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Large tree-cavities as key structures
for forest biodiversity



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CONTENTS

LIST OF ORIGINAL PUBLICATIONS	6
1. INTRODUCTION.....	7
1.1. Sustaining biodiversity in wooded ecosystems.....	7
1.2. Tree cavities as keystone structures	9
1.3. Large tree cavities – what is special?.....	11
1.4. Aims and objectives.....	12
2. MATERIALS AND METHODS	15
2.1. Literature reviews	15
2.2. Case studies (II–V)	16
2.2.1. Study areas	16
2.2.2. Field methods.....	18
2.2.3. Data analysis	20
3. RESULTS	21
3.1. Animal use of large tree-cavities	21
3.2. Distribution of large tree-cavities: from global to landscape scale.....	23
3.3. Development and dynamics of large tree cavities.....	25
4. DISCUSSION	28
4.1. Where, and what kind of large cavities are important for biodiversity?	28
4.2. Natural dynamics of the LTC supply	29
4.3. Gaps in knowledge.....	30
4.4. LTC as key structures in management for biodiversity	31
5. CONCLUSIONS	34
SUMMARY IN ENGLISH	35
REFERENCES.....	38
SUMMARY IN ESTONIAN	49
ACKNOWLEDGEMENTS	52
PUBLICATIONS	53
CURRICULUM VITAE	187
ELULOOKIRJELDUS.....	190

LIST OF ORIGINAL PUBLICATIONS

This thesis is the summary of the following papers, which are referred to in the thesis by their Roman numerals **I–IV**. The author of the thesis is highlighted in bold type. All published papers are reprinted here with permission from the copyright owners.

- I. Yatsiuk, Y.** & Lõhmus, A. Ecology of large tree-cavities: a review. Submitted manuscript.
- II. Yatsiuk, Y.**, Remm, J. & Lõhmus, A. Dynamic stocks of large tree-cavities in European temperate and hemiboreal forests. Submitted manuscript.
- III. Yatsiuk, Y.** (2024) The multi-functional use of large tree cavities by arboreal vertebrates in a temperate broadleaved forest of Eastern Europe. *Ecology and Evolution*, 14(11), e70521. <https://doi.org/10.1002/ece3.70521>
- IV. Yatsiuk, Y.** & Wesołowski, T. (2020) Diversity and abundance of large tree holes used by Tawny Owls *Strix aluco* in lowland temperate forests. *Bird Study*, 67(3), 331–343. <https://doi.org/10.1080/00063657.2020.1869179>
- V. Yatsiuk, Y.** & Viter, S. (2024) Black Woodpeckers recolonize south-eastern border of their European range. *Journal of Ornithology*, 165, 1097–1102. <https://doi.org/10.1007/s10336-024-02180-1>

Author's contribution (* moderate contribution; ** high contribution; *** leading role)

	I	II	III	IV	V
Original idea	*	**	***	***	***
Study design	*	**	***	***	**
Performing the work	**	**	***	**	**
Data collection	***	***	***	***	**
Data analysis	**	***	***	***	***
Manuscript writing	**	**	***	**	***

1. INTRODUCTION

1.1. Sustaining biodiversity in wooded ecosystems

Human impact on wooded ecosystems traces back to thousands of years but has intensified in recent centuries, causing large-scale fundamental changes in their structure and biodiversity (McGrath et al., 2015; Ellis et al., 2021). Nowadays, a large share of woodlands worldwide is human-transformed and under management for different purposes (Noble & Dirzo, 1997). For example, FAO estimates that 50.4% of the world's forests have management plans (FAO, 2020), but extensive management without plans is also shaping a large part of the remaining forests. A large part of other wooded ecosystems, like open woodlands or tree-dominated ecosystems in populated areas, are heavily influenced by agriculture or managed for recreational or safety purposes. Human-induced transformations of wooded ecosystems have already led to a global decline of biodiversity associated with forests and woodlands (Díaz et al., 2019).

Biodiversity in wooded ecosystems is closely linked with the diversity and characteristics of tree cover and tree-related structures (Thomas & Packham, 2007; Stokland et al., 2012). A common problem of biodiversity conservation in transformed wooded ecosystems originates from the truncation of mature and senescent stages of tree life, often over large areas, and disruption of natural disturbance dynamics. In production forestry or agricultural systems, it stems from the demand for tree products, and in settlements it is governed by safety considerations. Presence of multiple tree age stages and forest heterogeneity are key components that shape the biodiversity of different woodland types in landscapes. Managed woodlands become dominated with young to mid-aged trees, their spatial structure gets more homogenous and simplified (Thomas & Packham, 2007; Puettmann et al., 2012; Zeller et al., 2023), and it causes declines of tree-related biodiversity (e.g., Barlow et al., 2016; Mikusiński et al., 2018; Boonman et al., 2024). A variety of strategies from sharing (set aside protection areas and intensively use the remainder part) to various types of sparing (integrate close-to-nature approaches in management to support biodiversity) are considered worldwide. At least in populated regions with a long history of human transformation, an implementation of close-to-nature approaches to protect tree-related biodiversity is considered a necessary option (Betts et al., 2021). Thus, a major challenge for management is to determine elements important for biodiversity and ensure their presence.

A theoretical framework explaining biodiversity patterns in wooded ecosystems is based on the habitat heterogeneity hypothesis (MacArthur & MacArthur, 1961; Bazzaz, 1975). It states that the increase of habitat heterogeneity (spatial, temporal, or in amounts of resources) is associated with higher species diversity. Management should thus endeavour to maintain the heterogeneity of wooded ecosystems. However, the required spatial scale of heterogeneity differs for organisms of different sizes and levels of mobility. For example, the scale of

heterogeneity required for large mammals or birds of prey may result in fragmentation for small invertebrates with limited mobility. Some structures, while small in size, have disproportionate ecological importance for many species and their relationships: these are called “keystone structures” or “small natural features” (Tews et al., 2004; Hunter et al., 2017). An important task to management for biodiversity is to identify such keystone structures and promote their presence.

In wooded ecosystems keystone habitat structures include small wetlands, rock outcrops, treefall gaps, but large part of them is associated with trees and their parts (Lindenmayer & Laurance, 2017). Structures on trees, important for arboreal species, are called tree-related microhabitats (Paillet et al., 2018; Asbeck et al., 2021). They are defined as “distinct, well delineated structures occurring on living or standing dead trees, that constitute a particular and essential substrate or life site for species or species communities during at least a part of their life cycle” (Larrieu et al., 2018). Tree-related microhabitats include deadwood structures, injuries, epiphytes, sap runs, nests and tree cavities. They are important both to vertebrate and invertebrate animals by providing shelters or substrate, feeding opportunities and other resources. There are indications that presence of some tree-related microhabitats is positively correlated with biodiversity and influenced by management (Paillet et al., 2018), however, this relationship is more complex for some microhabitat types and taxonomic groups (Körkjas et al., 2023). Abundance and diversity of tree-related microhabitats serve as feasible biodiversity indicator (Winter & Möller, 2008; Martin et al., 2022). Comparing with old-growth natural forests, the diversity and abundance of tree-related microhabitats in forests managed for wood production is usually lower (Asbeck et al., 2022; Larrieu et al., 2012; Larrieu et al., 2014).

Given that tree-related microhabitats are important for biodiversity and influenced by management, the question is to how to integrate them in management for biodiversity in wooded ecosystems. Traditionally, it has been partly addressed by different types of retention approaches (in a broader sense), which involve retaining trees, deadwood, or other structures with recognized biodiversity values. For example, a concept of ‘habitat trees’ dates back to the origins of modern forestry and is implemented now in many systems (Mölder et al., 2020). When the knowledge of ecological role of tree microhabitats grew, questions of prioritizing different types, target densities and promoting their natural dynamics arose. Current questions related to the conservation of tree-related microhabitats embrace a wide variety of issues from selection of individual trees to shaping future landscapes, planning the presence of microhabitats in time and space. While different labour-intensive approaches to create microhabitats exist (e.g., tree veteranisation: Bengtsson et al., 2013), a priority is to be given to maintaining natural processes. It requires knowledge of the role of each microhabitat type in ecosystem functioning (and specifically for biodiversity), patterns of their natural occurrence, formation, dynamics and how these are shaped by various types of management.

1.2. Tree cavities as keystone structures

Tree cavities are among the most diverse and acknowledged tree-related microhabitats. They are defined as enclosed shelters in wood with external openings, formed by fungal decay, animal excavation or a combination of these processes. Tree cavities are well familiar to wider audience as dwellings of animals or sometimes having specific cultural values.

Tree cavities exist in a variety of forms. A European tree-related microhabitat classification distinguishes 20 types of cavities in standing trees based on their size, location and origin (Kraus et al., 2016). Cavity dimensions vary from millimetres (insect bore holes) to meters and are constrained only by the sizes of tree structures harbouring them. They can be located in trunks or branches of living or dead trees, varying in height from ground level to tens of meters. Cavities in lying deadwood are usually classified separately, and these are out of the scope of the current work. Tree cavities can be created by direct injuries of trees, boring activity of invertebrates (termites or wood-boring insects), excavation by vertebrates (mostly woodpeckers), but fungal decomposition of heartwood plays the key role (Gibbons & Lindenmayer, 2002; Wesolowski & Martin, 2018). Altogether, this variety of processes and characteristics can create a diversity of conditions inside cavities, including microclimate (O'Connell & Keppel, 2016), nutrient content and characteristics of the litter and internal substrate (Micó, 2018).

The main function of tree cavities for vertebrate animals is the provision of enclosed shelters that can protect from predators or adverse weather. For example, about 18% of the world's bird species nest in cavities (van der Hoek et al., 2017) and the overall breeding success of cavity-nesting birds is higher than of birds creating open nests (Wesolowski, 2007; Wesolowski & Martin, 2018). Mammals using tree cavities vary in size from small bats (Goldingay, 2009) to bears (Bull et al., 2000). Amphibians can use water-filled cavities for breeding (e.g., Yanovlak, 2001). Beyond breeding, tree cavities are used as temporary shelters for roosting or even hibernation (Godfrey et al., 2000; Bryant et al., 2012), but they are also sources of vertebrate (animals and their nests) and invertebrate (cavity-using invertebrates) food for animals (Wesolowski & Martin, 2018; Kobayashi et al., 2022). Water-filled cavities are used as drinking and bathing places (Sharma et al., 2016; Delgado-Martínez et al., 2022). In some cases, certain types of cavities are used exclusively for displays (e.g., by Palm cockatoos *Probosciger aterrimus*: Heinsohn et al., 2017).

The high variety of species using tree cavities and their forms of use suggest that landscape with a diverse supply of cavities supports more cavity-related functions. Important features in this diversity include dimensions (Renton et al., 2015; Lewis et al., 2023), spatial location of cavities (Gerhardt, 2004; Britt et al., 2014) and their microclimate (Kunz & Lumsden, 2003; Wei et al., 2019). Interspecific overlaps in preferred cavity characteristics and time of use increase competition (Newton, 1994). Studies on birds show that, even when entrance sizes appear suitable, only a variable proportion (5%–90%) of counted cavities appear suitable for a particular species (e.g., Gysel, 1961; Gibbons et al., 2002; Cockle et al., 2008; Stojanovic et al., 2014; Inoue et al., 2021). Limitation by

available cavities is significant in production forests and weaker in primeval forests (Wesołowski, 2007), but some limitation occurs even in cavity-rich habitats (Brightsmith, 2005; Löhmus & Remm, 2005; Bonaparte et al., 2024), especially when species require specific characteristics.

Tree cavities are present in all wooded ecosystems worldwide, but their densities vary widely: the main review on this topic estimated the global median density in forests at 16 ha⁻¹ but with a local variation between <1 and >900 cavities ha⁻¹ (Remm & Löhmus, 2011). Vertebrate animals able to excavate cavities (particularly woodpeckers) play an important role in ensuring cavity supply, but they are absent in some regions like Australia and New Zealand (van der Hoek et al., 2017). The main natural factors defining local cavity densities are the precipitation levels (positive relationship) and tree species composition (more in deciduous stands and in trees with high wood density). However, nowadays the strongest factor influencing cavity densities worldwide is management for timber production: densities are consistently lower in production forests (Remm & Löhmus, 2011).

Such strong influence of management on tree cavity stocks is explained by the fact that presence of cavities is associated with deterioration of wood properties and decreased tree stability. When stands are managed for tree production, traditional silvicultural approaches maximize presence of fast-growing trees with sound wood. It is achieved by selection of tree species for planting and by selective removal of trees with decay. When wooded ecosystems in settlements are managed, presence of decay indicates lower tree stability and danger to humans or property: such trees are removed more often (LaMontagne et al., 2015; Fröhlich et al., 2024). This leads to a predictable decline of cavity supply in managed settings (Gibbons & Lindenmayer, 1996; Gorrod et al., 2024). Agricultural intensification also leads to decreases of old trees and cavity availability in the landscape (e.g., Kajtoch, 2017). Many cavity-excavating animal species (mostly birds) are sensitive to management-induced habitat alterations, and occur in transformed ecosystems in lower densities than in natural ecosystems (van der Hoek et al., 2020).

Those problems, the known ecological role, and cultural recognition of tree cavities has resulted in their inclusion as a conservation management target. The existing approaches vary from the protection of cavity trees to installing artificial nest boxes or carving artificial cavities in trees (Ruegger, 2017). While the use of artificial structures may be justified in some cases, their wide implementation requires large amounts of resources for production and constant maintenance. Moreover, nest boxes and artificial cavities cannot mimic all characteristics of natural cavities (Wesołowski, 2011; Rowland et al., 2017). Thus, a promotion of natural cavities is considered a cheaper and more reliable way to support cavity-dependent fauna. In order to sustain sufficient pools of tree cavities, information about their abundance, dynamics and diversity in various settings is required. The existence of cavities suitable for fauna usually spans from years to decades (Körkjäs et al., 2021a) but wood decay processes involved in cavity formation require even longer time (Wagener & Davidson, 1954; Zheng et al., 2016). Because of such a low natural loss-development rate ratio, cavity densities can

decline even when all trees with existing cavities are protected. In order to ensure a long-term cavity supply, trees with decay have to survive for decades. Focusing on the most persistent cavity types is a complementary option for that.

1.3. Large tree cavities – what is special?

Physical dimensions of tree cavities define sets of animal species can enter, the microclimate characteristics inside, and their capacity as small ecosystems (e.g., hosting microorganisms and invertebrates). Even though there is a natural gradient of cavity sizes, the largest ones appear distinct in a number of characteristics. These characteristics include three major aspects, important for management: (i) the use by fauna, (ii) dynamics (including formation, persistence and loss) and (iii) distribution on the landscape.

- (i) Vertebrates breeding in cavities choose smallest available entrance sizes to protect from predation (Wesołowski & Martin, 2018), but larger animals require cavities with larger dimensions (Goldingay, 2009; Renton et al., 2015). Thus, sets of breeding species in large cavities will be distinct from small cavities. A larger size also makes cavities more attractive for non-breeding use: their increased resource capacity and large size makes them attractive and accessible for animals (Sharma et al., 2016; Kobayashi et al., 2022; Delgado-Martinez et al., 2023). For invertebrates, large cavities represent larger micro-ecosystems able to host richer communities and ecological relationships (Micó, 2018).
- (ii) Presence of cavity in wood undermines tree stability. Therefore, it is expected that only large trees are able to bear large cavities. Additional restrictions are put by main agents of formation and tree physiology. The largest animal species able to excavate cavities (*Campephilus*, *Dryocopus*, *Hylatomus* and *Mulleripicus* woodpeckers: Billerman et al., 2022) create entrances about 10-cm wide, but they serve as important providers of cavities in younger forests (Remm & Löhmus, 2011). Decay-formed tree cavities can reach much larger dimensions. Wood decay processes in trees are usually slow (Wagener & Davidson, 1954) and it means that trees have to remain stable throughout this time. Also, woodpeckers prefer to excavate cavities in trees softened by wood decay (Elliott et al., 2019). Therefore, with increasing cavity size, tree stability becomes increasingly important and, even if sometimes formed in smaller trees, large cavities are expected to be rapidly lost there.
- (iii) Association with larger trees and requirement for long-term stability defines distinct distribution and abundance of large cavities. On a global scale, this distinction has to be associated with the distribution of suitable tree species and a presence of cavity formation processes that can provide such cavities. On a local scale, it has to be associated with the presence of large trees.

There is no natural threshold of ‘large cavity’ size but a widely used tree-related microhabitat classification (Kraus et al., 2016) uses entrance width to distinguish the size classes. According to this classification, large excavated cavities are made by largest woodpeckers (black woodpecker, *Dryocopus martius*, in Europe) and have entrance width ca. 10 cm. Actual entrance width of cavities excavated by black woodpeckers are usually smaller: on average 8.6 cm (Glutz von Boltzheim et al., 1980). For various types of large decay-formed cavities, minimal entrance width is stated as 10 cm. Therefore, this study defines large excavated cavities as having minimal entrance width 8 cm and large decay-formed cavities as having entrance width 10 cm (hereafter LTC).

Despite the large number of publications focused on various aspects of tree cavities, a preliminary literature search showed the absence of studies testing the abovementioned statements about LTC. However, if at least one statement of LTC distinctness appear true, it means that special attention has to be paid on large cavities in management. If LTC have distinct ecosystem roles, so which of their specific functions cannot be substituted by other microhabitats and how these are related to characteristics and abundances of available cavities? If distributions are special, so which trees and habitats are important, and where the main management efforts have to be concentrated? If development processes and natural dynamics of LTC have specific features, to which extent it is possible to predict their presence on the level of individual trees and on a landscape level?

Two main issues are associated with answering these questions. The first issue is that LTC are usually rare and studying them requires special planning. The second issue is that research on three main aspects important for management (role for fauna, development and distribution) has been historically spread across several disciplines. Mechanics and survival of hollow trees has been traditionally addressed in arboricultural studies (e.g., Wagener, 1963; Kane, 2017). Development of decay and cavities in live trees was a focus of forest pathology (Wagener & Davidson, 1954; Boddy & Rayner, 1983; Schwarze et al., 2000) or recently for carbon pool assessments (Williams et al., 2005; Nogueira et al., 2006; Heineman et al., 2015; Zheng et al., 2016). Cavity-inhabiting wildlife initially has been a subject of game management (e.g., Baumgartner, 1939; Dalke, 1948; Bellrose et al., 1964; Prince, 1968; Sanderson, 1975; Dow & Fredga, 1985), later focus has shifted on biodiversity (McClelland et al., 1979), threatened vertebrates (e.g., Saunders, 1979; Poonswad, 1995; Isaac et al., 2014) saproxylic invertebrates (Ranius & Nilsson, 1997), and cavity provision by large woodpeckers (Johnsson et al., 1993; Bonar, 2000).

1.4. Aims and objectives

The general purpose of this thesis is to provide information about three distinct aspects of large tree-cavities (LTC) important for biodiversity conservation: their role for fauna, distribution patterns, and dynamics. These problems were first conceptualized and described in a literature review (I) that aggregates data from different fields and provides a summary of current knowledge relevant to these

three aspects on a global scale. Then, four case studies were carried out to provide new field data on LTC in temperate and hemiboreal European forests (II–V). Synthesizing both these approaches, the thesis finally suggests management recommendations across studies.

The thesis addresses four specific study questions:

1. Do LTC have distinct patterns of use by animals compared with smaller cavities?

LTC as breeding shelters for vertebrates. For vertebrates, the provision of safe breeding sites is the most important function of cavities (Gibbons & Lindenmayer, 2002; Wesołowski & Martin, 2018). LTC are accessible for larger number of predators, and their role as safe shelters has to be lower than of smaller cavities. Positive relationship between animal sizes and cavities used were established for regional sets of birds (Goldingay, 2009; Renton et al., 2015; Manikandan and Balasubramanian, 2018) and partly supported by selection of preferred cavity sizes in mammals (Goldingay, 2011). Perhaps, LTC are important breeding sites only for large species, but natural rarity of large cavities has to make their use opportunistic rather necessary. I expect that the value of LTC as breeding shelters for vertebrates will be expressed not in the number of species critically dependent on them, but in facilitating role of their presence (higher breeding success or lower competition). Predation will be the factor determining sets of species using LTC and preferred cavity characteristics (I, III).

The non-breeding use of LTC by vertebrates. Given that larger size defines potentially larger amounts of resources (food, water, nest material) and accessibility for fauna, I expect that other functions of LTC than providing breeding shelters will be available for the whole set of cavity-using fauna, making them an important link in community functioning and nutrient flows (I, III).

2. How abundant are LTC on global and landscape scales?

The tree species that provide most LTC. LTC are located in larger and older trees, but also tree species differ in their propensity to have cavities and that may vary regionally (Wormington et al., 2003; Ranius et al., 2009). I expect that LTC will be much scarcer than small cavities in conifer-dominated boreal regions but their patterns in tropical and subtropical regions do not differ much. In human-modified landscapes, due to the dependence on rare conditions, such as the distribution of certain large broadleaved trees, the LTCs are not necessary most frequent in production forests (I, II).

The role of large excavated cavities. Few bird species are able to excavate cavities larger than 8 cm entrance width, but some are relatively frequent in temperate and boreal regions where the abundance of decay-formed LTC is expected to be low. These include black woodpecker in Eurasia, pileated

woodpecker (*Hylatomus pileatus*) in North America and Magellanic woodpecker in temperate South America (*Campephilus magellanicus*) (Billerman et al., 2022). I expect that the role of large excavated cavities depends on such regional and landscape balance, and in some optimal habitats for woodpeckers their role can be significant (I, II, V).

Large cavities suitable for fauna are naturally rare. Taking into account a diversity of cavity formation processes and their characteristics, only small subsets of already rare LTC will meet the requirements of cavity-using animals. If so, the diversity of available LTC characteristics is valuable by allowing species to segregate, and this diversity is hard to be substituted by artificial structures (nest boxes). I am going to explore the diversity of available LTC characteristics and assess available cavity pools for selected target species (I, II, IV).

3. What features of LTC formation and dynamics are most relevant for conservation?

Factors of formation explaining the relative scarcity of LTC. Wood decay processes have crucial role in cavity formation. In living trees, decay proceeds slowly (Boddy & Rayner, 1983; Schwarze, 2007). Forming large cavities requires more time hence long-term stability. I am exploring how much time LTC formation requires and expect that only living trees provide large tree cavities in a long term (I, II).

Long-term dynamics of LTC. Cavity longevity depends on tree species, individual tree history, and the management and disturbance context (Körkjas et al., 2021a). LTC with longer persistence may have higher resulting value for fauna if their suitability does not decrease over time. The longer the cavity tree exists the more valuable it becomes for fauna if the cavity is suitable. From the other side, even short-living cavity trees may be important for fauna if the cavity stock is low or they have important characteristics. I use published (I) and own (II, IV) data to explore cavity longevity patterns and how they are associated with value for fauna.

A management priority list for LTC. To ensure a constant supply of LTC for fauna in a long term, the management options are distinct for each time perspective. Based on the literature review and case studies I derive an evidence-based priority list for LTC management. The case studies in temperate and hemiboreal European forests allow to specify the recommendations, taking into account the local context.

2. MATERIALS AND METHODS

2.1. Literature reviews

The main literature review (I) was aimed to characterize the specific features of the occurrence, dynamics and ecosystem roles of LTC. It started from a notion that there is a natural gradient of available cavity sizes without clear border between small and large sizes, but two sides of this continuum have clear ecological differences. Entrance size is the most often reported cavity dimension in published works, and the entrance width 10 cm is often used to define decay-formed LTC (Kraus et al., 2016). However, LTC also include cavities excavated by largest excavating birds (*Dryocopus*, *Hylatomus*, *Mulleripicus* and *Campephilus* woodpeckers) have entrances 8–10 cm wide (Beyer, 1900; Glutz von Blotzheim et al., 1980; Bull, 1987; Cockle et al., 2011; Gicaraya & Española, 2024). In the current work, a criterion of entrance width at least 8–10 cm was used to define large cavities.

The literature search was made in three steps. Initial searches in databases and search engines (Scopus, ISI WoS, Google Scholar) and previous reviews (Remm & Löhmus, 2011; Wesolowski & Martin, 2018) were made using terms “tree cavity”, “tree hole” and “hollow”. The papers found were scanned for relevance to three major topics: density data, development rates and role for fauna. The main selection criterion was an indication of the size of studied cavities, or at least when the dependence on the size was clearly stated for variables of interest. The following step included a snowballing approach: the extracted publications were checked for references and related studies or datasets. Additional searches were made to address specific topics (see below). In a final step, two outside reviewers proposed 35 possibly missed papers. A detailed analysis showed that only one paper corresponded search criteria, indicating reasonable coverage of the topic as for November, 2024.

The papers reporting cavity density estimates were included when LTCs were explicitly distinguishable or when it was possible to derive size classes from given statistics or plots. In some cases, papers with threshold sizes <8 cm were included: when reported statistics showed that most cavities were large or when LTC absence was reported. Studies based on very small samples (usually less than 10 cavities found) or subjective subsets of ‘suitable’ cavities for certain species were excluded. The densities of cavities were recalculated for ha⁻¹ but, for open woodlands or parks, usually only occurrences per numbers of trees were reported. The final set included 54 publications with reported LTC density estimates around the world.

When compiling data about LTC development and functions, the focus was on providing quantitative information on tree characteristics, factors, dynamic rates, and main relationships. Special searches were for rates of fungal decay spread and tree stability issues, mostly reported in the fields of biomechanics and

arboriculture. In this case, general relationships and conceptual ideas rather than exact cavity sizes were presented.

The role of LTC for fauna was described based on the papers where cavity dimensions were stated or clear dependence with cavity sizes were noted. Quantitative analyses were made on birds – a widely distributed and well-studied group of vertebrates. The full global list of cavity-nesting species was taken from a published review (van der Hoek et al., 2017); their conservation status was extracted from the IUCN database (at <https://www.iucnredlist.org> as of November 2024) using ‘taxize’ package (Chamberlain and Szöcs, 2013). A special search was made for publications reporting dimensions of breeding cavities with a final set totalling 360 bird species from 133 publications.

A separate review was aimed to document the dynamics of range expansion of the largest bird species creating cavities in east Europe – the black woodpecker (V). The species’ occurrence records were searched in faunistic publications from Ukraine and Russia since mid-twentieth century with the addition of data deposited in GBIF database (www.gbif.org). For each decade since the mid-1970s, the southernmost occurrences were plotted to estimate rates and directions of the range border.

2.2. Case studies (II–V)

2.2.1. Study areas

The field studies documented LTC availability, dynamics and use by vertebrate fauna in forests in four European countries: Estonia – in the hemiboreal zone; Ukraine, Poland and Austria – in the temperate zone (Fig. 1).

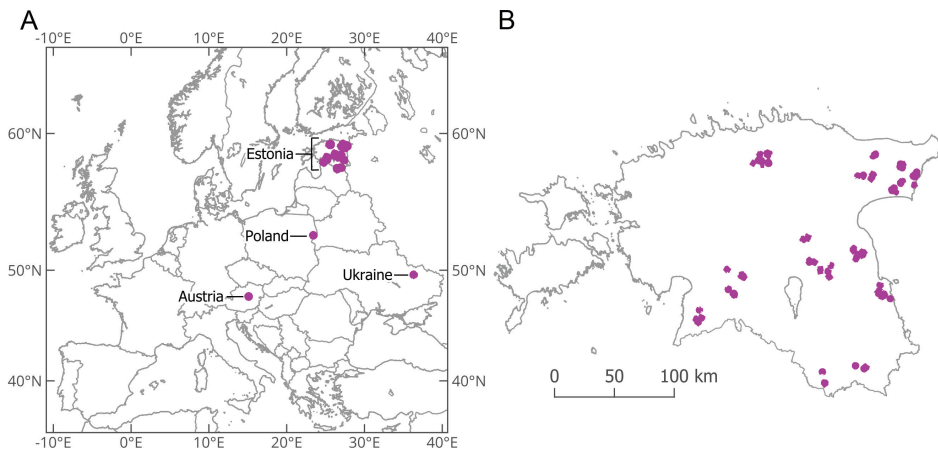


Fig. 1. Location of study areas (A) in Europe and (B) distribution of the 128 study plots in Estonia (II).

In Estonia, 128 study plots with a total area 541.5 ha were stratified by three forest site types and four stand age classes. The forest site types were (i) dry pine (*Pinus sylvestris*) dominated forests on nutrient-poor soils, (ii) spruce (*Picea abies*)-deciduous mixed forests on fertile soils, and (iii) birch (*Betula* sp.) and alder (*Alnus glutinosa*)-dominated forests on natural and drained swamps. The age classes were young even-aged post-clearcut stands (15–30 years), uneven-aged stands with retention trees (age classes <30 years and >80 years), mature even-aged (80–120 years) and old-growth (120–220 years for dominant layer) stands. Tree cavities on all study plots had been initially sampled in 2005–2006 by Remm et al. (2008). I made a resurvey in 2021–2024 to obtain longitudinal data on cavity survival.

In Ukraine, the field studies were made on a single 750-ha plot in the Natural Park Homilsha forest (Kharkiv region). The plot is dominated with mature (80–132 years) oak (*Quercus robur*) dominated deciduous stands. Before 2007, the territory was managed for productive clearcut-based silviculture. Between 2009 and 2022, all large cavities were controlled annually (some cavities since 2004).

Field studies in Poland were made in Białowieża National Park which represents the last remaining lowland primeval forest in Europe. The forest was mixed oak-spruce (*Picea abies*) with heterogeneous age structure and dominant trees reaching 300–400 years of age. In 2014 and 2018 I surveyed three plots there, with a total area 153 ha and previously subjected to long-term studies of breeding bird communities (Wesołowski et al., 2022).

The field studies in Austria were made in two plots (total area 70.4 ha) in Rothwald primeval forest in the Dürrenstein Wilderness Area. They were located at elevations between 960 and 1440 m, in montane mixed forests dominated by 500–600 years old beech (*Fagus sylvatica*) and fir (*Abies alba*), but a heterogeneous age structure.

Cross-sectional data about densities and characteristics of available LTC were obtained from all the study plots, while longitudinal data about LTC dynamics were obtained from the Ukrainian study plot and a set of plots in Estonia (II). The camera-trap study exploring the use of cavities by vertebrates was done in the study plot in Ukraine (III), where (in a 171-ha subplot) also the settlement of expanding black woodpeckers and accumulation of their excavated cavities were collected (V). The cavity requirements of a LTC-nester species, the Tawny owl (*Strix aluco*) were studied both in Ukraine and Poland (IV).

2.2.2. Field methods

Searching for tree cavities was the basic step performed in all plots. The cavities were searched from the ground in leafless period between October and April by the author. In the first pass, all cavities were described and trees measured from the ground. During the second visit, the trees were climbed using rope techniques to control for the presence of cavities, take measurements and sampling other data. Dead or unstable living trees were not climbed due to safety reasons. In total, 434 large cavities were measured (56% of counted).

Data on cavity and cavity-tree characteristics were used in papers **II** and **IV** to describe the diversity of cavity characteristics and species preferences. The tree-related data were: (1) tree species, (2) trunk diameter at the breast height (DBH), and (3) health status (living, dead). The cavity-related data were: (4) cavity type (according to Kraus et al., 2016 with modifications; see paper **II**), (5) entrance height above the ground, (6) maximal entrance width and (7) height, (8) depth to the cavity bottom, (9) maximum and (10) minimum diameter of the chamber, and (11) characteristics of the cavity base. Based on the measurements, two additional estimates were made (**II**): (i) the bias of ground counts – by subtracting false observations (visible entrance but absence of cavity) and cavities with several entrances; (ii) the set of potentially usable cavities – by applying two basic suitability criteria for vertebrate use, a 20–400 cm depth range (Goldingay, 2009; Koch et al., 2009; Cockle et al., 2011; Baldassarre, 2014; Bonaparte et al., 2020) and a 2-m minimal height above the ground (Bellrose, 1964; Cockle et al., 2011; Goldingay, 2011).

A camera trap study (**III**) was performed to describe the patterns and rates of vertebrate use of LTC at nine decay-formed side cavities in oaks and pears (*Pyrus communis*). The camera traps were installed in front of the cavity entrances (at 3.6–12 m height, Fig. 2a) between January 2018 and November 2023. The unit of observation was a photo-evidenced visit by a vertebrate; the visits were classified as breeding, roosting, entering cavities, and approaching and looking inside the cavities. All detectable feeding events or interactions with other animals were described. The interactions were treated as predation, aggression, mobbing of owls, and neutral. I also compared the relative visitation frequency of bird species between April and September with their share in the local breeding assemblage as recorded in the area (Vergeles et al., 1994; Nature Record of the National Nature Park Homilsha forest).

Original field data about distribution of the black woodpecker in Ukraine (**V**) were collected by distinguishing nesting territories based on all sightings of birds between 2013 (when first birds appeared on a territory) and 2023. The cavities excavated by black woodpeckers were searched in autumn 2019, seven years after the initial occupancy of the study plot.

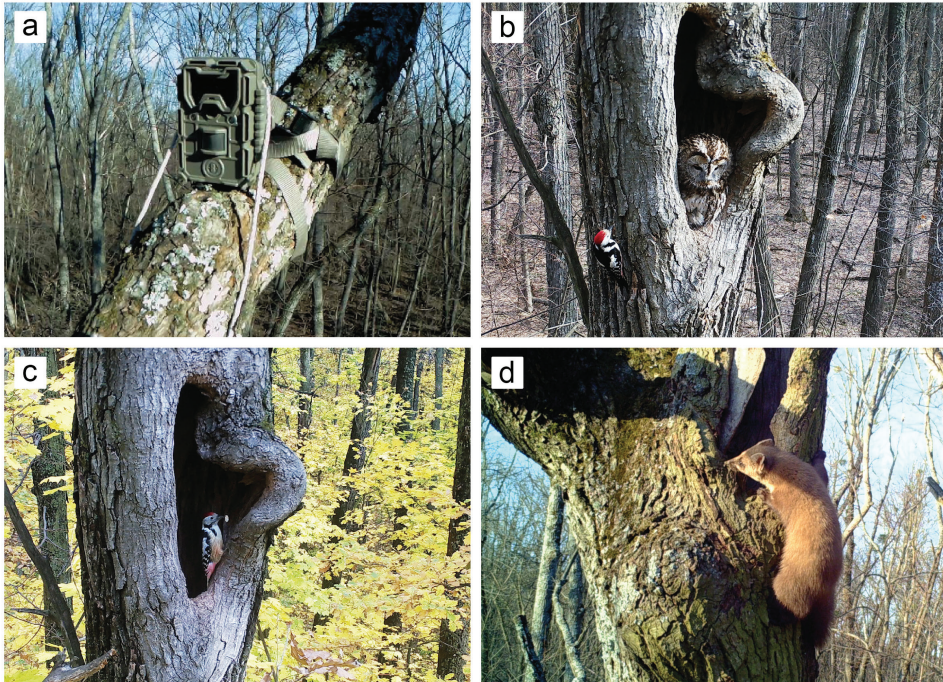


Fig. 2. The camera trap study (III) in a study plot in Ukraine: a – an example of camera installation in front of tree cavity entrance; b – middle spotted woodpecker (*Dendrocopos medius*) mobbing tawny owl (*Strix aluco*) roosting in a tree cavity; c – middle spotted woodpecker collecting food in a tree cavity; d – pine marten (*Martes martes*) inspecting tree cavity – predation of this species was the main factor shaping the use of LTC by other vertebrates.

2.2.3. Data analysis

The main approach to derive factors influencing LTC characteristics of interest was the use of statistical multi-factor models. All the calculations were performed in R version 4.4.2 (R Core Team, 2025). Initially, the candidate factors were separately tested to find basic dependencies. Then, full models including all studied factors were built. Selection of most important factors was made building models with different subsets of studied factors; then, all model subsets with $\Delta AIC < 2$ were selected and averaged using ‘MuMIn’ package (Bartoń, 2025) in R.

In study **I**, the relationship between bird sizes and preferred cavity entrance width was based on log-transformed values of adult weight. In study **II**, five factors of cavity persistence were considered: cavity type (excavated or decay-formed), tree species (aspen, birch, pine, lime and other species), and untransformed tree diameter at breast height, entrance height above the ground, and stand age. In study **IV**, the hole occupancy by tawny owls was a response variable, and tree DBH, cavity height above the ground, entrance width, minimum inner diameter and cavity depth were the factor variables. The predictor values were log-transformed to account for non-linearity.

In study **V**, the year of establishment of black woodpecker territories was related to the share of aspen stands in 700-m buffers (half of the nearest-neighbour distance). For that, all sightings of birds were first plotted using QGIS, and the centroids of each territory were calculated as average coordinates of all sighting. As controls, 12 buffers of similar size were analysed around random points in unoccupied parts of the same forest.

Image processing of camera trap data in study **III** was made using DigiKam software (www.digikam.org) and the ‘camtrapR’ package (Niedballa et al., 2016). Overlaps in diel visitation activity between predator visits and potential prey species were estimated using the ‘Activity’ package (Rowcliffe et al., 2014). Activity overlap coefficients were calculated performing 1000 bootstrap samples using the ‘Overlap’ package (Ridout & Linkie, 2009).

3. RESULTS

3.1. Animal use of large tree-cavities

The basic cavity use constraints for vertebrates are the **physical dimensions** of cavities, which determine the access for the target species, but also for their competitors and predators. My analysis of preferred cavity sizes in 354 bird species worldwide showed that the expected positive relationships between the cavity size and the user size ($r_s = 0.9$, $p < 0.0001$) across LTC thresholds is highly different for primary cavity-nesters (able to excavate cavities) and secondary cavity-nesters. Furthermore, there is increasing variability among larger secondary cavity-nesters (Fig. 3), which suggests that other factors like predation, competition or availability of suitable cavities influences cavity selection (**I**).

The case study on the tawny owl confirmed that requirements for temporary shelters are less constrained than for nesting: in particular, cavity depth (Fig. 4) and bottom characteristics have wider variation. This changes the LTCs available for this species during the year (**IV**).

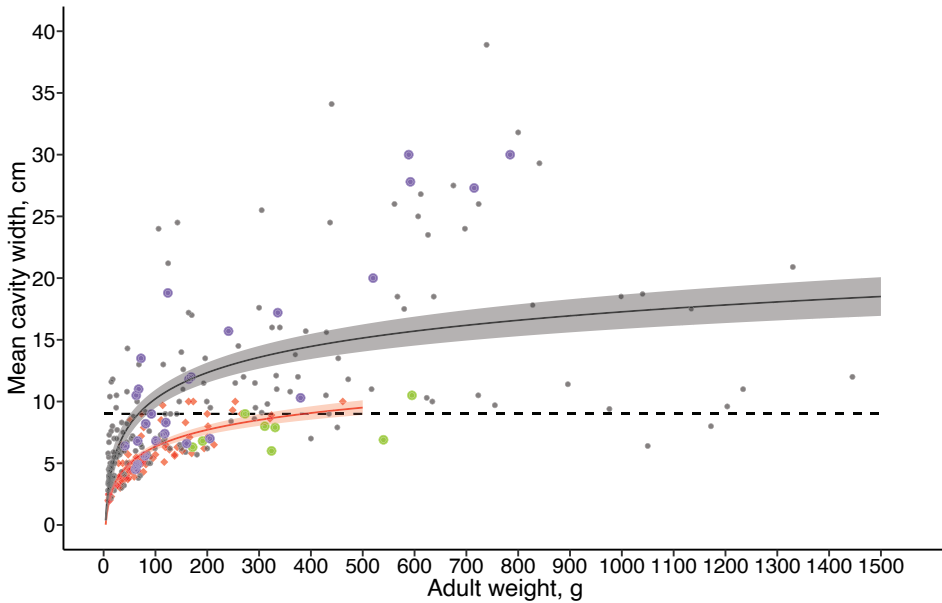


Fig. 3. Two basic relationships (mean $\pm$ 95% CI) between bird body weight and preferred breeding cavity width for 300 cavity-nesting bird species: red, primary cavity-nesters (able to excavate cavities); grey, secondary cavity-nesters. Two contrasting groups are shown among secondary cavity-nesters: toucans (Ramphastidae, larger green dots) using cavities with relatively narrow entrances, and owls (Strigidae and Tytonidae, larger violet dots) using relatively wide entrances. The horizontal dashed line indicates approximately the LTC limit (entrance width 9 cm) (**I**).

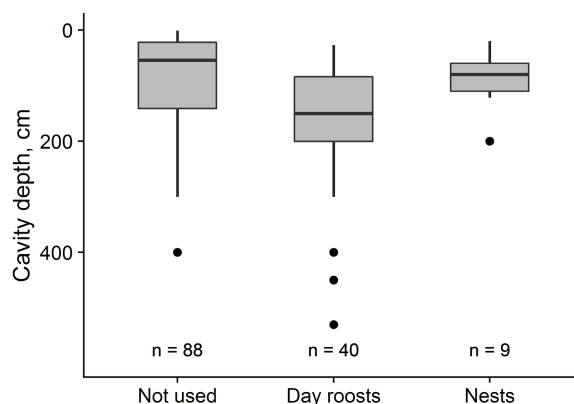


Fig. 4. Variation of depth characteristics in the tree cavities used and not used by tawny owl on a study plot in Ukraine (IV).

The review also revealed that at least in the temperate regions, most LTC breeding birds are able to exploit other sites like open nests or ground burrows (Lõhmus, 2003; Petty et al., 1994; Simmons et al., 1977; Baldassarre, 2014). The published review (van der Hoek et al., 2017) didn't show the lower share of obligate cavity-nesters in large species (body length >40 cm) but it is difficult to qualify the level of dependence on cavities without extensive comparative data on breeding success. At least, the use of alternative shelters is often associated with decreased breeding success (I). In parallel, a larger share of large cavity-nesting bird species is threatened (IUCN categories VU, EN, CR and EW in 2024: 23.9%) than of small cavity-nesters (10%) (I).

Regarding the presumed key role of predation risk in structuring LTC use, the camera-trap study in Ukraine identified pine marten (*Martes martes*) as the main predator (Fig. 2d) – it regularly visited each studied cavity on average every month. As a consequence, the only species breeding in LTC was the tawny owl that is able to actively defend its nests, while other animals can make short visits after inspecting the cavities for predator presence (III; Fig. 2c). The literature review provided additional evidence: it showed that competitive large parrots, owls or raptors tend to use cavities with larger entrances, possibly indicating their ability to defend nests (I). Other described anti-predator behaviours in LTC include plastering cavity entrances (hornbills; Kemp, 1969), selection of higher trees with smoother bark (Marsden & Jones, 1997; Kosiński et al., 2011) or deeper cavities. There are numerous indications of high competition for LTC in communities with rich fauna of cavity users (Brightsmith, 2005; Bonaparte et al., 2024) but it can be a relatively minor factor in communities with fewer species (III).

As the primary function, LTC appeared as prominent and well-known objects of short visits by the whole cavity-nester community of the surroundings, including smaller species to obtain food, water or control for predators (I, III; Fig. 5). Their large size allows more resources to be used in periods of potential shortages of resources (III, Delgado-Martínez et al. 2023). These data indicate that the role of LTC for vertebrates stretches beyond merely breeding sites and higher diversity of available cavity types enrich habitats of arboreal species.

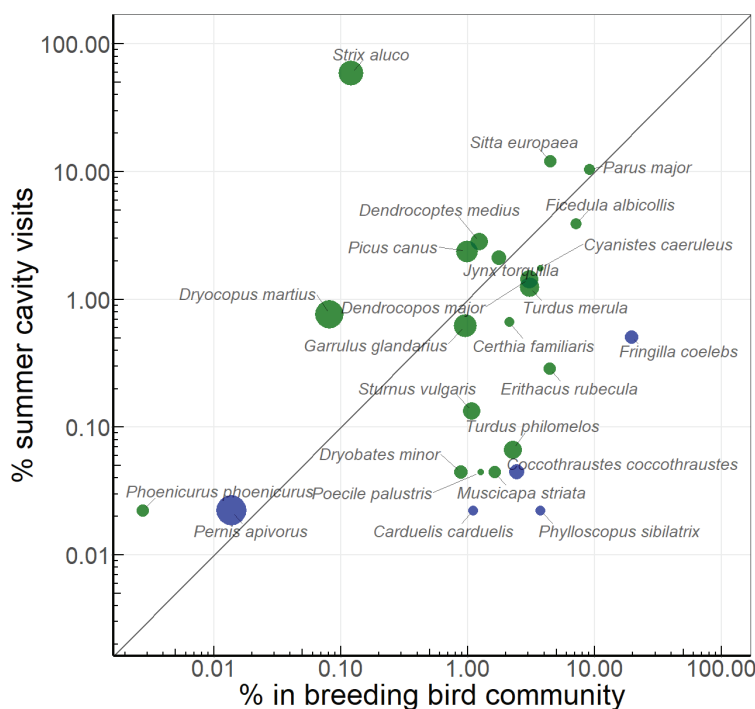


Fig. 5. Relative LTC visitation frequency of 25 breeding bird species in April–September compared with their share in the local breeding community in the Ukrainian study plot. Dot size is proportional to bird body length, and colour indicates its cavity nester status (van der Hoek et al., 2017): Green – obligate and facultative cavity nesters; blue – other birds (III).

3.2. Distribution of large tree-cavities: from global to landscape scale

The global median LTC density was 3.3 large cavities ha^{-1} based on 54 publications from different ecoregions (I), which forms 21% of a previously published global median density of all cavity types (16 cavities ha^{-1} ; Remm & Löhmus, 2011). Large angiosperm trees are the main source of LTC, but different species at given sizes vary up to 4.5-fold in cavity abundance. Conifers rarely produce decay-formed LTC unless trees reach very large size; this explains an overall rarity of large cavities in boreal forests. Standing dead trees contribute to LTC pools in a much lesser extent than to small cavity pools (I; Sedgwick and Knopf, 1986; Denton et al., 2012).

Compared with small cavities, LTC have distinct landscape distributions that depend on the distribution of large trees (I, Weier, 1966; Zudin et al., 2022). Notably, LTC densities in some open woodlands and selection-cutting silvicultural systems can be comparable with old-growth forests (I). Densities of decay-formed LTC appeared similar in old-growth forests in hemiboreal forests

(Estonia) and primeval forests in temperate Europe (Poland and Austria) (II). Management tends to decrease the occurrence of LTC to variable, often large extent (I; Fig. 6), by selectively cutting largest trees due to silvicultural or safety considerations. Without tree retention, post-clearcut forests lack any LTC for decades (II).

Where large cavity-excavating vertebrates are frequent, they can make large a contribution to LTC pools. In Estonian managed forests, cavities excavated by black woodpeckers formed >70% of all LTC, and patches of old pine stands can be hotspots of excavated cavities (II). Landscape distributions of large excavated cavities depend on habitat preferences of woodpeckers. In east Ukraine, newly established pairs of black woodpeckers tended to occupy aspen stands, quickly increasing their LTC supply in a few years (V).

My tree-climbing studies confirmed that ground counts tend to overestimate LTC stocks because of false detections of injuries without associated cavities or presence of cavities having several entrances. In excavated LTC the real numbers were only 44% (117 climbed cavity entrances) of ground estimates, while they were 87% (378 climbed cavity entrances) in decay-formed LTC. In turn, of these climbing-confirmed LTC, only 53% (excavated) and 82% (decay-formed) also met basic suitability criteria for vertebrate animals (cavity depth and entrance height above the ground). These results highlight the rarity of LTC, particularly when their suitability for fauna is considered (I, III). Chimney-type cavities (broken hollow tree trunks with entrances facing upwards) usually form in a fraction of trees with smallest size: they are usually considered of low importance for fauna but study IV showed their use by tawny owls. This cavity type can be important in stands with depleted cavity supply and younger trees.

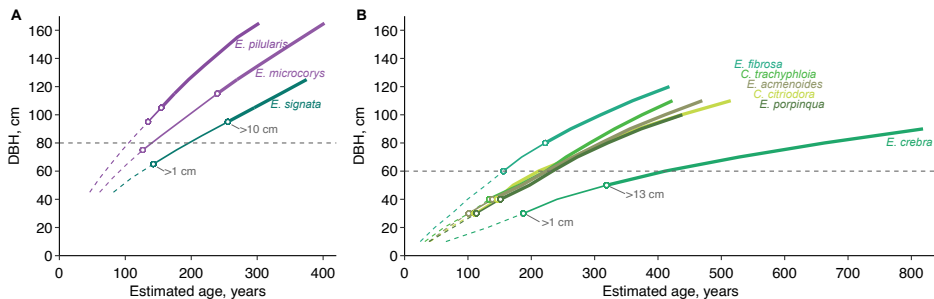


Fig. 6. Development of decay-formed cavities in Australian eucalypt species in relation to average growth rates: (A) wet (*Eucalyptus pilularis*, *E. microcorys*) and dry (*E. signata*) sclerophyll forests, 1600–1800 mm annual rainfall (data from: Wormington & Lamb, 1999); (B) dry sclerophyll forests, 900–1400 mm rainfall (data from: Wormington et al., 2003). Along each line, the two markers indicate appearance of small cavities (>1 cm entrance width), and LTC (entrance width >10 cm in A and >13 cm in B), respectively. The horizontal dashed lines are approximate threshold diameters of most trees harvested in these selection-cutting systems (I).

3.3. Development and dynamics of large tree cavities

Two pathways of LTC formation exist (**I**): slow fungal decay of heartwood and relatively fast animal excavation (Fig. 7). As cavity-excavating vertebrates prefer to use the softened wood (Conner et al., 1976; Zahner et al., 2012), fungal decay processes play critical role in LTC formation. A process of cavity formation is multi-staged and include separate processes of heartwood accumulation by tree, infection by heart rot fungi and injuring (needed for fungal infection and creation of entrances). Incidences and rates of different stages are influenced by multiple individual factors and prediction of cavity occurrence on individual tree level appears hardly predictable.

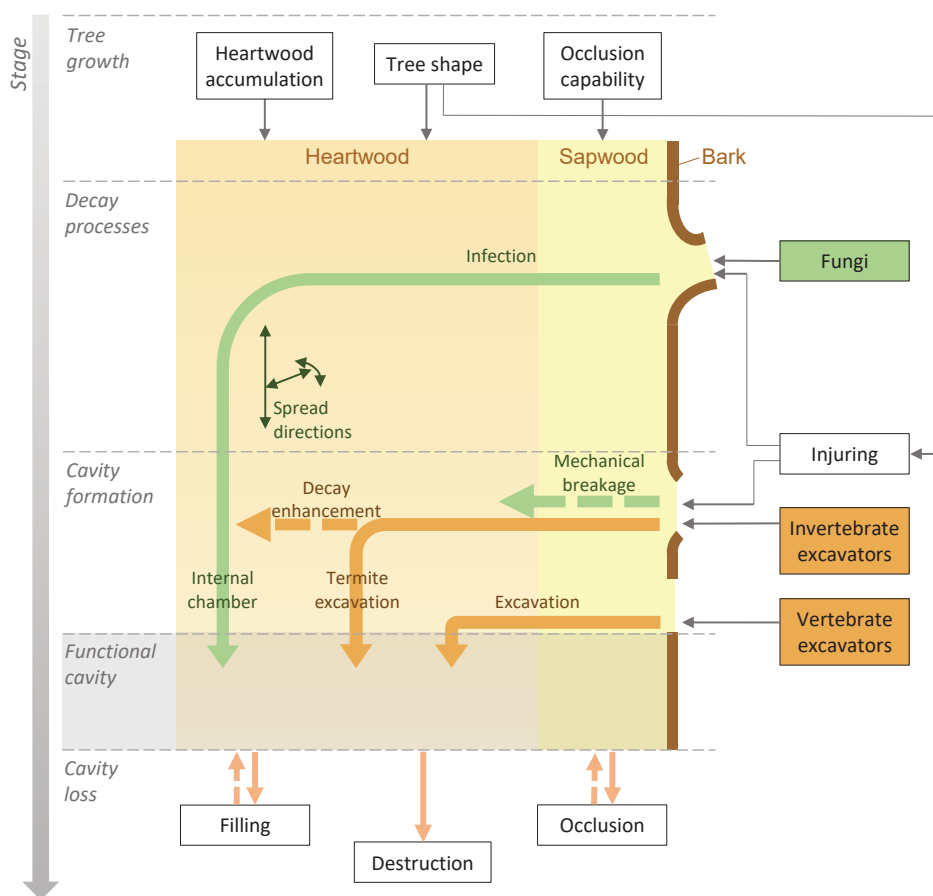


Fig. 7. Life-cycle of a large cavity, with the main pathways (including bark and sapwood breakage for entrance, and heartwood destruction to form internal cavities) shown by thick coloured arrows. The main stages are shown in grey on the left; processes are listed in white boxes, and the biological agents in filled boxes. Fungal decay dominates both pathways, as it also usually precedes or occurs simultaneously with vertebrate (woodpecker) and invertebrate (termite) excavation. Most of the elements depicted are additionally affected by tree species and growth conditions (**I**).

Stand-based models of cavity appearance for some regions are better developed (e.g., Ball et al., 1999). The general conclusion about the time frames is that decay processes leading to cavity formation are slow and take longer than the existence of cavity. Thus, approximately 75 years required to form 10-cm wide internal cavity in subtropical trees (Zheng et al., 2016), while most published studies and own data indicate that less than half of large cavities are expected to survive more than 20 years (**I, II**).

The mechanical models of tree stability, and their trade-offs, appear a useful framework to relate LTC with tree size, species, and condition, e.g., relatively low LTC occurrence and survival in snags (**I**, Table 1). The main trade-off comprises a slow decay progress in the heartwood, during with the sapwood has to maintain the tree stability. The bending stress models predict that probability of tree snapping exponentially increases when internal cavity exceeds 70% of trunk diameter (Kane et al., 2001). Another trade is between tree-growth rate and wood strength, with an important exception in oaks and other ring-porous deciduous trees that gain wood strength at higher growth rates (**I**).

Table 1. Averaged parameter estimates (β) and standard errors (*Adjusted SE*) of the model exploring the survival of 288 large tree cavities in Estonia between 2005–2007 and 2021–2024 (mean difference 16.8 years between controls). Significant factors are shown in bold (**II**).

Model term ^a	β	<i>Adjusted SE</i>	<i>Z</i>	<i>p</i>
Entrance height, cm	–0.07	0.05	1.58	0.114
Tree live state: live	3.37	0.62	5.41	<0.0001
Tree species: <i>Pinus sylvestris</i>	4.72	1.04	4.53	<0.0001
Tree species: <i>Populus tremula</i>	0.57	0.91	0.62	0.532
Tree species: <i>Tilia cordata</i>	0.74	0.95	0.78	0.436
Tree species: other	1.09	1.09	1.01	0.315
Age category: Mature	1.46	0.81	1.79	0.073
Age category: Old	0.47	0.47	1.00	0.317
Tree dbh, cm	0.01	0.01	0.49	0.623

^a Baseline categories for factors: Tree live state: dead trees; Tree species: *Betula* sp.; Age category: Uneven-aged with retention trees.

The only natural process able to quickly increase the LTC supply is excavation by large woodpeckers. Woodpecker populations are able to support relatively high densities of excavated cavities, sometimes concentrated in optimal habitats for the species. A case study in Ukraine showed that in 7 years after the appearance of black woodpecker in the region, local density of excavated cavities reached 1 ha^{–1}, which is roughly comparable to densities of decay-formed cavities (**II, V**). Most cavities were concentrated in aspen stands. If such local concentrations of cavities are combined with higher cavity survival in some tree species, it can create local hotspots of LTC concentration (**II**).

The constant recruitment of new cavities is important for long-term cavity supply. Repeated counts of LTC in a set of plots in Estonia, done with an average interval of 17 years, showed the increase of densities in most forest types and age classes (Fig. 8). LTC densities increased little in old-growth stands (from 235 to 259 counted cavities, 118% increase when corrected for detection accuracy) but considerably higher in uneven-aged stands with retention trees (16 to 32, 229%) and even-aged mature stands (30 to 50, 232%). It indicates presence of decay in managed stands in Estonia but long-term biodiversity values of these cavities remain understudied.

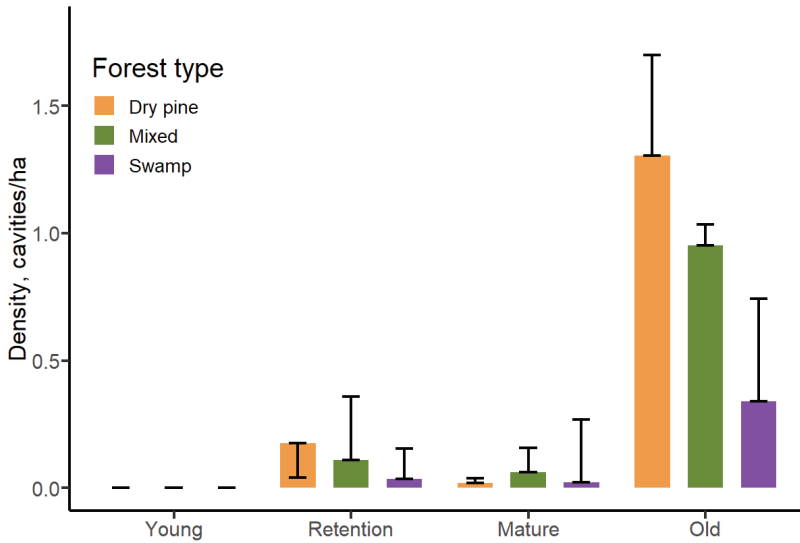


Fig 8. Changes in LTC densities on study plots in Estonia over 17 years. The columns indicate the mean densities for each combination of age class and forest types in 2005–2006 (Remm et al., 2008); black lines are densities in 2021–2024 (this study). The values have been corrected for detection accuracy (II).

4. DISCUSSION

4.1. Where, and what kind of large cavities are important for biodiversity?

The ecological role of large tree cavities (LTC) for biodiversity could be arbitrarily distinguished as two contrasting situations: where the cavities are critical for a particular species or ecological function to exist, and where their availability would have facilitating effects for the species and functions present. Regarding vertebrate fauna, LTC can be critical for strict cavity-breeding species – however, these appear to be relatively rare among large species, at least in temperate and boreal zones (cf. papers I, III).

Specifically, the relationship between bird body length and preferred cavity size estimated in paper I (Fig. 3) suggests that approximately 9% (body length at least 40 cm, 172 species) to 26% (body length at least 30 cm, 479 species) of the world's cavity-nester species may require large cavities (calculated based on van der Hoek et al., 2017). Most of these species are able to use other concealed structures or even open nests if tree cavities are absent, as reported for owls (Löhmus, 2003), ducks (Baldassarre, 2014), and many other large cavity-nester species. Such a tolerance to the absence of large cavities may be an evolutionary adaptation to naturally low abundances of cavities, facilitated by abilities of many large species to protect their nests. Perhaps, most species of strict LTC-nesters remain constrained to tropical regions where LTC supplies are naturally higher but insufficiently studied.

However, the role of LTC for vertebrate diversity appears most prominently through indirect effects. These effects can be described in terms of facilitation and segregation. For some large cavity-nesting birds, it has been demonstrated that, although they are able to nest in alternative structures, their breeding success remains higher in tree cavities (Saunders et al., 2014; Newton, 2002). Lower predation levels and better microclimate conditions may be the causal factors. Presence of a range of nest sites of varying quality, including diverse cavities, may thus create possibilities for segregation among potential competitor species and, eventually, richer co-occurring assemblages.

Furthermore, the study III showed that such effects extend much beyond cavity-nester assemblages – the study documented a high diversity of visiting species and a high frequency of visits to LTC in a temperate forest where very few species actually bred in those cavities. These non-breeding use types are probably rarely critical in the species' life cycle, but they form a part of the functioning of the local ecological networks. For example, among the species recorded in study III, the pine martens find prey in cavities only opportunistically and small birds might survive also without the food obtained in large cavities. A hypothesis to be yet properly tested is that such opportunities may become crucial in certain unfavourable periods, which would imply that LTC contribute to community resilience. For example, tree cavities containing water in seasonally-dry

cavities in Mexico are preferably used as watering sites by arboreal fauna, which presumably decreases predation risk for them (Delgado-Martínez et al., 2023).

One would expect that the extent of the facilitating effects is positively correlated with the abundance and diversity of available cavities. An example of a possible mechanism is an expected decrease of predation risk when many cavities are present in the landscapes. Such a diversity in different ecosystems across Europe was described in the study **II**, which highlighted the importance old-growth stands and multiple cavity-creating processes. Depending on what criteria are used for distinguishing “suitable” LTC for fauna, the density estimates in those ecosystems can differ manifold. It means that certain cavity types can be limiting for, and thus affect the distributions of, some species in any local landscape. It requires additional field studies to understand how frequent such effects are, for which species, and in which natural conditions. Notably important are the presence and conditions for large cavity-excavating vertebrates (woodpeckers) that were shown to be able to quickly increase the LTC stocks (**V**) and produce diverse cavities (**II**).

4.2. Natural dynamics of the LTC supply

The published information on LTC development processes and survival indicates that their density is largely a function of densities of large trees of particular species (**I**). It explains not only the (obviously) low densities in even-aged production forests (a distinct condition compared with smaller cavities), but also rapid increase of densities with the level of age heterogeneity: in selection-cutting and retention-forestry systems, and in old-growth and primeval forests (Table S1 in **I**, and **II**). An important conclusion was that in some regions there may be higher chances to find LTC in non-forested habitats: open woodlands (especially wood pastures), parks, cemeteries and ecosystems with pollarded trees (Dubois et al., 2009; LaMontagne et al., 2015). It shows that silvicultural systems have a pervasive effect on the occurrence of LTC.

In temperate and boreal zones, angiosperm trees or, more specifically, live broadleaved trees are most likely to provide large cavities (**I**, **II**). A case study in Europe (**II**) further showed how the local set of tree species providing most LTC is further influenced by management: which species are present in the landscapes and which are allowed to grow to old age. The importance of angiosperm trees emerges due to their ability to retain structural support of the outer wood (sapwood) while the heartwood remains susceptible to decay (Bunnell, 2013; Hararuk et al., 2020).

Differences in wood density and growth rates between species of angiosperm trees also determine rates of cavity formation and longevity of existing cavities. Slower-growing species and individuals may attain cavities in older age, but these cavities may exist longer (Körkjäs et al., 2021a). In turn, fast-growing species may be important in providing cavities in younger stands and trees. Thus, in Estonia, LTC were relatively often in fast-growing birches and alders in mature

managed stands compared with old-growth stands (II). Overall, a combination of old stands, presence of species excavating cavities, and high cavity survival can create local hotspots of LTC abundance, as it was seen in old-growth pine stands in Estonia (II).

Study II also illustrated that, compared with the long processes of cavity development, persistence of LTC is relatively short: less than one-third of all LTC were projected to persist more than 20 years. A surplus of trees with decay would be crucial to ensure LTC stocks despite such a high turnover (Sedgwick and Knopf, 1986; Manning et al., 2013). Particularly in forests managed for wood production, a diversity of tree species and tree sizes would be important for that. In smaller trees, chimney-type large cavities are more typical (II). Although they may not be preferred by vertebrates for breeding (due to exposure to precipitation, low height, and smaller dimensions), their presence may bridge the supply of LTC in relatively younger managed stands. However, it should be kept in mind that the lifespan of cavity trees in snags will be relatively short (Gibbons et al., 2000; Cockle et al., 2017) and their supply has to be maintained only by the constant recruitment of new cavity trees.

4.3. Gaps in knowledge

The ecology of tree cavities is generally a well-studied topic, receiving a lot of attention in scientific publications (major reviews by Gibbons and Lindenmayer, 2002; Remm and Lõhmus, 2011). However, despite several specific ecological features of LTC shown in this work, few ecological studies have so far distinguished and focused on cavities of large sizes. Partly, it is related to the relative scarcity of LTC in nature and challenges associated with obtaining direct cavity measurements. It should be also acknowledged as a possible limitation of the current work, notably the global review (I), that cavity dimension criteria have not been exactly determined. A relatively loose range of minimum entrance-width values between 8 and 10 cm allowed us to include more published data, but may have obscured some relationships (e.g., abrupt decrease of densities).

The main gaps of knowledge distinguished in this dissertation were related to three main issues: the LTC development processes, distribution, and use by fauna. As explained above, the development of LTC is a complex process which is difficult to predict on individual tree level. The review of published information (I) showed that there is little data on LTC incidence and its related process rates even for several well-studied tree species. Specifically, the development of decay-formed cavities is rarely tracked from earliest stages. A good example of field data on the presence of decay in living North American trees is provided by Basham (1991). The spread of decay is a long-term process and better to be studied in controlled conditions in inoculation studies (Silverborg & Larsen, 1967; Rayner, 1979; Edman et al., 2024). Injuring patterns across tree life determine infection by heart rot fungi and can be studied by tree microhabitat assessments (e.g., Großmann et al., 2020; Kõrkjas et al., 2021b; Zemlerová et al., 2023).

In human-transformed landscapes, non-forest habitats can provide the highest concentrations of LTC, while cavities are traditionally more studied in forests. Some studies in wood pastures (Ranius, 2002) or city parks (LaMontagne et al., 2015) provide good examples but should be expanded on other habitats. Few data about LTC stocks exist from the tropical regions, especially when compared with the relatively high diversity of large cavity-using species there. Analysed literature shows that density values are difficult to compare between forests and non-forests due to different measures used. Own field data were obtained only from forests. It indicates that studies in agricultural or populated areas are needed.

Despite a general recognition of the role of LTC for fauna, important gaps of knowledge remain associated with their indirect effects. Also, the limitation by the quality of available cavities is difficult to track, particularly in long-lived animals that may not breed in every season and use cavities only facultatively (Lõhmus, 2003). The study **III** indicated that the marten predation in large cavities was rather opportunistic, but considerable, taking into account the low densities of cavities. It could be studied whether predation levels decrease when more cavities are available. Finally, LTC apparently attract many arboreal species by either providing resources or as points of social interactions (**I**, **III**). In this respect, the role of large cavities in the transmission of pathogens or fungal spores could be studied.

4.4. LTC as key structures in management for biodiversity

My dissertation shows that LTC represent a special microhabitat type in terms of their role for fauna, distribution and development patterns. Their presence is critical for regionally varying sets of vertebrate species and supports many other arboreal species. In natural conditions, LTC distributions vary depending on the presence of angiosperm trees of old age and regional sets of large excavating animals. At the tree scale, the development of LTC is most dependent on long heartwood decay processes in living trees, triggered and supported by moderate levels of disturbances. Silviculture for wood production and tree management for safety and recreational reasons in populated areas heavily influence those processes in human-modified landscapes. It means that sites with present LTC are often biodiversity hotspots and the cavities themselves can indicate certain biodiversity values.

Approaches to sustain abundant and diverse LTC stocks vary from indirect measures aiming to facilitate natural processes in stands or across landscapes to retaining individual cavity trees or substituting cavities with artificially-created structures (**I**). Usually, the indirect approaches require less management effort and have wider effects on other biodiversity values in managed ecosystems. Two broad principles are critical: **allow presence of large trees** and **allow presence of decay**. These two principles imply shaping tree species composition in the landscapes, long-term planning of management interventions, and spatial planning to project future presence of LTC bearing trees in the landscapes.

More intensive measures to promote presence of LTC include manipulations with trees to speed up cavity formation, broadly treated as tree veteranisation. This includes inoculation of heart rot fungi in living trees (Wainhouse & Boddy, 2022), pruning to emulate injuring, or artificial carving of cavities (Rueegger, 2017; Ellis et al., 2022). Of these, pollarding is the best known effective way to promote formation of cavities in semi-open landscapes, but labour-intensive and requiring regular maintenance (Sebek et al., 2013). The effectiveness of inoculation of fungi for LTS remains unknown due to the lack of long-term studies. Artificial carving allows to create cavities with desired characteristics, but requires skilled workforce, time and long-term effectiveness of this approach is understudied. Finally, different nest boxes (including boxes with wood mould: Jansson et al., 2009) and structures emulating artificial cavities (Parker et al., 2022) are developed. The use of such intensive interventions and artificial structures is justified in the conditions of intensive management, in targeted conservation programs and mainly to bridge natural cavity supply. It is difficult to cover the full diversity of “naturally”-formed cavities, and promoting natural development has to be a priority in all settings.

Based on my thesis, the main management options for LTC are as follows:

1. **Protect existing LTC trees.** Retain large cavities at harvest operations, particularly those in living trees and with signs of animal use. Consider stand-scale protection for hotspots of LTC density ($>10 \text{ ha}^{-1}$).
2. **Sustain natural cavity development.** Whenever feasible, do not thin out all trees exhibiting signs of heartwood decay, and consider prolonging rotation periods beyond typical LTC formation age. Prioritize retention of larger trees with large injuries but showing signs of stability. Where possible, set aside old-growth or multi-aged stands from harvesting.
3. **Differentiate retention for LTC formation in a short term and in a long term.** Use a combination of aggregated retention (patches of trees) and single-tree retention (especially of large trees with injuries or signs of cavity development). Retain trees that provide cavities over different time horizons. In a short term, a priority should be given to trees exhibiting decay or developing cavities. For a longer perspective – to vigorous trees having chance to reach a large size and attain habitat value. The latter is especially important in current short-rotation forests.
4. **Ensure a diversity of LTC types.** This can be primarily achieved by a high diversity of tree species. In conifer-dominated stands in the temperate and hemiboreal zone, the presence of broadleaved species is important. The cavity-prone broadleaved species that do not have apparent economical value may require special attention.

Specific considerations apply to non-forest ecosystems where the human safety considerations are important:

- 6. Optimize the presence of cavity trees in landscapes.** While their presence is unwanted (sometimes prohibited) near houses, roads or other infrastructure, LTC bearing trees can be individually located and pre-planned in other places. In some cases, aggregated distributions of cavity trees may be advantageous for their management and both for connectivity of saproxylic communities.

5. CONCLUSIONS

In this thesis I investigated the specific features of large tree cavities (LTC) for biodiversity, their occurrence patterns and development. The main contribution of this work is synthesizing the published data about LTC ecology worldwide and complementing this with original field data from temperate and hemiboreal regions of Europe. The key findings of the work are:

1. **Role for fauna.** LTC host distinct sets of vertebrates compared with smaller cavities. A major factor shaping their use by animals is the predation risk, which makes them important breeding sites mainly for large species that tend to be rarer. The main advantages of LTC presence for vertebrates are associated with improved productivity and survival, and increasing possibilities to segregate habitats. Besides this, large size increases the importance of cavities as feeding or watering sites for arboreal vertebrates.
2. **Distribution.** LTC have naturally low densities; their distribution depends most on the presence of large broadleaved trees. In most ecosystems the LTC densities are $<5 \text{ ha}^{-1}$. On a global level, the highest densities have been recorded in subtropical and some temperate regions. On a landscape scale, the densities are highest in old-growth stands with a high share of broadleaved trees or in non-forest landscapes where large old trees are present (open woodlands, parks etc.).
3. **Development.** Heartwood decay processes play a critical role in the development of LTC, even when animal excavation is involved. Long-term stability of the trees and moderate levels of disturbances are important. The decay processes needed for LTC last decades and are much longer than time when cavities are available for fauna. It highlights the importance of continuous presence of trees with decay to ensure stable turnover of large cavities in the landscapes.
4. **Management.** LTC require special attention in management – specifically, through retention approaches and spatial planning in various woodlands to support natural processes of cavity formation and to retain the LTC present. The key approaches are facilitating an abundant and diverse supply of large angiosperm trees and to allow for their hollowing. Such management planning has to consider up to century-long time frames. Labour-intensive techniques like artificial wounding or the use of artificial structures are mostly feasible in short time frames to bridge shortages of natural cavity supply.

SUMMARY IN ENGLISH

A large proportion of the land surface is covered by ecosystems dominated by trees: naturally forests and various open woodlands, in anthropogenic landscapes also orchards, woods and trees in populated and agricultural lands. Nowadays, the majority of wooded ecosystems worldwide is shaped by human activity and is managed for different purposes. This often leads to simplified ecosystem structures and eventually causes decreases of tree-related biodiversity. Protected areas alone cannot sustain the full biodiversity of wooded ecosystems – it should be supported by increasing structural and spatial complexity also in landscapes managed for human needs. In order to do this, it is important to know, which structures are crucial for biodiversity and to promote their supply.

A large part of biodiversity in wooded ecosystems depends directly on tree-related microhabitats. Tree cavities are among the most diverse and well-recognized of such structures. For animals, they provide breeding or resting shelters and resources like food or water. Tree cavities also host fungal and microbial communities and play a role in nutrient cycling. A diversity of cavity shapes, formation pathways and sizes enable different patterns of use by animals: numerous studies demonstrate that tree cavities of different characteristics have to be present in landscapes to better sustain biodiversity.

In my dissertation, I focus on large tree cavities (LTC), which have entrances wider than 8–10 cm and can be created either by fungal decay or excavation by the largest woodpeckers. The main presumption is that LTC differ from smaller ones in their use by animals, occurrence and dynamics; they therefore require special attention in woodland management for biodiversity.

For the management, it is important to understand the natural LTC stocks and their dynamics; which characteristics of LTC are associated with highest biodiversity values; and how these are affected by land use. Long-term planning specifically requires knowledge about cavity development processes and loss rates to ensure the long-term LTC supply. In numerous studies on tree cavities this information often remains pooled with smaller cavities because LTC are rare and cavity dimensions cannot be accurately recorded without tree climbing. There has been no special research on the specific aspects of LTC ecology, and the relevant information is dispersed across fields of forest pathology, mycology, arboriculture, and animal ecology. This explains the overall rationale of this study: to aggregate such information from the literature and to complement this with original field data. The study is aimed to answer the following questions: In what, specifically, LTC have distinct patterns of use by animals? How abundant are LTC on global and landscape scales? What factors cause the specificity of LTC formation and dynamics? Based on this knowledge, the main principles of LTC management for biodiversity can be formulated.

The literature review (paper I) organizes the current knowledge on LTC from available publications worldwide. The four field case studies (papers II–IV) were made in various European forest types: Estonia (hemiboreal zone), Ukraine,

Poland and Austria (temperate zone). The patterns of animal use in a forest assemblage were studied using camera traps (III). Specific requirements of animals to cavity characteristics were exemplified based on a widespread European cavity nester, the tawny owl (*Strix aluco*) (IV). A case study of the black woodpecker (*Dryocopus martius*) expanding its range in east Europe demonstrates its role as the main species able to excavate LTC in increasing the cavity stocks (V). The LTC stocks and methodological issues in studying them are treated in detail by ground surveys supplemented with tree climbing and measuring the cavities in various European forest ecosystems (II). In a subset of the study plots, repeated controls of the cavities provided data about LTC dynamics over 15 years (II).

Regarding the function of providing safe breeding shelters for vertebrates, small animals tend to avoid breeding in large cavities due to their accessibility for predators. However, LTC provide important breeding sites for larger animals, which tend to be also more threatened (I, III). Besides breeding, LTC are important sources of food and water: their large size, visibility, and accessibility make them important structures that enrich the habitats of all arboreal species (I, III). For invertebrates LTC serve as small ecosystems which capacity is positively correlated with the chamber size but also depends on the location and microclimate (I). A diversity of cavities with different sizes and microclimate apparently allows animals to decrease predation and competition (II).

The global medium density of LTC in forests is 3.3 ha^{-1} , which can be compared with 16 ha^{-1} reported for all cavity size classes pooled (I). The distribution of LTC heavily depends on the presence of large angiosperm trees: the LTC densities are higher in temperate and subtropical zones and naturally low in the boreal zone. In human-modified landscapes, the presence of large trees is not always associated with closed (production) forests, and LTC densities may be higher in open woodlands and parks instead (I). Where vertebrates able to excavate large cavities are frequent, they can make a substantial contribution to LTC stocks (II), including quickly increasing the LTC supply in optimal habitats (V). Ground surveys tend to overestimate LTC abundance, and only less than 60% of available LTC appear suitable for vertebrate animal use (II). In many cases, animals use various types of cavities for different purposes: most important breeding cavities are usually in larger and older trees and have narrower range of dimensions, while presence of cavities with other characteristics remains important for non-breeding use (I, III, IV).

Wood decay processes heavily limit LTC dynamics in nature, since their rates are usually slow: at least 50 years of heart-rot are needed to produce a large cavity (I). Due to complexity of influencing factor and stochasticity of tree injuring, it is difficult to predict a formation of LTC on individual tree level in long term, but stand-based models of incidence are better developed. It means that long-term management goals have to be focused on supporting natural cavity formation rates. The trees have to remain stable during this whole time, which is best achieved in large trees that stay alive. Long-term observations show relatively short lifespan of LTC, comparing with the time needed for their formation

(I, II). It highlights the need for constant supply of decaying trees. Large woodpeckers are able to quickly increase LTC pools (V), sometimes creating hotspots of LTC abundance (II).

In conclusion, LTC are ecologically important in many ecosystems, but they are naturally rare and associated with large old trees. To sustain LTC stocks and functions, managed landscapes have to be planned for the cavity supplies while avoiding conflicts with human safety and production needs. In a short term, large trees with existing cavities and advanced hollowing can be protected. In a longer term, old-growth protection and retention forestry are the two useful approaches, particularly when combined with a silviculture that uses diverse tree compositions. Surrogate structures like nest boxes and artificially carved cavities cannot fully mimic natural cavities and are only feasible in targeted programs.

REFERENCES

- Asbeck, T., Großmann, J., Paillet, Y., Winiger, N. & Bauhus, J. (2021). The use of tree-related microhabitats as forest biodiversity indicators and to guide integrated forest management. *Current Forestry Reports*, 7(1), 59–68. <https://doi.org/10.1007/s40725-020-00132-5>
- Asbeck, T., Kozák, D., Spínu, A. P., Mikoláš, M., Zemlerová, V., & Svoboda, M. (2022). Tree-Related Microhabitats Follow Similar Patterns but are More Diverse in Primary Compared to Managed Temperate Mountain Forests. *Ecosystems*, 25, 712–726. <https://doi.org/10.1007/s10021-021-00681-1>
- Baldassarre, G., (2014). *Ducks, Geese, and Swans of North America*. John Hopkins University Press, Baltimore.
- Ball, I.R., Lindenmayer, D.B. & Possingham, H.P. (1999). A tree hollow dynamics simulation model. *Forest Ecology and Management*, 123, 179–194. [https://doi.org/10.1016/S0378-1127\(99\)00026-2](https://doi.org/10.1016/S0378-1127(99)00026-2)
- Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Nally, R.M., ... & Gardner, T. A. (2016). Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature*, 535(7610), 144–147. <https://doi.org/10.1038/nature18326>
- Bartoń, K. (2025). MuMIn: Multi-Model Inference. R package version 1.48.11, <https://CRAN.R-project.org/package=MuMIn>
- Basham, J.T. (1991). *Stem Decay in Living Trees in Ontario's Forests: A Users' Compendium and Guide*. Information report OX-Canadian Forestry Service, Great Lakes Forestry Centre.
- Baumgartner, L.L. (1939). Fox squirrel dens. *Journal of Mammalogy*, 20, 456–465. <https://doi.org/10.2307/1374592>
- Bazzaz, F. (1975). Plant species diversity in old-field successional ecosystems in southern Illinois. *Ecology*, 56(2), 485–488.
- Bellrose, F.C., Johnson, K.L. & Meyers, T.U. (1964). Relative value of natural cavities and nesting houses for wood ducks. *Journal of Wildlife Management*, 28, 661–676. <https://doi.org/10.2307/3798781>
- Bengtsson, V., Hedin, J., & Niklasson, M. (2013). Veteranisation of oak – Managing trees to speed up habitat production. *Trees Beyond the Wood: An Exploration of Concepts of Woods, Forests and Trees*, 61–68.
- Betts, M.G., Phalan, B.T., Wolf, C., Baker, S.C., Messier, C., Puettmann, K.J., Green, R., Harris, S.H., Edwards, D.P., Lindenmayer, D.B. & Balmford, A. (2021). Producing wood at least cost to biodiversity: Integrating Triad and sharing–sparing approaches to inform forest landscape management. *Biological Reviews*, 96(4), 1301–1317. <https://doi.org/10.1111/brv.12703>
- Beyer, G.E. (1900). The Ivory-billed Woodpecker in Louisiana. *Auk*, 17, 97–99.
- Billerman, S.M., Keeney, B.K., Rodewald, P.G. & Schulenberg, T.S. (Editors) (2022). *Birds of the World*. Cornell Laboratory of Ornithology, Ithaca, NY, USA. <https://birdsoftheworld.org/bow/home>
- Boddy, L. & Rayner, A.D.M. (1983). Origins of decay in living deciduous trees: the role of moisture content and a re-appraisal of the expanded concept of tree decay. *New Phytologist*, 94, 623–641. <https://doi.org/10.1111/j.1469-8137.1983.tb04871.x>
- Bonaparte, E.B., Cuatianquiz Lima, C., Ferreira-Xavier, H.D., da Hora Barros, J.S., Di Sallo, F.G., López, F.G., Cockle, K.L. & Núñez Montellano, M.G. (2024). Ecology and conservation of cavity-nesting birds in the Neotropics: Recent advances, future directions, and contributions to ornithology. *Ornithological Applications*, 126(4), duae042. <https://doi.org/10.1093/ornithapp/duae042>

- Bonaparte, E.B., Ibarra, J.T. & Cockle, K.L. (2020). Conserving nest trees used by cavity-nesting birds from endangered primary Atlantic forest to open farmland: Increased relevance of excavated cavities in large dead trees on farms. *Forest Ecology and Management*, 475, 118440. <https://doi.org/10.1016/j.foreco.2020.118440>
- Bonar, R.L. (2000). Availability of pileated woodpecker cavities and use by other species. *Journal of Wildlife Management*, 64, 52–59. <https://doi.org/10.2307/3802974>
- Boonman, C.C.F., Serra-Diaz, J.M., Hoeks, S., Guo, W.Y., Enquist, B.J., Maitner, B., Malhi, Y., Merow, C., Buitenwerf, R. & Svenning, J.C. (2024). More than 17,000 tree species are at risk from rapid global change. *Nature Communications* 15(166), 144–147. <https://doi.org/10.1038/s41467-023-44321-9>
- Brightsmith, D.J. (2005). Competition, predation and nest niche shifts among tropical cavity nesters: ecological evidence. *Journal of Avian Biology*, 36, 74–83. <https://doi.org/10.1111/j.0908-8857.2005.03311.x>
- Britt, C.R., García Anleu, R. & Desmond, M.J. (2014). Nest survival of a long-lived psittacid: Scarlet Macaws (*Ara macao cyanoptera*) in the Maya Biosphere Reserve of Guatemala and Chiquibul Forest of Belize. *The Condor: Ornithological Applications*, 116(2), 265–276. <https://doi.org/10.1650/CONDOR-12-141-R1.1>
- Bryant, G., Dundas, S., Fleming, P. & Bennett, N. (2012). Tree hollows are of conservation importance for a Near-Threatened python species. *Journal of Zoology*, 286, 81–92. <https://doi.org/10.1111/j.1469-7998.2011.00852.x>
- Bull, E.L. (1987). Ecology of the Pileated Woodpecker in northeastern Oregon. *Journal of Wildlife Management*, 51, 472–481. <https://doi.org/10.2307/3801036>
- Bull, E.L., Akenson, J.J. & Henjum, M.G. (2000). Characteristics of black bear dens in trees and logs in northeastern Oregon. *Northwestern Naturalist*, 81, 148–153. <https://doi.org/10.2307/3536825>
- Bunnell, F.L. (2013). Sustaining cavity-using species: patterns of cavity use and implications to forest management. *ISRN Forestry*, 2013, 1–33. <http://dx.doi.org/10.1155/2013/457698>
- Chamberlain, S.A., Szöcs, E. (2013). Taxize: taxonomic search and retrieval in R. *F1000Research*, 2, 191. <https://doi.org/10.12688/f1000research.2-191.v2>
- Cockle, K.L., Martin, K. & Bodrati, A. (2017). Persistence and loss of tree cavities used by birds in the subtropical Atlantic Forest. *Forest Ecology and Management*, 384, 200–207. <https://doi.org/10.1016/j.foreco.2016.10.052>
- Cockle, K., Martin, K. & Wiebe, K.L. (2008). Availability of cavities for nesting birds in the Atlantic Forest. Argentina. *Ornitologia Neotropical*, 19 (Suppl.), 269–278.
- Cockle, K., Martin, K. & Wiebe, K. (2011). Selection of nest trees by cavity-nesting birds in the Neotropical Atlantic forest. *Biotropica*, 43(2), 228–236.
- Conner, R.N., Miller Jr.O.K. & Adkisson, C.S. (1976). Woodpecker dependence on trees infected by fungal heart rots. *Wilson Bulletin*, 88, 575–581.
- Dalke, P.D. (1948). Some observations on den trees in the Missouri Ozarks. *Journal of Wildlife Management*, 12, 107–109. <https://doi.org/10.2307/3795752>
- Delgado-Martínez, C.M., Cudney-Valenzuela, S.J. & Mendoza, E. (2022). Camera trapping reveals multispecies use of water-filled tree holes by birds and mammals in a Neotropical forest. *Biotropica*, 54(1), 262–267.
- Delgado-Martínez, C.M., Kolb, M., Pascual-Ramírez, F. & Mendoza, E. (2023). Differential utilization of surface and arboreal water bodies by birds and mammals in a seasonally dry Neotropical forest in southern Mexico. *Ecology and Evolution*, 13(11), e10781. <https://doi.org/10.1002/ece3.10781>

- Denton, J.C., Roy, C.L., Soulliere, G.J. & Potter, B.A. (2012). Change in density of duck nest cavities at forests in the North Central United States. *Journal of Fish and Wildlife Management*, 3(1), 76–88. <https://doi.org/10.3996/112011-JFWM-067>
- Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Díaz, K.A.S., Brauman, K.A., Butchart, S.H.M., Chan, K.M.A., Garibaldi, L.A., Ichii, K., Liu, J., Subramanian, S.M., Midgeley, G.F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Chowdhury, R.R., Shin, Y.J., Visseren-Hamakers, I., Willis, K.J., Zayas, C.N. (Eds.) (2019). IPBES. *The Global Assessment Report on Biodiversity and Ecosystem Services – Summary for Policy Makers*. IPBES Secretariat, Bonn, Germany.
- Dow, H. & Fredga, S. (1985). Selection of nest sites by a hole-nesting duck, the Goldeneye *Bucephala clangula*. *Ibis*, 127, 16–30. <https://doi.org/10.1111/j.1474-919X.1985.tb05034.x>
- Dubois, G.F., Vignon, V., Delettre, Y.R., Rantier, Y., Vernon, P. & Burel, F. (2009). Factors affecting the occurrence of the endangered saproxylic beetle *Osmoderma eremita* (Scopoli, 1763) (Coleoptera: Cetoniidae) in an agricultural landscape. *Landsc. Urban Planning*, 91, 152–159. <https://doi.org/10.1016/j.landurbplan.2008.12.009>
- LaMontagne, J.M., Kilgour, R.J., Anderson, E.C. & Magle, S. (2015). Tree cavity availability across forest, park, and residential habitats in a highly urban area. *Urban Ecosystems*, 18(1), 151–167. <https://doi.org/10.1007/s11252-014-0383-y>
- Edman, M., Eriksson, A.M., Carlsson, F. & Rydkvist, T. (2024). Veteranising Scots pine trees by initiating tree hollowing: Inoculation with the fungal keystone species *Porodaedalia pini*. *Fungal Ecology*, 72, 101375. <https://doi.org/10.1016/j.funeco.2024.101375>
- Elliott, T.F., Jusino, M.A., Trappe, J.M., Lepp, H., Ballard, G.-A., Bruhl, J.J. & Vernes, K. (2019). A global review of the ecological significance of symbiotic associations between birds and fungi. *Fungal Diversity*, 98, 161–194. <https://doi.org/10.1007/s13225-019-00436-3>
- Ellis, E.C., Gauthier, N., Klein Goldewijk, K., Bliege Bird, R., Boivin, N., Díaz, S., Fuller, D.Q., Gill, J.L., Kaplan, J.O., Kingston, N., Locke, H., McMichael, C.N.H., Ranco, D., Rick, T.C., Shaw, M.R., Stephens, L., Svenning, J.-C. & Watson, J.E.M. (2021). People have shaped most of terrestrial nature for at least 12,000 years. *Proceedings of the National Academy of Sciences*, 118(17), e2023483118. <https://doi.org/10.1073/pnas.2023483118>
- Ellis, M.V., Taylor, J.E. & Rhind, S.G. (2022). Creating entrances to tree cavities attracts hollow-dependent fauna: proof of concept. *Restoration Ecology*, 30, e13713. <https://doi.org/10.1111/rec.13713>
- FAO (2020). *Global Forest Resources Assessment 2020: Main report*. Rome. <https://doi.org/10.4060/ca9825en>
- Fröhlich, A., Przepióra, F., Drobniak, S., Mikusiński, G. & Ciach, M. (2024). Public Safety Considerations Constraint the Conservation of Large Old Trees and Their Crucial Ecological Heritage in Urban Green Spaces. *Science of The Total Environment*, 948, 174919. <https://doi.org/10.1016/j.scitotenv.2024.174919>
- Gerhardt, R.P. (2004). Cavity nesting in raptors of Tikal National Park and vicinity, Petén, Guatemala. *Ornitologia Neotropical*, 15, 477–483.
- Gibbons, P. & Lindenmayer, D. (2002). Tree Hollows and Wildlife Conservation in Australia. *CSIRO Publishing, Collingwood*.
- Gibbons, P. & Lindenmayer, D.B. (1996). Issues associated with the retention of hollow-bearing trees within eucalypt forests managed for wood production. *Forest Ecology and Management*, 83(3), 245–279. [https://doi.org/10.1016/0378-1127\(95\)03692-X](https://doi.org/10.1016/0378-1127(95)03692-X)

- Gibbons, P., Lindenmayer, D., Barry, S.C. & Tanton, M. (2000). Hollow formation in eucalypts from temperate forests in south eastern Australia. *Pacific Conservation Biology*, 6, 218–228. <https://doi.org/10.1071/PC000217>
- Gibbons, P., Lindenmayer, D.B., Barry, S.C. & Tanton, M.T. (2002). Hollow selection by vertebrate fauna in forest of southeastern Australia and implications for forest management. *Biological Conservation*, 103, 1–12. [https://doi.org/10.1016/S0006-3207\(01\)00109-4](https://doi.org/10.1016/S0006-3207(01)00109-4)
- Gicaraya, V.A.G. & Española, C.P. (2024). First description of the breeding biology and behaviour of the near threatened northern sooty woodpecker *Mulleripicus funebris* (Valenciennes 1826) (Piciformes: Picidae) in Luzon Island, Philippines. *Natural History Sciences*, 11(1), 15–20. <https://doi.org/10.4081/nhs.2024.701>
- Glutz von Blotzheim, U.N., Bauer, K.M. & Bezzel, E. (Eds.). (1980). *Handbuch der Vögel Mitteleuropas*, Band 9. Columbiformes–Piciformes. 2nd ed. Wiesbaden: Aula-Verlag.
- Godfrey, C.L., Needham, K., Vaughan, M.R., Vashon, J.H., Martin, D.D. & Blank Jr, G.T. (2000). A technique for and risks associated with entering tree dens used by black bears. *Wildlife Society Bulletin*, 28(1), 131–140. <https://www.jstor.org/stable/4617294>
- Goldingay, R.L. (2009). Characteristics of tree hollows used by Australian birds and bats. *Wildlife Research*, 36, 394–409. <https://doi.org/10.1071/WR08172>
- Goldingay, R.L. (2011). Characteristics of tree hollows used by Australian arboreal and scansorial mammals. *Australian Journal of Zoology*, 59, 277–294. <https://doi.org/10.1071/ZO11081>
- Gorrod, E., Oliver, I., Bedward, M., McAllister, D., O’Kelly, T. & Lawrie, K. (2024). Tree hollow decline in new forest reserves with a long history of logging. *Austral Ecology*, 49(7), e13554. <https://doi.org/10.1111/aec.13554>
- 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 Forestry & Urban Greening*, 55, 126817. <https://doi.org/10.1016/j.ufug.2020.126817>
- Gysel, L.W. (1961). An ecological study of tree cavities and ground burrows in forest stands. *Journal of Wildlife Management*, 25(1), 12–20. <https://doi.org/10.2307/3796985>
- Hararuk, O., Kurz, W.A., Didion, M. (2020). Dynamics of dead wood decay in Swiss forests. *Forest Ecosystems*, 7, 36. <https://doi.org/10.1186/s40663-020-00248-x>
- Heineman, K.D., Russo, S.E., Baillie, I.C., Mamit, J.D., Chai, P.P.-K., Chai, L., Hindley, E.W., Lau, B.-T., Tan, S. & Ashton, P.S. (2015). Evaluation of stem rot in 339 Bornean tree species: implications of size, taxonomy, and soil-related variation for aboveground biomass estimates. *Biogeosciences*, 12, 5735–5751. <https://doi.org/10.5194/bg-12-5735-2015>
- Heinsohn, R., Zdenek, C.N., Cunningham, R.B., Endler, J.A. & Langmore, N.E. (2017). Tool-assisted rhythmic drumming in palm cockatoos shares key elements of human instrumental music. *Science advances*, 3(6), e1602399. <https://doi.org/10.1126/sciadv.1602399>
- Hunter, M.L., Acuña, V., Bauer, D.M., Bell, K.P., Calhoun, A.J.K., Felipe-Lucia, M.R., Fitzsimons, J.A., González, E., Kinnison, M., Lindenmayer, D., Lundquist, C.J., Medellin, R.A., Nelson, E.J. & Poschlod, P. (2017). Conserving small natural features with large ecological roles: A synthetic overview. *Biological Conservation*, 211, 88–95. <https://doi.org/10.1016/j.biocon.2016.12.020>

- Inoue, N., Inoue, T., Matsumoto, H., Sakai, M., Yoshida, T. & Washitani, I. (2021). Tree cavity abundance and formation in subtropical evergreen broad-leaved forests on Amami Oshima Island, Japan: Implications for conservation of cavity-using species. *Japanese Journal of Conservation Ecology*, 26, 15–32.
<https://doi.org/10.18960/hozen.2019>
- Isaac, B., White, J., Ierodiaconou, D. & Cooke, R. (2014). Urban to forest gradients: suitability for hollow bearing trees and implications for obligate hollow nesters. *Austral Ecology*, 39, 963–972. <https://doi.org/10.1111/aec.12164>
- Jansson, N., Ranius, T., Larsson, A. & Milberg, P. (2009). Boxes mimicking tree hollows can help conservation of saproxylic beetles. *Biodiversity and Conservation*, 18, 3891–3908. <https://doi.org/10.1007/s10531-009-9687-2>
- Johnsson, K., Nilsson, S.G. & Tjernberg, M. (1993). Characteristics and utilization of old Black Woodpecker *Dryocopus martius* holes by hole-nesting species. *Ibis*, 135, 410–416. <https://doi.org/10.1111/j.1474-919X.1993.tb02113.x>
- Kajtoch, Ł. (2017). The importance of traditional orchards for breeding birds: The preliminary study on Central European example. *Acta Oecologica*, 78, 53–60. <https://doi.org/10.1016/j.actao.2016.12.010>
- Kane, B., Ryan, D. & Bloniarz, D.V. (2001). Comparing formulae that assess strength loss due to decay in trees. *Arboriculture & Urban Forestry (AUF)*, 27, 78–87. <http://dx.doi.org/10.48044/jauf.2001.010>
- Kane, B. (2017). Assessing the likelihood of failure due to decay in trees. In: Ning, Z., Nowak, D.J., Watson, G. (Eds.), *Urban Forest Sustainability. International Society of Arboriculture*, Champaign, Illinois, pp. 274–280.
- Kemp, A.C. (1969). Some observations on the sealed-in nesting method of hornbills (family: Bucerotidae). *Ostrich*, 40(S1), 149–155.
<https://doi.org/10.1080/00306525.1969.9639117>
- Kobayashi, S., Kotaka, N., Nakata, K. & Takashima, A. (2022). Mammal and bird species using cavities among forests of different ages on Okinawajima Island in the Ryukyu Archipelago, Japan. *Journal of Forest Research*, 27(6), 439–449.
<https://doi.org/10.1080/13416979.2022.2060553>
- Koch, A.J., Munks, S.A. & Woehler, E.J. (2009). Hollow-using vertebrate fauna of Tasmania: distribution, hollow requirements and conservation status. *Australian Journal of Zoology*, 56, 323–349. <https://doi.org/10.1071/ZO08003>
- Kosiński, Z., Bilińska, E., Dereziński, J. & Kempa, M. (2011). Nest-sites used by Stock Doves *Columba oenas*: what determines their occupancy? *Acta Ornithologica*, 46, 155–163. <https://doi.org/10.3161/000164511X625928>
- Körkjas, M., Remm, L. & Lõhmus, A. (2021). Development rates and persistence of the microhabitats initiated by disease and injuries in live trees: A review. *Forest Ecology and Management*, 482, 118833. <https://doi.org/10.1016/j.foreco.2020.118833>
- Körkjas, M., Remm, L., Lõhmus, P. & Lõhmus, A. (2023). From tree-related microhabitats to ecosystem management: A tree-scale investigation in productive forests in Estonia. *Journal of Environmental Management*, 343, 118245.
<https://doi.org/10.1016/J.JENVMAN.2023.118245>
- 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. *European Forest Institute*.
<http://dx.doi.org/10.13140/RG.2.1.1500.6483>
- Kunz, T.H. & Lumsden, L.F. (2003). Ecology of cavity and foliage roosting bats. In: Kunz, T.H., Fenton, M.B. (Eds.), *Bat Ecology*. University of Chicago Press, Chicago, pp. 3–89.

- LaMontagne, J.M., Kilgour, R.J., Anderson, E.C. & Magle, S. (2015). Tree cavity availability across forest, park, and residential habitats in a highly urban area. *Urban Ecosystems*, 18(1), 151–167. <https://doi.org/10.1007/s11252-014-0383-y>
- 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. *Ecological Indicators*, 84, 194–207. <https://doi.org/10.1016/j.ecolind.2017.08.051>
- Larrieu, L., Cabanettes, A., Brin, A., Bouget, C., & Deconchat, M. (2014). Tree microhabitats at the stand scale in montane beech-fir forests: practical information for taxa conservation in forestry. *European Journal of Forest Research*, 133, 355–367. <https://doi.org/10.1007/s10342-013-0767-1>
- 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. *European Journal of Forest Research*, 131, 773–786. <https://doi.org/10.1007/s10342-011-0551-z>
- Lewis, T.C., Gutierrez Vargas, I., Vredenburg, C., Jimenez, M., Hatchwell, B., Beckerman, A. & Childs, D. (2023). Nest site selection and productivity of a critically endangered parrot, the great green macaw (*Ara ambiguus*) in an anthropogenic landscape. *Ibis*, 457, 1003. <https://doi.org/10.1101/2023.01.10.523381>
- Lindenmayer, D.B. & Laurance, W.F. (2017). The ecology, distribution, conservation and management of large old trees. *Biological Reviews*, 92, 1434–1458. <https://doi.org/10.1111/brv.12290>
- Löhms, A. (2003). Do Ural owls (*Strix uralensis*) suffer from the lack of nest sites in managed forests? *Biological Conservation*, 110, 1–9. [https://doi.org/10.1016/S0006-3207\(02\)00167-2](https://doi.org/10.1016/S0006-3207(02)00167-2)
- Löhms, A. & Remm, J. (2005). Nest quality limits the number of hole-nesting passerines in their natural cavity-rich habitat. *Acta Oecologica*, 27(2), 125–128. <https://doi.org/10.1016/j.actao.2004.11.001>
- MacArthur, R.H. & MacArthur, J.W. (1961). On bird species diversity. *Ecology*, 42(3), 594–598.
- Manikandan, P. & Balasubramanian, P. (2018). Sequential use of tree cavities by birds and nest web in a riparian forest in Southwest India. *Acta Ornithologica*, 53, 49–60. <https://doi.org/10.3161/00016454AO2018.53.1.005>
- Manning, A.D., Gibbons, P., Fischer, J., Oliver, D.L. & Lindenmayer, D.B. (2013). Hollow futures? Tree decline, lag effects and hollow-dependent species. *Animal Conservation*, 16, 395–403. <https://doi.org/10.1111/acv.12006>
- Marsden, S.J. & Jones, M.J. (1997). The nesting requirements of the parrots and hornbill of Sumba, Indonesia. *Biological Conservation*, 82, 279–287. [https://doi.org/10.1016/S0006-3207\(97\)00038-4](https://doi.org/10.1016/S0006-3207(97)00038-4)
- Martin, 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, 818474. <https://doi.org/10.3389/ffgc.2022.818474>
- McClelland, B.R., Frissell, S.S., Fischer, W.C. & Halvorson, C.H. (1979). Habitat management for hole-nesting birds in forests of western larch and Douglas-fir. *Journal of Forestry* 77(8), 480–483. <https://doi.org/10.1093/jof/77.8.480>

- McGrath, M.J., Luyssaert, S., Meyfroidt, P., Kaplan, J.O., Bürgi, M., Chen, Y., Erb, K., Gimmi, U., McInerney, D., Naudts, K., Otto, J., Pasztor, F., Ryder, J., Schelhaas M.-J. & Valade, A. (2015). Reconstructing European forest management from 1600 to 2010. *Biogeosciences*, 12(14), 4291–4316. <https://doi.org/10.5194/bg-12-4291-2015>
- Micó, E. (2018). Saproxylic insects in tree hollows. In: Ulyshen, M.D. (Ed.), *Saproxylic Insects: Diversity, Ecology and Conservation*. Springer, Cham, Switzerland, pp. 693–727. https://doi.org/10.1007/978-3-319-75937-1_21
- Mikusiński, G., Roberge, J.M. & Fuller, R.J. (Eds.). (2018). *Ecology and Conservation of Forest Birds* (Vol. 567). Cambridge: Cambridge University Press.
- Mölder, A., Schmidt, M., Plieninger, T. & Meyer, P. (2020). Habitat-tree protection concepts over 200 years. *Conservation Biology*, 34, 1444–1451. <https://doi.org/10.1111/cobi.13511>
- Newton, I. (1994). The role of nest sites in limiting the numbers of hole-nesting birds: A review. *Biological Conservation*, 70, 265–276. [https://doi.org/10.1016/0006-3207\(94\)90172-4](https://doi.org/10.1016/0006-3207(94)90172-4)
- Newton, I. (2002). Population limitation in Holarctic owls. In: Newton, I., Kavanagh, R., Olsen, J., Taylor, I. (Eds.), *Ecology and Conservation of Owls*. CSIRO Publishing, Collingwood, pp. 3–29.
- Niedballa, J., Sollmann, R., Courtiol, A. & Wilting, A. (2016). camtrapR: An R Package for Efficient Camera Trap Data Management. *Methods in Ecology and Evolution*, 7, 1457–1462. <https://doi.org/10.1111/2041-210X.12600>
- Noble, I. R. & Dirzo, R. (1997). Forests as human-dominated ecosystems. *Science*, 277(5325), 522–525. <https://doi.org/10.1126/science.277.5325.522>
- Nogueira, E.M., Nelson, B.W. & Fearnside, P.M. (2006). Volume and biomass of trees in central Amazonia: influence of irregularly shaped and hollow trunks. *Forest Ecology and Management*, 227, 14–21. <https://doi.org/10.1016/j.foreco.2006.02.004>
- O’Connell, C. & Keppel, G. (2016). Deep tree hollows: important refuges from extreme temperatures. *Wildlife Biology*, 22, 305–310. <https://doi.org/10.2981/wlb.00210>
- 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-taxa approach based on bats, birds and saproxylic beetles. *Journal of Applied Ecology*, 55(5), 2147–2159. <https://doi.org/10.1111/1365-2664.13181>
- Parker, D., Roudavski, S., Jones, T. M., Bradsworth, N., Isaac, B., Lockett, M. T. & Soanes, K. (2022). A framework for computer-aided design and manufacturing of habitat structures for cavity-dependent animals. *Methods in Ecology and Evolution*, 13(4), 826–841. <https://doi.org/10.1111/2041-210X.13806>
- Petty, S.J., Shaw, G. & Anderson, D.I.K. (1994). Value of nest boxes for population studies and conservation of owls in coniferous forests in Britain. *Journal of Raptor Research*, 28, 134–142.
- Poonswad, P. (1995). Nest site characteristics of four sympatric species of hornbills in Khao Yai National Park, Thailand. *Ibis*, 137, 183–191. <https://doi.org/10.1111/j.1474-919X.1995.tb03238.x>
- Prince, H.H. (1968). Nest sites used by wood ducks and common goldeneyes in New Brunswick. *Journal of Wildlife Management*, 32, 489–500. <https://doi.org/10.2307/3798927>
- Puettmann, K.J., Coates, K.D. & Messier, C.C. (2012). *A Critique of Silviculture: Managing for Complexity*. Island Press.
- R Core Team, 2025. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org>

- Ranius, T. (2002). Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. *Biological Conservation*, 103, 85–91.
[https://doi.org/10.1016/S0006-3207\(01\)00124-0](https://doi.org/10.1016/S0006-3207(01)00124-0)
- Ranius, T. & Nilsson, S.G. (1997). Habitat of *Osmoderma eremita* Scop. (Coleoptera: Scarabaeidae), a beetle living in hollow trees. *Journal of Insect Conservation*, 1, 193–204. <https://doi.org/10.1023/A:1018416000766>
- Ranius, T., Niklasson, M. & Berg, N. (2009). Development of tree hollows in pedunculate oak (*Quercus robur*). *Forest Ecology and Management*, 257, 303–310.
<https://doi.org/10.1016/j.foreco.2008.09.007>
- Rayner, A.D.M. (1979). Internal spread of fungi inoculated into hardwood stumps. *New Phytologist*, 82, 505–517. <https://doi.org/10.1111/j.1469-8137.1979.tb02677.x>
- Remm, J. & Löhmus, A. (2011). Tree cavities in forests – The broad distribution pattern of a keystone structure for biodiversity. *Forest Ecology and Management*, 262, 579–585. <https://doi.org/10.1016/j.foreco.2011.04.028>
- Remm, J., Löhmus, A. & Rosenvald, R. (2008). Density and diversity of hole-nesting passerines: dependence on the characteristics of cavities. *Acta Ornithologica*, 43, 83–91. <https://doi.org/10.3161/000164508X345365>
- Renton, K., Salinas-Melgoza, A., Labra-Hernández, D., Ángel, M. & de la Parra-Martínez, S.M. (2015). Resource requirements of parrots: nest site selectivity and dietary plasticity of Psittaciformes. *Journal of Ornithology*, 156, 73–90.
<https://doi.org/10.1007/s10336-015-1255-9>
- Ridout, M.S. & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, 14, 322–337. <https://doi.org/10.1198/jabes.2009.08038>
- Rowcliffe, J.M., Kays, R., Kranstauber, B., Carbone, C. & Jansen, P.A. (2014). Quantifying levels of animal activity using camera trap data. *Methods in Ecology and Evolution*, 5, 1170–1179. <https://doi.org/10.1111/2041-210X.12278>
- Rowland, J.A., Briscoe, N.J. & Handasyde, K.A. (2017). Comparing the thermal suitability of nest-boxes and tree-hollows for the conservation-management of arboreal marsupials. *Biological Conservation*, 209, 341–348.
<https://doi.org/10.1016/j.biocon.2017.02.006>
- Ruegger, N. (2017). Artificial tree hollow creation for cavity-using wildlife—trialling an alternative method to that of nest boxes. *Forest Ecology and Management*, 405, 404–412. <https://doi.org/10.1016/j.foreco.2017.09.062>
- Sanderson, H.R. (1975). Den-tree management for gray squirrels. *Wildlife Society Bulletin*, 3, 125–131. <https://www.jstor.org/stable/3781823>
- Saunders, D.A. (1979). The availability of tree hollows for use as nest sites by white-tailed black cockatoos. *Australian Wildlife Research*, 6, 205–216.
<https://doi.org/10.1071/WR9790205>
- Saunders, D.A., Mawson, P.R., Dawson, R. (2014). Use of tree hollows by Carnaby's cockatoo and the fate of large hollow-bearing trees at Coomallo Creek, Western Australia 1969–2013. *Biological Conservation*, 177, 185–193.
<https://doi.org/10.1016/j.biocon.2014.07.002>
- Schwarze, F.W. (2007). Wood decay under the microscope. *Fungal biology reviews*, 21, 133–170. <https://doi.org/10.1016/j.fbr.2007.09.001>
- Schwarze, F.W.M.R., Engels, J. & Mattheck, C. (2000). *Fungal Strategies of Wood Decay in Trees*. Springer, Berlin-Heidelberg.
<https://doi.org/10.1007/978-3-642-57302-6>

- Sebek, P., Altman, J., Platek, M. & Cizek, L. (2013). Is active management the key to the conservation of saproxylic biodiversity? Pollarding promotes the formation of tree hollows. *PloS ONE*, 8, e60456. <https://doi.org/10.1371/journal.pone.0060456>
- Sedgwick, J.A. & Knopf F.L. (1986). Cavity-nesting birds and the cavity-tree resource in plains cottonwood bottomlands. *Journal of Wildlife Management*, 50, 247–252. <https://doi.org/10.2307/3801906>
- Sharma, N., Huffman, M.A., Gupta, S., Nautiyal, H., Mendonça, R., Morino, L. & Sinha, A. (2016). Watering holes: The use of arboreal sources of drinking water by Old World monkeys and apes. *Behavioural Processes*, 129, 18–26. <https://doi.org/10.1016/j.beproc.2016.05.006>
- Silverborg S.B. & Larsen M.J. (1967). Rate of decay in *Pinus strobus* following artificial inoculation with *Fomes pini*. *Plant Disease Report*, 51, 829–831.
- Simmons, K.E.L., Ferguson-Lees, I.J., Gillmor, R., Hollom, P.A.D., Hudson, R., Nicholson, E.M., Ogilvie, M.A., Olney, P.J.S., Voous, K.H. & Wattel, J. 1977. *Handbook of the Birds of Europe the Middle East and North Africa. The Birds of the Western Palearctic, Vol. 1, Ostrich to Ducks*. Oxford University Press, Oxford.
- Stojanovic, D., Koch, A.J., Webb, M., Cunningham, R., Roshier, D., Heinsohn, R. (2014). Validation of a landscape-scale planning tool for cavity-dependent wildlife. *Austral Ecology*, 39(5), 579–586. <https://doi.org/10.1111/aec.12118>
- Stokland, J.N., Siitonen, J. & Jonsson, B.G. (2012). *Biodiversity in dead wood*. Cambridge University press.
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, 31(1), 79–92. <https://doi.org/10.1046/j.0305-0270.2003.00994.x>
- Thomas, P. & Packham, J. (2007). *Ecology of woodlands and forests: description, dynamics and diversity*. Cambridge University Press.
- Van der Hoek, Y., Gaona, G. V., Ciach, M. & Martin, K. (2020). Global relationships between tree-cavity excavators and forest bird richness. *Royal Society Open Science*, 7(7), 192177. <https://doi.org/10.1098/rsos.192177>
- van der Hoek, Y., Gaona, G.V. & Martin, K. (2017). The diversity, distribution and conservation status of the tree-cavity-nesting birds of the world. *Diversity and Distributions*, 23, 1120–1131. <https://doi.org/10.1111/ddi.12601>
- Vergeles, Y.I., Gorelova, L.N. & Drulyova, I.V. (1994). An essay on vegetation and bird population in the vicinities of the Kharkiv State University biological station (summer aspect). In: *The Birds of Seversky Donets River Basin 2: Proceedings of the 2nd Scientific Conference of the Working Group on Birds of the Seversky Donets River Basin*, Kharkiv, 29–33. [in Russian]
- Wagener, W.W. (1963). Judging hazard from native trees in California recreational areas: a guide for professional foresters, Vol. 1. *Pacific Southwest Forest and Range Experiment Station, Forest Service, US Department of Agriculture*.
- Wagener, W.W. & Davidson, R.W. (1954). Heart rots in living trees. *The Botanical Review*, 20, 61–134. <https://doi.org/10.1007/BF02872367>
- Wainhouse, M. & Boddy, L. (2022). Making hollow trees: Inoculating living trees with wood-decay fungi for the conservation of threatened taxa – A guide for conservationists. *Global Ecology and Conservation*, 33, e01967. <https://doi.org/10.1016/j.gecco.2021.e01967>

- Wei, W., Swaisgood, R.R., Owen, M.A., Pilfold, N.W., Han, H., Hong, M., Zhou, H., Wei, F., Nie, Y. & Zhang, Z. (2019). The role of den quality in giant panda conservation. *Biological Conservation*, 231, 189–196.
<https://doi.org/10.1016/j.biocon.2018.12.031>
- Weier, R.W. (1966). Survey of wood duck nest sites on Mingo Wildlife Refuge. In: *Wood Duck Management and Research: A Symposium*. Wildlife Management Institute, Washington, DC, pp. 91–108.
- Wesołowski, T. (2007). Lessons from long-term hole-nester studies in a primeval temperate forest. *Journal of Ornithology*, 148(Suppl 2), 395–405.
<https://doi.org/10.1007/s10336-007-0198-1>
- Wesołowski, T. (2011). Reports from nestbox studies: a review of inadequacies. *Acta Ornithologica*, 46, 13–17. <https://doi.org/10.3161/000164511X589866>
- Wesołowski, T., Czeszczewik, D., Hebda, G., Maziarz, M., Mitrus, C., Rowiński, P. & Neubauer, G. (2022). Long-term changes in breeding bird community of a primeval temperate forest: 45 years of censuses in the Białowieża National Park (Poland). *Acta Ornithologica*, 57(1), 71–100. <https://doi.org/10.3161/00016454AO2022.57.1.005>
- Wesołowski, T. & Martin, K. (2018). Tree holes and hole-nesting birds in European and North American forests. In: Mikusiński, G., Fuller, R.J., Roberge, J.-M. (Eds.), *Ecology and Conservation of Forest Birds*. Cambridge University Press, pp. 79–134.
- Williams, R.J., Zerihun, A., Montagu, K.D., Hoffman, M., Hutley, L.B. & Chen, X. (2005). Allometry for estimating aboveground tree biomass in tropical and subtropical eucalypt woodlands: Towards general predictive equations. *Australian Journal of Botany*, 53, 607–719. <https://doi.org/10.1071/BT04149>
- Winter, S. & Möller, G.C. (2008). Microhabitats in lowland beech forests as monitoring tool for nature conservation. *Forest Ecology and Management*, 255(3–4), 1251–1261. <https://doi.org/10.1016/j.foreco.2007.10.029>
- Wormington, K. & Lamb, D. (1999). Tree hollow development in wet and dry sclerophyll eucalypt forest in south-east Queensland, Australia. *Australian Forestry*, 62, 336–345. <https://doi.org/10.1080/00049158.1999.10674801>
- Wormington, K.R., Lamb, D., McCallum, H.I. & Moloney, D.J. (2003). The characteristics of six species of living hollow-bearing trees and their importance for arboreal marsupials in the dry sclerophyll forests of southeast Queensland, Australia. *Forest Ecology and Management*, 182, 75–92. [https://doi.org/10.1016/S0378-1127\(03\)00010-0](https://doi.org/10.1016/S0378-1127(03)00010-0)
- Yanovlak, S.P. (2001). The Macrofauna of Water-filled Tree Holes on Barro Colorado Island, Panama I. *Biotropica*, 33(1), 110–120. <https://doi.org/10.1111/j.1744-7429.2001.tb00161.x>
- Zahner, V., Sikora, L. & Pasinelli, G. (2012). Heart rot as a key factor for cavity tree selection in the black woodpecker. *Forest Ecology and Management*, 271, 98–103. <https://doi.org/10.1016/j.foreco.2012.01.041>
- Zeller, L., Förster, A., Keye, C., Meyer, P., Roschak, C. & Ammer, C. (2023). What does literature tell us about the relationship between forest structural attributes and species richness in temperate forests?—A review. *Ecological Indicators*, 153, 110383. <https://doi.org/10.1016/j.ecolind.2023.110383>
- Zemlerová, V., Kozák, D., Mikoláš, M., Svitok, M., Bače, R., Smyčková, M. ... & Svoboda, M. (2023). Natural disturbances are essential determinants of tree-related microhabitat availability in temperate forests. *Ecosystems*, 26(6), 1260–1274. <https://doi.org/10.1007/s10021-023-00830-8>

- Zheng, Z., Zhang, S., Baskin, C., Baskin, J., Schaefer, D., Yang, X. & Yang, L. (2016). Hollows in living trees develop slowly but considerably influence the estimate of forest biomass. *Functional Ecology*, 30, 830–838. <https://doi.org/10.1111/1365-2435.12566>
- Zudin, S., Heintz, W., Kraus, D., Krumm, F., Larrieu, L., Schuck, A., 2022. A spatially-explicit database of tree-related microhabitats in Europe and beyond. *Biodiversity Data Journal*, 10, e91385. <https://doi.org/10.3897/BDJ.10.e91385>

SUMMARY IN ESTONIAN

Suured puuõnsused metsade elurikkuse tugielemendina

Puud kasvavad ja kujundavad teistele liikidele elupaiku väga paljudes ökosüsteemides. Lisaks metsadele on puudega seotud elupaigad olulised erinevates poolavatud looduslikes ökosüsteemides, aga ka põllumajandusmaastikes, aedades ja inimasulates. Tänapäevaks on ka loodusliku päritoluga puistud valdavalt inimtegevusest mõjutatud ning neid majandatakse erinevatel eesmärkidel. Majandamine toob sageli kaasa puistute struktuuri lihtsustumise ja puudega seotud elurikkuse vähenemise.

Vastavalt võib eeldada ka vastupidist – et majandatavate alade struktuurilist ja ruumilist mitmekesisust suurendades saab nende elurikkuse seisundit parandada. Selleks, et seda tõhusalt teha, on tarvis teada, millised struktuurid ja kuidas täpselt on elurikkuse jaoks olulised ning kuidas nende hulka ja kvaliteeti suurendada. Need funktsioonid ja tekkeviisid on tihti väga spetsiifilised ja vajavad eriuuringuid.

Puuõnsused on puudega seotud mikroelupaikadest üks mitmekesisemaid. Hästi on tuntud asjaolu, et need pakuvad lindudele ja teistele selgroogsetele loomadele pesitsus- ja varjekohti ning ühtlasi ressursse nagu toit ja vesi. Lisaks on puuõõned aga elupaigaks eripärastele selgrootute, seene- ja bakterikooslustele ning neil on oma roll puistute toitaineringluses. Puuõõnte erinev kuju, tekkelugude ja suuruse mitmekesisus kujundab selle, kuidas eri liigid neid kasutavad: mitmed uuringud näitavad, et elurikkust toetab erinevate omadustega puuõõnte leidumine maastikes.

Käesolev väitekirj käsitleb suuri puuõõnsusi. Keskne väide on, et need erinevad väikestest puuõõntest mitme ökoloogilise näitaja poolest. Eeskätt on niisugusteks näitajateks esinemissagedus ja seda määravad faktorid puu, puistu ja maastiku tasemel, tekke ja hävimise dünaamika ning õõnsuste kasutamine loomade poolt. Viimati mainitud põhjusel väärivad suured puuõõned eraldi tähelepanu elurikkuse kaitsel. Seetõttu on ka praktiliselt oluline teada nende esinemissagedust nii looduslikes kui ka majandamisest mõjutatud oludes. Maa kasutuse pikaajaline planeerimine eeldab lisaks teadmisi puuõõnte kujunemise protsessi ja dünaamika kohta, et tagada nende järjepidev olemasolu.

Praktiliselt on suured puuõõned minu töös määratletud nende välisava laiuse põhjal, mis peab ületama 8–10 cm. Selliseid õõnsusi tekitavad puudes peamiselt üksnes puitu lagundavad seened või kõige suuremate kehämõõtmetega rähnid.

Suurte puuõõnsuste ökoloogilist eripära ei ole varem eraldi uuritud ja asjakohane info on hajutatud peamiselt metsapatoloogia, mükoloogia, arboristika ja loomaökoloogiliste uuringute vahel. Kuna suured õõnsused moodustavad ainult väikese osa kõigist puuõõnsustest ja õõnsuste täpseks mõõtmiseks tuleb kas nende juurde ronida või uuritavad puud langetada, siis on erineva suurusega õõnsusi enamasti käsitletud koos või keskendutud just väiksemate puuõõntele. Siit lähtub käesoleva uurimuse ülesehitus: koondada teemakohane informatsioon

kirjandusest ja teha seda täiendavaid väliuuringuid. Väitekirja sisuliseks eesmärgiks oli vastata järgnevatele küsimustele: 1) millised loomad, mis eesmärgil ja kui sageli suuri puuõõnsusi kasutavad; 2) kui palju suuri puuõõnsusi eri ökosüsteemides, maastikes ja bioomides leidub; 3) mis määrab suurte puuõõnsuste kujunemise ja dünaamika eripära. Eelneva põhjal sõnastatakse ka suurte puuõõnsuste majandamise põhimõtted elurikkuse kaitseks.

Teaduskirjanduse ülevaade (I) põhineb rohkem kui 400 publikatsioonil suurte õõnsuste hulga, tekke ja ökoloogia kohta kogu maailmas. Seda täiendavad väliuuringud (II–IV) tehti Euroopa sega- ja lehtmetsavööndi erinevates metsades: Eestis kolme tüüpi metsaökosüsteemide eri vanuseklassides ning Ukraina, Poola ja Austria loodus- ja põlismetsades. Kõigil neil aladel loendati suuri puuõõnsusi ja mõõdeti neid puudele ronides. See andis informatsiooni erinevate õõnsuste esinemissageduse, eri loendusviiside täpsuse ja (kahes piirkonnas 15 a jooksul korduvmõõtmisi tehes) ka suurte õõnte dünaamika kohta (II). Õõnsuste pikaajalist kasutamist selgroogsete loomade poolt uuriti automaatkaamerate abil Ukrainas 2018.–2023. aastal (III). Täpsemalt uuriti ainsa seal suurtes õõnsustes pesitseva liigi, kodukaku (*Strix aluco*) õõnekasutust võrdlevalt pesitsemiseks ja varjumiseks nii Ukraina kui ka Poola (Białowieża) andmetel (IV). Huvitava juhtumiuuringuna dokumenteeriti suurte õõnsuste ilmumist metsavööndi lõunaosa puistutesse Ukrainas seoses musträhni (*Dryocopus martius*) leviku laiennemisega (V).

Selgroogsete seas kipuvad väikesed loomad suuri õõnsusi sigimispaijana pigem vältima, sest need on kiskjatele ligipääsetavamad. Küll on suured puuõõned oluliseks sigimispaijaks suurematele loomadele, kes on sageli ka ohustatud (I, III). Lisaks on suured puuõõned ka olulised (spetsiifilise) toidu ja vee allikad ning nende silmapaistvus ja ligipääsetavus paljudele liikidele muudab need loomade käitumise seisukohalt olulisteks elupaigakomponentideks. Peamiselt teevad selgroogsed sinna lühikülastusi, mille iseloomu ja ajastust reguleerib oluliselt neid külastavate tippkiskjate käitumine. Ukraina õõnekaamerauuringutes tuvastati niisuguse tippkiskjana metsnugis (*Martes martes*), kes külastas õõnsusi keskmiselt kord kuus. Eeldatavasti oli see peamine põhjus, miks seal pesitses õõnsustes ainult kodukakk, kes potentsiaalselt on suuteline pesa nugise eest kaitsma (III). Selgrootute loomade jaoks toimivad suured puuõõned omaette väikeste ökosüsteemidena, mille maht oleneb esmaselt õõnsuse suuruselt, aga ka asukohast ja mikrokliimast (I).

Seniste uuringute põhjal leidub maailma metsades keskmiselt 3,3 suurt õõnsust hektaril (mediaantihedus) (I), mida saab võrrelda varasema hinnanguga kõigi õõnsuste kohta (16 õõnsust / ha). Samas kipuvad maapealsed loendused õõnsuste hulka üle hindama: näiteks Eestis moodustasid ainult 63% maast registreeritud rähniõõnsustest tegeliku (ronimisel tuvastatud) õõnsuse. Reaalselt selgroogsete jaoks kasutatavaid õõnsusi on veelgi vähem. Näiteks maapinnast vähemalt 2 m kõrgusel ja sügavusega 20–400 cm oli Euroopa metsades ainult 60% nendest, mis välisava mõõtmete ja siseõõne olemasolu põhjal suureks õõnsuseks kvalifitseerusid (II).

Suurte õõnsuste levik sõltub olulisel määral suurte lehtpuude hulgast maastikul. Vastavalt on tihedused looduslikult suuremad parasvöötmes ja väiksemad boreaalses vööndis. Kuna aga suured lehtpuud ei pruugi majandatud maastikes koonduda metsadesse (tulenevalt näiteks lühikestest raieringidest ja okaspuude eelistamisest), siis võivad ka suurte õõnsuste esinemissagedused olla isegi suuremad näiteks parkides ja teistes poolavatud ökosüsteemides (I).

Piirkondades, kus suured rähnid on sagedased, võib nende roll suurte õõnsuste tekitajana olla väga oluline. Näiteks Eesti metsades oli muusträhni rajatud >70% suurtest õõnsustest (II). Ukrainas kaasnes aga selle liigi levimisega õõnsuste hulga järsk suurenemine asustatud puistutes, nt ühel territooriumil rajati 10 õõnsust / km² seitsme aasta jooksul (V). Eri tüüpi õõnsuste mitmekesisus on samuti oluline, sest paljud loomad kasutavad erisuguseid õõnsusi erinevatel otstarvetel. Tüüpiliselt on kõige olulisemad sigimispaidad suurimates ja vanimates puudes, kuid teist tüüpi õõnsuste olemasolu on tähtis väljaspool sigimisaega (I, III, IV).

Keskne roll suurte puuõõnsuste dünaamikas on aga puidu lagunemise protsessidel. Tüüpiline õõnetekke on seotud kaugele arenenud südamemädanikuga puutüves, kuhu tekib välisava mõne suure oksa murdudes. Ka rähnid valivad õõnsuste rajamiseks südamemädanikuga puid. Üksnes kõduprotsesside tulemusel võtab suure õõnsuse väljakujunemine niisugusel moel vähemalt 50 aastat (I). Väitekirja üks keskseid tähelepanekuid seisneb selles, et kogu selle aja peavad puud püsima stabiilsena, mis seab suurte puuõõnsuste esinemisele looduses olulised mehaanilised piirangud. Kõige tõenäolisem on niisuguse õõne teke suurtes elusates puudes, kusjuures puude suured mõõtmed on seotud ka õõnte püsivuse ja sedakaudu suurema väärtusega elurikkusele (I, II). Ent noortes puistutes, kus suuri puid veel ei leidu, on väga olulised ka väiksemad õõnepuud (II).

Sega on suured, eri liikidele kasutatavad puuõõnsused juba looduslikult haruldased, aga majandatavates ökosüsteemides väheneb sobivate vanade puude hulk veelgi. Puuõõnsuste eripärase elurikkuse säilitamiseks tuleks maakasutust ja majandatavaid maastikke planeerida asjakohaseid erinevaid eesmärke ja piiranguid (nt inimeste ja nende vara ohutuse tagamine parkides) arvestades ning mitmes ajaperspektiivis (I). Lühiperspektiivis on esmane kaitsta suuri puid koos nendes juba olevate või tekkivate õõnsustega. Pikas perspektiivis on aga oluline hoida maastikel selliseid ökosüsteeme ja maakasutusvõtteid, mis võimaldaksid nii potentsiaalsete õõnepuude kui ka õõnetekke protsesside püsimist. Näiteks metsamaastikul tagab õõnsuste teket tulevikus säilikpuude jätmise praktika, kuid ainult juhul, kui metsades on raie-eelses puupõlvkonnas võimaldatud kasvada puuliikidel, kuhu tulevased õõnsused võiksid tekkida. Sellise planeerimise ajahorisont on elurikkuse kaitses üsna erakordne ning võib ületada sajandit. Asendusmeetmed, nagu pesakastid ja tehisoõned ei võimalda senistel andmetel looduslike õõnsuste kõiki funktsioone tagada ja neid on mõistlik rakendada üksnes konkreetse sihtotstarbega programmides.

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Yatsiuk, Y. & Viter, S. (2024) Black Woodpeckers recolonize south-eastern border of their European range. *Journal of Ornithology*, 165, 1097–1102. <https://doi.org/10.1007/s10336-024-02180-1>
Yatsiuk, Y., Löhmus, A. (2024) Habitat niche of the Crested Tit *Lophophanes cristatus* in central and peripheral parts of its range. *Journal of Ornithology*, 165, 591–602. <https://doi.org/10.1007/s10336-024-02152-5>

- Vlaschenko, A., Kravchenko, K., **Yatsiuk, Y.**, Hukov, V., Kramer-Schadt, S. & Radchuk, V. (2022). Bat Assemblages Are Shaped by Land Cover Types and Forest Age: A Case Study from Eastern Ukraine. *Forests*, 13(10), 1732. <https://doi.org/10.3390/f13101732>
- Vlaschenko, A., **Yatsiuk, Y.**, Hukov, V., Prylutska, A., Straka, T.M. & Kravchenko, K. (2021). Urban forest preserves local bat species diversity, but not forest dweller specialists—renewed study 65 years later (Kharkiv city, Ukraine). *Mammal Research*, 66(4), 615–626. <https://doi.org/10.1007/s13364-021-00580-9>
- Yatsiuk, Y.** & Wesołowski, T. (2020). Diversity and abundance of large tree holes used by Tawny Owls *Strix aluco* in lowland temperate forests. *Bird Study*, 67(3), 331–343. <https://doi.org/10.1080/00063657.2020.1869179>
- Balashov, I. & **Yatsiuk, Y.** (2017). The first record of a forest land snail *Macrogastra plicatula* in Central Ukraine (Stylommatophora, Clausiliidae). *Ruthenica*, 27(4), 167–170. [https://doi.org/10.35885/ruthenica.2017.27\(4\).4](https://doi.org/10.35885/ruthenica.2017.27(4).4)
- Yatsiuk, Y.** & Filatova, Y. (2016). Seasonal changes in Tawny owl (*Strix aluco*) diet in an oak forest in Eastern Ukraine. *Turkish Journal of Zoology*, 41, 130–137. <https://doi.org/10.3906/zoo-1509-43>
- Yatsyuk, Y.** (2011). Variability of the Tawny Owl (*Strix aluco*) winter and spring diet in a forest-steppe oak forest. *Zoologicheskii Zhurnal* 90(12), 1483–1491. (In Russian with English summary)

Other publications: datasets:

- Yatsiuk, Y.**, Brusentsova, N., Filatova, Y. (2023). Mammals in Tawny Owl (*Strix aluco*) pellets from Kharkiv Region, Ukraine. *Biodiversity Data Journal*, 11, e98772. <https://doi.org/10.3897/BDJ.11.e98772>

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- Yatsiuk, Y.**, Löhmus, A. Reduced habitat niche at a range border decreases adaptation potential to forest transformations in a pine forest specialist – Crested Tit (poster presentation). 21–25.08.2023. 14th Conference of the European Ornithologists' Union. Lund, Sweden.
- Yatsiuk, Y.** How distinct are large tree cavities as microhabitats for vertebrate animals? (oral presentation). 27–28.01.2023. PhD Student Conference of the Departments of Botany and Zoology 2023. Sangaste, Estonia.
- Yatsiuk, Y.** The role of large tree cavities for vertebrates (oral presentation). 06 May 2022. PhD Student Conference of the Departments of Botany and Zoology 2022. Cantervilla, Estonia.
- Yatsiuk Y.**, Wesołowski T. Diversity and abundance of large non-excavated tree holes in primeval and previously managed forests (oral presentation). 2–4 September 2019. Temperate and boreal primeval forests in the face of global change. Lviv, Ukraine.

Yatsiuk Y. The use of large non-excavated holes by tawny owls and other forest vertebrates in oak forest (poster presentation). 26–30 August 2019. 12th Conference of the European Ornithologists' Union. Cluj-Napoca, Romania.

Yatsiuk, Y. 10 years of monitoring a Tawny Owl *Strix aluco* population in oak forests of Eastern Ukraine (poster presentation). 26–30 September 2017. World Owl Conference 2017. Évora, Portugal.

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Yatsiuk, Y. (2024) The multi-functional use of large tree cavities by arboreal vertebrates in a temperate broadleaved forest of Eastern Europe. *Ecology and Evolution*, 14(11), e70521. <https://doi.org/10.1002/ece3.70521>
Yatsiuk, Y. & Viter, S. (2024) Black Woodpeckers recolonize south-eastern border of their European range. *Journal of Ornithology*, 165, 1097–1102. <https://doi.org/10.1007/s10336-024-02180-1>
Yatsiuk, Y., Lõhmus, A. (2024) Habitat niche of the Crested Tit *Lophophanes cristatus* in central and peripheral parts of its range. *Journal of Ornithology*, 165, 591–602. <https://doi.org/10.1007/s10336-024-02152-5>
Vlaschenko, A., Kravchenko, K., Yatsiuk, Y., Hukov, V., Kramer-Schadt, S. & Radchuk, V. (2022). Bat assemblages are shaped by land cover types and forest

age: A case study from Eastern Ukraine. *Forests*, 13(10), 1732.
<https://doi.org/10.3390/f13101732>

- Vlaschenko, A., **Yatsiuk, Y.**, Hukov, V., Prylutska, A., Straka, T.M. & Kravchenko, K. (2021). Urban forest preserves local bat species diversity, but not forest dweller specialists—renewed study 65 years later (Kharkiv city, Ukraine). *Mammal Research*, 66(4), 615–626.
<https://doi.org/10.1007/s13364-021-00580-9>
- Yatsiuk, Y.** & Wesołowski, T. (2020). Diversity and abundance of large tree holes used by Tawny Owls *Strix aluco* in lowland temperate forests. *Bird Study*, 67(3), 331–343. <https://doi.org/10.1080/00063657.2020.1869179>
- Balashov, I. & **Yatsiuk, Y.** (2017). The first record of a forest land snail *Macrogastra plicatula* in Central Ukraine (Stylommatophora, Clausiliidae). *Ruthenica*, 27(4), 167–170. [https://doi.org/10.35885/ruthenica.2017.27\(4\).4](https://doi.org/10.35885/ruthenica.2017.27(4).4)
- Yatsiuk, Y.** & Filatova, Y. (2016). Seasonal changes in Tawny owl (*Strix aluco*) diet in an oak forest in Eastern Ukraine. *Turkish Journal of Zoology*, 41, 130–137. <https://doi.org/10.3906/zoo-1509-43>
- Yatsyuk, Y.** (2011). Variability of the Tawny Owl (*Strix aluco*) winter and spring diet in a forest-steppe oak forest. *Zoologicheskii Zhurnal* 90(12), 1483–1491.

Andmeartiklid:

- Yatsiuk, Y.**, Brusentsova, N., Filatova, Y. (2023). Mammals in Tawny Owl (*Strix aluco*) pellets from Kharkiv Region, Ukraine. *Biodiversity Data Journal*, 11, e98772. <https://doi.org/10.3897/BDJ.11.e98772>

Konverentsiettekanded:

- Yatsiuk, Y.**, Lõhmus, A. Reduced habitat niche at a range border decreases adaptation potential to forest transformations in a pine forest specialist – Crested Tit (posterettekanne). 21–25.08.2023. 14th Conference of the European Ornithologists' Union. Lund, Sweden.
- Yatsiuk, Y.** How distinct are large tree cavities as microhabitats for vertebrate animals? (suuline ettekanne). 27.–28.01.2023. PhD Student Conference of the Departments of Botany and Zoology 2023. Sangaste, Estonia.
- Yatsiuk, Y.** The role of large tree cavities for vertebrates (oral presentation). 06 May 2022. PhD Student Conference of the Departments of Botany and Zoology 2022. Cantervilla, Estonia.
- Yatsiuk Y.**, Wesołowski T. Diversity and abundance of large non-excavated tree holes in primeval and previously managed forests (suuline ettekanne). 02.–04.9.2019. Temperate and boreal primeval forests in the face of global change. Lviv, Ukraine.
- Yatsiuk Y.** The use of large non-excavated holes by tawny owls and other forest vertebrates in oak forest (posterettekanne). 26.–30.08.2019. 12th Conference of the European Ornithologists' Union. Cluj-Napoca, Romania.

Yatsiuk, Y. 10 years of monitoring a Tawny Owl *Strix aluco* population in oak forests of Eastern Ukraine (posterettekanne). 26.–30.09.2017. World Owl Conference 2017. Évora, Portugal.

Yatsiuk Y. The availability and usage of tree hollows by Tawny owls in Oak forest of Eastern Ukraine (posterettekanne). 18.–22.08.2017. 11th Conference of the European Ornithologists' Union. Turku, Finland.

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Yatsiuk, Y., Novikov, A., Yatsiuk, I., Prylutskyi, O., Plyha, A., Vlaschenko, S., Leshchenko, Y. (2019). A book about the forest. "Pory Roku" in a partnership with IE Khalikov, R.K., 80 p. (ukrainakeelne populaarteaduslik raamat metsabioloogiast)

Yatsiuk, Y., Zemlyanskykh, I. (2015). Guardians of the night. Brovary, IE Bobko O.V., 48 p. (ukrainakeelne populaarteaduslik raamat kakulistest)

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