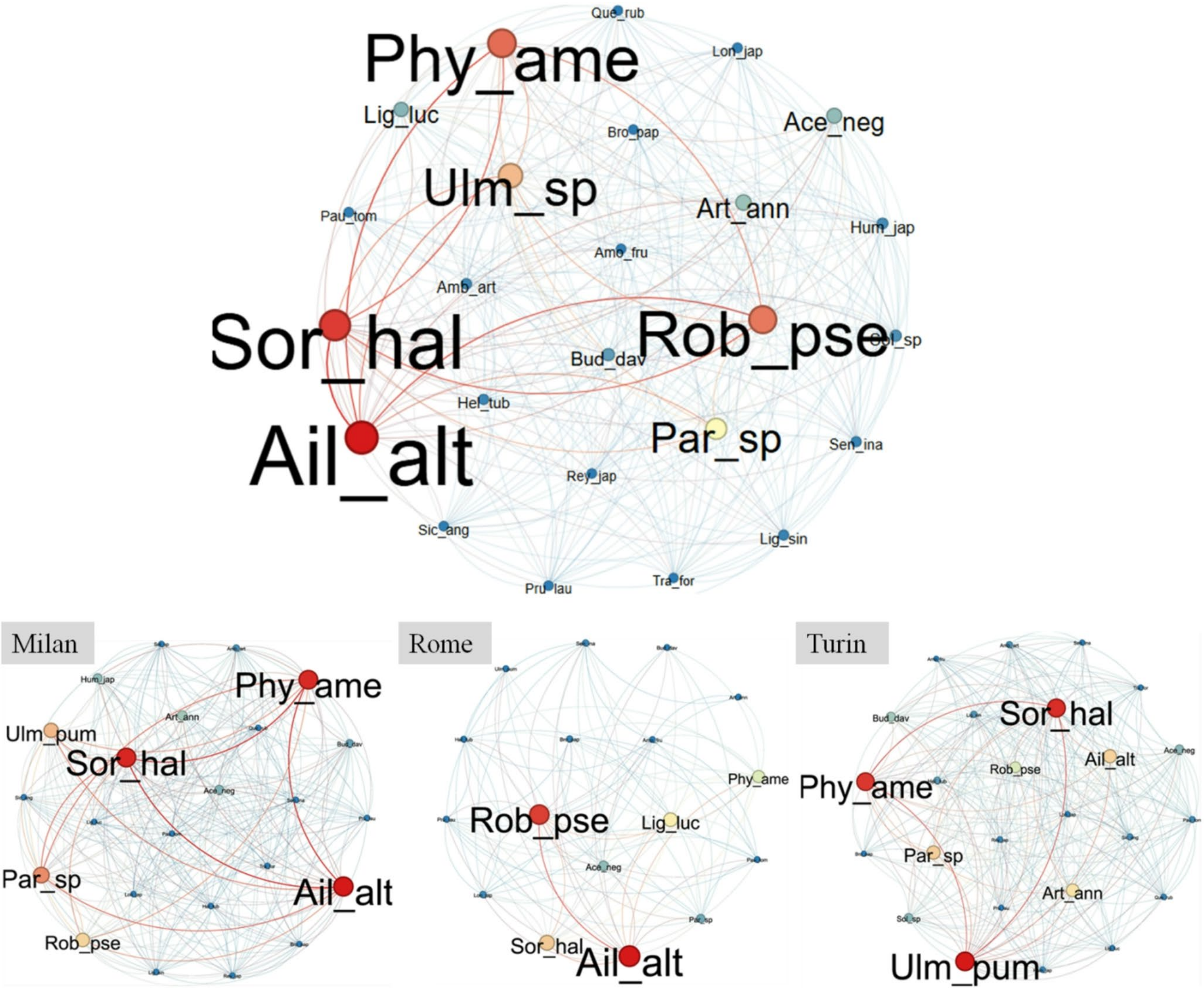


Fig. 3 Network analysis highlighting the most widespread and frequent spontaneous taxa in general and across cities. Nodes: colour and size gradient from the most central taxa (red, large dots) to less central taxa (blue, small dots). Edges: colour and size gradient from the strongest (red, thick) to weaker connections (blue, thin)

Despite the secondary status of *L. lucidum*, its centrality in Rome was notable.

Based on PERMANOVA, the significant dissimilarity of taxa assemblage across cities was confirmed (PERMANOVA: p (perm) $<$ 0.01; PAIRWISE test: p (perm) $<$ 0.01) (Table S3a). Rome also differed from the other two cities due to the absence of several taxa in our surveys: *A. artemisiifolia*, *H. japonicus*, *Ligustrum sinense*, *Q. rubra*, *Sicyos angulatus*, *R. japonica*, *Solidago* spp., *S. japonica* and *T. fortunei*. In contrast, the species not recorded in the other cities were very few: *Amorpha fruticosa* and *S. japonica* were not found in Milan and Turin, respectively.

Regarding cultivated species, *Prunus laurocerasus* and *Trachycarpus fortunei* emerged as the most frequently cultivated invasive alien plants (cultivated in 94% and 91% of their occurrences, respectively; Fig. 2). Following these, about half of the occurrences of *L. lucidum* and slightly less for *A. negundo* were of cultivated status in cities (55.6 and 38.5%, respectively).

Taxa richness, frequency and mean occupied surface across urban elements and categories

Based on univariate PERMANOVA (Table S4), dissimilarities were identified among urban (macro) elements considering the richness of taxa per cell as well as the number of records and the surface occupied by taxa (PERMANOVA: p (perm) = 0.0001). Specifically, a higher taxa richness (number of taxa per cell) was found in 'green areas', 'infrastructures', 'abandoned areas', 'agricultural areas' and 'water' than in other urban elements (Fig. S4a). The highest numbers of records were found in 'green areas' and ‘infrastructures’ (Fig. S4b), while taxa formed on average larger nuclei in ‘abandoned areas’, ‘agricultural areas’, ‘natural environments’ and ‘water’ than in any other category of urban elements (Fig. S4c). Comparing different urban categories, both taxa richness (HL < HM, ANOVA: $p = 0.015$) and number of records (HL < HM; Kruskal-Wallis test: $p = 0.048$) resulted significantly different only between HL and HM (Fig. S3d, S3e). As expected, the mean surface occupied by taxa was significantly lower in HL with respect to all the other categories (ANOVA: $p < 0.0001$) (Fig. S3f).

Distribution patterns of taxa across urban elements.

A. altissima was the most central species in the largest number of urban elements (Fig. 5, Table S2.3), but different combinations of species shared centrality in each urban element. In ‘abandoned areas’ *A. altissima* (1) was most central, followed closely by *R. pseudoacacia* (0.86); while in ‘agricultural areas’ *S. halepense* (1) and *P. americana* (0.93) ranked first. In ‘buildings’, the two most central species were *U. pumila* (1) and *P. americana* (0.94), with *A. altissima* (0.79) and *Parthenocissus* agg. (0.71) ranking as secondary taxa. In ‘green areas’, there were as new co-primaries *A. altissima* (1), *P. americana* (0.93) and *S. halepense* (0.95). In ‘infrastructures’ *A. altissima* ranked co-primary with *S. halepense*, while in ‘natural environments’ it ranked first (1) with *R. pseudoacacia* (0.95). ‘Service areas’ reveal a new central species: *Ligustrum lucidum* (1) with *A. altissima* (0.97) and followed by *P. americana* (0.90). Finally, in ‘water’ *Phytolacca americana* (1) was central, followed by *S. halepense* (0.86) and *R. pseudoacacia* (0.84), accompanied by the emergence of *H. japonicus* (0.65) as somewhat central. Generally, the most central taxa occupied smaller areas in ‘buildings’ and ‘service areas’ than in other urban elements (Fig. S5.1). *A. altissima* and *P. americana* occupied larger areas in ‘abandoned and ‘natural areas’, while *Parthenocissus* agg., *P. americana*, *R. pseudoacacia* and *S. halepense* occupied larger areas in ‘agricultural areas’. *A. altissima*, *Parthenocissus* agg., *S. halepense* and *U. pumila* were the most extensive in ‘green areas’, while in ‘infrastructures’ these four species were joined by *P. americana*. In ‘water’ *R. pseudoacacia* covered much larger areas than in most other urban elements. Two species showed strongly opposing affinities for certain urban elements: where *R. pseudoacacia* grew extensively, *A. altissima* covered only small areas (‘agricultural areas’), while where *A. altissima* dominated, *R. pseudoacacia* managed to colonize only smaller areas (‘green areas’ and ‘infrastructures’).

According to the PERMANOVA analysis, taxa composition was confirmed to be significantly dissimilar among all urban elements, with the only exception of comparing ‘natural environments’ vs ‘water’ (Table S3b). Again, dissimilarity mainly resulted from changes in frequency of the aforementioned taxa (Fig. S3a; Table S3.1), except for *H. japonicus* and *L. lucidum*, probably due to their marginal frequency.

Distribution patterns of taxa across meso-scaled urban elements

Patterns emerged within each macro-scaled urban element as well, with some meso-scaled elements preferentially colonized over others. Based on number of records, in ‘abandoned areas’ alien taxa were mostly found in wastelands on natural soil and secondarily in wastelands on artificial soil (Fig. 5). Both *A. altissima* and *R. pseudoacacia* were very frequent in wastelands mainly on natural soil, while *U. pumila* was frequent in wastelands but on artificial soil. In ‘agricultural areas’, *P. americana*, *R. pseudoacacia* and *S. halepense* were mainly found in uncultivated areas, while *S. halepense* was more frequent than the other two taxa in cultivated areas (multi-species fields and monocultures). In ‘buildings’ taxa were mostly found nearby (or on) residential or commercial buildings or abandoned buildings. There, *A. altissima* and *U. pumila* occurred mostly in association with residential and commercial buildings, while *P. americana* with abandoned buildings. In ‘green areas’, most occurrences were recorded in both public and, with a slight majority, private gardens, where *A. altissima* and *P. americana* were more frequent than other taxa; *S. halepense* was much more frequent in flowerbeds than in gardens. In ‘infrastructures’, it was mainly along roads that target plants were found, i.e. the frequency of *A. altissima* and *S. halepense* was higher along roads and secondarily along footpaths and cycle paths, as with *U. pumila* – though to a lesser degree. In ‘natural environments’, natural woods hosted more records and were mostly colonized by *A. altissima* and *R. pseudoacacia*, with the latter often dominating. In ‘service areas’, industrial complexes supported the most occurrences. However, there was an evident diversification: *A. altissima* mostly colonized outdoor sport facilities, industrial complexes and archaeological sites, while *P. americana* was much more frequent only in industrial complexes. The central role of *L. lucidum* in ‘service areas’ is due to its important occurrence in cemeteries. Finally, in ‘water’, target taxa were mainly found along perennial watercourses, primarily those minimally modified by human action. The only species to be found predominantly along perennial natural watercourses was *R. pseudoacacia*. In contrast, *P. americana* and *H. japonicus* were frequent along artificial perennial watercourses and *S. halepense* along periodically dry artificial watercourses.

Distribution patterns of taxa across urban categories.

A. altissima was the most central taxon in high artificial cover categories (HL, HM), and nearly so in the low artificial cover categories (LM, LH), where *S. halepense* and *R. pseudoacacia* were the most central (Fig. 6, Table S2.4). The centrality values of *R. pseudoacacia* increased from high to low artificial cover categories, while those of *U. pumila* increased in the opposite direction (Fig. 6, Table S2.4). Almost all species tended to occur in smaller populations in HL with respect to other categories, especially LH, although significant differences occurred only for *R. pseudoacacia* and *S. halepense* (Fig. S5.2).

Results by PERMANOVA analysis confirmed the dissimilar composition of taxa (p (perm) = 0.0003) (Table S3c). Pair-wise comparisons indicated significant dissimilarities in all comparisons, except that of low artificial cover categories (LM vs. LH) (Table 3c). Taxa generating dissimilarities (SIMPER test; Table S3.2) were mainly *A. altissima* and *S. halepense* followed by *R. pseudoacacia*, *Parthenocissus* agg., *P. americana* and *U. pumila* (Fig. S3b); *Artemisia annua* contributed minimally, and only when HM was compared to low cover categories (LM, LH) (Fig. S3b, Table S3.2).

Regarding the interaction of 'urban element × urban category', significant dissimilarities were identified for 'green areas' (PERMANOVA pair-wise test: p (perm) = 0.0001) and 'infrastructures' (PERMANOVA pair-wise test: p (perm) < 0.05). In 'green areas' of high artificial cover cells (HL and HM), some taxa were more frequent than in those of low artificial cover cells (LM and LH). These taxa were mainly *A. altissima*, *S. halepense* and *P. americana*. Also, the frequency of taxa in 'infrastructures' within HL and HM cells were dissimilar from those in the same urban element within LM and LH cells. Specifically, *A. altissima* and *U. pumila* were more frequent in HL and HM cells, while *S. halepense* and *R. pseudoacacia* in LM and LH cells.

Discussion

Our study highlights a pool of the most widespread and frequent invasive alien taxa in Milan, Rome and Turin, across different biogeographic regions. Although these species are widespread, they showed distinct responses to the physical characteristics of different urban elements.

Four out of the 26 taxa in the study were dominant

Among the 26 taxa considered, four species — *A. altissima*, *S. halepense*, *P. americana* and *R. pseudoacacia* — were dominant across the three cities (Fig. 3, Table S2.1). Consistent with previous studies, their broad ecological plasticity and efficient reproductive and dispersal strategies make them common components of the invasive alien flora in many European cities, spanning both Continental and Mediterranean regions (e.g., La Sorte et al. 2014). This is also evidenced by previous studies on the urban flora of our study cities (e.g. Banfi and Galasso 1998; Celesti-Grapow et al. 2013).For the species with less impressive repertoires, factors limiting their success became apparent. Climatic barriers restricted several taxa including *A. artemisiifolia*, *H. japonicus* and *R. japonica*, which were all absent from Rome, consistent with their limited adaptation to Mediterranean conditions (Gentili et al. 2017). *Buddleja davidii*, despite its invasive potential (Kriticos et al. 2011; Fanfarillo et al. 2024) and ability to colonize densely built-up areas (Tallent-Halsell et al. 2009; Godefroid and Ricotta 2018) appears less invasive in southern Italy (Galasso et al. 2024), which may explain its limited occurrence in Rome. Even in Milan and Turin, it was mostly restricted to dry, low-competition habitats such as wastelands, rubble and wall cracks. Some species' success, despite climate preferences, was influenced by historical or current cultivation practices. For instance, although more typical of temperate climates (Cierjacks et al. 2013), R. *pseudoacacia* was more frequent in Rome, probably due to its extensive historical planting there (Caneva et al. 2020). In contrast, the widespread cultivation of *P. laurocerasus* in our cities may not contribute to its spontaneous spread here. Its invasiveness elsewhere (Galasso et al. 2024) is likely curtailed here by the lack of suitable habitats and by frequent hedge pruning that prevents fruiting and, consequently, further spread (Conedera et al. 2018; Rusterholz et al. 2018).

Two taxa emerged as new expanding species: *U. pumila* and *L. lucidum* (Fig. 3; Table S2). In Turin and, to a lesser extent, Milan, *U. pumila* was abundant, but in Rome it was scarce. Introduced to Italy as a Dutch Elm Disease–resistant substitute for *U. minor* (Brunet et al. 2013), U. *pumila* was (and still is) widely cultivated along roadsides and in gardens in northern cities, facilitating the prolific seedling recruitment observed in nearby areas (Mainetti and Lonati 2017). *U. pumila*'s preference for temperate climates is reflected in the fact that it rarely becomes naturalized in Rome, despite its ornamental use there (Campagnaro et al. 2022; Bartoli et al. 2022).

Ligustrum lucidum is a highly adaptable species that can thrive and become invasive in diverse environments, both in Mediterranean and low-Alpine regions (Dreyer et al. 2019; Zischg et al. 2021). While the species primarily occurs in cultivation in Milan and Turin, it is widely naturalized and currently expanding in Rome (Celesti-Grapow and Ricotta 2021), largely due to its extensive ornamental use. Our meso-urban element analysis highlighted a notable presence of *L. lucidum* in cemeteries, where cultivated evergreen shrubs and trees create favourable microhabitat conditions that provide shade and shelter for *L. lucidum* seedling establishment and growth.

Urban elements as selective filters shaping the distribution of invasive alien plants

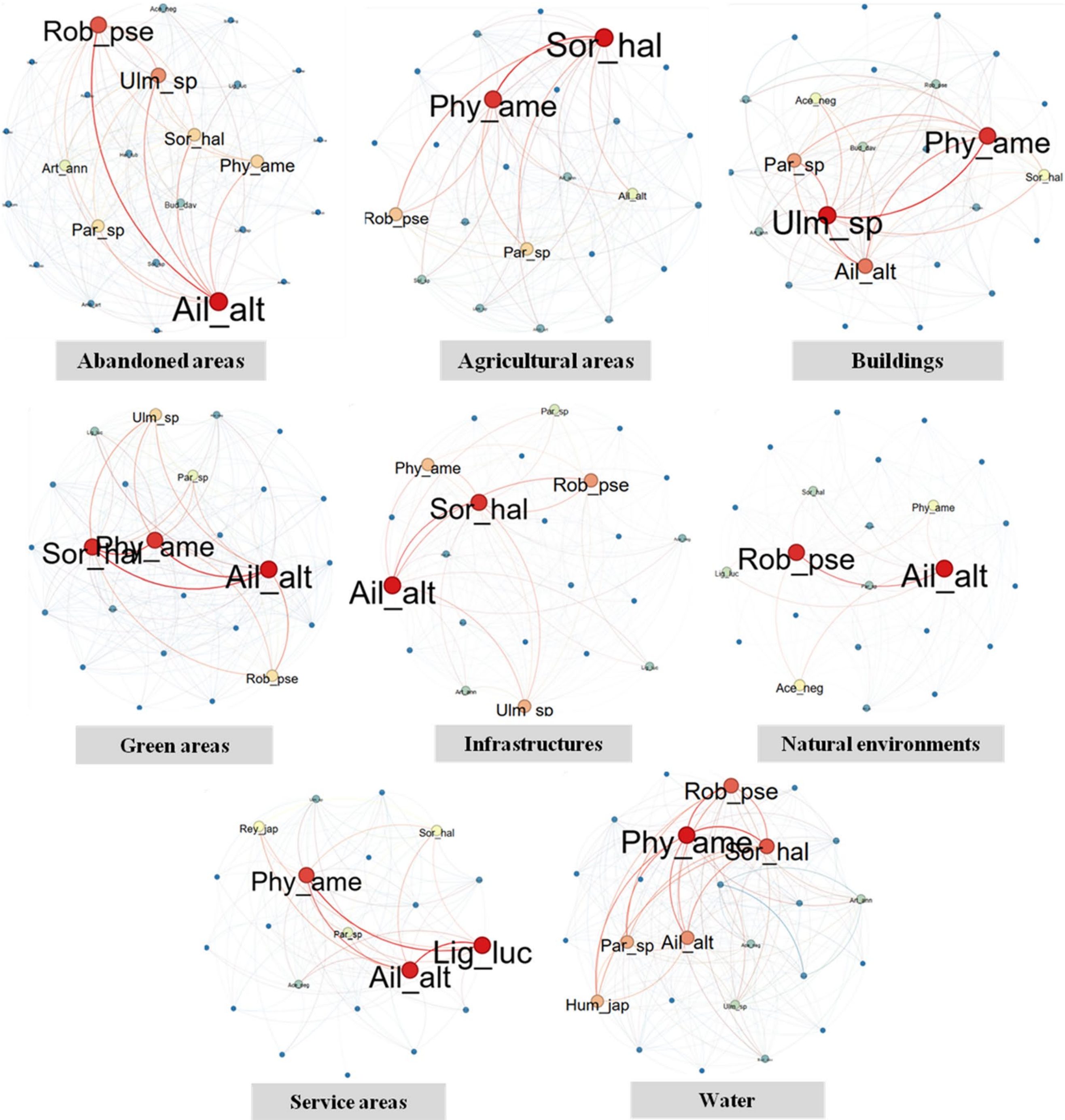
Our analysis showed clear differences in plant distribution across urban elements, revealing their variable permeability to alien plant colonization and distinct species responses.

The urban elements least prone to invasion were 'buildings', 'service areas', and 'natural environments', which hosted fewer taxa and occurrence records (Fig. S4, S5). In 'buildings' and 'service areas', limited permeability likely results from extensive hard surfaces and intensive management (Frazee et al. 2019). This was particularly evident in 'buildings', which nonetheless can act as bioreceptive elements for species adapted to dry, nutrient-poor substrates and extreme microclimates (Jim and Chen 2011; Chen et al. 2020). In our study, *U. pumila* and *P. americana* were the main taxa colonizing 'buildings', even more than *A. altissima*, a well-known example of invasive species on built structures (Trotta et al. 2020; Celesti-Grapow and Ricotta 2021). Like *A. altissima*, *U. pumila* combines rapid growth and drought tolerance; its sprawling root system allowing swift anchorage on walls and roofs (Kowarik and Säumel 2007; Park et al. 2016; Montagnoli et al. 2024). It resists management through re-sprouting and colonization of hard-to-reach impervious sites, which likely explains its presence in association with maintained structures such as residential and commercial buildings and poorly maintained public buildings (e.g. schools, hospitals) in this urban element (Fig. 5). Unlike *U. pumila*, *P. americana* – despite its plasticity – is prevented from establishing in the most impervious building parts (e.g. cracks or vertical surfaces), likely due to its bulky root system, which impedes growth in cracks or on vertical surfaces. As a result, it tends to colonize poorly managed ground-level areas, such as wall bases in abandoned buildings. The widespread ornamental climber *Parthenocissus* agg., though expected on city-centre walls, was mostly present there only in cultivation. In contrast, it was more often found naturalized on suburban walls, especially on abandoned buildings (Table S2.3, S2.4), where low disturbance and high propagule pressure from frugivorous birds favour its establishment (Reynolds et al. 2019).

In 'service areas', *A. altissima* and *P. americana* mainly colonized outdoor sports facilities and industrial sites, though both also occurred in archaeological areas, cemeteries, and working sites (Fig. 5). The role of outdoor sports facilities for *A. altissima* has been noted in other cities (Páz-Dyderska et al. 2020), while industrial areas favour colonization due to lower maintenance intensity than denser built-up sectors (Ricotta and Godefroid 2018). Aside from the suitable microhabitats for *L. lucidum* establishment (Fig. 4), cemeteries also provide dispersal opportunities via frugivorous birds utilizing these structurally complex urban meso-elements (Kowarik et al. 2016; Caneva and Bartoli 2017).

'Natural environments' hosted a low number of taxa (Fig. S4), but it was an underrepresented urban element in our cities and surveys. Nevertheless, some species dominated disturbed urban natural contexts, particularly *R. pseudoacacia* and *A. altissima* in natural woods (Figs. 4 and 5). *R. pseudoacacia* was frequently dominant, occupying extensive areas. These local-scale findings align with Campagnaro et al. (2022), confirming *R. pseudoacacia* and *A. altissima* as Italy's main forest woody invaders.

Over half of the urban elements were far more permeable to alien plant colonization: 'abandoned areas', 'agricultural areas', 'water', 'green areas' and 'infrastructures' yielded the highest numbers of records (Fig. S4a, S4b). Wastelands, agricultural lands and riverbanks provide suitable habitats and dispersal corridors for alien species through extensive unsealed and unmanaged areas (Aronson et al. 2017; Hou et al. 2023). This pattern is confirmed by the meso-scaled analysis, showing frequent occurrences in natural soils, uncultivated fields and verges, and the natural banks of watercourses (Fig. 5). Here, *R. pseudoacacia* prevailed in more peripheral elements and was particularly frequent in 'abandoned areas', 'water' and (secondarily) in 'agricultural areas' (Fig. 4, Table S2.3), consistent with previous findings (Cierjacks et al. 2013; Sádlo et al. 2017). In rural contexts, its persistence may also reflect historical planting and the accompanying generally positive perception linked to its resilience and multiple uses (e.g. hedges, timber, honey production) (Vítková et al. 2020). Conversely, *A. altissima* had a negligible role in 'agricultural areas' (Fig. 4, Table S2.3), probably due to control along field edges and its preference for other types of environments more suitable for thermophilous pioneer species (Motti et al. 2021). In these contexts — particularly in intensive periurban cultivated fields (e.g., around Milan) — the dominant weeds were the herbs *S. halepense* and *P. americana* (Fig. 4; Table S2.3), both typical agricultural weeds often found in fields and monocultures (Follak et al. 2022; Peerzada et al. 2023).In the urban matrix, watercourses act as major dispersal corridors (Wagner et al. 2020). *R. pseudoacacia* preferentially colonized natural riverbanks (Figs. 4 and 5, Table S2.3). In contrast, *P. americana* and *S. halepense* were common along artificial or periodically dry watercourses (Fig. 4), reflecting their adaptation to highly disturbed, often impervious habitats. *A. altissima* occurred secondarily in this element, likely limited by competition with riparian vegetation along natural banks. Notably, *H. japonicus* emerged as a common species along watercourses (Fig. 4, Table S2.3) particularly in disturbed artificial channels with high light availability and low competition, conditions that promote its spread (Fried et al. 2018).The richest urban elements for


Abandoned areas

Agricultural areas

Buildings

Green areas

Infrastructures

Natural environments

Service areas

Water

Fig. 4 Comparison of taxa centrality among urban elements through the weighted co-occurrence network. Nodes: colour and size gradient from the most central taxa (red, large dots) to less central taxa (blue, small dots). Edges: colour and size gradient from the strongest (red, thick) to weaker connections (blue, thin)

alien species were ‘infrastructures’, together with ‘green areas’ (Fig.S4). Roads and railways facilitate the spread of pioneer species through high abiotic stress, low competition and dispersal via vehicles and maintenance (Benedetti and Morelli 2017; Toffolo et al. 2021). It is no coincidence that most of alien species recorded along these elements are wind-dispersed (Kowarik and von der Lippe 2011). Roads and verges serve as primary pathways for *A. altissima* and *U. pumila* spread across the Mediterranean region (Motti et al. 2021; Reynolds et al. 2022). In peripheral areas, more permeable unsealed verges allow greater abundance of *R. pseudoacacia* (Toffolo et al. 2021).

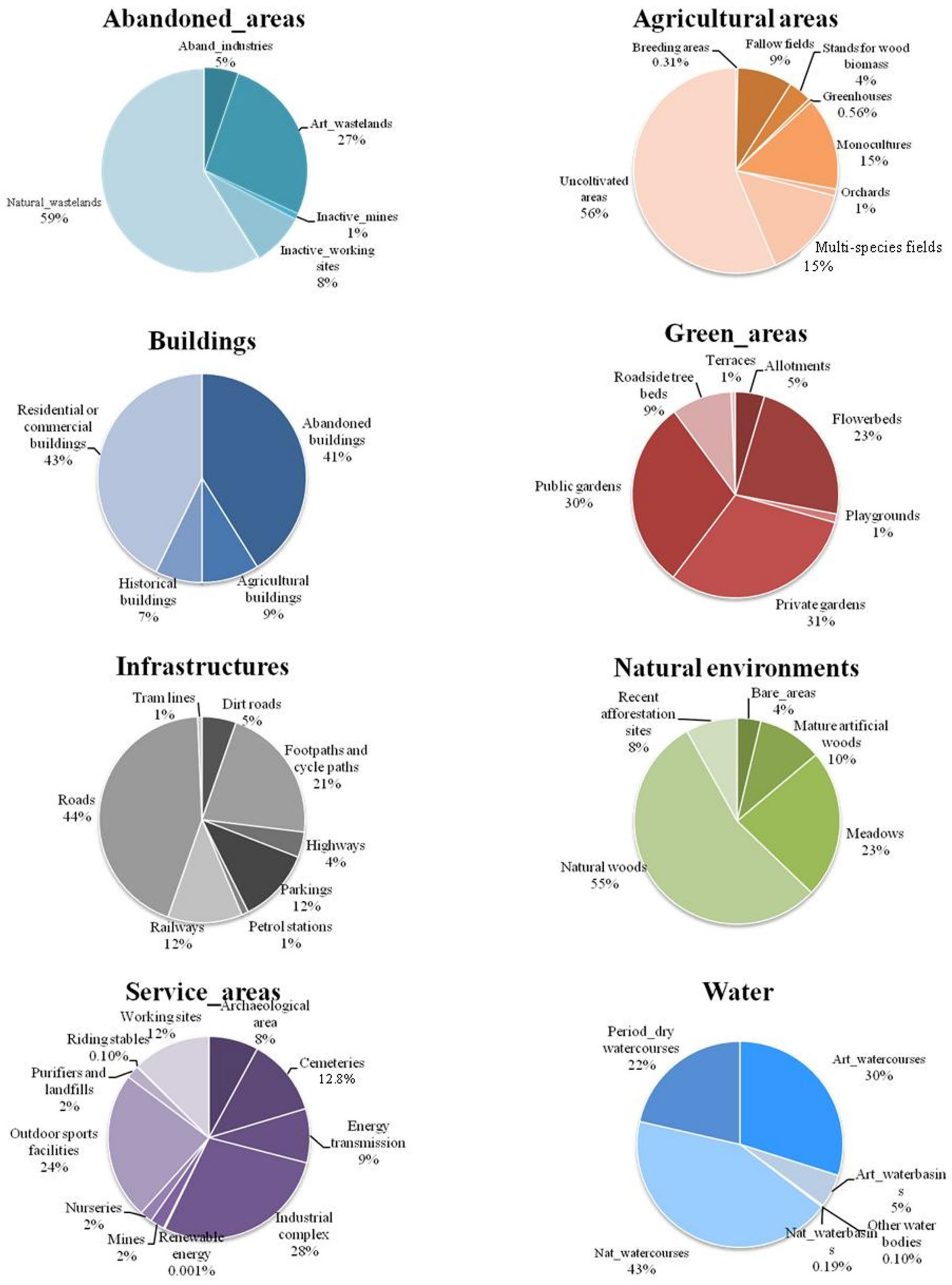

Abandoned_areas
Aband_industries 5%
Art_wastelands 27%
Inactive_mines 1%
Inactive_working sites 8%
Natural_wastelands 59%
Agricultural areas
Breeding areas 0.31%
Fallow fields 9%
Stands for wood biomass 4%
Greenhouses 0.56%
Monocultures 15%
Orchards 1%
Multi-species fields 15%
Uncoltivated areas 56%
Buildings
Residential or commercial buildings 43%
Abandoned buildings 41%
Historical buildings 7%
Agricultural buildings 9%
Green_areas
Roadside tree beds 9%
Terraces 1%
Allotments 5%
Flowerbeds 23%
Public gardens 30%
Playgrounds 1%
Private gardens 31%
Infrastructures
Tram lines 1%
Dirt roads 5%
Footpaths and cycle paths 21%
Roads 44%
Highways 4%
Parkings 12%
Railways 12%
Petrol stations 1%
Natural environments
Recent afforestation sites 8%
Bare_areas 4%
Mature artificial woods 10%
Meadows 23%
Natural woods 55%
Service_areas
Working sites 12%
Archaeological area 8%
Riding stables 0.10%
Purifiers and landfills 2%
Cemeteries 12.8%
Outdoor sports facilities 24%
Energy transmission 9%
Nurseries 2%
Mines 2%
Renewable energy 0.001%
Industrial complex 28%
Water
Period_dry watercourses 22%
Art_watercourses 30%
Art_waterbasins 5%
Other water bodies 0.10%
Nat_waterbasins 0.19%
Nat_watercourses 43%

Fig. 5 Distribution of the total number of occurrence records of taxa into meso-scaled urban elements for each (macro-scaled) urban element

In city centres, 'green areas' facilitate alien spread through ornamental introductions and management practices that create suitable microhabitats (e.g. irrigation, mowing) (Nielsen et al. 2014; Bayón et al. 2021). *S. halepense* and *P. americana* were frequent in 'green areas', together with *A. altissima* (Fig. 4, Table S2.3), but their frequency varied by green area type. In fact, *P. americana* and *A. altissima* occurred mainly in private gardens, whereas *S. halepense* preferred flowerbeds (Fig. 5). The abundance of *P. americana* likely reflects bird-mediated dispersal (Li et al. 2017; Mubamba et al. 2022). *A. altissima* may have been favoured by infrequent management (resprouting species) or citizen tolerance (Sladonja et al. 2015). *S. halepense* most likely reached flowerbeds through soil contamination (from rural areas) or from roadside vegetation (Fanfarillo et al. 2022), and once there probably benefitted from insufficient maintenance.

Urbanization gradient influences taxa distribution rather than their richness or frequency

In our analysis, the gradient of urbanization is expressed by the variation in cover and fragmentation of artificial surfaces, which gradually shifts from HL to LH urban categories (HL, HM, LM, LH). This generally represents a transition from highly built-up city centres to peripheral zones where buildings and infrastructures blend with rural landscapes. Overall, taxa richness and frequency did not vary significantly along the gradient (Fig. S4d, S4e). However, the HM category (high cover and medium fragmentation of artificial surfaces) showed higher values than HL (high cover and low fragmentation), consistent with previous studies identifying intermediate urbanization as favourable to plant richness (McKinney 2008), likely due to combined propagule pressure and increased habitat heterogeneity. The lower taxa richness observed in city centres (HL) aligns with Čeplová et al. (2017) for Central European cities.

Contrary to richness and frequency, the urbanization gradient influences taxa distribution patterns. *A. altissima* and *S. halepense* accounted for most dissimilarities among urban categories. Network analysis (Fig. 6) revealed two main patterns: species increasing from peripheries to city centres, and those showing the opposite trend, i.e. reflecting taxa more or less strictly associated with urban environments. *Ailanthus altissima* was among the most frequent and widespread taxa in all categories, confirming its adaptability to diverse urban elements. Its frequency slightly declined from city centres to peripheries (Fig. 6; Table S2.4) reflecting the high habitat suitability of *A. altissima* for 'buildings' and 'infrastructure', i.e. key urban elements in city centres. *U. pumila* exhibited an even clearer pattern (Fig. 6; Table S2.4). Conversely, *S. halepense*, *Parthenocissus* agg. and particularly *R. pseudoacacia* increased from central to peripheral areas, as did several secondary species (*A. artemisiifolia*, *Solidago* spp., *H. japonicus*, *T. fortunei*) (Fig. 6, Table S2.4), mainly associated with more natural suburban elements such as 'agricultural areas' and 'water'. These opposing trends likely arise from both environmental and anthropogenic factors, including species-specific adaptability, cultivation frequency, and management practices across the urban landscape.

We can add that, although highly urbanized city centres impose multiple stressors (i.e. disturbance, pollution and extensive hard surfaces) they can also host species adapted to the peculiar 'azonal' microclimates typical of these environments. A greater presence of thermophilous species in highly urbanized contexts compared with cooler, less urbanized peripheries has been widely documented (Schmidt et al. 2014; Géron et al. 2022). This pattern was evident for *A. altissima*, thriving in warmer city centres, and *R. pseudoacacia*, more abundant in suburbs. *Ailanthus altissima* thrives in urban environments due to its tolerance to heat, drought and soil compaction (Sladonja et al. 2015), while *R. pseudoacacia*, native to temperate North America, though widely planted, is less resilient to urban stressors (e.g. limited water availability; Wu et al. 2025) and more constrained by germination and light requirements (Vítková et al. 2017; Pepe et al. 2020), limiting its establishment in highly built-up areas. Among the secondary species, many temperate taxa (*Parthenocissus* agg., *A. artemisiifolia*, *Solidago* spp., *H. japonicus*, *T. fortunei*) were more frequent in suburbs over city centres, except *U. pumila*, which remained frequent in city centres. This contrast likely reflects life-history traits rather than temperature. *U. pumila* shares several adaptive features with *A. altissima* rather than with *R. pseudoacacia* or other temperate taxa; for example, its high climatic plasticity and drought resistance enable survival in harsh anthropogenic habitats (Ghelardini et al. 2010; Fragnière et al. 2021). Additionally, the shade tolerance of both *A. altissima* and *U. pumila* (Knüsel et al. 2017; Reynolds et al. 2022) likely favoured their persistence in densely built city centres with reduced direct sunlight availability due to the high density of buildings. In contrast, *R. pseudoacacia* and *S. halepense*, heliophilous taxa (Vítková et al. 2017; USDA NRCS 2024), prevailed in suburbs, consistent with the general increase of sun-loving species toward rural zones (Jogan et al. 2022). Moreover, *A. altissima* and *U. pumila* efficiently colonize highly managed city-centre sites due to their long-distance wind-dispersed seeds, high germination rates, and ability to persist as resprouting shrubs (Paź-Dyderska et al. 2020; Reynolds et al. 2022), i.e. traits more pronounced in these

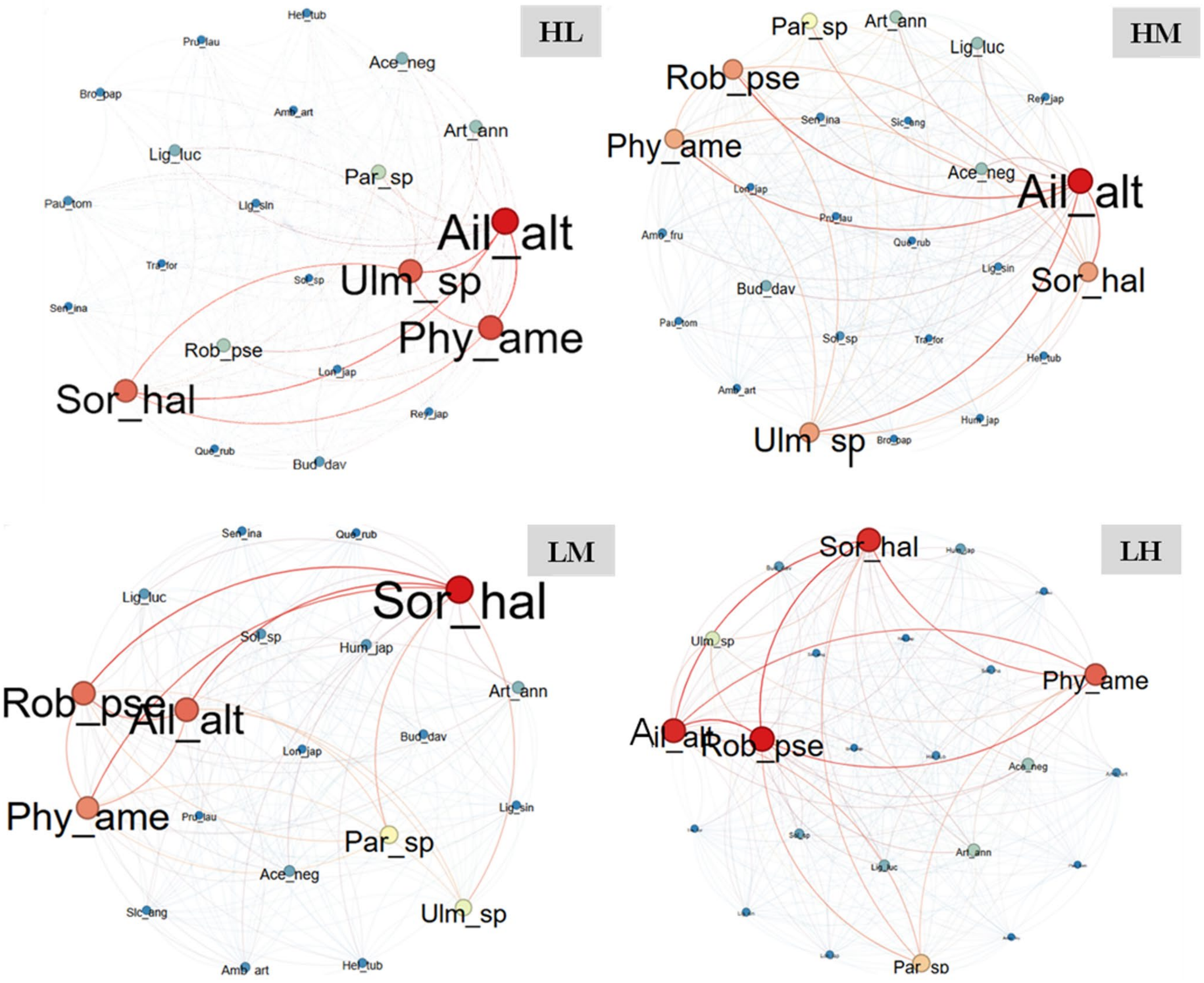


Fig. 6 Comparison of taxa centrality among urban categories through the weighted co-occurrence network. Nodes: colour and size gradient from the most central taxa (red, large dots) to less central taxa (blue, small dots). Edges: colour and size gradient from the strongest (red, thick) to weaker connections (blue, thin)

species than in *R. pseudoacacia* (Cabra-Rivas and Castro-Díez 2016; Vítková et al. 2017), which is therefore largely restricted to less disturbed peripheral areas where larger stands can develop.

Different distribution patterns also reflect changes in habitat availability along the gradient (Potgieter et al. 2024). *R. pseudoacacia*, *S. halepense* and several secondary taxa (*A. artemisiifolia*, *Solidago* spp., *H. japonicus*) are typical of rural and agricultural environments (Montagnani et al. 2017; Fried et al. 2018). Despite increased in importance toward the suburbs, *S. halepense* remained consistently represented along the entire gradient. Although *S. halepense* is a common agricultural weed, it easily shifts to non-agricultural habitats, as evidenced by its integration into a variety of vegetation types (Sezen et al. 2016; Fanfarillo et al. 2022). Finally, the major presence of *Parthenocissus* agg. in peripheral areas may result from less intensive vine management and more frequent cultivation of fleshy-fruited species in suburban gardens (Horvat et al. 2024), combined with broader habitat availability outside city centres.

Conclusions

Beyond a core group of widespread alien species found consistently across all three cities – namely *A. altissima*, *P. americana*, *R. pseudoacacia* and *S. halepense* – our analysis identified two additional noteworthy cases. *Ulmus pumila* was particularly widespread in Milan and Turin, where local climatic conditions seem especially favourable to its establishment. Conversely, in Rome *L. lucidum* was frequently recorded as spontaneously occurring, though typically confined to specific habitats. Our study highlighted the species most frequently associated with highly and less built-up areas and different urban zones. 'Green areas' and 'infrastructures' confirmed their role as key bioreceptive habitats promoting alien plant richness within urban environments. In contrast, buildings and commercial or 'service areas' proved to be the least permeable element to invasion by the target species.

According to our findings, urban planning and management should prioritize controlling the spread of *A. altissima*, *P. americana*, *R. pseudoacacia* and *S. halepense*. Urgent research is also needed on the taxonomy and invasiveness of *U. pumila* to clarify its current status and expansion in Italy. Our findings suggest that preventing and managing urban invasions requires strategies tailored to different levels of urbanization and fine-scale land use. Considering the potentially disruptive impacts of these species, species-specific actions should be incorporated into projects enhancing ecosystem services, citizen well-being, and the conservation of urban natural and historical heritage. Although the dominant taxa in our study were widespread and frequent, it is important not to overlook less common species, which may exert significant impacts at thelocal scale. Expanding the analysis to additional cities of varying size and biogeographical context would enhance our understanding of invasion dynamics and support more detailed assessments of urban invasion risk.

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Author contributions All authors contributed to the study conception and design. Material preparation was performed by all authors and data were collected by C.M., N.S., E.V., E.B., L.C-G, G.D., F.E., F.L. Analysis were performed by C.M., R.G. and S.C. The first draft of the manuscript was written by C.M. and N.S. and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability Species occurrence data will soon be available through the online repository of the project funding the work. At the moment, the data can be requested from the authors.

Declarations

Competing interests The authors declare no competing interests.

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