



Public safety considerations constraint the conservation of large old trees and their crucial ecological heritage in urban green spaces

Arkadiusz Fröhlich^{a,b,*}, Fabian Przepióra^a, Szymon Drobnik^c, Grzegorz Mikusiński^d, Michał Ciach^a

^a Faculty of Forestry, University of Agriculture, Kraków 31-425, Poland

^b Institute of Nature Conservation, Polish Academy of Sciences, Kraków 31-120, Poland

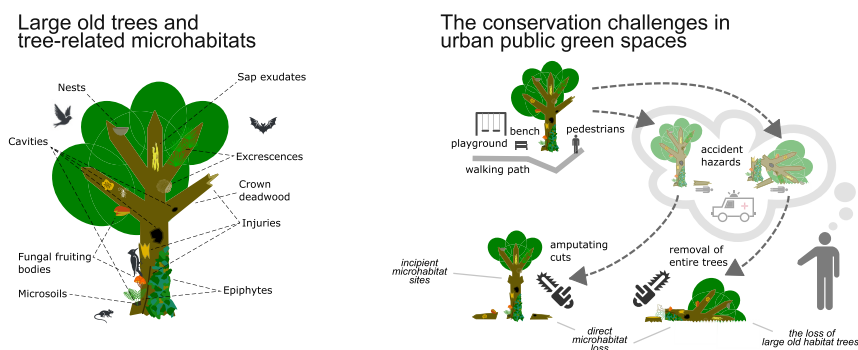
^c Institute of Environmental Sciences, Jagiellonian University, Kraków 30-387, Poland

^d School for Forest Management, Swedish University of Agricultural Sciences, Skinnkatteberg 739 21, Sweden

HIGHLIGHTS

- Conflict exists between public safety and the conservation of large old trees.
- Pedestrian traffic, infrastructure, and large tree size sum up to accident risk.
- Risky trees often require extensive surgeries, such as pruning and logging.
- This decimates large old trees and the microhabitats they provide for wildlife.
- Tree cavities, injuries, crown deadwood, and epiphytes are the most affected.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Shuqing Zhao

Keywords:

tree-related microhabitats
TreMs
habitat trees
evidence-based conservation
urban ecology
urban forestry
urban planning

ABSTRACT

Large old trees in urban public green spaces deliver a diversity of values essential for human well-being, including biodiversity conservation. Yet, the conservation of large old trees bearing key wildlife microhabitats interferes with safety considerations. This intuitive notion, however, is backed by an insufficient and scattered body of evidence. Here, we empirically examined this process using data on 5974 trees across 510 sample plots, organized as quintuplets within 102 sample sites, including urban parks, cemeteries, recreational forests, and historic reserves in the urban agglomeration of Kraków, Poland. Our analyses demonstrate that trees situated in areas frequently visited by people, or those near walking paths, benches, or playgrounds, have elevated accident hazards and, therefore, necessitate intensive tree surgeries (pruning and logging) to remain harmless. Large old trees, which bear the most diverse microhabitats and pose greater risks when they collapse, are especially affected by these measures. Accordingly, we found that the co-occurrence of large trees with elevated accident hazards results in significant losses of dead and sloped trees, and trees with cavities, injuries, crown deadwood, fungal fruiting bodies, or epiphytes, particularly in parks and, to a lesser extent, in recreational forests. Apparently, some tree-related microhabitats, such as injuries, cavities, and microsoils, also emerge in risky spots after pruning. Our findings underscore that the conservation of large old trees and their ecological functions faces

* Corresponding author at: Faculty of Forestry, University of Agriculture, Kraków 31-425, Poland.

E-mail address: frohlich@iop.krakow.pl (A. Fröhlich).

<https://doi.org/10.1016/j.scitotenv.2024.174919>

Received 26 April 2024; Received in revised form 4 July 2024; Accepted 18 July 2024

Available online 20 July 2024

0048-9697/© 2024 Elsevier B.V. All rights are reserved, including those for text and data mining, AI training, and similar technologies.

significant challenges due to safety considerations. To address conservation challenges and harmonize human coexistence with biodiversity, we recommend enhancing environmental awareness and reevaluating arboricultural and planning policies. This would involve establishing strategic and pocket reserves on city peripheries and interiors, allowing larger older trees to thrive and develop important microhabitats without compromising public safety. Otherwise, we risk losing many large old trees and/or their superior value for wildlife, which will regenerate over decades, if not centuries.

1. Introduction

In the era of a global ecological crisis, the presence of trees in urban areas is very important for broadly understood human well-being (Lindenmayer, 2017; Roy et al., 2012). This is especially true for large old trees (also known as ‘ancient trees’ or ‘veteran trees’), which are among the largest and scarcest living structures in the world, deeply embedded in human history, culture, and religion (Blicharska and Mikusiński, 2014; Mölder et al., 2020; Townsend and Barton, 2018), and provide a variety of fundamental ecosystem services, e.g., shading, water retention, nutrient cycling, carbon storage, aesthetic values, and the provision of wildlife habitats (Lindenmayer, 2017; Lindenmayer and Laurance, 2017; Piovesan et al., 2022). However, large old trees currently suffer from an amplified mortality rate (Lindenmayer et al., 2012) as a result of climate and land-use changes (Huang et al., 2023; Nolan et al., 2020; Skarpaas et al., 2017). Unfortunately, the development of large old trees usually takes centuries; hence, the rapid restoration of these structures is very difficult, if not impossible (Le Roux et al., 2014b; Lindenmayer et al., 2012; Lindenmayer, 2017). This calls for recognizing how common arboriculture policies influence large old trees (Le Roux et al., 2014a; Lindenmayer, 2017; Piovesan et al., 2022), while also taking into account the full array of services and disservices that these trees bring to humanity and biodiversity (Roy et al., 2012).

The conservation of biodiversity translates to human well-being (Blignaut and Aronson, 2008; Buckley et al., 2019; Díaz et al., 2018), for example, by enhancing mental (Hedblom et al., 2019) and physical health (Cirino et al., 2021). Large old trees play a fundamental role here (Gilhen-Baker et al., 2022), serving as vital hosts for cavities, injuries, crown deadwood, excrescences, fungal fruiting bodies, epiphytes, and other small structures (Lindenmayer, 2017; Lindenmayer and Laurance, 2017) identified as Tree-related Microhabitats (TreMs, see Fig. 1A) (Kraus et al., 2016; Larrieu et al., 2018). TreMs offer shelters for cavity-nesters, provide water resources, and supply nutrients for xylobionts,

fungivores, detritivores, and sap feeders, thus supporting a diversity of organisms at higher trophic levels (Kirsch et al., 2021; Martin et al., 2004; Maxence et al., 2022; Stokland et al., 2012). Trees hosting numerous TreMs, often referred to as ‘habitat trees’, are crucial for a variety of taxa, from microbes to vertebrates (Larrieu et al., 2018; Maxence et al., 2022), and the diversity of TreM assemblages reliably indicates the surrounding biodiversity (Basile et al., 2020; Paillet et al., 2018). Therefore, TreMs are ideal targets for systematic conservation efforts associated with large old trees (Augustynczyk et al., 2019). Over the past 50 years, evidence has accumulated showing that TreMs are more likely to be found on larger rather than smaller trees, as well as on dead trees and certain species that promote the formation of unique TreM groups (Asbeck et al., 2019; Kozák et al., 2018; Larrieu et al., 2012; Vuidot et al., 2011). This evidence primarily comes from natural and semi-natural forests, with only a few studies addressing urban green spaces (Carpaneto et al., 2010; Fröhlich and Ciach, 2020b; Großmann et al., 2020; LaMontagne et al., 2015).

Urbanization leads to significant losses of large old trees (Le Roux et al., 2014a; Le Roux et al., 2014b), but significant number of these trees persist as natural monuments in urban public green spaces, such as parks and cemeteries (Carpaneto et al., 2010; Fröhlich and Ciach, 2020a; Löhmus and Liira, 2013; Machar et al., 2021; Nolan et al., 2022). Although they receive a special care, they are also subject to strict arboriculture policies (Fröhlich and Ciach, 2020b; ISA, 2011; Sandström et al., 2006). While common urban policies generally value large old trees, this does not hold for those aging and accumulating TreMs, such as cavities, crown deadwood, or fungal fruiting bodies, due to the risk of unexpected collapse and potential accidents (Brookes, 2007; Nali and Lorenzini, 2009). Consequently, safety concerns often necessitate extensive tree surgeries on these habitat trees, including pruning (Avilés, 2019) or even complete removal (logging) (Carpaneto et al., 2010; Fröhlich and Ciach, 2020a). While these practices might create some artificial microhabitats (e.g., wounds, see Großmann et al., 2020), they

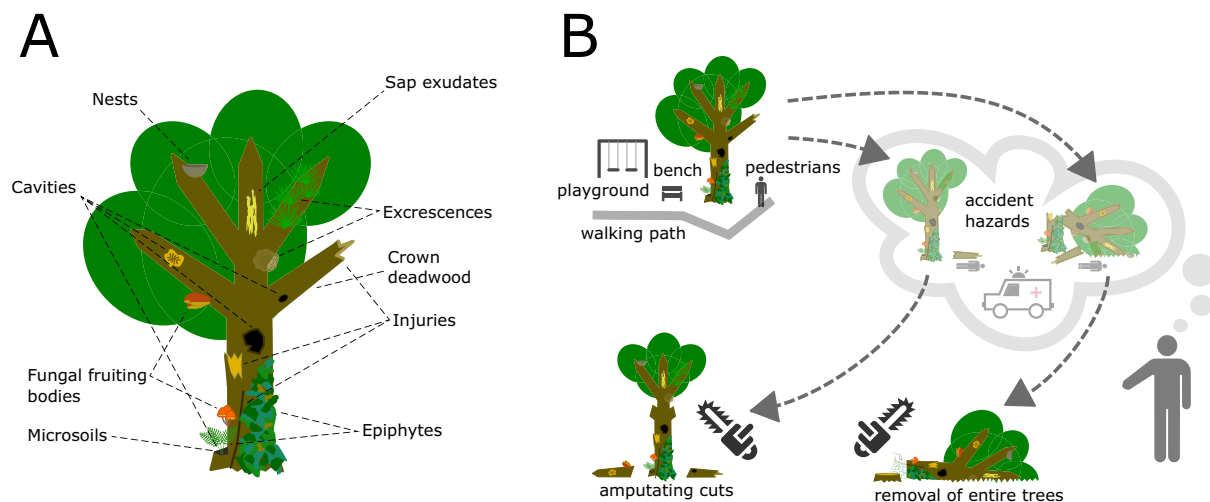


Fig. 1. Tree-related Microhabitats (TreMs) and the hypothesized constraints imposed by safety considerations on TreM conservation in urban public green spaces. Panel A shows TreMs as 15 distinct groups (woodpecker cavities, rot holes, insect galleries, concavities, exposed sapwood, exposed heartwood, crown deadwood, twig tangles, burrs and cankers, ephemeral fungal fruiting bodies, perennial fungal fruiting bodies, epiphytes, nests, microsoils, and sap exudates) categorized into nine families. Panel B outlines the hypothesized constraints affecting TreM conservation due to safety considerations.

generally have a negative impact on the abundance and diversity of TreMs. For instance, in an urban park in Rome (Italy), nearly all trees with TreMs were slated for removal due to perceived danger to visitors in 2000s (Carpaneto et al., 2010). In Montreal (Canada), trees under pruning regimes exhibited significantly lower abundance and diversity of TreMs compared to those unpruned in adjacent, non-managed forests (Großmann et al., 2020). The existing studies highlight the potential impacts of safety considerations on TreM preservation in urban environments. Yet, direct and high-resolution evidence of the process is still lacking, while it is essential for evaluating the constraints and opportunities for conserving large old trees within urban habitats.

The conservation of TreMs in public green spaces presents challenges due to safety concerns. Yet, significant variation in tree maintenance intensity is observed across and within cities globally (e.g., Carpaneto et al., 2010; Fröhlich and Ciach, 2020b; Großmann et al., 2020; Le Roux et al., 2014a; Sandström et al., 2006). This variation is attributed to diverse arboriculture policies, safety standards, and budgetary and practical limitations unique to each city. Tree surgeries, which are time-consuming and costly, are typically concentrated in strategically important parts of green spaces (Fröhlich and Ciach, 2020a; Sandström et al., 2006). Authorities base these decisions on known spatial variations in accident hazards, indicated by grey infrastructure and pedestrian activity (Ellison, 2005). Consequently, it could be hypothesized that trees near walking paths, benches, and playgrounds, which experience more frequent human activity, are subject to stricter arboriculture regimes (Fig. 1B). In contrast, trees located away from such infrastructure may receive less intensive maintenance (Fig. 1B). Moreover, we may assume that safety-driven surgeries primarily target large trees (Großmann et al., 2020; Avilés, 2019), which are more likely to harbor TreMs (Großmann et al., 2018; Kozák et al., 2018; Larrieu et al., 2012; Vuidot et al., 2011) and pose greater risks upon collapsing (Brookes, 2007; Ellison, 2005). Therefore, within individual parks, areas designated for recreation may not be suitable for conserving large old trees with TreMs, yet large trees positioned away from these areas can be left intact, allowing for the formation of natural TreM assemblages. Assessing these hypotheses is vital for understanding the interplay between safety considerations and TreM conservation in urban green spaces, highlighting both the constraints and opportunities for preserving arboreal biodiversity in a manner that harmonizes conservation efforts with human wellbeing.

Here, we examine the above hypotheses by comparing TreM assemblages across 5974 trees from over 50 species within 30 genera, spanning a gradient of human activity in urban public green spaces. These trees are organized into 510 sample plots, grouped as quintuplets within 102 sites, including parks, cemeteries, recreational forests, and historic reserves in Kraków, a historic settlement included in UNESCO's World Heritage Site list and one of the largest urban agglomerations in Poland. To test our hypotheses, we constructed Bayesian multi-level models (Rue et al., 2009, 2017) incorporating trees, plots, and sites as a nested random structure. First, we identify the influence of tree size and species on supporting TreM assemblages. Second, we evaluate how spatial variations in accident hazards—indicated by pedestrian activity and the presence of infrastructure across sample plots—affect tree management practices, as evidenced by pruning wounds and the removal of dead and sloped trees. Third, we assess the impact of intensive tree management on the prevalence of 15 TreM groups. Fourth, we quantify the constraints that safety considerations impose on TreM conservation by directly linking on-plot accident hazards with on-tree TreM occurrences. In all these analyses, we include a broad sample ranging from small to very large trees and control for tree size to determine whether the hypothesized conservation constraints apply universally or are predominantly relevant to larger trees, which are expected to pose greater safety concerns. Throughout these analyses, we also account for variations in green space types (parks, cemeteries, recreational forests, and historic reserves) to examine conservation challenges and opportunities under diverse arboriculture policies.

2. Materials and methods

2.1. Study area

This study was conducted in the Kraków agglomeration, encompassing the city of Kraków and several adjacent areas, with a combined population of approximately 1.4 million (in 2020, www.stat.gov.pl). The agglomeration radiates from Kraków's Old Town, one of Poland's oldest settlements. Its oldest sectors feature historic buildings, parks, and cemeteries, drawing 15 million tourists annually (www.krakow.pl). The responsibility for visitor safety lays on urban green space authorities, whom carefully monitor trees and remove or prune those deemed hazardous, sometimes prioritizing specific trees for surgery, such as those near playgrounds to safeguard children. In a few special cases, such as very large trees in crowded parks, green space authorities use acoustic tomography (see Arciniegas et al., 2014) to meticulously assess the tree's condition to inform maintenance decisions. However, in most cases, these services are outsourced to various private companies, which evaluate the risk of tree or branch falls based on trunk size, crown symmetry, and general tree health, including the presence of injuries, fungal fruiting bodies, or parasitic plants (ISA, 2011).

In the agglomeration's public green spaces, tree surgery intensity and types are governed by local arboriculture policies tailored to different green space types: parks, cemeteries, recreational forests, and historic reserves (Fig. 2A). Parks, under the municipal greenery authority's management (zsm.krakow.pl) for recreational and cultural purposes, undergo rigorous cleaning of trees and branches at high collapse risk. Cemeteries, managed by the municipal cemetery authority (www.zck-krakow.pl) and religious institutions, cater mainly to seniors with stringent safety expectations, resulting in even more rigorous tree maintenance than those in parks. Recreational forests, managed by either the municipal greenery authority (zsm.krakow.pl) or the state forest holding (www.lasy.gov.pl), lie at the agglomeration's edges but are frequented by both local residents and tourists. These forests are minimally used for timber production, focusing instead on wild-type recreation and conservation, leading to the removal of weakened trees and branches primarily along walking paths. Historic reserves, referring to parks around Austro-Hungarian fortifications managed by the state monument authority (www.wuoz.malopolska.pl), were established in the 18th century. Trees in these areas have been largely left intact, except for a few forts converted into commercial museums, which were considered non-public and excluded from this study. The selected historic reserves are seldom visited, with tree cutting limited to preventing damage to monumental structures.

2.2. Study design

The study area was defined as a 20 km × 20 km square (400 km²), centered on Kraków Main Square (Fig. 2B). We obtained the outlines of parks, cemeteries, forests, and historic reserves from www.openstreetmap.org in the form of spatial vector layers (depicted as greenish polygons in Fig. 2B). Utilizing satellite imagery (www.google.com/maps, accurate as of November 2019), we excluded patches of green space that were devoid of trees or contained only a few trees. Additionally, four forests near the northern boundary of the study area were excluded due to their status as spatial outliers, isolated by a vast expanse of cropland.

Within the remaining green spaces, we randomly selected 80-m-radius circles, termed 'sample sites' (Fig. 2C). Small or irregularly shaped patches that could not accommodate the desired circle were excluded; trees in these patches consistently intersected with transportation infrastructure, which fell outside the scope of the issues addressed in this study. We allocated one sample site per 100 ha of green space, ensuring a minimum distance of 500 m between sites. Most green spaces were smaller than 100 ha, thus having one centrally located sample site. Eight larger green spaces (114.9–131.2 ha) received two

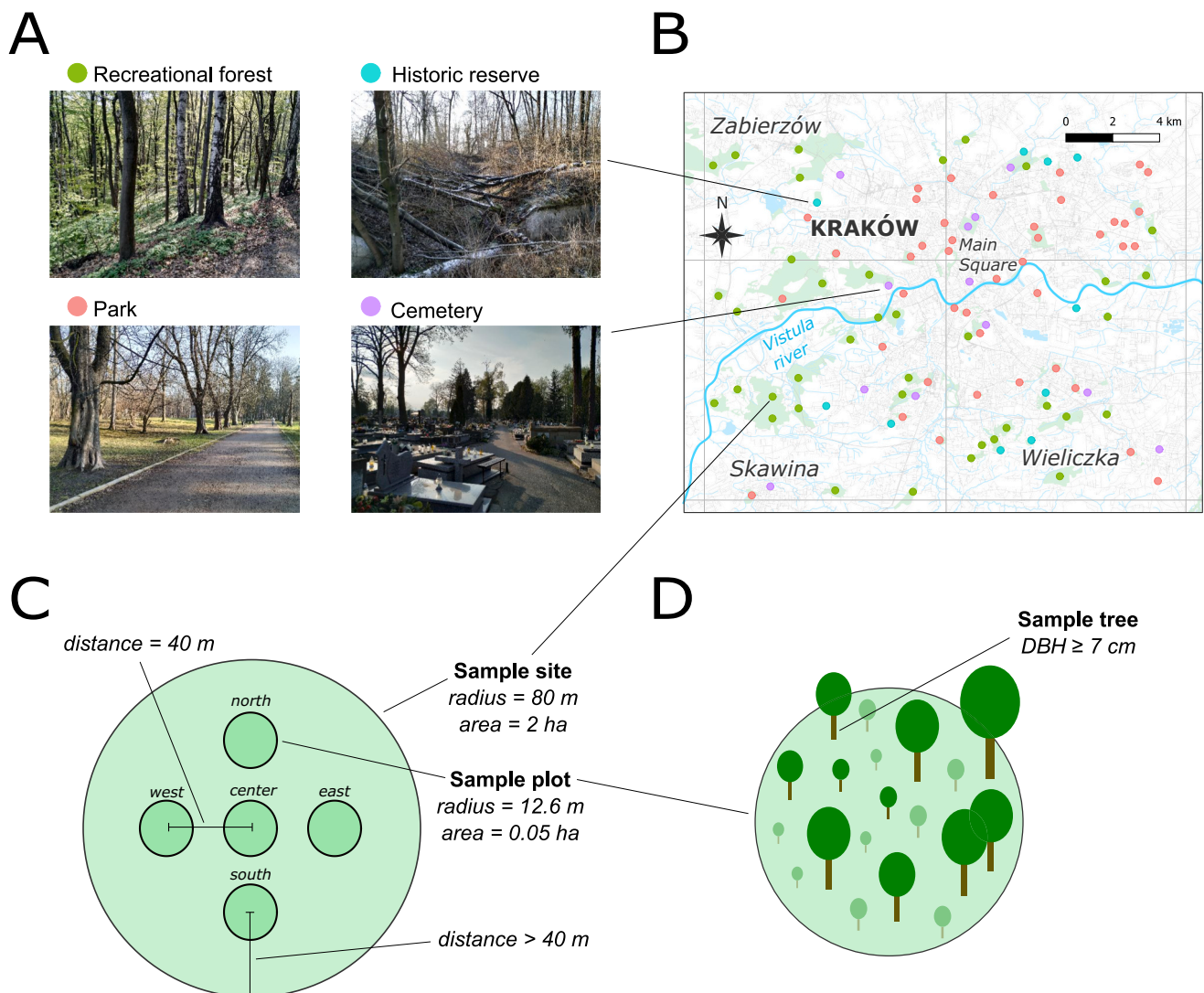


Fig. 2. Study design. In the urban agglomeration of Kraków (Southern Poland), we selected large, compact patches of publicly available green spaces, each classified as one of four green space types: recreational forest, historic reserve, park, or cemetery (A). Within selected green space patches, we selected 1 site per 100 ha, maintaining a minimum distance of 500 m between sites and 40 m to the edge of the green space patch, resulting in a total of $n = 102$ sample sites (B). For each sample site within a buffer of 80 m, we selected a quintuplet of regular sample plots, with the first plot located at the center and four located 40 m away toward the north, east, south, and west (C); this yielded a total of $n = 510$ sample plots. Within each sample plot, we surveyed all trees with a diameter at breast height (DBH) ≥ 7 cm (D), resulting in a total of $n = 5974$ sample trees. Pictures were taken by Arkadiusz Fröhlich.

sample sites each, while Wolski Forest (296.2 ha) was allocated three sample sites. This process resulted in a total of 102 sample sites, with 41 in parks, 12 in cemeteries, 39 in recreational forests, and 10 in historic reserves.

Within each sample site, five 12.6-m-radius circles (0.05 ha each), termed ‘sample plots,’ were selected in a regular manner: the first plot was centered on the sample site’s centroid, with subsequent plots placed directly to the north, east, south, and west, 40 m from the central plot (Fig. 2C). The 40-m distance, representing the maximum tree height in our study area, ensures that potential tree falls do not impact adjacent plots (Kozák et al., 2018). We also maintained a minimum 40-m distance from the green space’s outline to avoid edge effects on TreMs (Ouin et al., 2015) and exclude areas managed by transportation authorities, which typically enforce a more rigorous tree maintenance regime incompatible with conservation efforts.

All trees within the sample plots with a Diameter at Breast Height (DBH) of ≥ 7 cm, referred to as ‘sample trees’ (Fig. 2D), were included in the survey. The total count of sample trees was 5974, ranging from 1 to 193 trees per sample site (median = 53, quartile range = 30–76) and

from 1 to 57 trees per sample plot (median = 10, quartile range = 5–16). At these three levels of spatial organization—sample trees, sample plots, and sample sites—we evaluated a set of variables through fieldwork, geospatial, and statistical analyses (Table 1).

2.3. Fieldwork

We conducted fieldwork from January 5th to March 12th, 2020, during the leafless period to ensure better detectability of small structures (TreMs) within the crowns of sampled trees. Binoculars were used to identify significant visual traits present on the tree trunks and crowns at higher elevations. The DBH of each sampled tree was measured using a tree caliper with an accuracy of 1 cm.

Tree species were identified using the local authorized key (Szweczyk et al., 2011), based on characteristic traits of bark, crown habit, twigs, and/or buds. In our study area, at least 16 tree genera contain species with tendencies for hybridization (e.g., *Tilia* sp., birches, *Populus* sp., and *Salix* sp.), which exhibit intermediate phenotypic traits (Senta et al., 2021). This difficulty, coupled with the leafless conditions,

Table 1

The summary of variables assessed across sample trees (n = 5974), sample plots (n = 510), and sample sites (n = 102), a random-effect-levels in our analyses.

Variable name	Random level	Type	Description	Statistics	Method
Principal tree traits					
diameter at breast height (DBH)	tree	continuous, non-Gaussian	The diameter (cm) at breast height of the sample tree	median = 23; q. range = 12–39; range = 7–196	fieldworks
tree genus	tree	categorical, 31 levels	The taxonomic genus of the sample tree	see Table 2	fieldworks (Szewczyk et al., 2011)
Indicators of tree surgeries					
large pruning wound	tree	binary	Whether the sample tree has a pruning wound with a surface diameter ≥ 20 cm.	TRUE, n = 437 (7.3 %)	fieldworks (Grüebler et al., 2013)
dead tree	tree	binary	Whether the sample tree is dead	TRUE, n = 211 (3.5 %)	fieldworks (Fröhlich and Ciach, 2020b)
sloped tree	tree	binary	Whether the sample tree is sloped by $\geq 15^\circ$	TRUE, n = 522 (8.7 %)	fieldworks
Measures of accident hazards					
human activity	plot	continuous, Gaussian (Fig. S1B)	The probability of pedestrian presence recorded within the boundaries of sample plot, reduced by the effect of hour and month of the survey (see Fig. S1)	mean = 0.0 \pm 1.9	fieldworks (Corsini et al., 2019), statistical analyses (Rue et al., 2009)
path	plot	binary	Whether any walking path crosses the sample plot's outlines	TRUE, n = 255 (50 %)	geospatial analyses (Padgham et al., 2017)
bench	plot	binary	Whether the sample plot has at least one bench	TRUE, n = 82 (16.1 %)	fieldworks
playground	plot	binary	Whether the sample plot has at least one playground device	TRUE, n = 16 (3.1 %)	fieldworks
Proxies of arboriculture policies					
green space type	site	categorical, 4 levels	Whether the sample site is a recreational forest, historic reserve, park, or cemetery.	forests, n = 39; reserves, n = 10; parks, n = 41; cemeteries, n = 12	city council (Dubiel and Szwagrzyk, 2008)

prevented us from identifying every species. Consequently, we were able to assign species to only 48.1 % of the sampled trees (Table S1). Nevertheless, we identified 98.2 % of trees to the genus level (Table 2), which we then used as a proxy for species in all analyses. The sampled trees spanned 30 genera; completely dead individuals, lacking distinctive traits due to severe bark decay, were categorized as an additional 31st category (Table 2). This approach allowed us to include all trees in the analyses, thereby capturing a wider variation in green space properties and producing more general findings.

We inspected all sampled trees for the presence of TreMs, following the criteria outlined in the field handbook (Kraus et al., 2016). We classified these TreMs into 15 distinct groups following a widely accepted typology (Larrieu et al., 2018), including: woodpecker cavities, rot holes, insect galleries, concavities, exposed sapwood, exposed heartwood, crown deadwood, twig tangles, burrs and cankers, ephemeral fungal fruiting bodies, perennial fungal fruiting bodies, epiphytes, animal nests, microsoils, and sap exudates (refer to Fig. 1A). For each sampled tree, we recorded the presence of each TreM group as a binary attribute (TRUE/FALSE).

2.4. Indicators of tree surgeries

Historic data on tree surgeries was available only for a fraction of the trees analyzed. Therefore, we utilized three binary variables at the sample tree level as proxies for tree surgeries: the presence of large pruning wounds, dead trees, and sloped trees. Recent pruning intensity is commonly measured by the presence of a fresh pruning wound on a tree, which meets a certain surface diameter threshold (Avilés, 2019; Großmann et al., 2020; Grüebler et al., 2013). Since we used a 20 cm threshold to distinguish (natural) exposed heartwood (Kraus et al.,

2016), we assigned TRUE to all trees with at least one fresh pruning wound larger than 20 cm in diameter and FALSE to trees without such wounds. Additionally, we attributed the presence of exposed heartwood to all trees with pruning wounds (Großmann et al., 2020).

Dead and sloped trees are primarily targeted for removal within public green spaces (Ellison, 2005; ISA, 2011; Fröhlich and Ciach, 2020a; Le Roux et al., 2014a), thus their presence or absence serves as an indicator of the recent cessation or intensification of risky tree removal activities within a plot or site. Dead trees were identified as those completely lacking leaves, twigs, or buds, often broken at the trunk, missing branches and/or bark, and frequently unclassified to a genus. Sloped trees were defined as those leaning at an angle of at least 15° , a critical threshold for static inspection and removal recommendation by Kraków's authorities. The angle was measured using the 'Bubble Level' app (version 1.0) for android. We expressed the occurrence of dead and sloped trees as two separate binary variables (TRUE/FALSE) for each sampled tree.

2.5. Accident hazards

We quantified the spatial variation in accident hazards using four measures assessed at the sample plot level: human activity, and the presence of a walking path, bench, or playground. We defined 'human activity' as the extent to which a given plot is more or less frequently visited by people compared to an average plot; this measure is a primary criterion for determining the necessity of removing risky trees or branches (Ellison, 2005). To assess this, we conducted 4080 surveys of pedestrian presence, with eight surveys carried out on each plot, conducted once a month from January to August. The surveys were performed only on weekdays. Each site was visited monthly at various times

Table 2

The summary of tree genus across sample trees ($n = 5974$), sample plots ($n = 510$) and sample sites ($n = 102$). See Table S1 for information on species appearing within genera.

Genus common name	Scientific Name	n	Frequency		
			trees	plots	sites
Oak	<i>Quercus</i> sp.	759	12.7 %	10.4 %	7.6 %
Maple	<i>Acer</i> sp.	662	11.1 %	10.9 %	9.0 %
Prunus	<i>Prunus</i> sp.	478	8.0 %	7.0 %	7.0 %
Alder	<i>Alnus</i> sp.	450	7.5 %	4.2 %	3.9 %
Elder	<i>Sambucus</i> sp.	324	5.4 %	4.9 %	4.9 %
Locust	<i>Robinia</i> sp.	314	5.3 %	4.6 %	4.7 %
Beech	<i>Fagus</i> sp.	317	5.3 %	4.4 %	3.8 %
Pine	<i>Pinus</i> sp.	295	4.9 %	3.8 %	2.7 %
Birch	<i>Betula</i> sp.	284	4.8 %	6.6 %	6.5 %
Lime	<i>Tilia</i> sp.	268	4.5 %	6.4 %	7.1 %
Hornbeam	<i>Carpinus</i> sp.	254	4.3 %	3.3 %	2.7 %
Willow	<i>Salix</i> sp.	188	3.1 %	3.8 %	4.1 %
Elm	<i>Ulmus</i> sp.	178	3.0 %	4.0 %	4.8 %
Ash	<i>Fraxinus</i> sp.	182	3.0 %	5.2 %	5.1 %
Hawthorn	<i>Crataegus</i> sp.	174	2.9 %	3.5 %	4.3 %
Hazel	<i>Corylus</i> sp.	152	2.5 %	1.5 %	1.4 %
Larch	<i>Larix</i> sp.	144	2.4 %	2.3 %	2.4 %
Poplar	<i>Populus</i> sp.	139	2.3 %	3.5 %	3.6 %
Thuja	<i>Thuja</i> sp.	112	1.9 %	1.3 %	1.3 %
Chestnut	<i>Aesculus</i> sp.	49	0.8 %	2.3 %	3.3 %
Walnut	<i>Juglans</i> sp.	36	0.6 %	0.7 %	1.3 %
Lilac	<i>Syringa</i> sp.	38	0.6 %	0.1 %	0.3 %
Spruce	<i>Picea</i> sp.	27	0.5 %	0.7 %	1.0 %
Whitebeam	<i>Sorbus</i> sp.	23	0.4 %	1.0 %	1.4 %
Yew	<i>Taxus</i> sp.	5	0.1 %	0.1 %	0.1 %
Dogwood	<i>Cornus</i> sp.	6	0.1 %	0.2 %	0.4 %
Sumac	<i>Sumac</i> sp.	2	<0.1 %	0.1 %	0.3 %
Honey locust	<i>Gleditsia</i> sp.	2	<0.1 %	0.1 %	0.3 %
Fir	<i>Abies</i> sp.	2	<0.1 %	0.1 %	0.3 %
Catalpa	<i>Catalpa</i> sp.	1	<0.1 %	0.1 %	0.1 %
Juniper	<i>Juniperus</i> sp.	1	<0.1 %	0.1 %	0.1 %
Unknown	Unknown	108	1.8 %	2.9 %	4.4 %

between 6:00 and 20:00 CET, and the surveys on each plot were conducted in random order. We then estimated the average probability of human presence within each sample plot (adjusted for the month and time of the survey) using a generalized linear mixed model (see Fig. S1A). This variable followed a normal distribution (Fig. S1B).

The presence of a walking path within a sample plot was determined using the 'osmdata' (version 0.2.1) and 'sf' (version 1.0–12) packages in R. We utilized line vector layers of pavements, walking trails, paths, and bike roads to calculate the total length (in meters) of these features within the boundaries of each sample plot. The median path length across sample plots was 0.6 m (interquartile range = 0–28.9 m; range = 0–100.6 m). Due to significant skewness, we transformed the path length into a binary variable, assigning TRUE to plots with a path length > 0 m and FALSE to those without. The presence of a walking path correlated perfectly with field observations and was significantly associated with human activity across sample plots (estimate = 1.4, credible intervals = 1.2–1.6), as determined by a binomial generalized linear mixed model with the sample site as a random effect.

The presence of benches and playgrounds was recorded during fieldwork on each sample plot as binary variables. A playground was defined as entertainment equipment intended for children (e.g., swings, slides, or merry-go-rounds) or adults (e.g., courts, skateboard ramps, or exercise machines). Playgrounds were only found in parks, while benches were present in all types of green spaces except historic reserves.

2.6. Data handling and analyses

All analyses were conducted using the R statistical language (version 4.2.3) (R Development Core Team, 2023). The study design encompassed three levels of spatial organization: sample trees, sample plots,

and sample sites, all treated as nested random effects. Additionally, tree genus was included as a cross-random effect to control for its influence. A binomial type of the response variable, coupled with the varying number of trees and the uneven distribution of tree genera across plots and sites (see Table 2) posed a challenges to the convergence of standard linear mixed models. To address this, we employed Integrated Nested Laplace Approximations (INLA) (Rue et al., 2009), an efficient method for estimating patterns in structured data that demands less computational time compared to other Bayesian models (Rue et al., 2017). Thus, INLA (R package version 22.08.24) was utilized in all analyses, with non-informative (default) priors (see Rue et al., 2009) applied in each model. Since INLA does not include p -values in model summaries, the model performance was evaluated using the Deviance Information Criterion (DIC), considering models with Δ DIC < 4 relative to the null model as informative. It was used to assess the random effects structure (see Figs. S2 and S3), fixed effects, and interactions. The interactions were deemed informative if Δ DIC < 4 compared to the model with same fixed terms, but excluding the interaction.

Although The global dataset, structured into three sub-nested levels: sample sites ($n = 102$), sample plots ($n = 510$), and sample trees ($n = 5974$, corresponding to data points) across $n = 31$ genera, was analyzed. The modelling procedure is detailed in Supplementary Methods 1. Additionally, to accommodate varying arboriculture policies across different types of green spaces, the dataset was segmented to analyze patterns within parks (1780 trees across 28 genera, 205 plots, and 41 sites), cemeteries (302 trees across 18 genera, 60 plots, and 12 sites), recreational forests (3328 trees across 23 genera, 195 plots, and 39 sites), and historic reserves (564 trees across 15 genera, 50 plots, and 10 sites) separately.

3. Results

Among the sampled trees, we found TreMs representing all fifteen distinct groups (Fig. 3A and B). The most common were crown deadwood, exposed heartwood, epiphytes, and exposed sapwood, each occurring in > 10 % of sampled trees (Fig. 3A). The scarcest TreMs included woodpecker cavities, ephemeral and perennial fungal fruiting bodies, and sap exudates, found in < 2 % of sampled trees (Fig. 3A). The presence of each TreM was primarily determined by fundamental tree traits – tree size and genus – when considered as sole predictors (Fig. S4A). Large DBH was a crucial factor for the occurrence of each TreM (Fig. S4A and B). However, some groups were more tightly linked with larger trees than others; for example, perennial fungal fruiting bodies or twig tangles required, on average, double the DBH compared to crown deadwood (Fig. S4B). Additionally, tree genus played an important role, with most TreMs more commonly forming on beeches *Fagus* sp., birches *Betula* sp., willows, and poplars, and less so on elders *Sambucus* sp., pines *Pinus* sp., ashes *Fraxinus* sp., and larches *Larix* sp. (Fig. S4C).

Our analyses suggest that pruning and removal of dead and sloped trees predominantly target the largest trees associated with accident hazards. Specifically, large trees (Fig. 4A), and especially those located on plots with high human activity (Fig. 4B), a walking path (Fig. 4C), a bench (Fig. 4D), or a playground (Fig. 4E), were more likely to be pruned and/or less likely to be left on trunk if dead or sloped. The presence of a bench and playground predicted pruning within parks (Fig. S6A), while paths determined pruning within cemeteries (Fig. S6B) and recreational forests (Fig. S6C); no pattern was found within historic reserves (Fig. S6D). Additionally, our results indicate that exacerbated surgeries lead to significant losses of woodpecker cavities, rot holes, insect galleries, concavities, exposed sapwood, crown deadwood, perennial and ephemeral fungal fruiting bodies, and microsoils (Fig. S7A–D). However, exposed heartwood increased in prevalence after pruning in smaller trees (Fig. S4B).

Further analyses revealed a direct association between spatial variation in accident hazards and the occurrence of TreMs. Large trees on

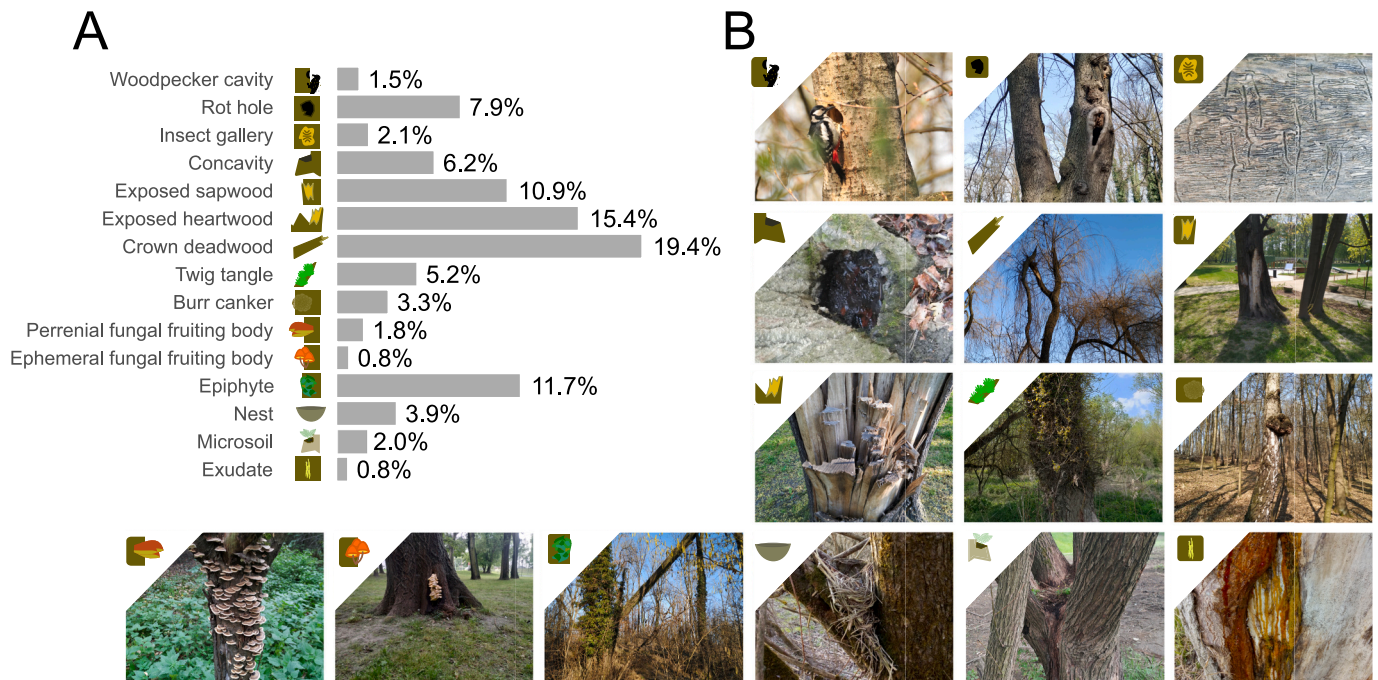


Fig. 3. Tree-related microhabitats (TreMs) found among 5974 sample trees situated within publicly available urban green spaces of the Kraków agglomeration. The prevalence of 15 TreM groups (A) and exemplary photographs for each (B). Pictures were taken by Arkadiusz Fröhlich and Fabian Przepióra.

plots with higher human activity were less likely to accumulate rot holes, exposed sapwood, crown deadwood, perennial and ephemeral fungal fruiting bodies, and epiphytic plants compared to trees on plots with lower human activity (Fig. 5). Similarly, large trees on plots with walking paths were less likely to bear concavities, exposed sapwood, and ephemeral fungal fruiting bodies (Fig. 5). Crown deadwood was less probable on plots with benches, while concavities and perennial fungal fruiting bodies were negatively associated with playground presence (Fig. 5). Notably, negative associations between accident hazards and TreM occurrences were generally more significant for larger than smaller trees (Fig. 5).

In parks, ephemeral fungal fruiting bodies were linked to low human activity and the absence of paths; rot holes appeared on plots without paths, while crown deadwood was found in areas without benches or playgrounds (Fig. S9). In cemeteries, nest presence was associated with high human activity, and epiphytes on smaller trees were observed near benches (Fig. S10). In recreational forests, both rot holes and ephemeral fungal fruiting bodies correlated with low human activity, whereas the opposite was true for microsoils (Fig. S11). No such associations were found in historic reserves (Fig. S12).

4. Discussion

The conflict between safety considerations and the conservation of the ecological values of large trees is a widespread problem across the world's cultural landscapes, as it has been extensively discussed across both non-urban (Avilés, 2019; Grüebler et al., 2013; Suchocka et al., 2019) and urban contexts (Carpaneto et al., 2010; Fröhlich and Ciach, 2020b; Großmann et al., 2020; Le Roux et al., 2014a). Our research provides the first empirical evidence of this interaction, demonstrating that elevated accident hazards lead to intensified tree surgeries, which, in turn, reduce the prevalence of most TreMs on urban trees, especially large ones. While previous studies have explored the potential loss of TreMs in single locations (Carpaneto et al., 2010) or compared TreM assemblages between managed and unmanaged habitats (Großmann et al., 2020), our study incorporates more detailed resolution. This includes direct surrogates for accident hazards and a finer spatial scale, addressing not only cross-green space variation but also within-green

space variation. Taking into account the safety standards and arboriculture policies of Kraków, our models reveal that the observed spatial variation in (perceived) accident hazards is significant enough to influence the pattern of tree maintenance intensity that affects TreM assemblages. This understanding can be potentially generalized to urban landscapes worldwide and is vital for developing sustainable management strategies that reconcile human well-being with the conservation of urban biodiversity.

Despite the impact of urban arboriculture practices, the presence of TreMs is still largely dictated by natural factors, such as tree size and species. Our findings concur with the well-documented reality that larger trees are invaluable hosts for TreMs (Carpaneto et al., 2010; Kozák et al., 2018; Larrieu et al., 2012; Lindenmayer and Laurance, 2017; Przepióra and Ciach, 2022; Vuidot et al., 2011; Großmann et al., 2020), emphasizing the essential role of large old trees in supporting urban biodiversity. The importance of certain genera, such as beeches, birches, willows, and poplars, in maintaining diverse TreM assemblages, is consistent with recent research in non-urban settings (Asbeck et al., 2019; Kozák et al., 2018; Larrieu et al., 2012; Przepióra and Ciach, 2022; Vuidot et al., 2011). Moreover, our observations indicate that a broader range of tree genera is important, as each supports unique TreM groups. Although perhaps expected (Le Roux et al., 2014a; Threlfall et al., 2016; Großmann et al., 2020), these insights offer crucial guidance for developing ecologically-oriented urban arboriculture policies: the preservation of old and diverse tree stands is imperative for conserving biodiversity.

The pivotal finding of our study is that spatial variation in accident hazards both produces constraints and opportunities for the conservation of TreMs. Spaces designed for recreational access, characterized by high human activity and the presence of recreational infrastructure such as walking paths, benches, or playgrounds, face significant challenges in conserving TreMs due to the necessity of frequent pruning and logging of risky trees to meet safety standards. Another important finding of our study is that the influence of spatial risk variation on TreM assemblages depends on tree size. Large old trees are crucial hosts for TreMs (Asbeck et al., 2019; Kozák et al., 2018; Larrieu et al., 2012; Vuidot et al., 2011), but they also pose the greatest risk of causing severe harm if they collapse (Brookes, 2007; Ellison, 2005). Consequently, they are often

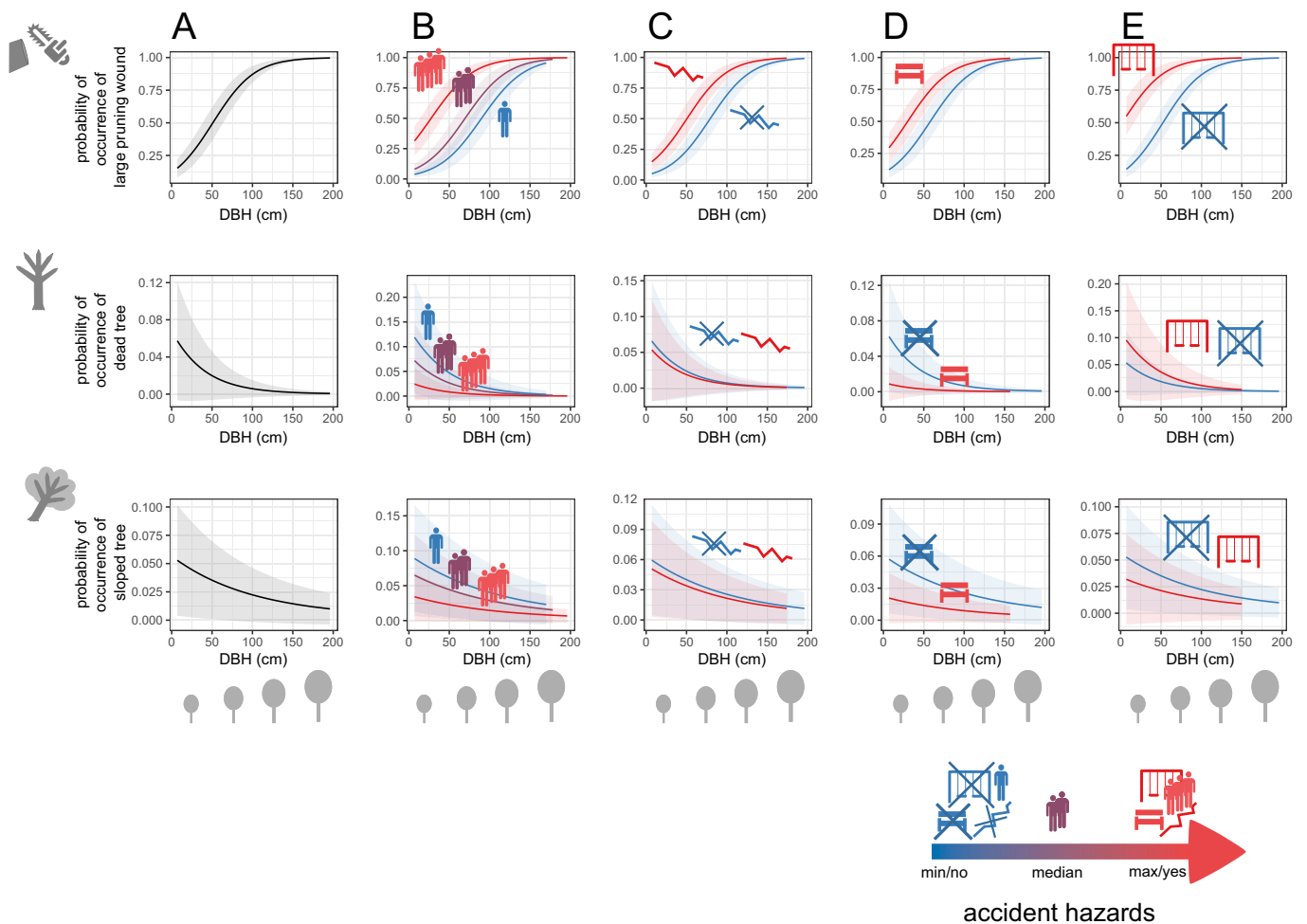


Fig. 4. Spatial variation in accident hazards governing tree surgeries. We evaluated the diameter at height (DBH) and spatial variation in accident hazards as factors governing tree surgeries across 5974 sample trees belonging to 30 genera, growing on 510 sample plots nested as quintuplets in 102 sample sites situated in publicly available green spaces of the Kraków urban agglomeration. We ran Integrated Nested Laplace Approximations (INLA) binomial-family models with the response of the presence of a large pruning wound (1st row), a dead tree (2nd row), and a sloped tree (3rd row), while including the sample site, sample plot, and tree genus as random effects. Through the model selection procedure, we evaluated the performance of models including only DBH (null) and models with DBH altogether with either of four indicators of accident hazards (specific to the sample plot) as a fixed or interaction term: human activity and the presence of a walking path, bench, or playground (see Fig. S2). Here, we illustrated only informative models, those with $\Delta\text{DIC} \leq 4$ compared to the null model, and models with interaction considered when $\Delta\text{DIC} \leq 4$ compared to similar models without interaction. Charts show how the probability of occurrence of a pruning wound, dead tree, and sloped tree vary as a function of tree size (A) under the maximum (red trends), median (purple trends), and minimum (blue trends) human activity (B) or the presence (red trends) or absence (blue trends) of elements of recreational infrastructure, such as walking path (C), bench (D), or playground (E); ribbons and error bars indicate 95 % credible intervals. These results suggest that the co-occurrence of large old trees with increased accident hazards necessitates exacerbated tree surgeries due to safety reasons.

removed or pruned for safety reasons (Avilés, 2019; Großmann et al., 2020; Gruebler et al., 2013). The exceptional ecological value of these large old trees, coupled with their long regeneration periods, necessitates a reconsideration of management strategies.

Our results show that the TreMs most sensitive to conflicts with public safety include rot holes, exposed sapwood, crown deadwood, perennial and ephemeral fungal fruiting bodies, and epiphytic plants. This finding was to be highly expected given that such structures are often cited as indicators of tree collapse risk (ISA, 2011; Nali and Lorenzini, 2009). The diminished prevalence of these structures in public green spaces can have cascading effects on associated organisms, such as woodpeckers (Fröhlich and Ciach, 2020a), secondary cavity nesters (Blewett and Marzluff, 2005), saproxylic beetles (Carpaneto et al., 2010), and fungi (Meyer et al., 2021). Instead of using the presence of TreMs as tree condition indicators, it is worthwhile to promote acoustic tomography, which, although costly, is a promising non-invasive method to assess the true condition and collapse risk of trees (Arciniegas et al., 2014), and could therefore save numerous trees from

removal or pruning. However, our results also align with previous observations that under certain circumstances, some TreM groups may be positively linked to intensive arboriculture practices (Avilés, 2019; Großmann et al., 2020; Gruebler et al., 2013). For example, exacerbated pruning directly produces exposed heartwood (Fig. S13A). The correlated increase of avian nests with human activity observed in this study may result from high densities of synanthropic birds (Ciach and Fröhlich, 2017; Morelli et al., 2018) attracted to anthropogenic food sources (Fig. S13B). Similarly, some epiphyte species are often preserved to enhance scenic beauty, as in the case of ivy *Hedera helix* in cemeteries (Fig. S13C). The positive association between microsoils and human activity in the studied forests resulted from frequent pruning and thinning that produced coppice shoots, accumulating more litter than regular trees (Fig. S13D). These TreMs might be more common in managed than unmanaged tree stands, but they are marginal compared to those disappearing because of exacerbated tree maintenance induced by safety considerations.

The intersection of tree size and spatial variation in accident hazards

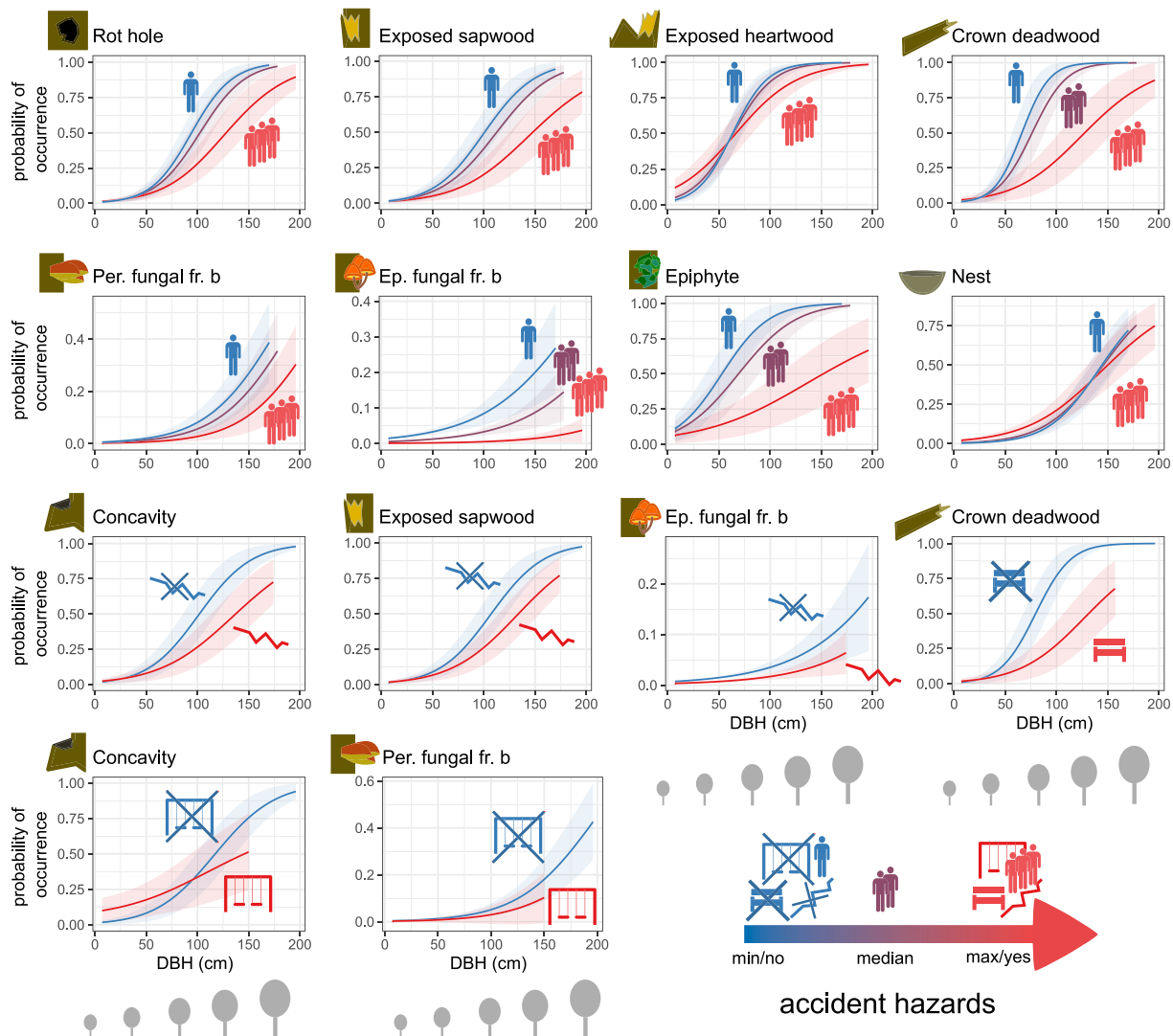


Fig. 5. Constraints that safety considerations impose on the conservation of Tree-related Microhabitats (TreMs) in urban public green spaces. We evaluated the diameter at breast height (DBH) and spatial variation in accident hazards as determinants for the occurrence of TreMs across 5974 sample trees belonging to 30 genera, growing on 510 sample plots nested as quintuplets in 102 sample sites situated in publicly available green spaces of the Kraków urban agglomeration. We ran Integrated Nested Laplace Approximations binomial-family models with the response of the occurrence of either of 15 TreM groups while including sample plot, sample site, and tree genus as random effects. Through the model selection procedure, we evaluated the performance of models including only DBH (null) and models with DBH altogether with either of four indicators of accident hazards (specific to the sample plot) as a fixed or interaction term: human activity and the presence of a walking path, bench, or playground (see Fig. S5). Here, we illustrated only informative models, those with $\Delta\text{DIC} \leq 4$ compared to the null model, and models with interaction considered when $\Delta\text{DIC} \leq 4$ compared to similar models without interaction. Charts show how the probability of occurrence of TreMs increases as a function of tree size under the maximum (red trends), median (purple trends), and minimum (blue trends) human activity or the presence (red trends) or absence (blue trends) of elements of recreational infrastructure; ribbons and error bars indicate 95 % credible intervals. These results suggest that the co-occurrence of large old trees with increased accident hazards constrains the formation of TreMs due to exacerbated tree surgeries driven by safety reasons.

indicates obstacles to conservation but also uncovers multiple implications for sustainable urban forestry. While the conservation of TreMs encounters substantial constraints in risky areas, these constraints are minimal or absent in other spaces, allowing large trees to thrive intact, forming a diversity of microstructures important for biodiversity. Importantly, accident hazards vary both among and within green spaces (as observed across sample sites and sample plots, respectively), pointing toward two key opportunities for large old trees conservation. The first is maintaining strategic refuges for large old trees in certain wooded patches located in sparsely populated districts of the city—a concept corresponding to land sparing (Green et al., 2005; Phalan et al., 2011), as previously discussed in tree-management literature (Fröhlich and Ciach, 2020b; Großmann et al., 2020; Le Roux et al., 2014a). The second opportunity—unconsidered in existing literature—involves maintaining similar refuges in green spaces that are moderately amenitized for

recreation but have specific areas set apart from infrastructure which could be considered ‘pocket reserves’. This yet overlooked opportunity aligns with the land sharing concept (Soga et al., 2014). Our study indicates that pocket reserves have already emerged in many green spaces from the center to the peripheries (Fig. 6A-D), perhaps unintentionally due to random and/or practical reasons. However, intentionally expanding such spaces through smart, nature-friendly urban planning could significantly enhance the persistence of habitat trees within the city’s interior, bringing humans closer to nature and thus positively influencing well-being (Cirino et al., 2021; Hedblom et al., 2019).

We found that the intersection of safety considerations with large old trees and their TreM assemblages depends on the arboriculture policies applied in various types of green spaces. The most significant constraints were observed in parks, where a mix of infrastructure elements, combined with spatially variable human activity, produced spatial patterns

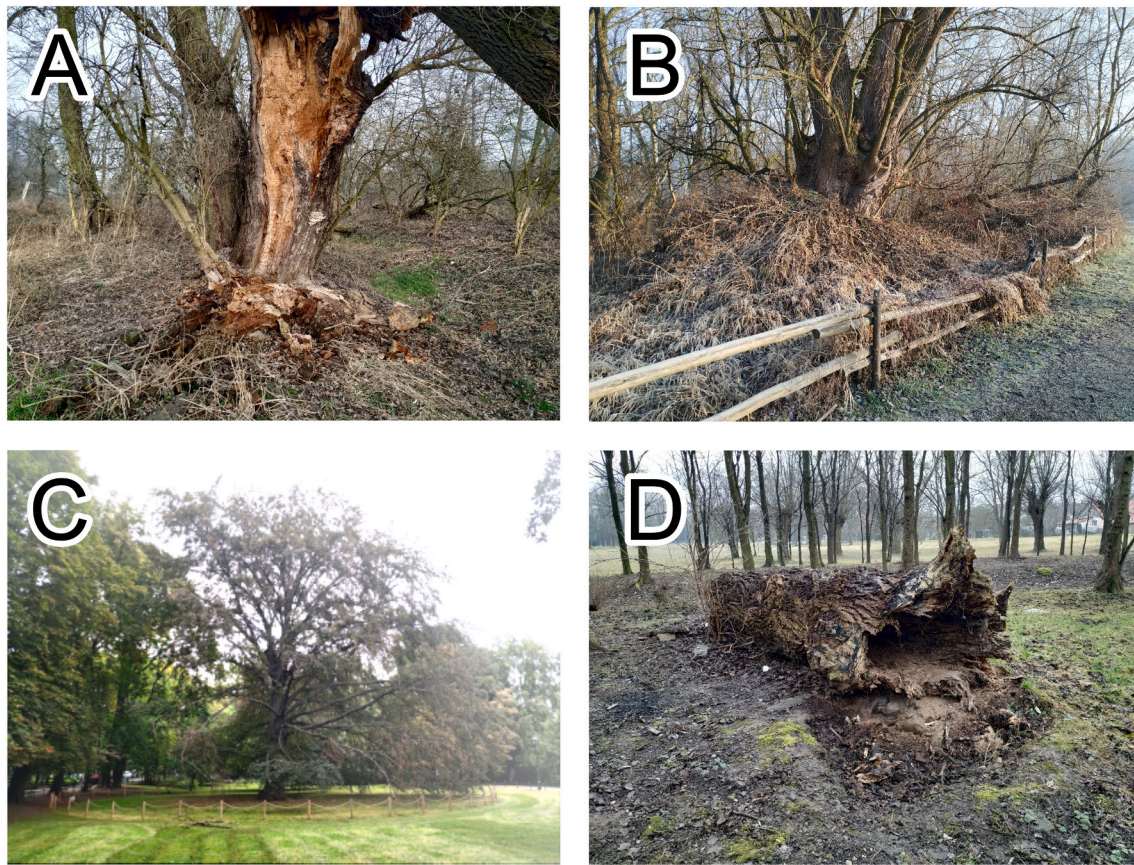


Fig. 6. We found many large old trees with diverse assemblages of Tree-related Microhabitats (TreMs). Such spaces occurred both in recreational forests (a) and historic reserves and parks (b, c, and d), from Kraków's center to the peripheries, but always away from walking paths and other infrastructure elements: (a) large decayed crack willow *Salix fragilis* in Dolina Prądnika Forest in Kraków; (b) large old white willow *Salix alba* in Józef Piłsudski Park in Skawina; (c) ancient beech *Fagus sylvatica* covered by monumental protection in Planty Park in Kraków; (d) large decaying trunk of crack willow in Płaszów Park in Kraków. These spaces might be considered pocket nature reserves, where large old trees are left intact and allowed to form various TreMs without decreasing public safety (such as in c). Pocket reserves might also provide an opportunity to conserve debris produced by these large trees (d). Importantly, the number of these pocket reserves might be multiplied by implementing smart infrastructure designs. Pictures were taken by Arkadiusz Fröhlich.

in certain TreM types. These patterns were less evident in recreational forests, which are maintained more naturally, yet rot holes and fungal fruiting bodies were still negatively associated with human activity levels. In cemeteries, the dense network of infrastructure necessitates strict arboriculture regimes, thus accident hazards did not produce the pattern in TreMs, highlighting the lack of opportunities for conservation. In historic reserves, where trees are almost entirely unmanaged, accident hazards did not result in notable patterns, thus again suggesting that there is nothing to do to conserve TreMs in the habitat. This demonstrates that sustainable management of large old trees, while upholding safety standards, could be viable in parks and to a lesser extent in recreational forests, underscoring the complexity of the issue and the need for tailored conservation solutions that do not interfere with the principal purposes of green space maintenance.

It is noteworthy that the conservation of large old trees and their ecological properties is impossible without environmental awareness, which, in democratic societies, shapes public debate and indirectly translates into future policies. The understanding of the key value of veteran large old trees and their TreMs is already substantial among professionals (Martin and Almas, 2023) and passionate naturalists (Nolan et al., 2020, 2022), but this knowledge has not yet been widely adopted by the general public (Brookes, 2007; Gilles, 2004; Hauru et al., 2014; Nali and Lorenzini, 2009; Tyrväinen et al., 2003). Thus, it is essential to inform society about the ecological value of TreMs to foster broader support for conservation efforts. Citizen science platforms could be of great value for increasing awareness in this matter (Nolan et al.,

2020, 2022). Further highlighting iconic species that rely on TreMs, such as cavity-nesting birds or bats (Blewett and Marzluff, 2005; Fröhlich and Ciach, 2020a; Larrieu et al., 2018; Paillet et al., 2018), could help change the perception of veteran trees within urban spaces and thereby introduce conservation purposes into common arboricultural practices. Importantly, besides pruning and logging, many other commonly applied practices, such as the plugging of tree cavities, thinning of twig tangles, trimming of loose bark, removal of fungal fruiting bodies, epiphytic plants, wasp or bird nests, and the application of fungicides or insecticides, are not aligned with TreM conservation. Therefore, current arboriculture and greening practices should be reconsidered within the framework of nature-oriented sustainable management.

Our findings suggest that the careful allocation of tree maintenance efforts toward large old trees is a critical, yet often overlooked, aspect of current arboriculture policies. The proposed conservation strategies can not only increase the prevalence of TreMs on large trees but also enhance the longevity of significantly large old and mature trees, which are valued for multiple reasons (Roy et al., 2012) and constitute nearly non-renewable landscape elements (Le Roux et al., 2014b). Integrating the conservation concept into practice can boost biodiversity and protect other tree-associated ecosystem services, such as aesthetics, shading, water retention, and pollutant filtration (Lindenmayer, 2017; Lindenmayer and Laurance, 2017; Piovesan et al., 2022; Qiu et al., 2020; Roy et al., 2012; Smithers et al., 2018). This is particularly crucial in the current era, where land use and climate changes significantly impact

natural environments (Huang et al., 2023; Le Roux et al., 2014a; Le Roux et al., 2014b; Nolan et al., 2020; Skarpaas et al., 2017) and pose limitations to everyday life. Additionally, maintaining large old trees involves substantial costs (Roy et al., 2012), so reducing tree surgeries on these trees can also lower overall maintenance expenses. By considering the conservation of large old trees, urban planners and policymakers can create greener, more resilient cities that support wildlife and offer numerous benefits to urban residents. This approach is essential for developing nature-oriented urban green infrastructure plans that adhere to sustainable urban development principles.

Although our study was conducted in a single urban agglomeration, it offers a universal conceptual model that could be applied to most urban areas worldwide, where safety considerations serve as a bottleneck for biodiversity conservation, while multifaceted management perspective is often set aside (Carpaneto et al., 2010; Fröhlich and Ciach, 2020a, 2020b; Großmann et al., 2020; Le Roux et al., 2014a; Sandström et al., 2006). We present the most straightforward and robust empirical evidence to date of the apparent conflict between public safety and the conservation of habitat trees. Our work suggests that promising solutions exist to mitigate this conflict, such as delineating strategic green spaces for conservation purposes in less populated districts and intelligently designing recreational infrastructure within public green spaces to manage accident risks and reduce the necessity for invasive tree surgeries. Given the undeniable link between biodiversity, physical stress, and human health (Buckley et al., 2019; Cirino et al., 2021; Gilhen-Baker et al., 2022; Hedblom et al., 2019), this issue warrants attention, with potential solutions explored and incorporated into urban arboriculture policies. Our findings offer valuable insights for future studies on designing grey infrastructure in urban areas and beyond, such as in historic rural parks (Löhmus and Liira, 2013) and along roadsides (Avilés, 2019; Suchocka et al., 2019), adhering to sustainable development principles.

Funding

Polish National Science Centre grant Preludium 2018/31/N/NZ9/03067.

CRediT authorship contribution statement

Arkadiusz Fröhlich: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Fabian Przepióra:** Writing – review & editing, Investigation. **Szymon Drobnik:** Writing – review & editing, Validation, Formal analysis. **Grzegorz Mikusiński:** Writing – review & editing, Validation. **Michał Ciach:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization.

Declaration of competing interest

Authors declare that they have no competing interests.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.174919>.

References

- Arciniegas, A., Prieto, F., Brancheriau, L., Lasaygues, P., 2014. Literature review of acoustic and ultrasonic tomography in standing trees. *Trees* 28 (6), 1559–1567. <https://doi.org/10.1007/s00468-014-1062-6>.
- Asbeck, T., Pyttel, P., Frey, J., Bauhus, J., 2019. Predicting abundance and diversity of tree-related microhabitats in central European montane forests from common forest attributes. *For. Ecol. Manage.* 432, 400–408. <https://doi.org/10.1016/j.foreco.2018.09.043>.
- Augustynczyk, A.L.D., Asbeck, T., Basile, M., Bauhus, J., Storch, I., Mikusiński, G., Yousefpour, R., Hanewinkel, M., 2019. Diversification of forest management regimes secures tree microhabitats and bird abundance under climate change. *Sci. Total Environ.* 650, 2717–2730. <https://doi.org/10.1016/j.scitotenv.2018.09.366>.
- Avilés, J.M., 2019. Pruning promotes the formation of an insufficient number of cavities for hollow-dependent birds in Iberian Holm-oak dehesas. *For. Ecol. Manage.* 453, 117627 <https://doi.org/10.1016/j.foreco.2019.117627>.
- Basile, M., Asbeck, T., Jonker, M., Knuff, A.K., Bauhus, J., 2020. What do tree-related microhabitats tell us about the abundance of forest-dwelling bats, birds, and insects? *J. Environ. Manage.* 264 (August 2019), 110401 <https://doi.org/10.1016/j.jenvman.2020.110401>.
- Blewett, C.M., Marzluff, J.M., 2005. Effects of urban sprawl on snags and the abundance and productivity of cavity-nesting birds. *Condor* 107, 678–693. <https://doi.org/10.2307/4096552>.
- Blicharska, M., Mikusiński, G., 2014. Incorporating social and cultural significance of large old trees in conservation policy. *Conserv. Biol.* 28 (6), 1558–1567. <https://doi.org/10.1111/cobi.12341>.
- Blignaut, J., Aronson, J., 2008. Getting serious about maintaining biodiversity. *Conserv. Lett.* 1 (1), 12–17. <https://doi.org/10.1111/j.1755-263X.2008.00006.x>.
- Brookes, A., 2007. Preventing death and serious injury from falling trees and branches. *Aust. J. Outdoor Educ.* 11, 50–59.
- Buckley, R., Brough, P., Hague, L., Chauvenet, A., Fleming, C., Roche, E., Sofija, E., Harris, N., 2019. Economic value of protected areas via visitor mental health. *Nat. Commun.* 10 (1), 1 <https://doi.org/10.1038/s41467-019-12631-6>.
- Carpaneto, G.M., Mazziotta, A., Coletti, G., Luiselli, L., Audisio, P., 2010. Conflict between insect conservation and public safety: the case study of a saproxylic beetle (*Osmoderma eremita*) in urban parks. *J. Insect Conserv.* 14 (5), 555–565. <https://doi.org/10.1007/s10841-010-9283-5>.
- Ciach, M., Fröhlich, A., 2017. Habitat type, food resources, noise and light pollution explain the species composition, abundance and stability of a winter bird assemblage in an urban environment. *Urban Ecosyst.* 20, 547. <https://doi.org/10.1007/s11252-016-0613-6>.
- Cirino, D.W., Tambosi, L.R., de Freitas, S.R., Mauad, T., Metzger, J.P., 2021. Exploring the role of land-sharing on urban green and cardiovascular health. *The Lancet Planetary Health* 5, S20. [https://doi.org/10.1016/S2542-5196\(21\)00104-2](https://doi.org/10.1016/S2542-5196(21)00104-2).
- Corsini, M., Marrot, P., Szulkin, M., 2019. Quantifying human presence in a heterogeneous urban landscape. *Behav. Ecol.* 30 (6), 1632–1641. <https://doi.org/10.1093/beheco/arz128>.
- Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R.T., Molnár, Z., Hill, R., Chan, K.M.A., Baste, I.A., Brauman, K.A., Polasky, S., Church, A., Lonsdale, M., Larigauderie, A., Leadley, P.W., van Oudenhoven, A.P.E., van der Plaats, F., Schröter, M., Lavorel, S., Shirayama, Y., 2018. Assessing nature's contributions to people. *Science* 359 (6373), 270–272. <https://doi.org/10.1126/science.aap8826>.
- Dubiel, E., Szwagrzyk, Jerzy, 2008. Atlas Roślinności Rzeczywistej Krakowa. Urząd Miasta Krakowa, Wydział Kształtowania Środowiska.
- Ellison, M.J., 2005. Quantified tree risk assessment used in the management of amenity trees. *J. Arboric.* 31 (2).
- Fröhlich, A., Ciach, M., 2020a. Dead tree branches in urban forests and private gardens are key habitat components for woodpeckers in a city matrix. *Landsc. Urban Plan.* 202 <https://doi.org/10.1016/j.landurbplan.2020.103869>.
- Fröhlich, A., Ciach, M., 2020b. Dead wood resources vary across different types of urban green spaces and depend on property prices. *Landsc. Urban Plan.* 197, 103747 <https://doi.org/10.1016/j.landurbplan.2020.103747>.
- Gilhen-Baker, M., Roviello, V., Beresford-Kroeger, D., Roviello, G.N., 2022. Old growth forests and large old trees as critical organisms connecting ecosystems and human health. A review. *Environ. Chem. Lett.* 20 (2), 1529–1538. <https://doi.org/10.1007/s10311-021-01372-y>.
- Gilles, B.K., 2004. Tree cutting and pruning to benefit urban wildlife. In: Shaw, W.W., Harris, L.K., Vandruff, L. (Eds.), *Proceedings 4th International Urban Wildlife Symposium*, pp. 325–329.
- Green, R.E., Cornell, S.J., Scharlemann, J.P.W., Balmford, A., 2005. Farming and the fate of wild nature. *Science* 307 (5709), 550–555. <https://doi.org/10.1126/science.1106049>.
- Großmann, J., Schultze, J., Bauhus, J., Pyttel, P., 2018. Predictors of microhabitat frequency and diversity in mixed mountain forests in South-Western Germany. *Forests* 9 (3), 104. <https://doi.org/10.3390/f9030104>.
- Großmann, J., Pyttel, P., Bauhus, J., Lecigne, B., Messier, C., 2020. The benefits of tree wounds: microhabitat development in urban trees as affected by intensive tree maintenance. *Urban For. Urban Green.* 55, 126817 <https://doi.org/10.1016/j.ufug.2020.126817>.
- Griebler, M.U., Schaller, S., Keil, H., Naef-Daenzer, B., 2013. The occurrence of cavities in fruit trees: effects of tree age and management on biodiversity in traditional European orchards. *Biodivers. Conserv.* 22 (13–14), 3233–3246. <https://doi.org/10.1007/s10531-013-0581-6>.
- Hauri, K., Koskinen, S., Kotze, D.J., Lehvavirta, S., 2014. The effects of decaying logs on the aesthetic experience and acceptability of urban forests – implications for forest

- management. *Landscape Urban Plan.* 123, 114–123. <https://doi.org/10.1016/j.landurbplan.2013.12.014>.
- Hedblom, M., Gunnarsson, B., Irvani, B., Knez, I., Schaefer, M., Thorsson, P., Lundström, J.N., 2019. Reduction of physiological stress by urban green space in a multisensory virtual experiment. *Sci. Rep.* 9 (1) <https://doi.org/10.1038/s41598-019-46099-7>.
- Huang, L., Jin, C., Pan, Y., Zhou, L., Hu, S., Guo, Y., Meng, Y., Song, K., Pang, M., Li, H., Lin, D., Xu, X., Minor, J., Coggins, C., Jim, C.Y., Yan, E., Yang, Y., Tang, Z., Lindenmayer, D.B., 2023. Human activities and species biological traits drive the long-term persistence of old trees in human-dominated landscapes. *Nature Plants* 1–10. <https://doi.org/10.1038/s41477-023-01412-1>.
- International Society of Arboriculture (ISA), 2011. Recognizing Tree Risk. <https://www.isa-arbor.com/>.
- Kirsch, J.-J., Sermon, J., Jonker, M., Asbeck, T., Gossner, M.M., Petermann, J.S., Basile, M., 2021. The use of water-filled tree holes by vertebrates in temperate forests. *Wildl. Biol.* 2021 (1) <https://doi.org/10.2981/wlb.00786> wlb.00786.
- Kozák, D., Mikoláš, M., Svitok, M., Bače, R., Paillet, Y., Larrieu, L., Nagel, T.A., Begović, K., Čada, V., Diku, A., Franković, M., Janda, P., Kameniar, O., Keren, S., Kjučukov, P., Lábusová, J., Langbehn, T., Málek, J., Mikac, S., Svoboda, M., 2018. Profile of tree-related microhabitats in European primary beech-dominated forests. *For. Ecol. Manage.* 429, 363–374. <https://doi.org/10.1016/j.foreco.2018.07.021>.
- Kraus, D., Büttler, R., Krumm, F., Lachat, T., Larrieu, L., Mergner, U., Paillet, Y., Rydkvist, T., Schuck, A., Winter, S., 2016. Catalogue of tree microhabitats – Reference field list. Integrate+ Technical Paper, p. 16. www.integrateplus.org.
- LaMontagne, J., Kilgour, R., Anderson, E., Magle, S., 2015. Tree cavity availability across forest, park, and residential habitats in a highly urban area. *Urban Ecosyst.* <https://doi.org/10.1007/s11252-014-0383-y>.
- Larrieu, L., Cabanettes, A., Delarue, A., 2012. Impact of silviculture on dead wood and on the distribution and frequency of tree microhabitats in montane beech-fir forests of the Pyrenees. *Eur. J. For. Res.* 131 (3), 773–786. <https://doi.org/10.1007/s10342-011-0551-z>.
- Larrieu, L., Paillet, Y., Winter, S., Büttler, R., Kraus, D., Krumm, F., Lachat, T., Michel, A. K., Regnery, B., Vandekerckhove, K., 2018. Tree related microhabitats in temperate and Mediterranean European forests: a hierarchical typology for inventory standardization. *Ecol. Indic.* 84, 194–207. <https://doi.org/10.1016/j.ecolind.2017.08.051>.
- Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Blanchard, W., Manning, A.D., Gibbons, P., 2014a. Reduced availability of habitat structures in urban landscapes: implications for policy and practice. *Landscape Urban Plan.* 125, 57–64. <https://doi.org/10.1016/j.landurbplan.2014.01.015>.
- Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Manning, A.D., Gibbons, P., 2014b. The future of large old trees in urban landscapes. *PloS One* 9 (6), e99403. <https://doi.org/10.1371/journal.pone.0099403>.
- Lindenmayer, D.B., 2017. Conserving large old trees as small natural features. *Biol. Conserv.* 211, 51–59. <https://doi.org/10.1016/j.biocon.2016.11.012>.
- Lindenmayer, D.B., Laurance, W.F., 2017. The ecology, distribution, conservation and management of large old trees. *Biol. Rev.* 92 (3), 1434–1458. <https://doi.org/10.1111/brv.12290>.
- Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., 2012. Global decline in large old trees. *Science* 338 (6112), 1305–1306. <https://doi.org/10.1126/science.1231070>.
- Löhms, K., Liira, J., 2013. Old rural parks support higher biodiversity than forest remnants. *Basics Appl. Ecol.* 14 (2), 165–173. <https://doi.org/10.1016/j.baec.2012.12.009>.
- Maehar, I., Poprach, K., Praus, L., Úradníček, L., 2021. Floodplain forests and urban parks – a brief comparison of bird diversity. *J. Landsc. Ecol.* 14 (3), 1–11. <https://doi.org/10.2478/jlecol-2021-0015>.
- Martin, A.J.F., Almas, A.D., 2023. Urban wildlife and arborists: environmental governance and the protection of wildlife during tree care operations. *J. Urban Ecol.* 9 (1) <https://doi.org/10.1093/jue/juad002> juad002.
- Martin, K., Aitken, K.E.H., Wiebe, K.L., 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: Nest characteristics and niche partitioning. *The Condor* 106 (1). <https://doi.org/10.1650/7482>.
- Maxeune, M., Paillet, Y., Larrieu, L., Kern, C.C., Raymond, P., Drapeau, P., Fenton, N.J., 2022. Tree-related microhabitats are promising yet underused tools for biodiversity and nature conservation: a systematic review for international perspectives. *Frontiers in Forests and Global Change* 5. <https://doi.org/10.3389/ffgc.2022.818474>.
- Meyer, S., Rusterholz, H.-P., Baur, B., 2021. Saproxyllic insects and fungi in deciduous forests along a rural-urban gradient. *Ecol. Evol.* 11 (4), 1634–1652. <https://doi.org/10.1002/ece3.7152>.
- Mölder, A., Schmidt, M., Plieninger, T., Meyer, P., 2020. Habitat-tree protection concepts over 200 years. *Conserv. Biol.* 34 (6), 1444–1451. <https://doi.org/10.1111/cobi.13511>.
- Morelli, F., Mikula, P., Benedetti, Y., Bussièrè, R., Jerzak, L., Tryjanowski, P., 2018. Escape behaviour of birds in urban parks and cemeteries across Europe: evidence of behavioural adaptation to human activity. *Sci. Total Environ.* 631–632, 803–810. <https://doi.org/10.1016/j.scitotenv.2018.03.118>.
- Nali, C., Lorenzini, G., 2009. Residents' perception of tree diseases in the urban environment. *Arboricult. Urban For.* 35 (2), 87–93.
- Nolan, V., Reader, T., Gilbert, F., Atkinson, N., 2020. The ancient tree inventory: a summary of the results of a 15 year citizen science project recording ancient, veteran and notable trees across the UK. *Biodivers. Conserv.* 29 (11–12), 3103–3129. <https://doi.org/10.1007/s10531-020-02033-2>.
- Nolan, V., Gilbert, F., Reed, T., Reader, T., 2022. Distribution models calibrated with independent field data predict two million ancient and veteran trees in England. *Ecol. Appl.* 32 (8), e2695 <https://doi.org/10.1002/eap.2695>.
- Ouin, A., Cabanettes, A., Andrieu, E., Deconchat, M., Roume, A., Vigan, M., Larrieu, L., 2015. Comparison of tree microhabitat abundance and diversity in the edges and interior of small temperate woodlands. *For. Ecol. Manage.* 340, 31–39. <https://doi.org/10.1016/j.foreco.2014.12.009>.
- Padgham, M., Lovelace, R., Salmon, M., Rudis, B., 2017. OSMDATA. *Journal of Open Source Software* 2, 305. <https://doi.org/10.21105/joss.00305>.
- Paillet, Y., Archaux, F., du Puy, S., Bouget, C., Boulanger, V., Debaive, N., Gilg, O., Gosselin, F., Guilbert, E., 2018. The indicator side of tree microhabitats: a multi-taxon approach based on bats, birds and saproxylic beetles. *J. Appl. Ecol.* 55 (5), 2147–2159. <https://doi.org/10.1111/1365-2664.13181>.
- Phalan, B., Onial, M., Balmford, A., Green, R.E., 2011. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science* 333 (6047), 1289–1291. <https://doi.org/10.1126/science.1208742>.
- Piovesan, G., Cannon, C.H., Liu, J., Munné-Bosch, S., 2022. Ancient trees: irreplaceable conservation resource for ecosystem restoration. *Trends Ecol. Evol.* 37 (12), 1025–1028. <https://doi.org/10.1016/j.tree.2022.09.003>.
- Przepióra, F., Ciach, M., 2022. Tree microhabitats in natural temperate riparian forests: an ultra-rich biological complex in a globally vanishing habitat. *Sci. Total Environ.* 803, 149881 <https://doi.org/10.1016/j.scitotenv.2021.149881>.
- Qiu, L., Yu, N., Gao, Y., Zhang, T., Gao, T., 2020. Public visual preference for dead wood in different types of landscape. *Forests* 2021 12 (1), 44. <https://doi.org/10.3390/F12010044>.
- R Development Core Team, 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing (4.3.1.) [Computer software]. <http://www.r-project.org>.
- Roy, S., Byrne, J., Pickering, C., 2012. A systematic quantitative review of urban tree benefits, costs, and assessment methods across cities in different climatic zones. *Urban For. Urban Green.* 11 (4), 351–363. <https://doi.org/10.1016/j.ufug.2012.06.006>.
- Rue, H., Martino, S., Chopin, N., 2009. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *J. R. Stat. Soc. Series B Stat. Methodology* 71 (2), 319–392. <https://doi.org/10.1111/J.1467-9868.2008.00700.X>.
- Rue, H., Riebler, A., Sørbye, S.H., Illian, J.B., Simpson, D.P., Lindgren, F.K., 2017. Bayesian computing with INLA: a review. *Annual Review of Statistics and Its Application* 4 (1), 395–421. <https://doi.org/10.1146/annurev-statistics-060116-054045>.
- Sandström, U.G., Angelstam, P., Mikusiński, G., 2006. Ecological diversity of birds in relation to the structure of urban green space. *Landscape Urban Plan.* 77 (1–2), 39–53. <https://doi.org/10.1016/j.landurbplan.2005.01.004>.
- Senta, W., Dolatowski, J., Zieliński, J., 2021. *Dendrologia*, 5th ed. (PWN.).
- Skarpaas, O., Blumentrath, S., Evju, M., Sverdrup-Thygeson, A., 2017. Prediction of biodiversity hotspots in the Anthropocene: the case of veteran oaks. *Ecol. Evol.* 7 (19), 7987–7997. <https://doi.org/10.1002/ece3.3305>.
- Smithers, R.J., Doick, K.J., Burton, A., Sibille, R., Steinbach, D., Harris, R., Groves, L., Blicharska, M., 2018. Comparing the relative abilities of tree species to cool the urban environment. *Urban Ecosyst.* 21 (5), 851–862. <https://doi.org/10.1007/s11252-018-0761-y>.
- Soga, M., Yamaura, Y., Koike, S., Gaston, K.J., 2014. Land sharing vs. land sparing: does the compact city reconcile urban development and biodiversity conservation? *J. Appl. Ecol.* 51 (5), 1378–1386. <https://doi.org/10.1111/1365-2664.12280>.
- Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. *Biodiversity in Dead Wood*. Cambridge University Press.
- Suchocka, M., Błaszczak, M., Juźwiak, A., Duriasz, J., Bohdan, A., Stolarczyk, J., 2019. Transit versus nature. Depreciation of environmental values of the road alleys. *Case Study: Gamerki-Jonkowo*, Poland. *Sustainability* 11 (6), 1816. <https://doi.org/10.3390/su11061816>.
- Szewczyk, J., Gazda, A., Szwagrzyk, J., 2011. *Dendrologia. Materiały pomocnicze do ćwiczeń*. Wydawnictwo Uniwersytetu Rolniczego w Krakowie.
- Threlfall, C.G., Ossola, A., Hahs, A.K., Williams, N.S.G., Wilson, L., Livesley, S.J., 2016. Variation in vegetation structure and composition across urban green space types. *Front. Ecol. Evol.* 4 (JUN) <https://doi.org/10.3389/fevo.2016.00066>.
- Townsend, J.B., Barton, S., 2018. The impact of ancient tree form on modern landscape preferences. *Urban For. Urban Green.* 34, 205–216. <https://doi.org/10.1016/j.ufug.2018.06.004>.
- Tyrväinen, L., Silvennoinen, H., Kolehmainen, O., 2003. Ecological and aesthetic values in urban forest management. *Urban For. Urban Green.* 1 (3), 135–149. <https://doi.org/10.1078/1618-8667-00014>.
- Vuidot, A., Paillet, Y., Archaux, F., Gosselin, F., 2011. Influence of tree characteristics and forest management on tree microhabitats. *Biol. Conserv.* 144 (1), 441–450. <https://doi.org/10.1016/j.biocon.2010.09.030>.