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Where the not-so-wild things are in cities? The influence of social-ecological factors in urban trees at multiple scales

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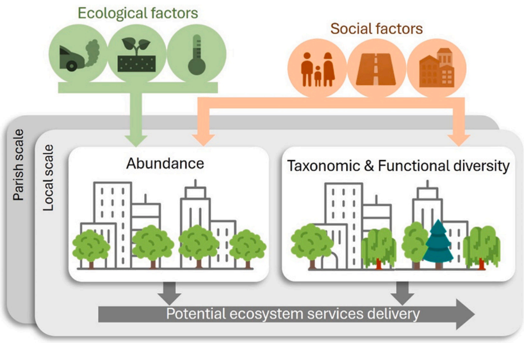
HIGHLIGHTS

- Urban tree abundance, and taxonomic and functional diversity vary spatially.
- Social factors linked to all indices; ecological factors linked to abundance.
- Factors can act as filters affecting functional expression and ecosystem services.
- Need for long-term studies to understand specific cause-effect relationships.

GRAPHICAL ABSTRACT



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ABSTRACT

Green infrastructure plays an essential role in cities due to the ecosystem services it provides. However, these elements are shaped by social and ecological factors that influence their distribution and diversity, affecting ecological functions and human well-being. Here, we analyzed neighborhood tree distribution - trees in pocket parks, squares and along streets – in Lisbon (Portugal) and modelled tree abundance and taxonomic and functional diversity, at the parish and local scales, considering a comprehensive list of social and ecological factors. For the functional analyses, we included functional traits linked to dispersal, resilience to important perturbations in coastal Mediterranean cities, and ecosystem services delivery. Our results show not only that trees are unevenly distributed across the city, but that there is a strong influence of social factors on all biological indices considered. At the parish and local scales, abundance and diversity responded to different factors, with abundance being linked to both social and ecological variables. Although the influence of social factors on urban trees can be expected, by modelling their influence we can quantify how much humans modify urban landscapes at a structural and functional level. These associations can underlie potential biodiversity filters and should be

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analyzed over time to inform decisions that support long-term ecological resilience, maximize trait functional expression, and increase equity in ecosystem services delivery.

1. Introduction

As human populations grow and urbanization expands, the diversity and dynamics of urban green infrastructure reflect social and ecological contexts, embodying the complexity of urban areas throughout time (Grimm et al., 2008; McPhearson et al., 2022). These local contexts are known to shape green infrastructure's composition and distribution, often leading to an uneven delivery of ecosystem services (Grilo et al., 2022).

The distribution and diversity of urban trees, in particular, are shaped by ecological and social factors that often interact and influence tree location, survival, establishment, and growth (Mullaney et al., 2015). The ecological factors include abiotic conditions such as climate, hydrology, soil type, pollution, and land use, as well as biotic interactions (Bigsby et al., 2014; Bourne and Conway, 2014; Groffman et al., 2014; Nitoslawski et al., 2017; Roman et al., 2018; Smart et al., 2020). The social factors reflect specific cultural and socio-demographic backgrounds, influencing species symbolism and landscape periodic trends (Avolio et al., 2018; D'Amato et al., 2023). For instance, areas of higher income and educational status have been linked to a higher abundance of street trees (Neckerman et al., 2009; Kirkpatrick et al., 2011; Pham et al., 2017; Shams et al., 2020), which enhances walkability and livability, often leading to environmental injustices (Tooke et al., 2010; Sarkar et al., 2015). Urban trees can also be influence by economic incentives and constraints, as well as governance decisions, due to their role in city beautification movements and vegetation management systems (Huang et al., 2007; Nitoslawski et al., 2017; Pham et al., 2017; Roman et al., 2018, 2021; Berghauser Pont et al., 2019; Smart et al., 2020). The built infrastructure of cities, including development history and street type, can condition the space allocated for trees, affecting their establishment and growth (Pham et al., 2017; Smart et al., 2020).

These complex and interacting social-ecological variables can also affect tree functional traits by filtering their functional expression, with consequences on fitness and survival (Williams et al., 2009; Grilo et al., 2022). Furthermore, given that higher functional diversity is associated with higher ecological resilience and delivery of multiple ecosystem services, social-ecological filtering processes can also affect citizens' health and quality of life (McPhearson et al., 2023). For example, hindering climatic conditions or management budget constraints that prevent the irrigation of plants can affect specific traits like Specific Leaf Area. This, in turn, may affect the delivery of important ecosystem services for human well-being, such as climate regulation (Grilo et al., 2022; McPhearson et al., 2022).

The social-ecological factors that influence urban trees can act at broader or finer scales (Kendal et al., 2012), according to city expansion patterns, extreme weather events (Luck et al., 2009), different governance regimes within a city (Troy et al., 2007), and microclimatic conditions (Grilo et al., 2020). However, to date, few studies have addressed the complex relationships between biodiversity and social-ecological contexts in urban areas at different spatial scales (Pham et al., 2017; Roman et al., 2018; D'Amato et al., 2023). These studies either analyze few factors and a single scale of analysis, or compare street trees across different cities, or limited areas, within a city (Pham et al., 2017). These approaches do not reflect potential biodiversity filtering processes nor consider other trees at the neighborhood level, as they focus only on urban forests or street trees. Nonetheless, both street trees, and the trees of small pocket parks and squares - hereafter neighborhood trees - are particularly important in older and denser urban matrixes (Breger et al., 2019), since they are the most abundant public green element in heavily built-up areas, that lack space for sizable green areas (Keller and Konijnendijk, 2012; Graça et al., 2018). These trees have a vital role in ensuring cities' livability and citizens' well-being (Bartens et al., 2009; Nowak et al., 2018; Dodman et al., 2022), and serve as ecological corridors that connect larger green spaces, allowing for the dispersal of fauna (Mullaney et al., 2015).

In this study, we look at different facets of neighborhood trees' diversity: i) at the taxonomic (abundance, species richness, Shannon diversity index, evenness, beta diversity) and ii) at the functional (divergence and evenness) levels, across two spatial scales (civil parish and local scales). We then analyze the relationship between each biological index and a comprehensive and diverse list of social and ecological factors that can act as potential biodiversity filters. Specifically, this study asks: i. How are neighborhood trees taxonomically and functionally distributed across the city? ii. Are they mostly associated with social or ecological factors? iii. Do these relationships differ if we analyze broader and finer scales? By exploring these questions, we aim to identify the most important variables that can act as biodiversity filters. We conducted this study in Lisbon, Portugal, a historical city with strong environmental commitments, including an increase in the area occupied by green infrastructure and the creation of local biodiversity and climate change adaptation plans (Luz et al., 2019), which led to the city receiving the 2020 European Green Capital award. By analyzing multiple biological indices and spatial scales, we can gain a better understanding of how social-ecological factors may be affecting neighborhood trees and potential ecosystem services delivery, providing useful and spatialized information for urban planning and management strategies.

2. Methodology

2.1. Study area

The study was performed in Lisbon, the capital of Portugal, a coastal city on the north bank of the mouth of the Tagus river (38°43′00" N; 9°07′59" W). Lisbon has a Mediterranean climate, characterized by hot and dry summers and cold and rainy winters, with an annual mean temperature of 17.2 °C, and a mean annual precipitation of 704.8 mm (1960–2022 average; PORDATA, 2023). It covers an area of 8545 ha (ha), with a resident population of 545,000, though it surpasses 1 million people daily due to tourism and commuting movements (INE, 2021). The city has expanded along the river into the interior, growing steadily until the 1950s, when many new neighborhoods and avenues were built, and experienced a sharp growth after the 1970s. Currently, it includes 24 civil parishes, which represent the smallest administrative jurisdiction in Portugal, and 2823 census tracts, relatively small and permanent statistical subdivisions within each parish at which census are analyzed (INE, 2021) (Fig. 1). For the purposes of this paper, the local scale considered represents these census tracts.

2.2. Neighborhood trees and traits data

Lisbon's tree data (n = 65,796) was retrieved from a publicly available tree census database currently being developed by the municipality of Lisbon (CML, 2022). This dataset includes the location and, when available, the species identification of trees that are not embedded in large green spaces (Fig. 1). Trees that are not considered neighborhood trees (for example, trees in cemeteries that are not experienced by the overall public) were excluded from this study. To calculate taxonomic and functional indices, we excluded trees not identified at the species level, and analyzed species synonyms according to The Plant List (2010) to uniformize all species names. In the few cases where some individuals were only identified to the genus level, as a matter of probability we considered them as the species with most individuals. For functional analyzes, we considered the species collectively attaining 70 % of the relative abundance, seeing that this has been considered an adequate proportion to functionally characterize a plant community (Pakeman and Quested, 2007), making up a total of 20 taxa. Within these, 1528 individuals were identified as *Platanus sp.*, which we have considered as *Platanus x hybrida* due to a clear higher abundance of this species over other *Platanus* species (Table S1). In order to increase result robustness at the finer scale, only census tracts with >3 species were used to compute functional indices.

For functional analyses, we retrieved trait information at the species level from several publicly available information sources, prioritized according to the following criteria: 1) Portuguese databases; 2) Iberian databases; 3) urban trees databases; 4) other databases (Table S2). The traits selected for this study were intended to consider a number of potential functions linked to traits, namely: i. survival and regeneration, ii. resilience to relevant disturbances in Mediterranean and coastal cities – heat, drought, pests, and sea proximity, iii. Capacity to regulate climate, iv. capacity to provide aesthetic experiences, and v. allergenicity. The specific traits considered are listed in Table 1. Here, our goal was not to analyze each trait individually, rather to compare the overall potential functional diversity of different areas within the city, and associate the spatial patterns found with social-ecological variables. By doing so, we can understand which locations have higher and lower potential ecological resilience and can potentially provide multiple ecosystem services (Gross et al., 2017).

The continuous numerical traits (longevity, height, leaf, flower, seed size) were categorized as ordinal (coded as 1 for low, 2 for medium, 3 for high) using Jenks natural breaks. Traits already categorized as high, medium, or low in trait databases were used as such. When discrepancies were found in species categories among datasets, we used the database prioritization criteria. Some categorical traits were transformed into binary traits (coded as 0 for no and 1 for yes), namely dispersal mode (abiotic and biotic dispersal), leaf phenology (deciduous leaves), reproduction strategy (monoecious flowers), leaf arrangement (broad leaves), and leaf shape (simple leaves) (Table S3).

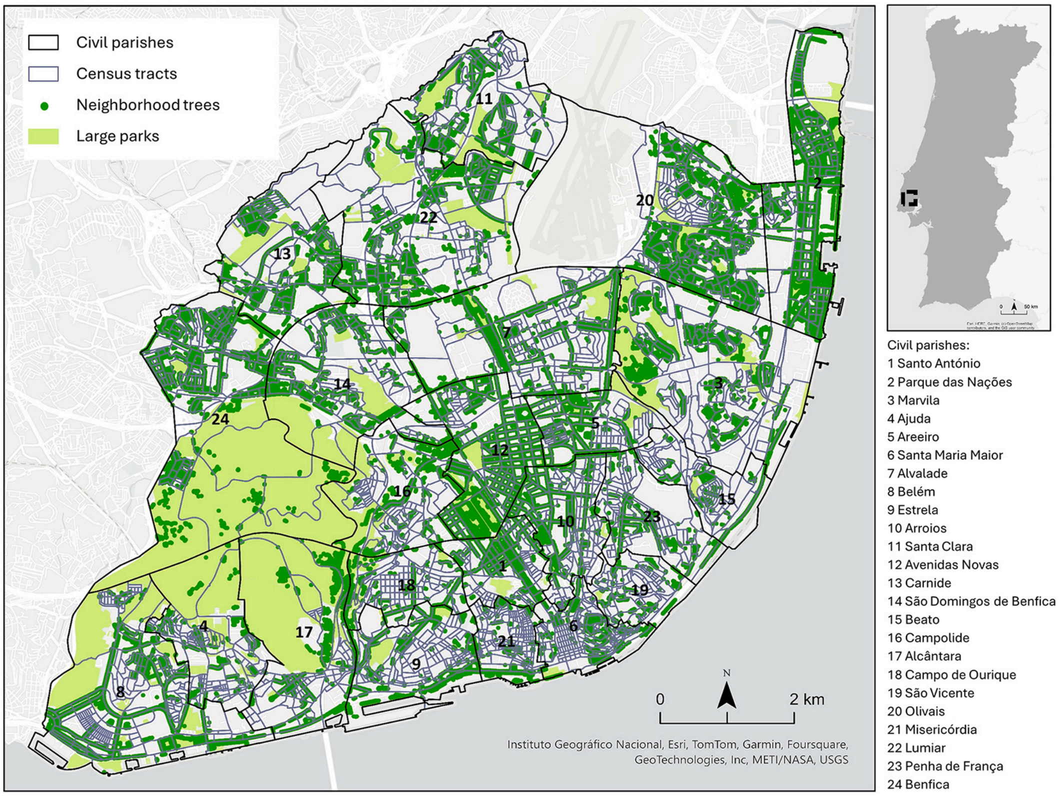
2.3. Social-ecological variables

A comprehensive set of social and ecological factors was selected based on a bibliographic analysis, in order to understand which variables can potentially influence urban tree abundance and diversity (Grilo et al., 2022). The ecological variables analyzed encompassed a range of environmental, biophysical, and ecological landscape components, including climatic variables at the macro and microscale, hydrology, soil type, atmospheric pollution, and land use (Tables 2, S4) (Nitoslawski et al., 2017; Pham et al., 2017; Roman et al., 2018; Smart et al., 2020). As in other studies, we have considered noise pollution a proxy of urbanization level (Sordello et al., 2020). The social factors analyzed included walking potential, residents' social-demographic characteristics, city amenities, and development year (Tables 2, S4). At the local scale, to enhance the robustness of the analysis, we have only considered the social-ecological variables that have values in >50 % of the census tracts. Further details on methodological approaches are provided in Table S5. All spatial analyzes were performed using ArcMap v10.8.1.

2.4. Statistical analysis

2.4.1. Taxonomic and functional analysis

We analyzed neighborhood trees i. abundance, ii. species richness; iii. Shannon diversity index (which includes species abundance, with lower values indicating lower diversity); and iii. evenness (regularity of distribution of species abundances, with lower values indicating uneven distributions; Jost, 2010). Simpson diversity index and Simpson's inverse were performed but presented similar results to the Shannon diversity index, and therefore, are not shown. All statistical analyzes were performed in R (R Core Team, 2022). Species richness and Shannon



Instituto Geográfico Nacional, Esri, TomTom, Garmin, Foursquare, GeoTechnologies, Inc, METI/NASA, USGS

Fig. 1. Location of Lisbon's neighborhood trees and large parks within the civil parishes and census tracts.

Table 1
List of traits considered for functional analysis and respective rationale.

Function	Individual traits	Rationale (examples)
Survival and regeneration	Dispersal mode - abiotic, biotic; Flower reproduction - monoecious; Growth rate; Mean longevity; Mean seed size	More dispersal strategies and fast growth rate are linked to higher spread and regeneration (Larson and Funk, 2016, Pan et al., 2020, Niu et al., 2023). Small seeds have longer dispersal distances, but lower probabilities of successful establishment (Westoby et al., 1996).
Drought resistance	Mean height; Mean leaf size; Minimum required precipitation	Small trees with small leaves are associated with lower susceptibility to drought-induced mortality (Greenwood et al., 2017, Stovall et al., 2019).
Heat resistance	Mean height; Mean leaf size; Resistance to heat; Resistance to pests	Small species have lower water stress from water loss through leaves at high temperatures (Michaletz et al., 2016). High temperatures can increase insect herbivory (Youngsteadt et al., 2015, Dale and Frank, 2017).
–	Resistance to pests	Herbivorous pests are often abundant in urban areas, therefore, a higher resistance to pests favors tree survival (Raupp et al., 2010, Meineke et al., 2013).
–	Resistance to salinity	Resistance to salinity increases tree survival in coastal areas since these trees are subject to sea water spray or penetration into the soil (Zhu, 2001, Lukac et al., 2011).
Climate regulation	Canopy projected width; Leaf arrangement - broad leaves; Leaf density; Leaf phenology - deciduous leaves; Leaf shape - simple leaves; Mean leaf size	Coniferous trees with large leaves, with dense and large canopies are associated with higher levels of climatic regulation (Pretzsch et al., 2015, Stratopoulos et al., 2018).
Aesthetic experiences	Leaf arrangement - broad leaves; Mean flower size; Leaf phenology - deciduous leaves; Leaf shape - simple leaves; Mean height; Mean leaf size	Large trees with oval dense canopies, broadleaves and large flowers are often considered aesthetically appealing (Lohr and Pearson-Mims, 2006, Goodness et al., 2016).
–	Allergenicity	Trees with high allergenicity values can negatively impact human health (Cariñanos et al., 2019).

Table 2
Type of social and ecological variables analyzed to test their association with neighborhood trees, the aggregate variables they represent, and the list of individual variables considered. Average and median were calculated for each spatial unit, at both scales; area and number of elements were calculated in proportion to each spatial unit area, at both scales.

Variable type	Aggregated variables	Variables analyzed and respective description
Ecological	Macroclimate	**Bio1**: average annual mean temperature; **Bio8**: average mean temperature of the wettest quarter; **Bio9**: average mean temperature of the driest quarter; **Bio10**: average mean temperature of warmest quarter; **Bio11**: average mean temperature of coldest quarter; **Bio12**: average annual precipitation; **Bio16**: average precipitation of wettest quarter; **Bio17**: average precipitation of driest quarter; **Bio18**: average precipitation of warmest quarter; **Bio19**: average precipitation of coldest quarter; **LST**: average summer land surface temperature
	Microclimate	**PSR**: average potential solar radiation; **Coast**: distance to the nearest coastline
	Terrain hydrology	**Humid**: humid system area
	Soil type	**Alluvial**: alluvial soil area; **Arenitic**: arenitic soil area; **Basaltic**: basaltic soil area; **Carbonate**: carbonate soil area; **Clay**: clayish soil area; **Limestone**: limestone soil area
	Pollution	**CO**: median carbon monoxide; **NO**: median nitrogen monoxide; **NO_2**: median nitrogen dioxide; **O_3**: median ozone; **$PM_{2.5}$**: median particulate matter 2.5; **PM_{10}**: median particulate matter 10; **Day_noise**: average daily noise; **Night_noise**: average nocturnal noise
	Landuse	**NDVI**: average normalized difference vegetation index; **SAVI**: average soil adjusted vegetation index; **Urban**: urban fabric area; **Crops**: crops area; **Forests**: forested area; **Green**: green spaces area; **Vacant_land**: land without use area; **Herbs**: pastures/herbs area
Social	Walking potential	**Walking:** predictive model that indicates where people are most likely to walk
	Socio-demographic characteristics	**Families1–2**: resident families with 1–2 people; **Families $\geq$ 3**: resident families with $\geq$3 people; **Residents**: residents; **Residents0–14**: residents with 0–14 years old; **Residents15–24**: residents with 15–24 years old; **Residents25–64**: residents with 25–64 years old; **Residents $\geq$ 65**: residents with $\geq$65 years old
	City elements	**Bike_lanes**: bike lane area; **Roads**: total road length; **Cultural**: libraries, cultural centers, cinemas, museums, theaters; **Education**: schools, universities; **Health**: health centers, hospitals, pharmacies; **Public**: streetlamps, viewpoints, playgrounds, kiosks; **Traffic**: parking lots, crossings, roundabouts, traffic signals, gas stations; **Amenities**: commerce, health, tourism, education, leisure amenities, historical points; **Buildings(ar)**: building area; **Buildings(n)**: buildings
	Development history	**Buildings < 1945**: buildings built before 1945; **Buildings1946–1980**: buildings built between 1946 and 1980; **Buildings1981–2000**: buildings built between 1981 and 2000; **Buildings2001–2021**: buildings built between 2001 and 2021

diversity index were calculated using the *specnumber* and *diversity* functions, respectively, within the *vegan* package (Oksanen et al., 2022). Evenness was calculated by dividing the inverse Simpson index by species richness. Associations between tree abundance and species richness and spatial unit area were examined with Spearman correlations. At the functional level, to evaluate functional diversity we considered i. functional divergence (degree of functional dissimilarity within the community, with higher values indicating high degree of niche differentiation and possible increased ecosystem function; Mason et al., 2005, Villéger et al., 2008); and ii. functional evenness (regularity with which species abundances are distributed in the functional space, with lower values meaning uneven distributions; Mason et al., 2005, Mason and de Bello, 2013). Non-binary traits were scaled, and Gower distances were calculated with the *gowdis* function. All functional indices were calculated with the *dbFD* function within the *FD* package with the *cailliez* correction (Laliberté et al., 2014).

2.4.2. *Beta diversity*

To measure variability in species composition across spatial units within each spatial scale, we calculated beta diversity using a site per species matrix with species presence-absence data for Sørensen dissimilarity measures. The Sørensen dissimilarity index measures the proportion of exclusive species among assemblages and can be partitioned into turnover and nestedness. Turnover (Simpson dissimilarity) reflects the effect of species replacement among sites, while nestedness (difference between Sørensen and Simpson dissimilarities) indicates differences in species richness when species-poor assemblages are nested in species-rich assemblages (Xu et al., 2020). Beta diversity was calculated using the *beta.multi* and *beta.pair* functions within the *betapart* package (Baselga et al., 2023).

2.4.3. *Modelling*

To account for possible spatial autocorrelation, we performed Moran tests at the parish and local scales, using the coordinates of each parish and census tract geometric center to build distance matrixes. This analysis was performed with the *Moran.I* function within the *ape* package (Paradis and Schliep, 2019). Spatial autocorrelation was significative at the local level. To model tree distribution and diversity, all social-ecological variables values were normalized. To understand which social-ecological variables presented the strongest associations with neighborhood trees, we performed Spearman correlations. At the parish scale, the best candidate variables were considered for generalized additive modelling (GAM), to account for non-linear relationships. Considering the significative spatial autocorrelation found at the local scale, we performed generalized additive mixed models (GAMM) with the parishes of each census tract used as smoothed terms. At the local

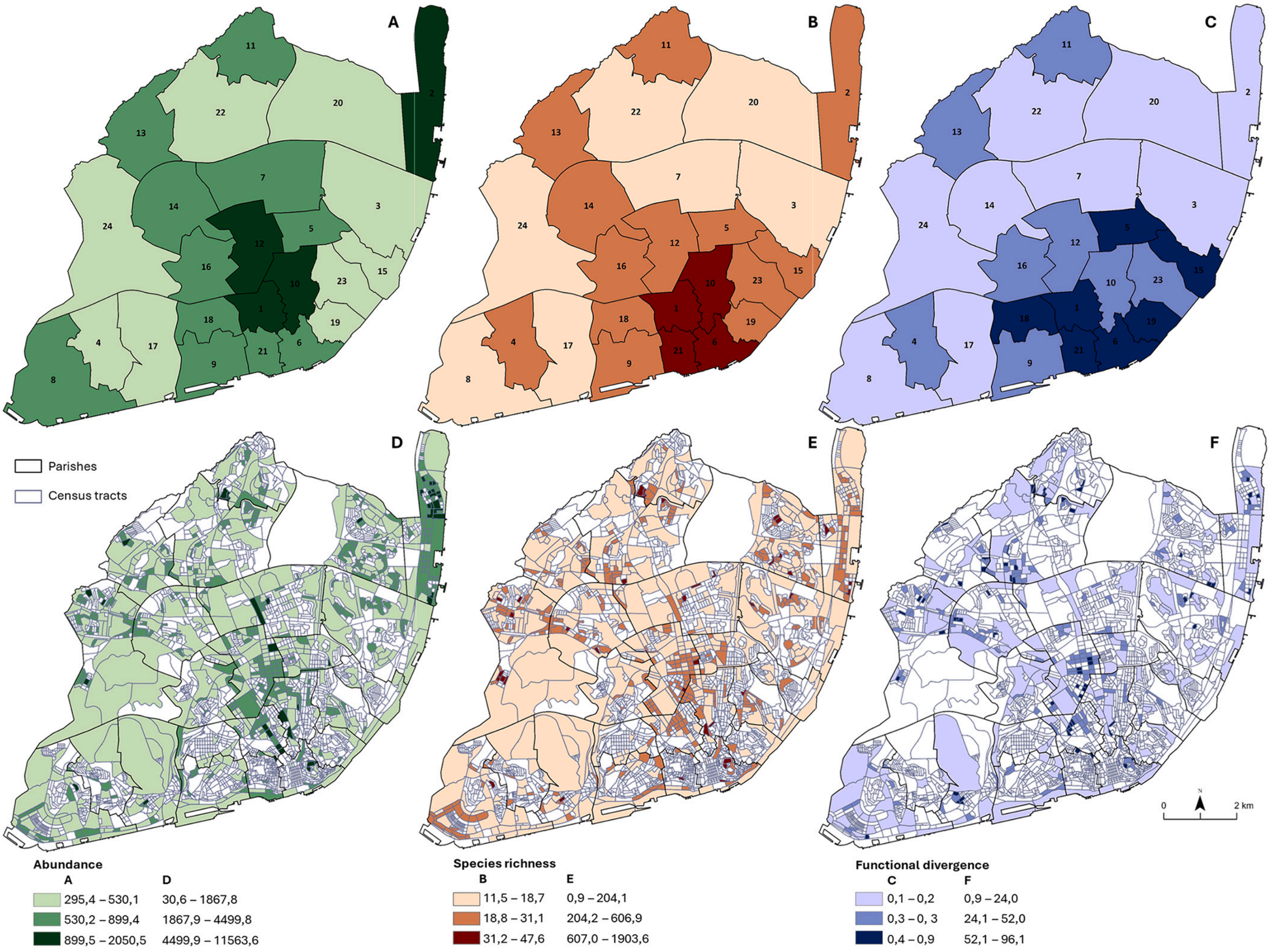


Fig. 2. Spatial distribution of the abundance (A, E), species richness (B, F), and functional divergence (C, G) of neighborhood trees in Lisbon, Portugal. A, B, C represent the results at the parish scale, and E, F, G represent the results at the local scale. At the local scale, only census tracts with >10 ha and 20 neighborhood trees were considered. For functional divergence, only census tracts with 70 % of identified trees were included (the census tracts not analyzed are represented in blank). Indices are shown in proportion to the spatial unit area in km^2. Parishes names are specified in Fig. 1.

level, we only considered tracts with >10 ha and 20 neighborhood trees to enhance the robustness of the analysis. We restricted the number of variables included in the models to five, to avoid GAM/GAMM overfitting. To minimize co-linearity effects in the regression models, among the independent variables with >70 % correlation, only one variable was retained. From all possible models for each dependent variable, we retained the best-performing one (lowest AIC and highest R^2), for which all participating independent variables presented a significant contribution. To avoid overfitting, we reduced the number of nods in the smoothed functions and used a restricted maximum likelihood estimator. Models were obtained using the *gam* and *gamm* functions and the fitting procedure and results of each model were analyzed with *gam.check*, within the *mgcv* package (Wood, 2011).

3. Results

3.1. Neighborhood tree distribution and diversity

To account for the influence of parish and census tract area on tree abundance and species richness, all results below were calculated in proportion to the respective area (parish area and i. tree abundance: $r = 0.78$, $p < 0.001$, ii. species richness: $r = 0.74$, $p < 0.001$; census tract area and i. $r = -0.66$, $p < 0.001$, and ii. $r = -0.65$, $p < 0.001$). At both spatial scales, the distribution of these indices varied across Lisbon (Figs. 2, S1, S2). At the parish scale, tree abundance was higher in the city's central and most urbanized area – Santo António, Parque das Nações, Arroios and Avenidas Novas. The parishes with a lower abundance of neighborhood trees are highly covered by an urban forest - Ajuda, Beato, Alcântara, and Benfica. The most abundant neighborhood trees in Lisbon comprise 15 genera: *Celtis sp., Jacaranda sp., Platanus sp., Pinea sp., Acer sp., Populus sp., Cercis sp., Fraxinus sp., Tipuana sp., Prunus sp., Olea sp., Melia sp., Grevillea sp., Robinia sp., Tilia sp.,* with one species (*Celtis australis*) presenting a much higher abundance than other species (Figs. 3, S1).

Regarding species richness, parishes within the city center presented a higher diversity, namely Santa Maria Maior, Misericórdia, Santo António and Arroios. Lower species richness was found in northern and eastern parishes, and in parishes largely covered by an urban forest (Fig. 2). Trees' Shannon diversity index and evenness were higher in most parishes of the historic center and adjacent areas (Fig. S1). The composition of neighborhood trees analyzed through beta diversity, showed that the total variation in species composition between parishes was 0.86, with 0.78 related to species turnover. Therefore, Lisbon's parishes have a high variation in neighborhood trees, which is mainly explained by species replacement. The most built-up areas of the city have higher values of beta diversity (Fig. S1). At the functional level, divergence and evenness also showed higher values in the most urbanized areas of Lisbon, and the lowest values were mainly found in oriental and northern parishes (Figs. 2, S1).

At the local scale, our results show that few locations within each parish account for the highest values found for all indices (Figs. 2, S2). For beta diversity, variation in species composition between census tracts was 0.99, which is explained by species turnover.

3.2. Tree associations with social-ecological factors

At both scales, the strongest correlations between neighborhood trees' taxonomic and functional indices and the social-ecological variables analyzed, showed that species richness, Shannon diversity index, and evenness were mostly associated with social factors (Tables 3, 4, S5, S6, S7, S8). City amenities and residents' socio-demographic characteristics presented the highest positive correlations. Abundance was strongly associated with both ecological and social factors at broader and finer scales, including positive associations with city elements and negative associations with green areas (Tables 3, 4, S5, S6).

Overall, both GAM and GAMM results showed that the best statistical

Fig. 3. Images of locations in Lisbon without neighborhood trees (A), with neighborhood trees in a pocket park (B), with high abundance of neighborhood trees with low diversity (*Platanus x hybrida* and *Celtis australis*) (C), and with high abundance of neighborhood trees with high diversity (D). Photos by Filipa Grilo.

Table 3

The 10 highest Spearman correlations between neighborhood tree abundance, species richness, Shannon diversity index, evenness, functional divergence (Fdiv) and functional evenness (Feve), and the social (S) and ecological (E) variables analyzed, for the parish level. Variables names are specified in Table 2. Significant correlations are marked: * - $p < 0.05$; ** - $p < 0.01$; *** - $p < 0.001$.

Variables	Abundance	Variables	Species richness	Variables	Shannon index	Variables	Evenness	Variables	Fdiv	Variables	Feve
(S) Public	0.72***	(S) Buildings(n)	0.80***	(S) Buildings(n)	0.89***	(S) Buildings(n)	0.66***	(S) Buildings(n)	0.90***	(S) Buildings(n)	0.88***
(S) Walking	0.64***	(S) Residents25–64	0.80***	(S) Buildings<1945	0.86***	(S) Buildings<1945	0.65***	(S) Buildings<1945	0.88***	(S) Buildings<1945	0.85***
(S) Amenities	0.58**	(S) Amenities	0.78***	(S) Residents25–64	0.78***	(S) Residents25–64	0.64***	(S) Families1–2	0.79***	(S) Families1–2	0.82***
(S) Roads	0.57**	(S) Buildings(ar)	0.77***	(S) Families1–2	0.78***	(S) Families1–2	0.63**	(S) Residents25–64	0.79***	(S) Residents25–64	0.81***
(E) NDVI	−0.56**	(S) Residents	0.76***	(S) Residents	0.76***	(S) Residents	0.62**	(S) Residents	0.77***	(S) Residents	0.80***
(E) NO	−0.52**	(S) Families1–2	0.75***	(S) Buildings(ar)	0.75***	(E) NDVI	−0.58**	(S) Buildings(ar)	0.75***	(S) Residents≥65	0.72***
(S) Buildings(ar)	0.51*	(S) Public	0.75***	(S) Amenities	0.74***	(E) SAVI	−0.58**	(S) Amenities	0.75***	(S) Residents15–24	0.71***
(S) Buildings2001–2021	0.46*	(E) NDVI	−0.75***	(E) NDVI	−0.73***	(S) Buildings(ar)	0.57**	(E) NDVI	−0.72***	(S) Buildings(ar)	0.70***
(E) Clay	0.46*	(S) Buildings<1945	0.71***	(S) Walking	0.69***	(S) Residents≥65	0.57**	(E) CO	0.71***	(E) CO	0.69***
(E) Vacant_land	−0.46*	(S) Residents15–24	0.71***	(S) Public	0.68***	(S) Residents15–24	0.53**	(S) Walking	0.70***	(S) Buildings1946–1980	0.69***

Table 4

The 10 highest Spearman correlations between neighborhood tree abundance, species richness, Shannon diversity index, evenness, functional divergence (Fdiv) and functional evenness (Feve), and the social (S) and ecological (E) variables analyzed, for the local level. Variables names are specified in Table 2. Significant correlations are marked: * - $p < 0.05$; ** - $p < 0.01$; *** - $p < 0.001$.

Variables	Abundance	Variables	Species richness	Variables	Shannon index	Variables	Evenness	Variables	Fdiv	Variables	Feve
(S) Roads	0.60***	(S) Roads	0.60***	(S) Roads	0.68***	(S) Roads	0.81***	(S) Roads	0.88***	(S) Roads	0.84***
(S) Public	0.54***	(S) Public	0.46***	(S) Public	0.47***	(S) Buildings(n)	0.51***	(S) Public	0.58***	(S) Residents	0.57***
(S) Amenities	0.47***	(S) Amenities	0.41***	(S) Residents	0.43***	(S) Residents	0.48***	(S) Buildings(n)	0.55***	(S) Families1–2	0.56***
(S) Traffic(n)	0.47***	(S) Families1–2	0.38***	(S) Amenities	0.42***	(S) Residents25–64	0.48***	(S) Residents	0.54***	(S) Residents25–64	0.56***
(S) Families≥3	0.32***	(S) Residents≥65	0.38***	(S) Families1–2	0.42***	(S) Families≥3	0.48***	(S) Families1–2	0.54***	(S) Families≥3	0.56***
(S) Residents	0.32***	(S) Residents	0.37***	(S) Residents≥65	0.42***	(S) Residents15–24	0.47***	(S) Residents25–64	0.53***	(S) Buildings(n)	0.56***
(S) Residents25–64	0.32***	(S) Residents25–64	0.37***	(S) Residents25–64	0.42***	(S) Public	0.46***	(S) Families≥3	0.52***	(S) Residents≥65	0.56***
(S) Residents15–24	0.31***	(S) Families≥3	0.35***	(S) Families≥3	0.42***	(S) Residents0–14	0.46***	(S) Residents≥65	0.52***	(S) Residents15–24	0.55***
(S) Families1–2	0.30***	(S) Traffic(n)	0.35***	(S) Residents15–24	0.41***	(S) Buildings(ar)	0.46***	(S) Residents15–24	0.51***	(S) Public	0.54***
(S) Residents0–14	0.30***	(S) Residents15–24	0.34***	(S) Traffic(n)	0.39***	(S) Families1–2	0.45***	(S) Residents0–14	0.48***	(S) Residents0–14	0.52***

Table 5
Summary statistics for the smoothed function from each final GAM model used to analyze the relationship between abundance, species richness, Shannon diversity index, evenness, functional divergence (Fdiv), functional evenness (Feve) and the social (S) and ecological (E) variables analyzed. Includes estimated degrees of freedom (edf), F and P statistics, deviance and adjusted R^2. Variables names are specified in Table 2.

Indices	Scale	Social-ecological factors	Trend	edf	F	ρ value	Adj. R^2
Abundance	Parish	(E) Clay	U	1.9	5.0	0.02	0.58
		(E) NO	–	1.0	17.6	0.001	
		(S) Buildings(ar)	+	1.8	9.2	0.002	
	Local	(E) LST	∩	3.5	17.7	<0.001	0.35
		(S) Public	+	1.0	58.2	<0.001	
		(S) Roads	∩	3.6	30.0	<0.001	
Species richness	Parish	(S) Buildings(n)	+	1.0	17.9	0.0004	0.80
		(S) Public	+	1.0	17.2	0.0004	
	Local	(S) Public	+	1.8	22.5	<0.001	0.25
		(S) Roads	∩	3.7	28.0	<0.001	
Shannon index	Parish	(S) Buildings(n)	+	1.0	81.8	<0.001	0.78
	Local	(S) Public	+	1.0	25.6	<0.001	0.43
		(S) Roads	∩	3.8	86.7	<0.001	
Evenness	Parish	(S) Families1–2	∩	1.9	10.7	0.001	0.45
	Local	(S) Buildings(ar)	∩	3.4	15.4	<0.001	(0.58
		(S) Roads	+	3.7	173.8	<0.001	
Fdiv	Parish	(S) Buildings<1945	+	1.0	65.0	<0.001	0.74
	Local	(S) Roads	+	3.7	242.9	<0.001	0.71
Feve	Parish	(S) Buildings(n)	+	1.0	65.7	<0.001	0.74
	Local	(S) Roads	+	3.5	163.9	<0.001	0.62

models for the indices considered highlight the importance of social factors, particularly city elements, to urban tree distribution and diversity, at both spatial scales (Table 5, Figs. S3, S4). Taxonomic and functional diversity showed positive associations with the presence of buildings at broader scales, and total road length and number of public elements at finer scales. For abundance, the best models included social and ecological variables at both scales: soil type (clay), pollution (nitrogen oxide) and city elements (area of buildings) at the parish scale, and macroclimate (land surface temperature) and city elements (road length and number of public elements) at the local scale (Table 5, Figs. S3, S4).

4. Discussion

Our study showed that neighborhood tree abundance and taxonomic and functional diversity vary spatially with social-ecological factors. The models obtained revealed strong associations between all biological indices and social factors, at broader and finer scales. Tree abundance was linked to both ecological and social factors. By considering multiple spatial scales, we were able to analyze the factors influencing trees at an administrative scale (parish scale) and at an ecosystem services delivery scale (local scale). Since neighborhood trees are mostly chosen and planted by humans, the demonstrated influence of social factors could be expected. Nonetheless, by modelling the importance of these factors, our study was able to quantify how much humans modify urban landscapes at structural and functional levels. This information can help policy makers to make informed decisions that promote ecological resilience and long-term ecosystem services delivery.

Overall, neighborhood trees were associated with higher urbanization levels, namely buildings (broader scale) and roads (finer scale). At the parish scale, the areas with the highest values for all indices are older than those with lower values, and have recently been subject to strong ecological rehabilitation measures. These include abundant and diverse tree planting by the municipality, and active management, conducted by both parish councils and the municipality. Seeing that Lisbon is a consolidated city, and most built-up areas have a smaller surface of large parks and gardens, these actions are important to reduce the urban heat island effect, increase walkability, promote ecological corridors and increase citizens' well-being. The models obtained showcase this top-down awareness in having an abundant and diverse landscape where most citizens live. However, it is important to highlight that the distribution of all indices at the finer scale showed that these trees are concentrated in few census tracts, and therefore, their benefits are provided to a small percentage of the population. In addition, evenness and beta diversity values indicate that throughout the city, only a few species are dominating (particularly *Celtis australis*). This tendency occurs in other cities worldwide, where despite there being a high species richness, only a reduced number of species dominate, which decreases the overall diversity of urban biodiversity (Lohr et al., 2014; Ma et al., 2020; Galle et al., 2021; Jiao et al., 2021). This could be of concern since it could imply lower ecological functioning and ecosystem services delivery, with consequences on ecological resilience and human well-being (McPhearson et al., 2023).

Other studies have shown linkages between urban morphology and social-economic factors, and street tree abundance and diversity, particularly in more recently developed cities in North America (Pham et al., 2013; Bigsby et al., 2014; Ma et al., 2020). Yet, in these cities, street trees are more abundant and diverse in wealthier and more recently built areas. This occurs due to development patterns of urban sprawl that account for larger planting areas that can accommodate more species (Nitoslawski et al., 2017), increasing taxonomic diversity outside the city center (Pham et al., 2017; Roman et al., 2021). Still, as opposed to our study, most of these studies do not analyze diversity in proportion to the area, which can greatly influence the results, given that most cities have different sized neighborhoods or boroughs (Galle et al., 2021).

The municipal efforts to green the most built-up areas within the city are also seen at the functional level. The positive linkages between functional indices and urbanization reveal that areas where dwellers live or work potentially benefit from multiple ecosystem services delivery and have higher levels of ecological resilience. However, at the broader scale, functional divergence distribution showed that despite the high tree coverage and species richness, trees in the oriental and more recently built part of the city, are functionally similar. In other studies that focus on entire sets of trees within cities, it is shown that cities with high species richness in densely urbanized areas tend to have functionally similar species (Knapp et al., 2008, 2012; Nock et al., 2013). This could be of concern, considering that low functional diversity is associated with a lower capacity to respond to environmental changes and provide multiple ecosystem services (Cadotte et al., 2011). Still, despite the importance of functional diversity, few studies and municipal management plans are centered around functional traits (Nock et al., 2013).

In our models, tree abundance was strongly associated with social and ecological variables at both scales. These models show the importance of both factors for tree abundance, since they influence tree establishment and survival (Nitoslawski et al., 2017; Smart et al., 2020). The associations with soil type could reflect the increasing concern by urban planners to plant adequate species to local hydrological and edaphic conditions (expressed in Lisbon's tree regulation), to guarantee trees' survival, and increase abundance (Roman et al., 2018). On the other hand, trees' negative association with air pollution (broad scale) and an inverted-U-shaped curve association with summer surface temperatures (fine scale), can indicate positive links between tree abundance and ecosystem services delivery (air quality mitigation and microclimate regulation, respectively), contributing to human health and well-being (Muyshondt et al., 2022). To specifically understand cause-effect relationships between indices and these variables, long-term studies are needed.

An aspect that should be accounted for is the possible influence of these social-ecological factors on the ability of traits to functionally express and generate benefits, acting as biodiversity filters (Coleman et al., 2022; Grilo et al., 2022). For example, high levels of urbanization can affect traits' functional expression due to limited space for the trees' healthy development (McElhinney and Harper, 2019). In addition, air pollution emissions and adverse soil type can negatively affect tree establishment and growth (Canetti et al., 2017; Mukherjee and Agrawal, 2018), and increase vulnerability to pests (Ball et al., 2007); high temperatures can decrease leaf area development, and accelerate flowering, affecting climate regulation and pollination services (Cleland et al., 2007; Teskey et al., 2015). Therefore, an important next step for research would be to analyze direct cause-effect relationships between trees and social-ecological variables, in order to better understand if these are acting as biodiversity filters and inform management strategies to prevent the loss of desired ecosystem services. To do so, it would be essential to analyze these biological indices and social-ecological variables across a wide temporal scale, as well as consider trees' eco-physiological status. Such long-term studies are rare but critical to advance knowledge, as they can help local practitioners plan targeted actions to increase and diversify urban trees, fostering effective management and policy making, contributing to multifunctionality and local resilience.

Our study builds knowledge on the importance of social-ecological factors for urban tree abundance, as well as taxonomic and functional diversity. However, some limitations to this study should be considered for a more comprehensive understanding of the results, namely the inability to analyze the entire set of i. neighborhood trees, due to the lack of species identification (n ≈ 16,600); ii. census tracts, due to having very few trees and/or social-ecological variables. Nonetheless, our study provides insights about the importance of analyzing urban trees at multiple biological levels and spatial scales to support planning decisions.

5. Conclusions

In this study, we analyzed neighborhood tree distribution and diversity across Lisbon at broader and local scales, from taxonomic and functional perspectives, while focusing on their association with social-ecological factors. We found strong associations between social variables and all the indices analyzed. Ecological factors were associated with tree abundance. These relationships should be analyzed in the long-term, to ensure that ecosystem services are continuously being delivered. By comparing tree abundance and diversity at broader and finer scales, our study showed how important it is to not generalize results at larger scales due to the possibility of overestimations, with higher resolutions highlighting critical areas where trees are needed. This is particularly important in older cities, due to the lack of green spaces and inability to reconfigure the urban morphology.

CRediT authorship contribution statement

Filipa Grilo: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Timon McPhearson:** Writing – review & editing, Conceptualization. **Alice Nunes:** Methodology, Writing – review & editing. **Cristiana Aleixo:** Writing – review & editing, Methodology. **Margarida Santos-Reis:** Writing – review & editing. **Cristina Branquinho:** Writing – review & editing, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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