



Large cemetery trees are vital for ecosystem services and tree-related microhabitats: A study from Karlsruhe city, southwest Germany

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ABSTRACT

Urban trees play vital roles in climate regulation, improving air quality, sequestering carbon, and supporting biodiversity. However, the ecological significance of cemetery trees remains understudied. We analyzed 200 large trees from five common broadleaved species across three cemeteries in Karlsruhe, Germany. Field measurements assessed tree size, crown health, pruning, and tree-related microhabitats (TreMs). Using i-Tree Eco v6, we then estimated carbon storage and sequestration, oxygen generation, pollutant removal, and transpiration from these inputs. We employed species comparisons, ordination, generalized linear models, and Spearman correlations to explore differences and relationships among these ecosystem services. Results showed species differed in ecosystem service profiles, reflecting complementary ecological roles rather than one species dominating all services. Larger DBH (diameter at 1.3 m height) correlated positively with TreM richness, abundance, and leaf-area-dependent services. Crown dieback was linked to higher TreM abundance but reduced leaf area, pollutant removal, and transpiration. TreM richness and abundance significantly positively correlated with carbon storage, though not with carbon sequestration or oxygen production. A positive relationship was observed between TreM richness and a composite of canopy-mediated ecosystem services. These findings suggest that large, structurally diverse cemetery trees can jointly store carbon and host various microhabitats, though annual physiological regulating ecosystem services may not always complement TreM diversity. Due to their high ecological value, cemetery trees should be conserved as much as possible, and conservation efforts should balance tree health, habitat continuity, and public safety.

1. Introduction

Urban trees are widely acknowledged for providing key ecosystem services. They absorb and store carbon, aiding climate-change mitigation [1], and filter gaseous and particulate air pollutants, improving air quality [2]. They also provide habitat structures. Tree-related microhabitats (TreMs) are distinct features borne by living or dead trees—including cavities, cracks, exposed wood, crown deadwood, fungal fruiting bodies, and epiphytic structures—that offer shelter, breeding sites, or substrates for other organisms [3]. TreM richness and abundance are therefore useful structural indicators of potential biodiversity support, although they are not direct measures of species occurrence [4–7]. Despite their value, TreMs remain rarely integrated into urban ecosystem-service assessments (but see recent works by

[6–9]). This is especially true for trees growing in cemeteries, a unique type of urban green space often overlooked in ecological studies, including their habitat values and other ecosystem services. Found in nearly every city, cemeteries serve cultural and ecological purposes: they are places of memory and reflection and possess mature trees, diverse vegetation, and low disturbance, making them important ecological refuges [10]. Although evidence shows that cemeteries can support notable biodiversity—ranging from tree species [11] to birds [12] and other taxa [13]—systematic evaluation of ecosystem services and TreMs on cemetery trees has not yet been conducted in the literature. Understanding how ecosystem services differ among species, which factors influence these differences, and the trade-offs between service categories is essential for promoting urban sustainability and human well-being.

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Evidence strongly indicates that different tree species provide varying ecosystem services. For example, species with high leaf area index, such as *Carpinus betulus*, tend to remove more pollutants and transpire more [14], while fast-growing species, such as *Acer platanoides*, are associated with greater carbon sequestration [15]. Regarding supporting services, TreMs also differ significantly among species: *Quercus robur* offers more woodpecker cavities and crown deadwood than *Quercus rubra*, whereas *Carpinus betulus* often develops rot holes and cavities [6, 16,17]. Beyond species, traits like size, health, and management practices are greatly associated with ecosystem service delivery. Larger trees consistently store and sequester more carbon and support microhabitats [18–20]. Tree vitality, as indicated by crown dieback, has mixed effects: it can increase microhabitats through deadwood and decay, but it can also diminish services such as carbon sequestration and pollutant removal [21,22]. i-Tree Eco is a modeling system that combines field-observed tree attributes with species information, weather records, and air-pollution data to estimate urban-forest structure and associated services [14,23]. Its outputs are modeled estimates rather than direct physiological measurements; this distinction is important when interpreting differences among species or individual trees. Nevertheless, the literature on assessing ecosystem services using i-tree-eco is limited for cemetery trees, and knowledge gaps remain regarding the quantitative assessment of ecosystem services from cemetery trees.

Ecosystem services often involve trade-offs or synergies—for example, in urban trees, declining vitality can weaken regulation functions while creating more microhabitats [21,24]. Therefore, caring for and preserving large, old trees is essential. These keystone structures support biodiversity and provide critical services but are becoming scarce in cities due to safety, space, land-use conflict, or aesthetic issues [25,26]. Cemeteries, with their mature trees and lower disturbance from daily commercial and anthropogenic activities in cities, offer a unique opportunity to explore the ecological significance of large trees in urban environments. However, a thorough assessment of their potential value is still missing.

This study examined five common broadleaved tree species across three cemeteries in Karlsruhe, Germany. Our primary goal was to evaluate how large cemetery trees contribute to regulating ecosystem services and provision as habitats for flora and fauna. In 2023, we used field surveys and i-Tree Eco modeling to identify TreMs and estimate provisioning and regulating ecosystem services. Specifically, we (1) conducted standardized TreM surveys as indicators of potential biodiversity support; (2) used i-Tree Eco, ordination, and generalized linear models (GLM) to analyze variation in services and their statistical relationships with tree characteristics; and (3) investigated whether TreM richness and abundance correlated with individual and multivariate ecosystem service dimensions.

2. Materials and methods

2.1. Study area

This research was conducted in Karlsruhe, Baden-Württemberg, Germany. Karlsruhe has a temperate climate, with an average temperature of 11.2 °C annually and yearly rainfall of 871 mm [27]. Established in 1715, the city spans 17,342 ha and has a population of 301,749; about 40% of its land is dedicated to built environments or transportation, while forests and farmland make up 26% and 23%, respectively [28]. We focused on three cemeteries with significant green space, diverse histories, and areas exceeding 4 ha: the Main Cemetery, Durlach Cemetery, and Rüppurr Cemetery (Fig. 1). Species distribution was uneven across cemeteries; this was managed via a fixed-block sensitivity analysis and considered in evaluating species differences.

2.2. Selected tree species and sampling design

Because the cemeteries are managed by the cemetery and burial office rather than the municipal horticultural department, no digital tree cadaster was available for the study area at the time when fieldwork was

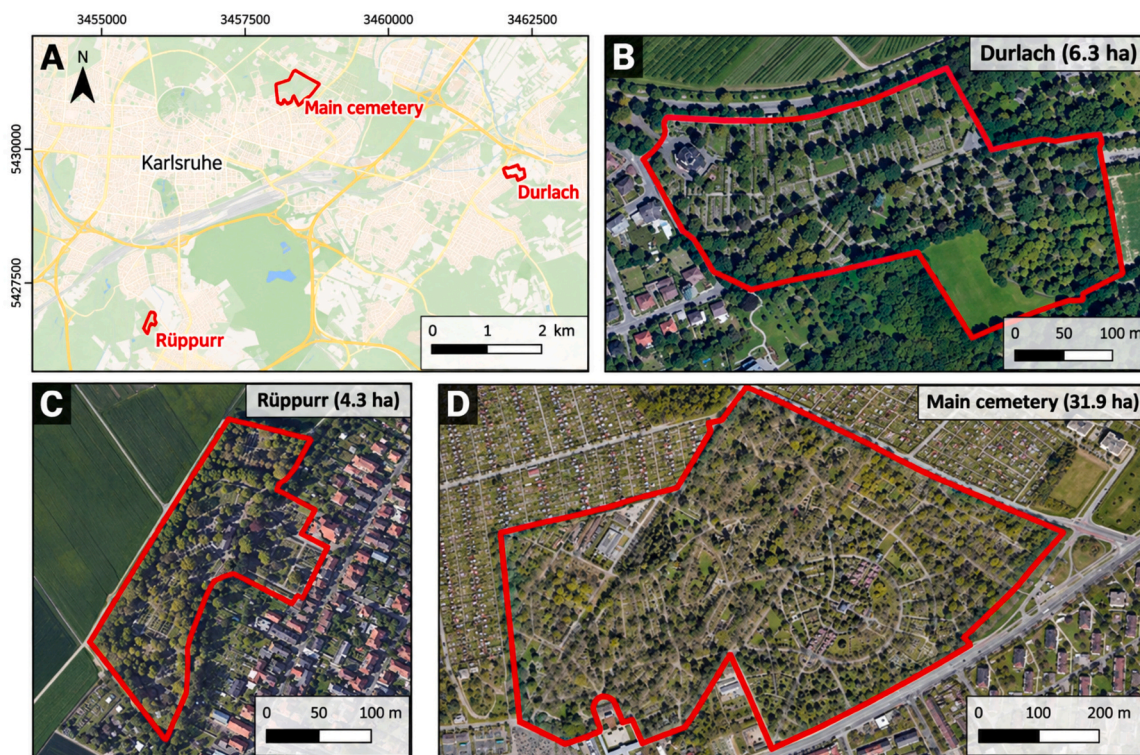


Fig. 1. Location and spatial extent of the three selected cemetery study sites in Karlsruhe, Germany. (A) Overview map showing the locations of the Main Cemetery, Durlach Cemetery, and Rüppurr Cemetery within Karlsruhe. Satellite images show the boundaries and spatial configuration of (B) Durlach Cemetery (6.3 ha), (C) Rüppurr Cemetery (4.3 ha), and (D) Main Cemetery (31.9 ha). Red outlines indicate the boundaries of the respective study areas.

conducted. Therefore, we conducted a brief preliminary survey in July 2023 to record all target trees with a diameter at breast height (DBH) of 40 cm or more. For each tree, we measured DBH with a 3-m diameter tape, recorded GPS coordinates with a handheld device, and identified the species (Fig. S1a in the [Supplementary Materials](#)). The survey systematically covered all three cemeteries, resulting in a total of 483 trees.

Following the preliminary survey, *Quercus rubra* was excluded due to its low abundance, clustered distribution, and primarily small planted patches rather than scattered trees. We then focused on *Acer platanoides* (Norway maple), *Carpinus betulus* (European hornbeam), *Fagus sylvatica* (European beech), *Platanus × acerifolia* (London plane tree), and *Quercus robur* (English oak), chosen for their abundance and contrasting ecological traits such as shade tolerance, drought tolerance, and growth rate (see Table S1 in [Supplementary Materials](#)). Among these, *Platanus × acerifolia* was especially common. The total sample included 136 trees from the Main Cemetery, 38 from Durlach, and 26 from Ruppurr. To balance workload and representativeness, a two-stage sampling method was used for this species: first, 90 trees were randomly preselected using QGIS 3.28, their DBH measured, and then 40 trees were randomly chosen from this subset. For the other four species, nearly all recorded individuals (close to or just above 40) were included, and 40 trees per species were randomly selected. The total sample comprised 200 trees (40 per species) with DBH ≥ 40 cm (see Fig. S1b in [Supplementary Materials](#)). To ensure spatial coverage, a minimum distance of 10 m between trees of the same species was maintained. Satellite imagery was used for visual inspection to confirm even distribution across the three cemeteries. Random selection in QGIS helped prevent bias, and trees that were inaccessible or unsafe were excluded. For multi-stemmed trees, DBH was calculated as the quadratic mean diameter of all stems, following the method described by Curtis & Marshall [29], which is standard in forestry for determining a single DBH value for such trees.

2.3. Data collection

Field data collection was divided into two periods. During summer (4–30 August 2023), we recorded field-measured dendrometric and crown-condition variables, including DBH, tree height, crown dimensions, crown missing, crown dieback, pruning intensity, crown light exposure (CLE), defoliation, and ground-cover types beneath the canopy (Table S2 in the [Supplementary Materials](#)). Visual crown assessments were made from four directions, averaged, and recorded in 5% increments following i-Tree Eco protocols [30]. After leaf fall (16 October–24 November 2023), we surveyed TreMs using the hierarchical typology of Larrieu et al. [3] that consisted of 47 types (Table S3 in the [Supplementary Materials](#)). Each tree was inspected from base to crown in all directions, with binoculars used for higher crown sections. We measured TreM richness by counting the different types and assessed TreM abundance using a semi-quantitative index based on how often TreMs were recorded during fieldwork, as explained in detail in sub-sections 2.4.2.1 and 2.4.2.2. Bryophytes, lichens, ivy, and lianas were visually estimated for percentage cover and then mapped to ordinal cover classes to be included in the abundance index.

2.4. Data processing

2.4.1. Provisioning and regulating ecosystem service quantification

2.4.1.1. Crown projection area (CPA). CPA is a key parameter used to normalize ecosystem services by tree size. It is defined as the portion of the forest floor covered by the vertical projection of tree crowns [31]. The unit of CPA is m², and it is calculated using the following equation:

$$CPA = \pi * CR^2 \quad (2)$$

CR (crown radius) was derived from the crown width (north-south and east-west). CR was calculated as half of the average of the two

measured crown widths (north-south and east-west).

2.4.1.2. Crown volume (CV). To analyze tree size and its relationship with ecosystem services [18], crown volume was determined using species-specific shape equations [32]. These equations incorporate measured crown dimensions such as length and radius, and also account for the estimated percentage of crown missing (Fig. S2 in the [Supplementary Materials](#)). The specific shape equations used are presented in Fig. S3 in the [Supplementary Materials](#). An ovoid shape was assumed for *Acer platanoides*, *Platanus × acerifolia*, *Quercus robur*, and *Carpinus betulus*, while a half-ellipsoid shape was applied for *Fagus sylvatica* [32].

2.4.1.3. i-Tree Eco modeling. Ecosystem services were estimated using i-Tree Eco v6 [23] following Nowak [14]. Field data included species, DBH, total height, crown height and width, crown missing, dieback, and CLE. Model outputs included leaf area, leaf-area index, carbon storage, leaf biomass, annual carbon sequestration, oxygen production, air-pollutant removal, potential evapotranspiration, and transpiration. These estimates are based on measured inputs and model calculations rather than direct measurements of carbon fluxes or pollutant removal. To compare species, service metrics were also normalized by crown projection area (CPA). Meteorological data for 2015 were obtained from the Baden-Baden station, and air-quality data came from Karlsruhe monitoring stations. Species-specific growth rates, shading coefficients, and biomass conversion factors are detailed in Tables S1, S4, and S5 in the [Supplementary Materials](#).

2.4.2. Calculation of microhabitat abundance and richness

2.4.2.1. Microhabitat abundance. Microhabitat abundance was measured using a semi-quantitative composite index. TreMs that could be directly counted were summed based on their occurrences. Epiphytes such as mosses, lichens, and ivy, recorded as percentage cover, were categorized into five ordinal classes—0: 0%; 1: 1–< 25%; 2: 25–< 50%; 3: 50–< 75%; 4: 75–100%—and then combined. This index allows for relative comparisons among trees but does not represent an exact count of habitat units. TreM richness indicates the number of distinct TreM types per tree, ranging from 0 to 47.

2.4.2.2. Microhabitat richness. Microhabitat richness was calculated as the total number of distinct microhabitat types present on each tree. Given that Larrieu et al. [3] classified and defined 47 microhabitat types in their hierarchical typology, the maximum microhabitat richness a tree can have is 47, and the minimum is 0.

2.5. Data analysis

The species comparisons, ordinations, and regression analyses were conducted in R 4.1.2 [33]. Kruskal–Wallis tests followed by pairwise Wilcoxon tests with Bonferroni correction were used to compare species because distributional assumptions were not met. TreM accumulation curves and non-metric multidimensional scaling (NMDS) were performed using vegan [34] with Bray–Curtis dissimilarity. A preliminary detrended correspondence analysis yielded a first-axis length of 4.07 SD (standard deviation for microhabitat types' turnover). The two-dimensional NMDS had a stress of 0.229; a three-dimensional solution (stress 0.172) was examined as a robustness check. Graphics were produced with ggplot2 [35].

GLM quantified statistical associations between tree attributes and service metrics. The GLM related to TreM richness assumed a Poisson distribution of the response variable that was TreM richness. Whereas GLM models with response variables such as TreM abundance, leaf area, carbon storage, carbon sequestration, pollutant removal, and transpiration, assumed Gaussian models after Box–Cox transformation where

required [36]. Candidate predictors were species, DBH, crown dieback, cut-branch count, and CLE; predictors already used by i-Tree Eco to calculate a response were excluded from that response model to reduce mathematical circularity (Tables S6–S7 in Supplementary Materials). Residual and collinearity diagnostics followed the submitted workflow; HC3 heteroskedasticity-consistent covariance matrix estimates were used for carbon sequestration. Because trees were nested within only three cemeteries, random-effects estimation or cluster-robust inference would be unreliable. We therefore refitted each GLM with cemetery as a fixed blocking factor as a sensitivity analysis. Species and cemetery were unevenly crossed, so cemetery coefficients were not interpreted ecologically; the analysis tested whether the reported tree-level associations remained stable after adjusting for site.

Direct relationships between TreM abundance or richness and ten ecosystem-service variables were assessed using Spearman rank correlations, which are appropriate for monotonic associations involving

skewed or ordinal data. *P* values were adjusted across each family of tests using the Benjamini–Hochberg false-discovery-rate (FDR) procedure [37]. To avoid allowing the seven strongly collinear canopy-mediated outputs to dominate interpretation, we also defined three ecologically balanced dimensions from standardized variables: annual production (mean *z* score of carbon sequestration and oxygen production), canopy-mediated services (mean *z* score of potential evapotranspiration, transpiration, and five pollutant-removal variables), and carbon storage as a separate long-term stock. An ecosystem-service-only principal component analysis (PCA; standardized variables) summarized covariance among services, and co-inertia analysis assessed overall shared multivariate structure between the TreM and service matrices, with significance evaluated using 9999 permutations [38,39]. These additional analyses were conducted in R 4.5.1 using stats, ade4 1.7–24, dplyr 1.2.1, ggplot2 4.0.3, and factoextra 2.2.0.

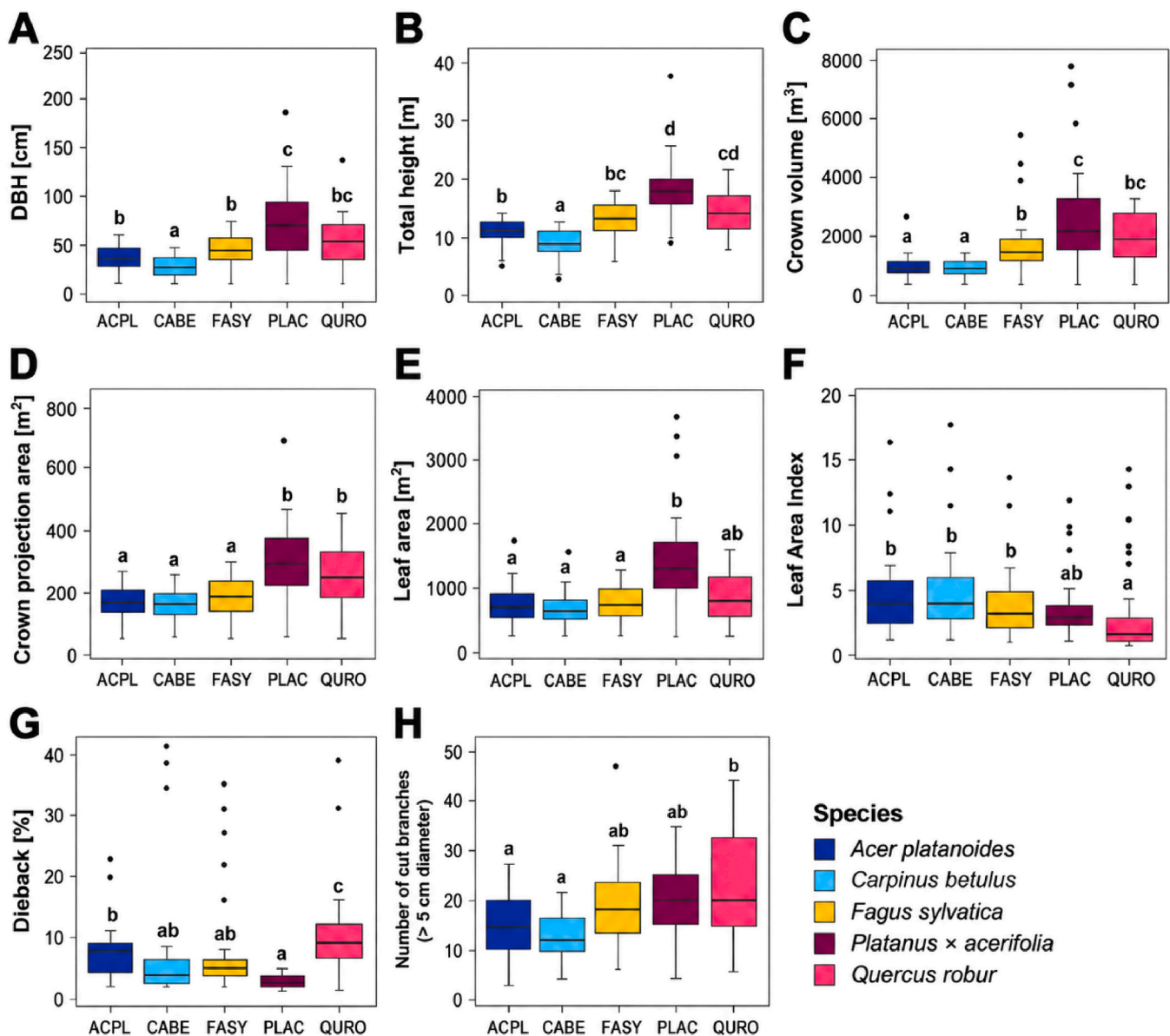


Fig. 2. Comparison of (A) diameter at breast height (DBH), (B) total height, (C) crown volume, (D) crown projection area, (E) leaf area, (F) leaf area index, (G) dieback, and (H) number of cut branches among the tree species *Acer platanoides* (ACPL), *Carpinus betulus* (CABE), *Fagus sylvatica* (FASY), *Platanus × acerifolia* (PLAC), and *Quercus robur* (QURO). Boxplots show the median (horizontal black line), interquartile range (IQR; box), whiskers extending to values within $1.5 \times$ IQR, and outliers (points). Different lowercase letters above the boxplots indicate significant differences among species based on pairwise Wilcoxon rank-sum tests ($p < 0.05$); species sharing at least one letter are not significantly different.

3. Results

3.1. Tree morphological and health characteristics

Among the 200 trees examined, *Carpinus betulus* had the smallest DBH and height, being noticeably smaller than all other species. Conversely, *Platanus × acerifolia* had the largest DBH at 148 cm and the tallest height at 30.7 m, greatly exceeding all other species except *Quercus robur* in DBH ($p < 0.001$) and in height ($p < 0.001$). These differences in crown volume mirrored those in DBH and height (Fig. 2A-C). *Platanus × acerifolia* also demonstrated the highest CPA and leaf area (LA), with LA at least double that of any other species. The leaf area index (LAI) was significantly lower in *Quercus robur* than in all others ($p < 0.001$), while *Carpinus betulus* had the highest LAI (Fig. 2D-F). Crown dieback was most pronounced in *Quercus robur* and *Acer platanoides*, with median values of 5%, and least in *Platanus × acerifolia* at 0% (Table 1). *Fagus sylvatica* and *Quercus robur* showed the highest pruning intensity (more branches removed > 5 cm), whereas it was lowest in *Carpinus betulus* (Fig. 2G-H).

3.2. Microhabitats as supporting ecosystem services

Among 200 trees, 33 out of 47 possible microhabitat types were identified, totaling 2353 individual microhabitats. Microhabitat richness (ranging from 0 to 13) and abundance (ranging from 0 to 51) varied significantly among species (Fig. 3). *Carpinus betulus* had the highest median richness and abundance, whereas *Fagus sylvatica* had the lowest. *Platanus × acerifolia* displayed the broadest range in both variables, including trees with no microhabitats and those with the maximum recorded richness of 13 types. The microhabitat accumulation curve for all 200 trees (Fig. 4A) rose sharply up to about 40 trees, then plateaued and neared an asymptote at 200, indicating most TreM types in the community were captured. For individual species (Fig. 4B), the curves did not level off as quickly within 40 trees per species. *Fagus sylvatica* showed the shallowest slope, reaching 20 TreM types at 40 individuals and nearing its asymptote. *Carpinus betulus* had a steeper initial slope, leveling at 21 TreM types. *Acer platanoides* and *Platanus × acerifolia* showed the highest cumulative TreM types (24 and 27, respectively), with curves still rising, suggesting more microhabitat types could be found with larger samples.

A two-dimensional metaMDS based on Bray-Curtis dissimilarity revealed clear differences in microhabitat composition among species (Fig. 5A). The stress value of 0.2293 indicates a moderate stress level. TreMs from *Platanus × acerifolia* formed a distinct cluster, clearly separated from the other four species. *Fagus sylvatica*, *Acer platanoides*, and *Carpinus betulus* clustered tightly together, while *Quercus robur* partially overlapped with them but showed some divergence. The three-dimensional metaMDS confirmed the same clustering pattern with a lower stress value of 0.172 (Fig. 5B).

The distribution of ecologically significant microhabitat groups

(Fig. 6) revealed that rot holes and concavities were most common on *Carpinus betulus* and *Platanus × acerifolia*. Woodpecker cavities appeared only on *Quercus robur*, *Platanus × acerifolia*, and *Acer platanoides*, with the highest count on *Q. robur*. Crown deadwood was mainly found on *Q. robur* ($> 50\%$ of observations). Insect galleries were most frequently seen on *Q. robur*. Fungi were primarily recorded on *P. × acerifolia* and *Fagus sylvatica*. Epiphytes showed an even distribution, except for a lower presence on *P. × acerifolia*. Vertebrate nests (birds, squirrels) were twice as common on *Q. robur* as on other species. Invertebrate nests (bees, hornets, spiders) were mostly observed on *Carpinus betulus* and *P. × acerifolia*.

GLM identified tree species, DBH, and crown dieback as the primary drivers of microhabitat richness and abundance (Table 2 and Fig. S4 in the Supplementary Materials). DBH had a significant positive effect on both richness ($p < 0.001$) and abundance ($p < 0.001$). Crown dieback positively influenced abundance ($p < 0.001$) but not richness. Compared with the reference species *Platanus × acerifolia*, all other species showed significantly higher microhabitat richness and abundance ($p < 0.05$ or better). Pruning intensity and CLE had no consistent significant effects. Adding cemetery as a fixed blocking factor did not significantly change TreM richness and abundance (Table S8 in the Supplementary Materials).

3.3. Provisioning and regulating ecosystem services

For the provisioning services, Carbon storage per m^2 CPA was significantly higher in *Fagus sylvatica* than in all other species ($p < 0.001$) (Fig. 7A). Stem volume per m^2 CPA was largest in *Platanus × acerifolia*, significantly exceeding all other species ($p < 0.001$), and smallest in *Carpinus betulus* ($p < 0.001$) (Fig. 7B). Leaf biomass per m^2 CPA was highest in *Carpinus betulus*, significantly higher than in *Platanus × acerifolia* ($p < 0.05$) and *Quercus robur* ($p < 0.001$); no significant difference was found between *Carpinus betulus* and *Acer platanoides* (Fig. 7C).

For regulating services, annual carbon sequestration per m^2 CPA was highest in *Acer platanoides* and lowest in *Carpinus betulus* ($p < 0.001$; Fig. 7D). The near-zero position of *C. betulus* in the normalized plot reflects a small but non-zero median of $0.007 \text{ kg C m}^{-2} \text{ CPA yr}^{-1}$ (absolute median $1.10 \text{ kg tree}^{-1} \text{ yr}^{-1}$) and rounding at the plotted scale; it should not be interpreted as zero carbon uptake. These values are i-Tree Eco estimates and reflect species growth assumptions, crown condition, and normalization by CPA. Oxygen production followed the same pattern because i-Tree derives it directly from sequestration (Fig. 7E). Pollution removal per m^2 CPA was lowest in *Quercus robur*, whereas *Carpinus betulus* showed the highest rate (Fig. 7F). Transpiration followed the same species pattern (Fig. 7G).

3.4. Factors influencing the supply of ecosystem services

The GLM analyses revealed that the DBH, crown dieback, and species

Table 1

Morphological, environmental, and crown health variables of surveyed trees per species (CPA: Crown Projection Area, CV: Crown Volume; CLE: Crown Light Exposure).

Species	DBH	Tree height	CPA	CV	Dieback	Cut branches	CLE	Defoliation
	[cm]	[m]	[m ²]	[m ³]	[%]	[N]	(0–5)	[%]
<i>Acer platanoides</i>	60 (40, 83)	17.4 (11.5, 21.6)	141 (72, 333)	711 (255, 2514)	5 (0, 25)	15 (0, 33)	3 (1, 5)	1 (0, 25)
<i>Carpinus betulus</i>	54 (41, 82)	15 (8.9, 20.4)	149 (70, 281)	690 (223, 1909)	1 (0, 40)	12 (0, 31)	3 (1, 5)	2 (0, 50)
<i>Fagus sylvatica</i>	68 (40.5, 107)	18.1 (11.5, 23.8)	170 (65, 340)	1420 (478, 4064)	1.5 (0, 18)	18 (6, 42)	2 (1, 4)	0 (0, 3)
<i>Platanus × acerifolia</i>	89 (40, 148)	21.6 (16.5, 30.7)	293 (64, 684)	1904 (117, 7182)	0 (0, 3)	16 (4, 37)	2 (1, 4)	0 (0, 2)
<i>Quercus robur</i>	75.3 (41, 143)	18.1 (13.6, 25.9)	225 (36, 605)	1278 (70, 4500)	5.5 (1, 30)	18 (4, 40)	3 (1, 5)	0 (0, 10)

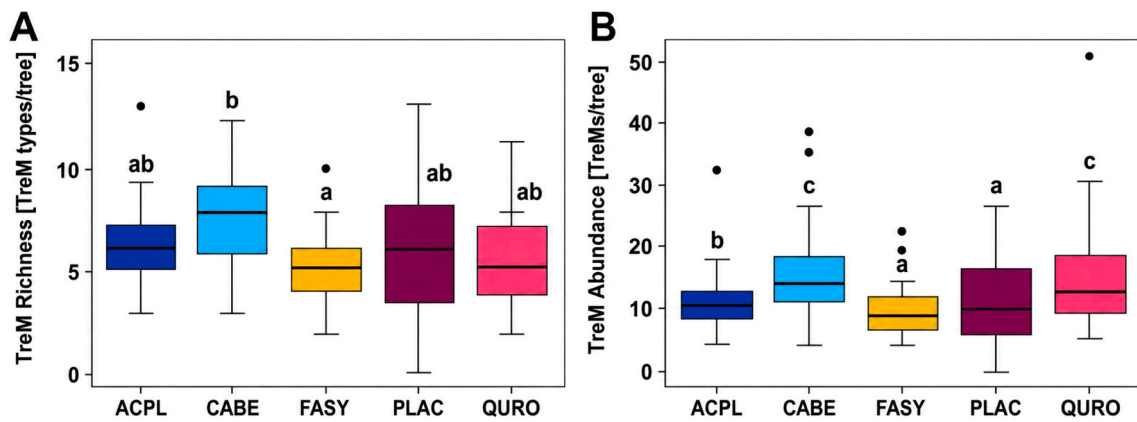


Fig. 3. Comparison of microhabitat richness (A) and microhabitat abundance (B) among the tree species *Acer platanoides* (ACPL), *Carpinus betulus* (CABB), *Fagus sylvatica* (FASY), *Platanus × acerifolia* (PLAC), and *Quercus robur* (QURO). Boxplots show the median (horizontal black line), interquartile range (IQR; box), whiskers extending to values within $1.5 \times$ IQR, and outliers (points). Different lowercase letters above the boxplots indicate significant differences among species based on pairwise Wilcoxon rank-sum tests ($p < 0.05$); species sharing at least one letter are not significantly different.

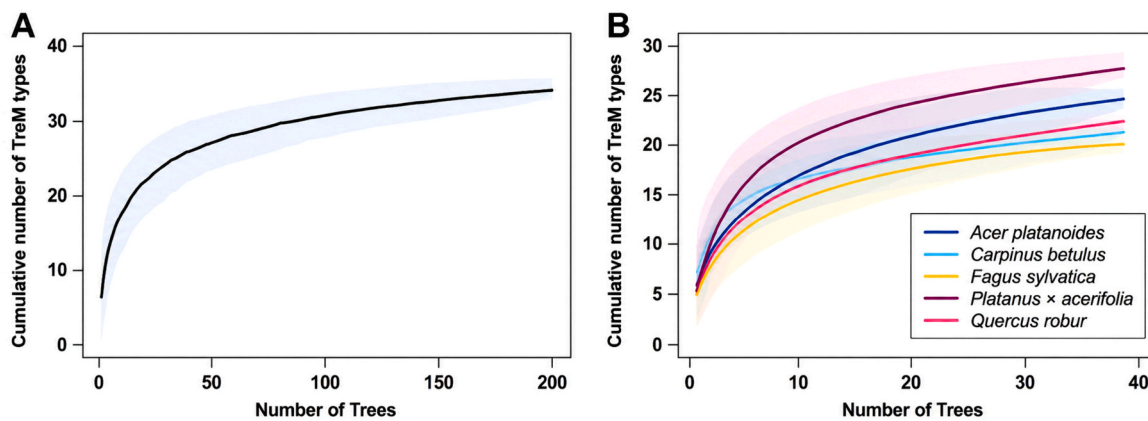


Fig. 4. Microhabitat accumulation curves for all 200 trees (A) and separately for each tree species (B).

were the principal statistical predictors of service variation, whereas pruning intensity and CLE were generally not associated (Table 3). Leaf area, pollution removal, and transpiration showed parallel patterns: DBH was positively associated and crown dieback negatively associated with all three ($p < 0.001$). Carbon storage was negatively associated with crown dieback and positively associated with cut-branch count. Carbon sequestration was not significantly associated with cut-branch count, the only eligible predictor not already used in its i-Tree calculation. Adding cemetery as a fixed blocking factor improved the leaf-area, carbon-storage, pollution-removal, and transpiration models (joint $p = 0.003$ – 0.004), but did not materially change the signs or significance of the principal tree-level predictors. Cemetery as a fixed blocking factor did not associate with carbon sequestration (Table S8 in the Supplementary Materials).

Overall, larger DBH was positively associated with provisioning, regulating, and TreM metrics, whereas greater crown dieback was associated with lower modeled leaf-area-dependent services and greater TreM abundance.

3.5. Relationships between TreMs and ecosystem services

TreM richness and abundance were strongly correlated with one another ($\rho = 0.81$, $p < 0.001$), but their relationships with ecosystem services were selective rather than universal. At the individual-variable level, carbon storage was positively related to both TreM abundance ($\rho = 0.28$) and richness ($\rho = 0.38$; both FDR $q < 0.001$; Fig. 8). TreM richness showed weak positive correlations with potential

evapotranspiration, transpiration, and each pollutant-removal estimate ($\rho = 0.16$; FDR $q = 0.047$), whereas the corresponding abundance correlations were small and non-significant ($\rho = 0.06$). Neither TreM metric was significantly related to annual carbon sequestration or oxygen production ($|\rho| \leq 0.09$).

The balanced dimensions confirmed these patterns (Table 4). The ecosystem-service PCA was dominated by two axes explaining 74.4% and 20.0% of variance, respectively, separating the tightly covarying canopy-mediated services from annual production (Figure S5 in the Supplementary Materials). Co-inertia analysis detected a statistically significant but small shared structure between the TreM and balanced ecosystem-service matrices ($RV = 0.063$, permutation $p < 0.001$; Tables S9–S11 in the Supplementary Materials), indicating modest multivariate concordance rather than a strong common gradient.

4. Discussion

4.1. Functional complementarity among tree species

The five tree species showed notable differences in microhabitat provision (supporting services) and in provisioning and regulating services, revealing a pattern of functional complementarity. *Carpinus betulus* exhibited the greatest microhabitat diversity and abundance, particularly in rot holes and concavities, which are vital microhabitats [3,8]. This is due to species-specific traits: hornbeam trunks and branches are prone to necrosis, attracting fungi and insects that accelerate wood decay and cavity creation [16,40,41]. Its irregular growth

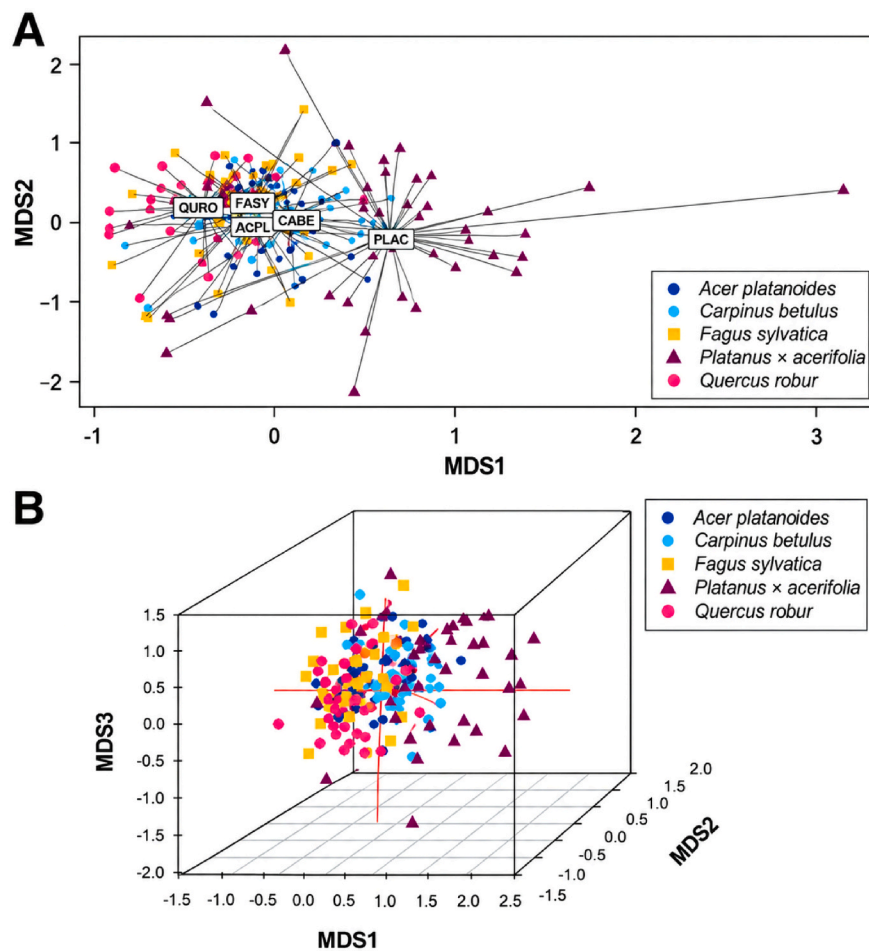


Fig. 5. Results of two-dimensional *metaMDS* of microhabitats showing the patterns of TreM type occurrence for each tree species (A) and 3D *metaMDS* of microhabitats showing the patterns of TreM occurrence for each tree species with a stress value of 0.1715 (B).

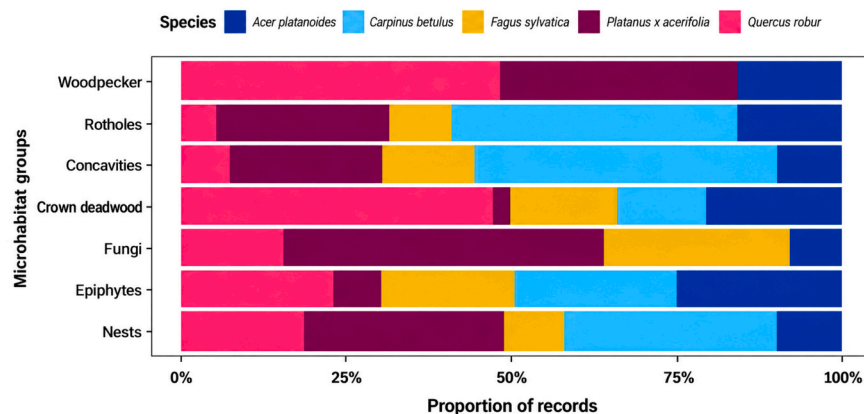


Fig. 6. Selected ecologically relevant microhabitat groups and their occurrence among tree species (*Acer platanoides* (ACPL), *Carpinus betulus* (CABB), *Fagus sylvatica* (FASY), *Platanus × acerifolia* (PLAC), and *Quercus robur* (QURO)). Stacked bars show the proportional contribution (%) of each tree species to the records within each microhabitat group. The groups “perennial fungal fruiting bodies” and “ephemeral fungal fruiting bodies and slime moulds” were combined into the group “fungi” due to the low number of occurrences.

form, marked by low, dense branching, provides additional microhabitats such as dendrotelms and nests [42,43]. Regarding provisioning and regulating services, *Carpinus betulus* had the highest leaf biomass and pollution removal per m² CPA, thanks to its high shading factor and leaf area index [14]. However, it recorded the lowest carbon sequestration rate among the five species because most individuals were in the late life stage, with significantly reduced growth [14].

Quercus robur, on the other hand, contributed the most woodpecker cavities, insect galleries, and crown deadwood. The abundance of dead branches in oak crowns creates ideal sites for woodpecker excavation [16,44]. Its fissured bark supports a rich invertebrate community, which attracts insect-eating birds [45]. Additionally, acorns are a crucial food source for birds and mammals [46,47]. Consequently, *Q. robur* plays an essential and irreplaceable role in supporting urban wildlife. Regarding

Table 2

Regression results for microhabitat richness and abundance. Estimates with significance level of influence indicated with asterisk (" " p-value > 0.1; "." p-value < 0.1; * p-value < 0.05; ** p-value < 0.01; *** p-value < 0.001) and arrow for influence type (▲ for positive influence; ▼ for negative influence; not adequate for more complex functions of CLE). Values of significantly influencing predictors are highlighted in bold (p-value < 0.05). *P. acerifolia* (PLAC) is used as reference for the other four species in the models.

	Dependent variable	
	Microhabitat richness	Microhabitat abundance
DBH	0.0125 *** ▲	0.0423 *** ▲
Dieback	0.0076 ▲	0.0775 *** ▲
Nr. cut branches	-0.0023 ▼	0.0030 ▲
CLE (linear)	-0.0914 ▼	-0.4992 ▼
CLE (quadratic)	0.0887	0.0890
CLE (cubic)	-0.0825	-0.5806 *
CLE (quartic)	-0.1112 .	-0.3099
Species ACPL vs. PLAC	0.4909 *** ▲	1.8495 *** ▲
Species CAGE vs. PLAC	0.7400 *** ▲	3.0201 *** ▲
Species FASY vs. PLAC	0.2451 * ▲	1.1708 *** ▲
Species QURO vs. PLAC	0.1863 . ▲	1.6822 *** ▲
Intercept	0.5942	-0.7390
Adjusted R-squared	0.3634	0.4289
AIC	872.54	691.38

regulating services, *Quercus robur* showed the lowest pollution removal rate per CPA, likely due to its low leaf area index [2,48]. Its carbon sequestration rate was notably higher than that of *Platanus × acerifolia*, although this difference may be influenced by growth rate assumptions in i-Tree Eco rather than actual field performance [49].

Platanus × acerifolia showed the greatest variety of microhabitats and the highest total number of microhabitat types. It was especially common to find fungi, burrs, and sap flows on larger, older trees, consistent with the presence of xylophagous fungi on older plane trees [50]. Despite being non-native, *Platanus × acerifolia* still offers important habitat features, including cavities used by bats and birds [51,52]. However, it supported fewer epiphytes than the other four species, likely because its exfoliating bark hampers long-term growth of bryophytes and lichens [53,54]. Regarding provisioning services, *Platanus × acerifolia* had the highest stem volume per CPA, indicating significant biomass buildup in older trees [55]. Its leaf biomass per CPA was the lowest, which matches the unusual decrease in leaf area index with increasing DBH noted for this species [56].

Acer platanoides exhibited the highest rate of carbon sequestration per unit crown area, aligning with its rapid growth and moderate height that allows ongoing development [15]. In an earlier study in Karlsruhe, Germany, Petridis [9] found that *Acer platanoides* trees growing in parks had higher microhabitat diversity than those growing on streets. The microhabitat diversity we found on *Acer platanoides* trees in cemeteries was similar to that in park trees and exceeded that of street trees observed by Petridis [9], suggesting that *Acer platanoides* trees in cemeteries provide higher habitat quality than street trees. In contrast, *Carpinus betulus* showed the lowest rate, significantly below that of other species. This difference can be attributed to the size and age of the trees relative to their species-specific lifespans. Hornbeam has a shorter lifespan and reaches maturity at a smaller size compared to the other four species. Our study's dataset mainly includes large trees with DBH over 40 cm, which largely surpass the typical height at maturity for this species per i-Tree Eco data. Most hornbeams in the dataset are in late life stages and are no longer growing rapidly [14]. Since carbon sequestration estimates depend on growth rates, the i-Tree Eco model significantly reduces these estimates once trees reach their species' maturity size, as noted in [14]. *Fagus sylvatica* had the lowest microhabitat richness among the five species but significantly contributes to provisioning services by storing the most carbon per CPA, indicating its high resource-use efficiency [57]. Overall, our results indicate that no single tree species can provide all ecosystem services. Each species offers a

unique set of benefits with specific strengths. Therefore, maintaining high species diversity is crucial for supporting multifunctional urban green spaces [4,20,58].

4.2. The central role of large trees

Large trees are reliably associated with an array of ecosystem services. Specifically, DBH greatly increased microhabitat diversity and quantity (supporting services) and all evaluated provisioning and regulating services. Their extended lifespans enable larger trees to accumulate wounds from weather, pathogens, and wood-boring insects [20,59]. Over time, these processes produce more deadwood and a complex bark structure, creating diverse substrates and microsites such as cracks, cavities, and decayed wood that support many taxa [26,60], acting as biodiversity hotspots in urban green spaces. Large trees also serve as keystone structures for provisioning and regulation, with attributes such as extensive crowns, large leaf areas, complex bark, and abundant deadwood that increase carbon sequestration, pollutant removal, and transpiration rates [14,61]. They also contain more woody biomass than smaller trees [18,19]. Although sequestration may decrease during senescence, the total contribution of large trees remains high due to their size [62]. Thus, large trees function as "ecological hubs," integrating multiple functions—supporting biodiversity and providing high levels of regulating and provisioning services [25,26]. Preserving large trees is a beneficial strategy that supports biodiversity, climate regulation, and air quality. However, in urban settings, large old trees are becoming scarcer, often removed due to safety issues, limited space, or aesthetic reasons [25,26]. Urban green space management should therefore focus on conserving existing large trees and planning for future ones by ensuring adequate space for growth and minimizing unnecessary removals [51,63].

4.3. The trade-off between tree vitality, ecosystem services, and safety

Our results reveal a fundamental trade-off associated with tree vitality. Crown dieback significantly increased microhabitat abundance and supporting services while simultaneously reducing all measured provisioning and regulating services.

The positive influence of crown dieback on microhabitat abundance aligns with findings from both forest and urban studies [8,20,22]. Dead branches and crown deadwood provide critical nesting and foraging sites for woodpeckers, which prefer weakened trees for cavity excavation [16,64]. Moreover, the onset of decay creates rot holes, bark crevices, and other microsites that are colonized by saproxylic insects, fungi, and epiphytes [20,22]. In our research, *Quercus robur*, which had the highest crown dieback, also had the highest numbers of woodpecker cavities and crown deadwood, illustrating this relationship.

In contrast, crown dieback consistently reduced provisioning and regulating services. Dieback directly reduces leaf area, thereby diminishing photosynthetic capacity, carbon sequestration, and oxygen production [14,65]. It also lowers the surface area available for pollutant capture and reduces transpiration rates, both of which depend on leaf area and crown volume [61]. Furthermore, dieback is an indicator of underlying tree stress, whether from drought, disease, or mechanical injury, which can suppress growth and productivity [66]. Consequently, trees in poor health contribute less to climate regulation and air quality improvement.

The contrasting effects of tree vitality on supporting, provisioning, and regulating services highlight a key trade-off in urban green space management. Promoting tree health—through pruning, disease control, or removing declining trees—can boost regulating and provisioning benefits but might decrease microhabitat availability. Conversely, leaving trees with dieback supports biodiversity but can compromise climate regulation and air purification [21]. This trade-off is especially critical in cities and requires a context-specific approach [24]. When safety allows, deliberately retaining standing deadwood or trees with

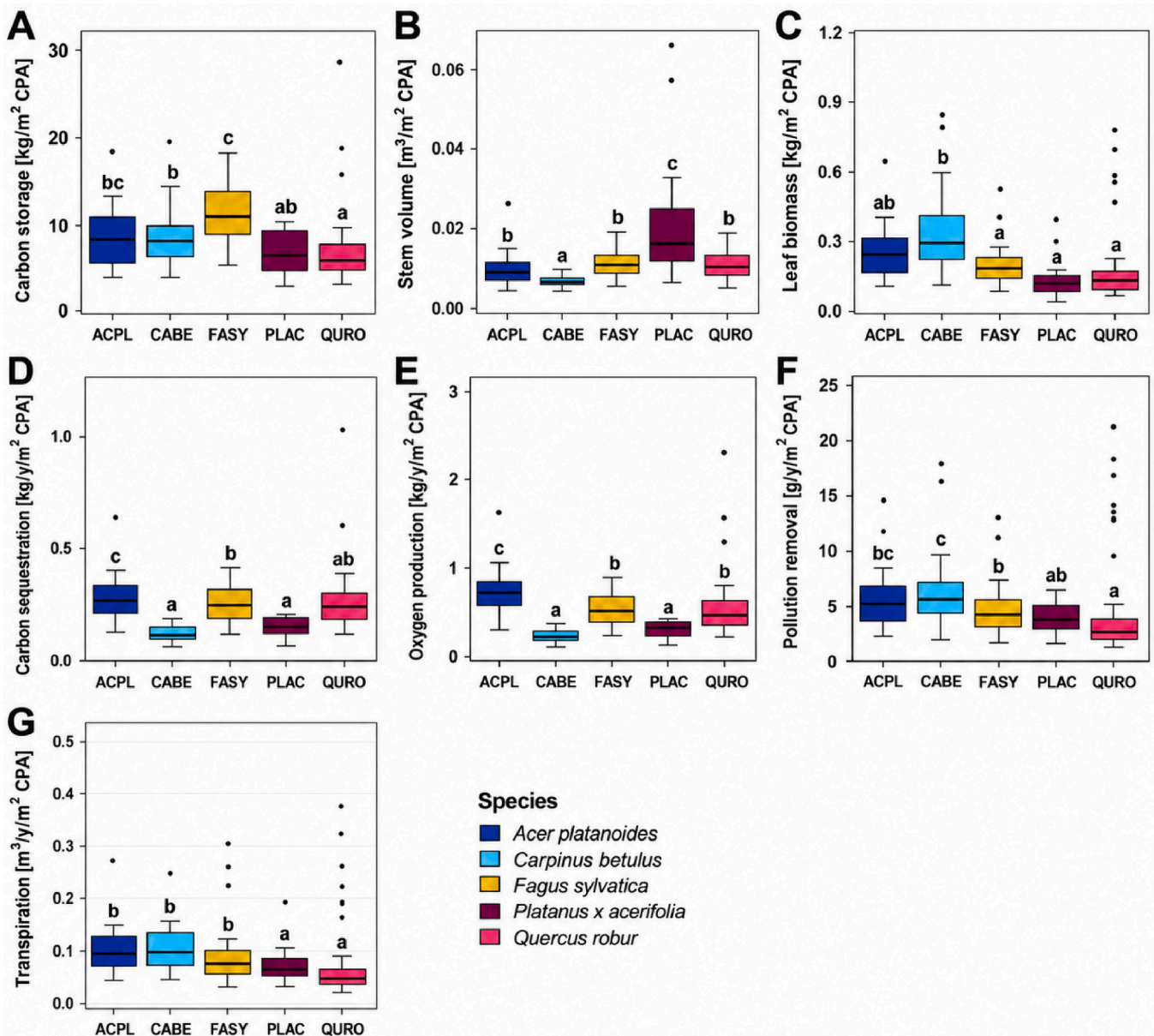


Fig. 7. Comparison of (A) carbon storage, (B) stem volume, (C) leaf biomass, (D) carbon sequestration, (E) oxygen production, (F) pollution removal, and (G) transpiration among *Acer platanoides* (ACPL), *Carpinus betulus* (CABE), *Fagus sylvatica* (FASY), *Platanus × acerifolia* (PLAC), and *Quercus robur* (QURO). Ecosystem-service estimates were standardized per 1 m² of crown projection area (CPA) to enable comparison on a per-unit-area basis. Boxplots show the median (horizontal black line), interquartile range (IQR; box), whiskers extending to values within 1.5 × IQR, and outliers (points). Different lowercase letters above boxes indicate significant differences among species based on pairwise Wilcoxon rank-sum tests ($p < 0.05$); species sharing at least one letter are not significantly different.

dieback can help support urban biodiversity [51,63]. For hazard trees, less invasive strategies like crown reduction or branch removal can maintain some habitat values while reducing risks. Public acceptance may improve through signage explaining the ecological importance of deadwood [67]. In cemeteries, where visitors often appreciate natural elements, there may be greater tolerance for trees as habitat [67]. Therefore, vitality isn't always beneficial—senescence can be an asset. Achieving a balance between biodiversity and climate resilience is central to sustainable urban green space management.

4.4. Relationships between habitat structures and other ecosystem services

The direct analyses refine the initial interpretation of the trade-off. TreM richness and abundance did not consistently correlate with every ecosystem service. Their strongest link was with carbon storage, which reflects a long-term stock of woody biomass. Ecologically, this

makes sense because large, old, structurally complex trees have had more time to accumulate carbon in their stems and branches, and to develop features like cavities, exposed wood, deadwood, and other TreMs. The fact that richness correlates more strongly than abundance suggests that habitat structure diversity may better indicate long-term tree structural complexity than the semi-quantitative abundance index, which also includes ordinal epiphyte-cover classes. Conversely, annual carbon sequestration and oxygen production showed no relation to TreM metrics. Only TreM richness exhibited a weak association with canopy-related services, indicating that a tree with many habitat structures isn't necessarily a tree with high current physiological output. The species-specific findings highlight this complementarity: *Carpinus betulus* combined high TreM richness and abundance with high canopy-mediated services but low modeled annual sequestration; *Fagus sylvatica* stored significant carbon per canopy area despite lower TreM richness; and *Quercus robur* provided unique deadwood and cavity habitats but

Table 3
Regression results for factors influencing dependent variables such as Leaf area, Carbon storage, carbon sequestration, air pollution removal, and transpiration. Estimates with significance level indicated with asterisk (“ ” p-value > 0.1; “.” p-value < 0.1; * p-value < 0.05; ** p-value < 0.01; *** p-value < 0.001) and arrow for influence type (▲ for positive influence; ▼ for negative influence; not adequate for more complex functions of CLE). Values of significantly influential predictors are highlighted in bold (p-value < 0.05). “-” if the predictor was not used in the model.

	Dependent variable									
	Leaf area		Carbon storage		Carbon sequestration		Air pollution removal		Transpiration	
DBH	0.0133 ***	▲	-	-	-	-	0.0134 ***	▲	0.0123 ***	▲
Dieback	-0.0263 ***	▼	-0.0122 **	▼	-	-	-0.0265 ***	▼	-0.0245 ***	▼
Nr. cut branches	0.0004	▲	0.0216 ***	▲	0.1519	▲	0.0004	▲	0.0003	▲
CLE (linear)	-0.1192	▼	-	-	-	-	-0.1202	▼	-0.1088	▼
CLE (quadratic)	-0.0605		-	-	-	-	-0.0610		-0.0565	
CLE (cubic)	-0.0020		-	-	-	-	-0.0021		-0.0017	
CLE (quartic)	-0.0964 .		-	-	-	-	-0.0971 .		-0.0899 .	
Intercept	6.4044 ***		5.5938 ***		31.876 ***		6.8096 ***		2.4290 ***	
Adjusted R-squared	0.4831		0.2341		0.0024		0.4831		0.4834	
AIC	175.98		148.64		1306.9		178.88		146.36	

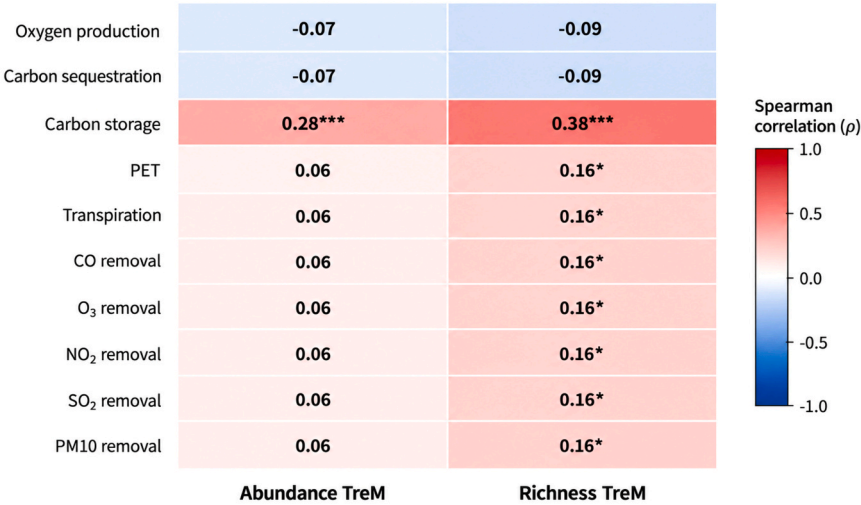


Fig. 8. Associations between tree-related microhabitat (TreM) metrics and individual ecosystem services. Values within cells are Spearman correlation coefficients (ρ) between TreM abundance or richness and individual ecosystem-service estimates. Cell colors indicate the direction and magnitude of the correlations, ranging from negative (blue) to positive (red) associations. Asterisks indicate statistically significant correlations after Benjamini–Hochberg false discovery rate (FDR) correction ($q < 0.05$; * $q < 0.01$; ** $q < 0.001$).

Table 4
Spearman relationships between TreM metrics and balanced ecosystem-service dimensions. Annual production is the mean standardized score of carbon sequestration and oxygen production; canopy-mediated services combine potential evapotranspiration, transpiration, and five pollutant-removal estimates. q values are Benjamini–Hochberg FDR-adjusted. “Significant” denotes $q < 0.05$; ns = not significant.

TreM metric	Annual production, ρ (q)	Canopy-mediated services, ρ (q)	Carbon storage, ρ (q)
Abundance	−0.07 (0.417), ns	0.06 (0.431), ns	0.28 (<0.001), significant
Richness	−0.09 (0.306), ns	0.16 (0.041), significant	0.38 (<0.001), significant

had lower pollutant removal per crown area. These contrasting profiles support the value of preserving multiple species and life stages but do not prove that species interact synergistically. Because the correlations include multiple species and sizes, shared factors like DBH, age, crown architecture, and i-Tree assumptions are likely; understanding causal mechanisms requires long-term experimental observation of cemetery trees.

4.5. Implications for management and limitations

The three cemeteries featured large trees with varying ecosystem service profiles and habitat structures, highlighting their contribution to Karlsruhe’s green infrastructure. Management advice should, however, be proportional to the evidence. This observational case study, based on five species and trees with a DBH of 40 cm or more in one city, limits the ability to generalize findings to other locations, species, size groups, or cemetery designs. Only three cemeteries were examined, with uneven species distribution across sites. Fixed-block sensitivity analyses helped control for site context but cannot fully distinguish species effects from cemetery conditions or support broad conclusions about cemetery influences. TreM abundance, a semi-quantitative index combining direct counts with ordinal epiphyte cover classes, indicates potential habitat rather than confirmed organism presence. The i-tree-eco modeling of ecosystem service estimation had a limitation for some ecosystem services, such as carbon sequestration, for large trees with low longevity, as we reported earlier in the case of *Carpinus betulus*. Lastly, the cross-sectional design and rank correlations identify associations, not causation or changes over time. Future research should include more cemeteries and cities, balanced species sampling within sites, smaller trees, more taxa, repeated TreM monitoring, direct biodiversity assessments, and field validation of physiological services. Within these parameters, management should focus on retaining large trees while also managing

and mitigating risks, maintaining diverse species and age classes, and preserving habitat structures through proportionate arboricultural interventions.

5. Conclusion

This case study combines field-recorded TreMs with modeled provisioning and regulating services by using tree size and vitality data collected from large cemetery trees in Karlsruhe. Different species played complementary ecological roles, with no single species ranking highest in all services. Larger DBH consistently correlated with increased habitat structural diversity and higher modeled services, while crown dieback was linked to more TreMs but lower leaf-area-dependent services. Analysis revealed that TreM richness and abundance were most strongly connected to carbon storage, with weak or inconsistent links to canopy-mediated services and no relation to annual carbon sequestration and oxygen production. These findings suggest that long-term structural growth can support both woody carbon stocks and habitat features without necessarily implying high current physiological productivity. Considering the limitations of data from three unevenly sampled cemeteries, model estimates, and the cross-sectional approach, we finally conclude that cemetery management and municipal administrations should prioritize conserving large, habitat-supporting trees where safety allows, maintain species and age diversity, and opt for proportionate rather than routine removal interventions.

Authors' contributions

Somidh Saha conceptualized the study, authored the manuscript, supervised Lisa Strunk, and performed some data analyses. Lisa Strunk gathered the data, built the databases, carried out most of the analyses, and co-authored the paper. Jinchun Wang also contributed as a co-author. Zoe Petridis participated in field data collection, co-wrote the paper, and co-supervised Lisa Strunk.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, we used ChatGPT Plus to develop preliminary versions of R scripts. Afterward, we reviewed and edited the R scripts as needed, and we take full responsibility for the content of the published article.

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.cpb.2026.100673](https://doi.org/10.1016/j.cpb.2026.100673).

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