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Original article

Urban trees through a functional traits' lens: Exploring the interplay between tree functional groups and social-ecological factors

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ABSTRACT

Urban trees' functional traits influence their resilience to environmental changes and the delivery of ecosystem services. However, research on classifying urban trees into functional groups based on species traits - clusters of species with similar responses to environmental stressors and providing similar ecosystem services - and exploring the factors that shape their distribution is limited. This study classified a subset of urban trees in Lisbon, Portugal, into functional groups using 20 traits related to survival, establishment, tolerance, and ecosystem services delivery. We analyzed their distribution patterns across the city and modelled their abundance at the local scale, considering various social and ecological factors. These results were integrated with the municipality's tree selection criteria. Our results revealed three functional groups - temperate, mediterranean, and tropical - each with the potential to deliver complementary ecosystem services. The distribution of the temperate functional group, the most abundant, was primarily associated with social factors, such as proximity to roads and public spaces. However, the temperate group had lower potential resilience to climate change due to its association with humid temperate climates, raising concerns in areas dominated by these species. In contrast, the mediterranean and tropical groups were influenced by both social and ecological factors, with trait data suggesting their potential to thrive under future climate conditions. These findings emphasize the need to enhance local functional diversity to increase ecological resilience and ensure a wider range of ecosystem services, especially in the context of climate adaptation. Overall, this analysis demonstrates the importance of social-ecological factors in shaping the functional composition of urban green spaces, offering insights into the roles of traits in sustainable species selection and urban tree management.

1. Introduction

Urban green infrastructure is central to shaping ecological and aesthetic landscapes in cities, providing essential ecosystem services that enhance human well-being (Childers et al., 2019). Urban trees, as a key aspect of nature-based solutions, contribute to sustainable urban planning by delivering various benefits. These benefits include air quality improvement, microclimate regulation, aesthetics, and recreational spaces, which support the ecological, social, and economic resilience of urban environments (Roy et al., 2012; Nesbitt et al., 2019). The strategic placement, abundance, and diversity of trees amplify these benefits, making them integral to nature-based solutions initiatives aimed at creating healthier and more resilient urban environments.

Urban areas often exhibit high levels of species richness, primarily due to the intentional introduction of regionally non-native species by humans (Wang and Zhang, 2022). However, this diversity is often unevenly distributed, with a reliance on a few species from one or two higher taxa leading to low evenness at the local level (Kendal et al., 2014; Jiao et al., 2021). Consequently, local tree diversity tends to be low, with functionally similar species dominating the landscape (Nock

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et al., 2013; Ma et al., 2020).

These functional patterns of urban trees are influenced by social and ecological factors acting as biodiversity filters (Roman et al., 2018, Grilo et al., 2022), affecting tree distribution, survival, and establishment (Kendal et al., 2014). Ecological factors include abiotic and biotic pressures, such as atmospheric pollution, heat stress, and pest outbreaks. Social factors encompass human actions determined by socio-cultural preferences, governance decisions, and economic constraints (Avolio et al., 2021, Grilo et al., 2022; Hilbert et al., 2023b). The influence of these factors varies across cities, as urban trees are found in a mosaic of privately and publicly managed spaces, each subjected to different ecological pressures and planting preferences (Kirkpatrick et al., 2011). For example, trees in private backyards are often chosen for their aesthetic qualities, such as flowering and fruiting characteristics (Kendal et al., 2012), while street trees are selected for their adaptability to extreme conditions, availability in nurseries, and ease of maintenance (Conway and Vecht, 2015).

Understanding trees from a functional perspective, i.e., by the composition of their functional traits - such as leaf size, root structure, and drought tolerance - offers insights into how species contribute to different ecosystem services. Functional traits can directly affect how well trees mitigate urban challenges like air pollution, stormwater runoff, and extreme temperatures (Vogt et al., 2017). Therefore, low local functional diversity can potentially reduce urban ecological resilience to environmental changes and undermine the delivery of ecosystem services (McPhearson et al., 2023; Grilo et al., 2024).

To address this, a more strategic approach to urban forestry is needed, moving beyond the analysis of individual tree traits to classifying trees into functional groups. Trees within a functional group exhibit similar responses to environmental disturbances and provide comparable ecosystem services (Blondel, 2003) (Fig. 1). This categorization helps urban planners select species groups best suited to specific urban conditions, enhancing tree survival, maximizing environmental benefits, and reducing maintenance costs (Gómez-Baggethun et al., 2013; Roy et al., 2012). Furthermore, functional grouping promotes urban biodiversity and ecological balance, as diverse tree populations are more resilient to pests and diseases and support various faunal communities (McPherson et al., 2017). By anticipating the demand for specific tolerances or functions (i.e., specific functional groups), nurseries can optimize production schedules and manage inventory, preventing shortages and surpluses while ensuring a consistent supply for urban greening efforts (Miller et al., 2015). This approach can also improve tree quality, as nurseries can adjust growing conditions to produce healthier, more resilient stock (Jim and Chen, 2009).

Despite the importance of classifying urban trees into functional groups for understanding ecological resilience and informing urban planning, this approach remains underexplored, with the abundance and distribution of functional groups often overlooked (Dylewski et al., 2023; Lokatis et al., 2023; Hilbert et al. 2023a). This study categorizes a subset of urban trees into functional groups and analyze their distribution, abundance, dominance patterns, and associations with social and ecological factors in Lisbon, Portugal - a historic city with strong environmental commitments (Luz et al., 2019). Specifically, this study asks: i. What tree functional groups exist in a historical Mediterranean city? ii. How are these groups influenced by different social and ecological factors? Additionally, we apply a multi-faceted approach to understand species and trait selection by the Lisbon municipality, linking these findings to the broader results of the study.

2. Methods

2.1. Study area

The study was performed in Lisbon, the capital of Portugal, located on the coast of the Atlantic Ocean (38°43'00" N; 9°07'59" W). Lisbon has a Mediterranean climate and a population of approximately 545,000 residents. The city covers 8 545 ha, divided into 24 parishes (smallest administrative jurisdiction) and 2823 census tracts (statistical subdivisions that reflect the neighborhoods at which census are evaluated) (INE, 2021). Approximately 74 % of Lisbon is urban fabric, including roads and residential, commercial, and industrial buildings, while 20 % comprises green infrastructure, such as an urban forest, parks, gardens, neighborhood trees, agricultural land, and semi-natural areas (Fig. 2).

2.2. Tree selection and trait collection

Urban tree data (n = 65,796) were retrieved from a public database provided by the municipality of Lisbon (CML, 2022). This dataset primarily includes street trees and trees in pocket parks and squares (hereafter referred to as neighborhood trees), which are the most abundant public green element in most cities, providing numerous ecosystem services (Breger et al., 2019). Trees in larger parks and those

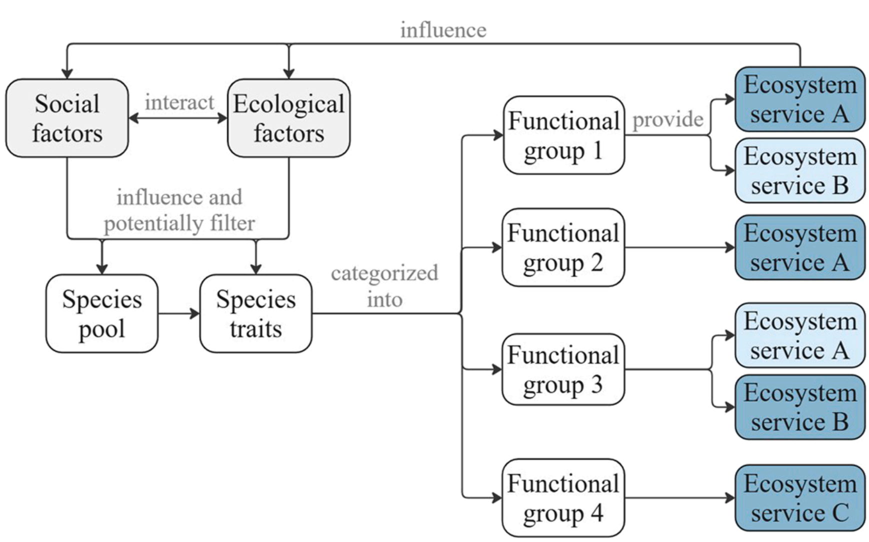

Fig. 1. Conceptual diagram illustrating the influence of social and ecological factors on the filtering of species pools and functional traits in urban environments. These factors shape the composition of distinct functional groups, each characterized by similar functions within the group and dissimilar functions across groups. Different colors represent varying levels of ecosystem service provision by each functional group, highlighting the potential for functional redundancy and complementarity among groups.

Fig. 2. Distribution of neighborhood trees and main land uses across the civil parishes and census tracts of Lisbon, Portugal. Land use classes were derived from EEA (2018), with several categories grouped into aggregated variables as follows: Crops, pastures, herbaceous vegetation=arable land, herbaceous vegetation associations, pastures, permanent crops; Roads=fast transit roads and associated land, railways and associated land, other roads and associated land; Urban fabric=continuous urban fabric, discontinuous dense urban fabric, discontinuous low density urban fabric, discontinuous medium density urban fabric, discontinuous very low density urban fabric, industrial, commercial, public, military and private units, isolated structures, airports, port areas.

not identified to at least the genus level were excluded. Species synonyms were standardized using the Plants of the World Online (POWO, 2023), resulting in 323 identified species. Trait data were collected for 21,312 trees, representing about 70 % of the identified neighborhood trees - a suitable percentage for functionally characterizing a plant community (Pakeman and Quested, 2007) (Table S1). When trees were identified only to the genus level, we assigned the species with the most individuals within that genus. To ensure robust results, we focused on census tracts with more than 10 ha, 20 individuals and at least one species, resulting in a total of 436 census tracts (out of 1363).

Trait information was obtained from various databases, prioritizing Portuguese databases, followed by Spanish, urban, and other sources (Table S2). The selected 22 traits describe species' potential for survival and spread, their tolerance to environmental stressors in a Mediterranean coastal city (heat, drought, shade, wind, pests, and salinity), and their capacity to provide ecosystem services recognized as important by urban planners, namely climate regulation and aesthetic experiences (Table 1). These traits encompass various aspects of tree functionality, including dispersal mode, growth rate, longevity, tolerances to environmental stressors, and contributions to climate regulation and aesthetic experiences, and collectively represent the functional diversity considered in this study.

Continuous numerical traits were categorized as ordinal using Jenks natural breaks (coded as 1 for low, 2 for medium, 3 for high). Traits already categorized as high, medium, or low in the databases were used as such. Dispersal mode, leaf phenology, arrangement, and shape were

Table 1
List of individual traits considered to perform cluster analysis, respective function and references.

Function	Individual traits	Function description	References
Survival and spread	Dispersal mode; growth rate; mean longevity; mean seed size; preferred climate – humid temperate, mediterranean, subtropical	Influences how species establish and persist in the urban environment	Jenerette et al. (2016), Larson and Funk (2016), Pan et al. (2020), Niu et al. (2023)
Tolerances	Heat tolerance; minimum required precipitation; shade tolerance; wind tolerance; pest tolerance; salinity tolerance	Reflects species' ability to withstand various environmental stressors	Lukac et al. (2011), Meineke et al. (2013), Michaletz et al. (2016), Stovall et al. (2019)
Climate regulation	Canopy projected width; leaf density, arrangement, phenology, shape, and mean size	Contributes to climate-related ecosystem services and climate change adaptation	Stratopoulos et al. (2018), Rahman et al. (2020), Sharmin et al. (2023),
Aesthetic experiences	Mean height; leaf arrangement, phenology, shape, mean size; mean flower size; nativeness	Relates to the visual appeal and cultural significance of trees	Goodness et al. (2016), Zhao et al. (2017)

transformed into binary variables, specifically whether a species dispersed its seeds abiotically, had deciduous leaves, broadleaves, and simple leaves (Table S3). Discrepancies in species traits among datasets were resolved by prioritizing databases as described previously. The goal was not to analyze each trait individually, but to obtain functional groups that share similar traits and can be distinguished based on their ability to tolerate disturbances and provide ecosystem services.

2.3. Social and ecological factors

For a preliminary exploratory approach, we considered a comprehensive set of ecological and social variables identified through a literature review that could potentially influence species distribution in urban areas. Ecological variables included those related to climate, terrain hydrology, lithology, land use, and atmospheric and noise pollution (used as a proxy of urbanization intensity; Sordello et al., 2020). Social factors included the social-demographic characteristics of residents, urban infrastructure, building development history, and mobility. The specific list of variables considered, and respective methodologies are described in Table 2 and Table S4. To enhance the robustness of the results, only social and ecological variables present in more than 30 % of all census tracts were considered.

2.4. Tree selection criteria by the municipality

To understand how the municipality of Lisbon selected tree species and traits, we used a multi-faceted approach. First, we reviewed the scientific literature and local regulations on tree selection criteria. This provided a foundation for understanding the theoretical and regulatory frameworks guiding urban tree selection. Second, we discussed the topic with key municipal stakeholders: the head of Lisbon's green infrastructure and the head of division responsible for maintaining and requalifying green infrastructure. This discussion aimed to deepen our understanding of the most critical traits considered in the selection of urban trees, both historically and in the present day. We specifically sought to identify which physiological traits, tolerances, and requirements were prioritized, as well as preferred planting locations and how these priorities might have evolved over time.

Table 2
Social (s) and ecological (e) aggregate and individual variables eanalyzed to test their association with each functional group of neighborhood trees, and respective description. Average and median were calculated for census tract; area and number were calculated in proportion to the census tract area.

Aggregate variables	Variables analyzed and respective description
Climate (e)	BIO1 =average annual mean temperature; BIO10 =warmest quarter average mean temperature; BIO11 =coldest quarter average mean temperature; BIO12 =average annual precipitation; BIO16 =wettest quarter average precipitation; BIO17 =driest quarter average precipitation; LST=average summer land surface temperature; PSR=average potential solar radiation; Coast_distance=distance to the nearest coastline
Hydrology (e)	Humid_system=humid system area
Lithology (e)	Alluvial=alluvial soil area; Arenitic=arenitic soil area; Clay=clayish soil area; Limestone=limestone soil area
Pollution (e)	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
Land use (e)	NDVI=average normalized difference vegetation index; SAVI=average soil adjusted vegetation index; UI=average urbanization index
Mobility (s)	Walking_potential=predictive model that indicates where people are most likely to walk
Socio-demographic characteristics (s)	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≥ 65 =residents with more than 65 years old
Urban infrastructure (s)	Bike_lanes=bike lane area; Roads=total road length; Public_elements= streetlamps, viewpoints, playgrounds, kiosks; Amenities=commerce, health, tourism, education, and leisure amenities, historical points; Buildings=buildings
Buildings' development history (s)	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

2.5. Statistical analysis

2.5.1. Cluster analysis and PCoA

To obtain tree functional groups and perform cluster analysis, we first normalized the non-binary traits by subtracting the mean of each trait and dividing by its standard deviation. This ensured that all traits contributed equally to the analysis. Next, we performed a hierarchical cluster analysis on the trait matrix using Euclidean distance to measure dissimilarity between species and applying the Ward's d2 method to minimize the sum of squared deviations within clusters, to create compact and balanced clusters (Ward, 1963; Laliberté et al., 2010). We examined the results for two to five functional groups and selected three clusters based on silhouette values, which measure how similar an object is to its own cluster compared to other clusters. We validated the groups by checking for significant segregation using analysis of similarity tests (ANOSIM). In ANOSIM, $R < 0.25$ indicates no separation, $0.25 < R < 0.50$ indicates overlap, $0.50 < R < 0.75$ indicates slight overlap, and $R > 0.75$ indicates well-segregated groups. We visualized the functional groups and their traits using a principal coordinate analysis (PCoA) with Gower's distance, which gives equal weight to all traits (Gower, 1971). Finally, we calculated and mapped the abundance of each functional group within Lisbon's census tracts, as well as their proportion within each tract, to understand dominance patterns. A functional group was considered dominant if its abundance exceeds 50 % compared to other groups.

2.5.2. Modelling

To account for spatial patterns in tree abundance across census tracts, we tested for spatial autocorrelation by performing Moran's I tests. We used the coordinates of each census tract's geometric center to create distance matrixes. Spatial autocorrelation was found to be significant. To model each functional group's abundance across census tracts, we normalized all social and ecological variables and calculated Spearman's rank correlations between each functional group's abundance and those variables. We then selected the most important social-ecological variables as candidates for modelling each functional group's abundance. Given the significant spatial autocorrelation between trees across census tracts, we used generalized additive mixed models (GAMM) to account for non-linear relationships between the response and independent variables. We used the parishes of each census tract used as smoothed terms. To avoid overfitting, we restricted the models to a maximum of five variables. To minimize collinearity, when social-ecological variables had correlations exceeding 70 %, we retained only the variable with the highest correlation to the functional group. We analyzed all alternative models and chose the best-performing model for each functional group (with the lowest AIC and highest R^2) that included significant independent variables. To further mitigate overfitting, we reduced the number of nodes in the smoothed functions and used a restricted maximum likelihood estimator.

All spatial analyses were performed in ArcMap v10.8.1. Statistical analyses were conducted in R v4.2.3 (R Core Team, 2022) using the packages stats, vegan (Oksanen et al., 2022), NbClust (Charrad et al., 2014), StatMatch (D'Orazio, 2022), cluster (Maechler et al., 2022), mgcv (Wood, 2011), and ape (Paradis and Schliep, 2019).

3. Results

The results presented are normalized by census tract area to account for variations in census tract size across the city.

3.1. Functional groups and traits

Out of the 22 traits considered for Ward's hierarchical clustering, 17 were statistically significant (no significance found for leaf arrangement and density, canopy projected width, and tolerance to heat and salinity). These traits defined three functional groups, which we named the "temperate functional group" (12 species, 11,167 individuals), the "mediterranean functional group" (3 species, 6960 individuals), and the "tropical functional group" (3 species, 3185 individuals) (Fig. 3 A). Pairwise comparisons indicated a clear segregation between the functional groups ($R_{ANOSIM} > 0.81$, $p = 0.001$). The corresponding PCoA (Fig. 3B, Table S5) showed the following characteristics for each functional group: i. the temperate functional group includes native and exotic species that tolerate wind, shade, and pests. These species mostly prefer humid temperate climates and require more frequent irrigation. They are typically tall, with abiotic dispersal, deciduous and simple leaves, rapid growth rates, short lifespans, and small leaves, flowers, and seeds; ii. the mediterranean functional group comprises native species to Portugal that prefer Mediterranean climates and tolerate drought and

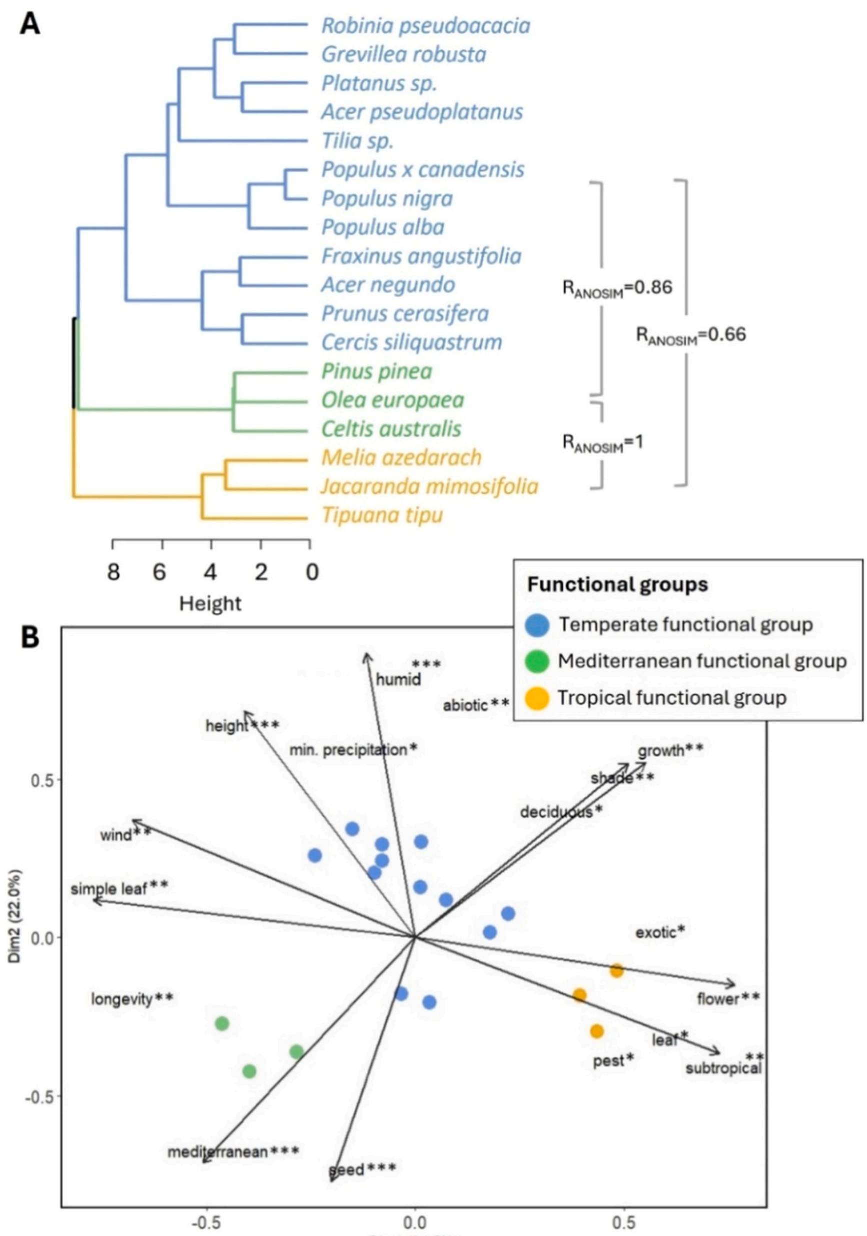

Fig. 3. (A) Dendrogram of species clustered using Ward's algorithm with an Euclidean similarity. The three colors in the dendrogram indicate the three functional groups selected using silhouette values, that measure how similar an object is to its own cluster compared to other clusters. (B) Principal coordinates analysis (PCoA) of species clustered by traits into functional groups. Trait significance is showed as * - p < 0.05; ** - p < 0.01; *** - p < 0.001. Traits are shown in the PCoA ordination space over points that correspond to each species, colored by functional group. Trait legend: abiotic= abiotic dispersal, deciduous=deciduous leaves, exotic=exotic species, flower=mean flower size, growth=growth rate, height=mean height, humid=humid temperate climate, leaf=mean leaf size, longevity=mean longevity, mediterranean=mediterranean climate, min. precipitation=minimum required precipitation, pest=tolerance to pests, seed=mean seed size, shade=tolerance to shade, subtropical=subtropical climate, wind=tolerance to wind.

wind. They have large seeds, long lifespans, simple leaves, small flowers, and slow growth rates; iii. the tropical functional group includes exotic species that prefer subtropical climates. They have large compound, and deciduous leaves, large flowers, short lifespans, and high tolerance to pests and shade.

3.2. Distribution and dominance

The distribution of the functional groups reveals unequal patterns of abundance across Lisbon (Fig. 4). The temperate functional group is the most common, present in most census tracts (only 26 of the 436 census tracts considered lack trees from this group). The mediterranean functional group has a higher abundance in the city center (located in the geometric center of Lisbon) and newer areas (located in the northeastern part of Lisbon), with 119 census tracts across the city not containing these species. The tropical functional group has the lowest abundance, absent in 204 census tracts, and is concentrated mainly in the city center. In terms of dominance, the temperate functional group is dominant in 250 census tracts, the mediterranean group in 95, and the tropical group in 51. The remaining census tracts have a balanced abundance of two or three functional groups (Fig. 4).

3.3. Associations with social and ecological factors

Spearman's rank correlations showed that the temperate functional group had strong positive associations with social variables, such as roads, public and transportation elements, and the number of residents and buildings. The mediterranean and tropical functional groups showed stronger associations with both ecological and social factors. The mediterranean group was positively associated with amenities, walking potential, vegetation indices (NDVI and SAVI), and negatively associated with summer land surface temperature (LST), potential solar radiation (PSR), and coast distance. The tropical group was negatively associated with NDVI, mobility slope, limestone soil, and LST, and positively associated with recently built buildings, urbanization index (UI), bike lanes, terrain hydrology, and walking potential (Table S6).

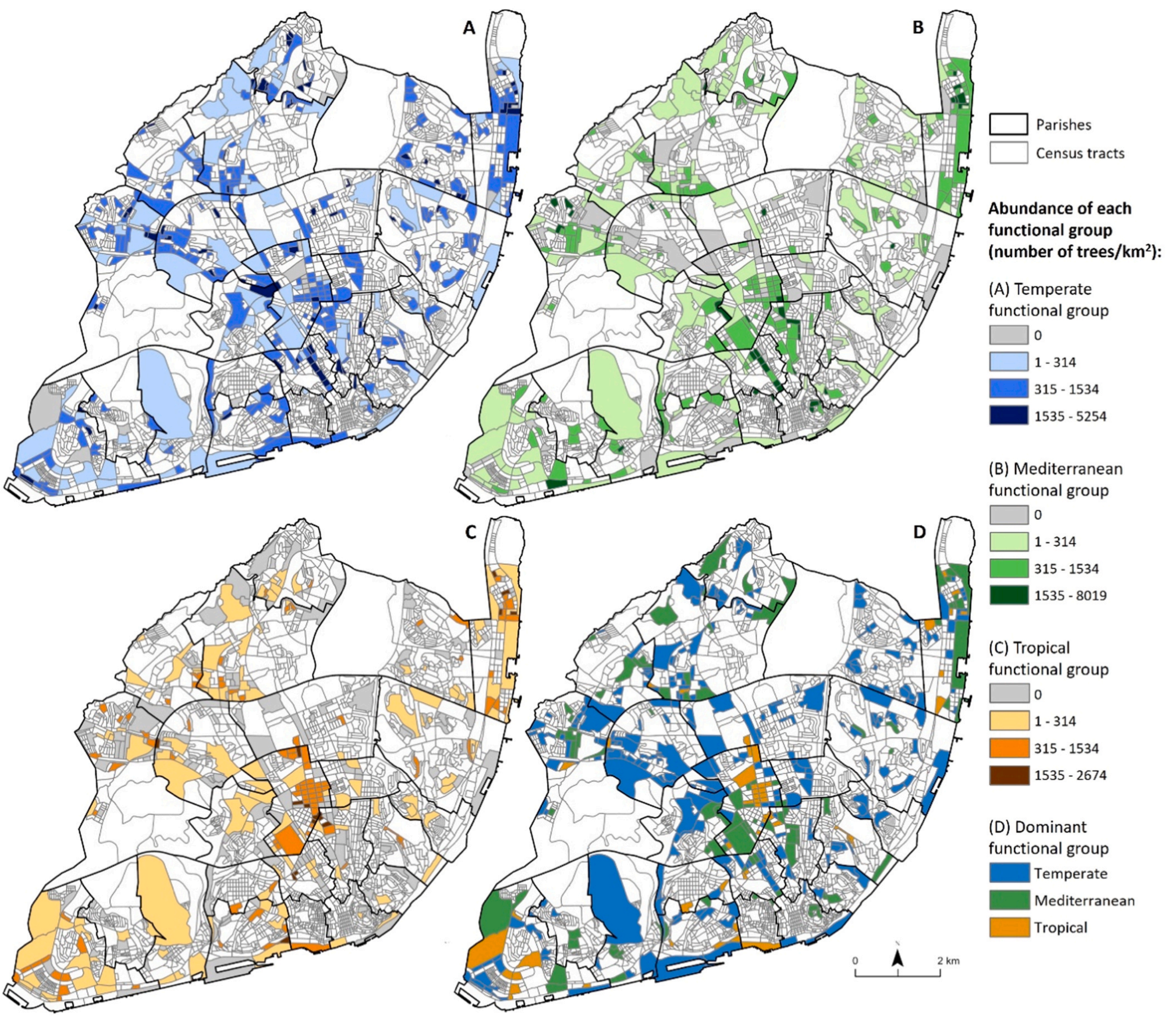

Fig. 4. Spatial distribution of the abundance of the functional groups found for Lisbon's (Portugal) neighborhood trees at the census tract scale - temperate functional group (A), mediterranean functional group (B), tropical functional group (C) -, and the dominant functional group in each census tract (D) Only census tracts with more than 10 ha, 20 neighborhood trees and at least one species were considered (those without these characteristics are represented in white). Functional group abundance is normalized by census tract area (number of trees per km^2).

3.4. Modelling functional group abundance

The best-performing statistical models for the abundance of each functional group showed that the temperate functional group was positively associated with public elements and roads (social variables). The mediterranean group had maximum abundance at intermediate LST and UI (ecological variables) and was positively associated with amenities (social variable). The tropical group had maximum abundance at intermediate LST, negative associations with NDVI (ecological variables), and positive associations with walking potential (social variable) (Table 3, Fig. S1).

3.5. Tree selection criteria by the municipality

Our multi-faceted approach to understanding Lisbon municipality's tree selection criteria revealed a strategic focus on species with traits that support climate regulation, particularly evergreen trees with dense canopies. However, the findings also highlighted the importance of a structurally and functionally diverse arrangement of species with varying characteristics. This includes a mix of canopy widths, root systems, growth rates, and other traits to provide a wide range of ecosystem services and reduce maintenance. The municipality also prioritizes trees with low allergenicity and volatile organic compounds emissions. In terms of tolerances, the municipality prioritizes trees that can withstand drought, heat, solar radiation, and pollution. Planting efforts are directed toward warmer areas, areas with higher pollution levels, and areas lacking vegetation. Lastly, there has been a shift towards selecting species resilient to climate change and capable of greater climate mitigation benefits over aesthetics.

4. Discussion

Our study demonstrates that categorizing neighborhood trees into functional groups using species traits and analyzing their distribution reveals distinct spatial patterns in their potential to respond to environmental changes and provide ecosystem services across Lisbon. Model results showed that the temperate functional group has strong associations with social variables, while the mediterranean and tropical functional groups were associated with both social and ecological factors. The composition, distribution, and dominance patterns of these groups highlight the need to increase local functional diversity and prioritize trees that can withstand future climate changes.

4.1. The distribution of functional groups

The most abundant functional group in Lisbon, the temperate group, is widely distributed across the city and positively associated with roads and public elements, indicating that these trees are primarily street trees exposed to air pollution, soil compaction, and limited space. Given these challenging conditions, and with tree selection and management in Lisbon overseen by the municipality and civil parishes, the findings suggest top-down social filters that favor species with acquisitive strategies (e.g., fast growth, short lifespan, abiotic dispersal). These strategies enable trees to mature quickly (Song et al., 2019; Matos et al., 2019; Grilo et al., 2022) and deliver key ecosystem services, such as air purification, more rapidly. However, only one species in this group has evergreen foliage - a trait that enhances particulate matter deposition and reduces exposure to air pollution - indicating the potential to further improve this ecosystem service (Barwise et al., 2024).

The mediterranean functional group, composed of native species with slower resource acquisition strategies, is particularly prominent in the city center and newer areas. Native species are often linked to cultural ecosystem services, fostering feelings of familiarity, a sense of place and belonging, cultural identity, and connection with nature, which can contribute to reducing vandalism (Kaplan et al., 2023). Additionally, trait data suggest this group is more resilient to key stressors in Mediterranean regions, such as drought and heat. However, despite the growing interest in species with these traits (also revealed by the municipality), their proportion remains significantly lower than that of the temperate functional group. The least represented group, the tropical functional group, features species with highly aesthetic traits, such as larger leaves and flowers (Goodness et al., 2016) and demonstrates tolerance to key challenges like pests and shade. The large deciduous leaves of these species provide shade in summer, cooling nearby buildings, while their leaf loss in winter prevents sun blockage, reducing unnecessary heating needs (Massetti et al., 2019).

Associations between these groups reveal that the mediterranean group is linked to local amenities, while the tropical group is more connected to walkable areas. These patterns suggest top-down social filters that place species evoking a sense of place near everyday locations (mediterranean group), while species with aesthetic appeal are prioritized in walkable areas lacking other green elements (tropical group). This pattern is consistent with findings in other cities, where trees with visually pleasing traits are often prioritized in walkable zones, where residents may lack other ways to connect with nature (Lindemann-Matthies & Bose, 2007; Goodness et al., 2016; Browning et al., 2024). These results highlight the importance of these trees in highly urbanized areas to help address environmental inequalities (Baró et al., 2019). Additionally, the abundance of these groups is linked to reduced summer land surface temperatures, suggesting their role in climate mitigation (Grilo et al., 2020). These findings emphasize the influence of social factors on urban biodiversity, showing how humans modify urban landscapes structurally and functionally. However, long-term monitoring is needed to fully understand cause-effect relationships.

Lisbon's tree functional group distribution reflects varying capacities for environmental adaptation and ecosystem service provision, highlighting the potential of urban greening as an effective nature-based solution. The temperate group primarily supports regulating services, the mediterranean group fosters a connection with nature and a sense of place, while the tropical group offers aesthetic experiences. These findings align with trends in other cities, where aesthetic preferences, desired ecosystem services, ease of maintenance, and availability are key factors in species selection (Conway & Vecht, 2015; Gillner et al.,

Table 3

Summary statistics for the smoothed function from the final GAMM models for the abundance of each neighborhood trees' functional groups in Lisbon, Portugal, and the social (s) and ecological (e) variables analyzed. Legend: edf=estimated degrees of freedom for the model, adj. R^2=adjusted R^2, LST=land surface temperature of summer, NDVI=normalized difference vegetation index, UI=urbanization index. The scatterplots with each fitted final GAMM model are shown in Fig. S1.

Response variable	Independent variables	Trend	edf	F	ρ value	Adj. R^2
	Roads (s)	+	2.1	19.5	< 0.001	
Temperate functional group	Public_elements (s)	+	2.2	11.3	< 0.001	0.21
	Amenities (s)	+	2.3	38.2	< 0.001	
	LST (e)	∩	3.6	8.3	< 0.001	
Mediterranean functional group	UI (e)	∩	2.9	6.9	< 0.001	0.30
	NDVI (e)	-	1.0	45.3	< 0.001	
	LST (e)	∩	2.8	8.9	< 0.001	
Tropical functional group	Walking_potential (s)	+	3.4	6.9	< 0.001	0.21

2016; Avolio et al., 2018). In addition, Lisbon's municipality highlighted a growing focus on creating functionally diverse tree communities, a practice common in other urban areas where planners integrate large and ornamental trees to minimize interference with building structures (Roman et al., 2021). This marks a shift from 20th century species selection, which prioritized rapid growth, pest resistance, and low costs (Conway & Vecht, 2015; Sjöman et al., 2016; Roman & Eisenman, 2022). In Lisbon, traits like growth rate, availability, and reduced management needs are now of lower importance, reflecting a proactive response to climate change, ensuring the urban forest is both sustainable and effective in delivering essential ecosystem services, with less emphasis on aesthetic experiences than in previous decades (Roman et al., 2018).

4.2. The importance of functional diversity

However, most functional tree groups in Lisbon are concentrated in specific census tracts, meaning the ecosystem services they provide may benefit only a small proportion of the population. Furthermore, dominance patterns reveal that one group predominates in many locations, indicating low local functional diversity. This situation raises two key concerns: i. There is a need to enhance functional diversity by increasing the representation of underrepresented groups, which would improve ecological resilience and support the delivery of multiple ecosystem services to local communities, ii. Despite ongoing efforts to increase species with higher climate resilience, the predominance of the temperate group in most census tracts is concerning, especially as Mediterranean regions are projected to face rising temperatures and decreasing precipitation (Cos et al., 2022). This group is likely the least resilient to climate change due to its preference for humid temperate conditions and consequent potentially higher irrigation needs. In fact, 67 % of the analyzed trees belong to this group, contributing to the reduced local functional diversity. This finding aligns with studies indicating low functional diversity in highly urbanized areas (Song et al., 2019; Hu et al., 2022; Dylewski et al., 2023). Moreover, despite the high number of species (minimum of 323 taxa) compared to other cities (Ma et al., 2020), 18 represented 70 % of the total abundance of identified individuals, with *Celtis australis* accounting for 24 % of the analyzed trees. This implies that most ecological functions are provided by few species, as in other cities (Nock et al., 2013).

Until recently, urban planning in many cities focused primarily on increasing tree diversity (Hilbert et al., 2023a). However, this study highlights the importance of understanding urban landscapes from a functional perspective. As seen in this study, categorizing species into meaningful functional groups offers several advantages for species selection: it provides insights beyond functional diversity indices, emphasizing the need to enhance the representativeness of underrepresented groups to increase multifunctionality and resilience to disturbances; it enables the identification of critical areas more sensitive to climate change; and, when spatialized at high resolutions, it facilitates targeted management strategies, which is particularly useful in older cities such as those in the Mediterranean area, where there is less capacity to reconfigure the urban morphology. However, we emphasize the need for both functional diversity and functional redundancy in urban ecosystems. While functional diversity emphasizes the importance of incorporating a variety of species with distinct ecological roles into urban green spaces, enhancing ecosystem health and sustainability (Elmqvist et al., 2003), functional redundancy acknowledges the potential benefits of having multiple species performing similar functions, maintaining critical functions despite environmental changes (Laliberté et al. 2010). To support species selection based on functional groups, further research should focus on assessing tree phytosanitary status and analyzing long-term cause-effect relationships between trees and social-ecological variables, supported by accessible trait databases that include critical urban traits, such as root characteristics (Roman et al., 2021).

4.3. Limitations and future research

This study represents a snapshot in time and has limitations, including potential biases in trait selection, and the availability of trait data. Future research could explore different functional diversity indices, develop more comprehensive trait databases, and investigate the relationship between functional diversity and other aspects of urban ecosystems, such as biodiversity, ecosystem services, and human well-being. This would provide a more holistic understanding of the role of functional diversity in urban sustainability. For example, we suggest prioritizing species from underrepresented functional groups to enhance functional diversity and resilience and recommend specific species with traits that are well-suited to particular urban conditions (e.g., drought tolerance for areas with limited water availability).

Our study was also limited by the availability of tree data, particularly for trees in parks and privately owned properties. Future research should include these trees to gain a more complete understanding of urban forest structure and function. Additionally, long-term monitoring is needed to fully understand the cause-effect relationships between trees and social-ecological factors and assess the effectiveness of management strategies aimed at increasing functional diversity and resilience to climate change. Finally, future research could explore potential biases in the municipality's selection of tree species and traits and their implications for urban forest management.

5. Conclusions

This study analyzed the functional composition and distribution of neighborhood trees at a local scale in Lisbon, Portugal, and their association with social and ecological variables. Our findings underscore the importance of considering functional groups in urban tree management to enhance ecological resilience and the provision of ecosystem services. By categorizing trees into temperate, mediterranean, and tropical functional groups, we demonstrated distinct spatial patterns that align with different social-ecological factors. The predominance of the temperate group suggests a legacy of tree selection that prioritizes rapid growth and the delivery of immediate regulating services. However, the limited representation of the mediterranean and tropical groups indicates untapped potential for increasing local functional diversity, which could bolster resilience to climate change, particularly in light of Lisbon's Mediterranean climate.

Our findings highlight the need for more proactive urban planning strategies that enhance the functional diversity of Lisbon's urban forest to improve ecosystem service delivery and contribute to environmental justice by expanding the benefits of urban greening to more communities. Furthermore, this trait-based approach allows for more targeted management interventions, particularly in areas more vulnerable to climate stressors. Future research should explore the contribution of trees in private properties to the urban forest and investigate the phytosanitary status of trees and the long-term cause-effect relationships between trees and social-ecological variables.

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

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ufug.2025.128749.

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