DEADWOOD AND WOOD-INHABITING FUNGI IN URBAN FORESTS

BIODIVERSITY CONSERVATION POTENTIAL IN CITIES

Aku Korhonen

DOCTORAL DISSERTATION

To be presented for public discussion with the permission of the Faculty of Biological and Environmental Sciences of the University of Helsinki, in Building C, hall K111 (Latokartanonkaari 5, Helsinki), on the 30th of March, 2022, at one o’clock in the afternoon.

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ABSTRACT

Forests and other natural environments retained in cities and their surroundings provide recreational opportunities for urban residents and refuges for urban wildlife. From the perspective of biodiversity conservation, urban forests offer interesting prospects for creating habitat structures, such as old and dead trees, that are scarce in surrounding rural forest landscapes. Yet, habitat fragmentation and urban environmental stressors may deteriorate habitat quality for species that are not well adapted to living in human-altered landscapes. In this thesis, I investigate how availability of deadwood, forest fragmentation and urbanization together play out to shape wood-inhabiting fungal diversity across a rural-urban gradient.

The study was conducted in spruce-dominated forests in southern Finland, mainly in the Helsinki metropolitan area and the surrounding region. This area provides an interesting setting for addressing the relationships between urbanization and wood-inhabiting biodiversity as the region is relatively urbanized but retains high forest cover where deadwood has been retained in variable quantities. The study consists of three interrelated parts. Firstly, urban forests were characterized based on forest stand measurements to outline the current and potential resource availability in urban forests and to evaluate these with respect to corresponding rural forest types. Secondly, fungal fruiting-body survey data was collected and analyzed to identify which landscape-level characteristics and processes are relevant in shaping diversity patterns of wood-inhabiting polypore fungi in urbanized environments. Thirdly, fungal communities of decaying spruce trunks were studied by means of DNA sequencing to identify possible substrate-scale mechanisms, by which wood-inhabiting fungi could be affected by urbanization.

The results showed that spruce-dominated urban forests in southern Finland differed from respective rural forests in terms of living and deadwood composition. Quantities of deadwood in typical urban forests were relatively low and close to the levels in production forests, but stands with high amounts of deadwood were also present in the urban forest landscape. Polypore species richness across a rural-urban gradient was driven primarily by local availability of deadwood and forest connectivity. Urbanization had a negligible role in explaining patterns of species occurrences and the overall species richness. However, the species richness of red-listed polypores was negatively associated with urbanization. Downed, intermediately decayed spruce trunks in urban forests were drier, had less epiphyte cover and hosted fewer red-listed fungal species than respective trunks in semi-natural rural forests. Differences in fungal community composition between spruce trunks in urban and semi-natural forests corresponded more with wood-microclimatic variability than with variability in epiphyte cover.

Overall, this thesis demonstrates that, despite some negative effects associated with urbanization, urban forests can still host diverse wood-inhabiting fungal assemblages, when deadwood resources are made available. However, if the conservation of threatened spruce-associated species is to be promoted in urban forests, it is necessary to retain adequately large intact forest areas to ensure habitat continuity and to buffer against urban environmental stressors.
ACKNOWLEDGEMENTS

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Viikin toimiston väki: Ikävöin naapurihuoneista kantautuvia ääniänne ja kohtaamisiamme käytävillä ja kahvihuoneessa!

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<table>
<thead>
<tr>
<th>Section</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>Results and discussion......................................................................</td>
<td>25</td>
</tr>
<tr>
<td>3.1</td>
<td>Urban forests along the naturalness continuum...............................</td>
<td>25</td>
</tr>
<tr>
<td>3.1.1</td>
<td>Urban forests are characterized by a distinctive combination of stand structural features</td>
<td>25</td>
</tr>
<tr>
<td>3.1.2</td>
<td>Urban spruce forests have low amounts of large coniferous deadwood</td>
<td>26</td>
</tr>
<tr>
<td>3.2</td>
<td>Effects of urbanization on wood-inhabiting fungi............................</td>
<td>27</td>
</tr>
<tr>
<td>3.2.1</td>
<td>Landscape scale patterns of fungal diversity</td>
<td>27</td>
</tr>
<tr>
<td>3.2.2</td>
<td>Urban effects on deadwood characteristics</td>
<td>28</td>
</tr>
<tr>
<td>3.2.3</td>
<td>Fungal winners in urban deadwood</td>
<td>31</td>
</tr>
<tr>
<td>3.3</td>
<td>Conclusions</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>Appendices</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>References</td>
<td>38</td>
</tr>
</tbody>
</table>

Original publications

Article I
Stand characteristics and dead wood in urban forests: Potential biodiversity hotspots in managed boreal landscapes

Article II
Urban forests host rich polypore assemblages in a Nordic metropolitan area

Article III
Landscape context and substrate characteristics shape fungal communities of dead spruce in urban and semi-natural forests
LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications:


The publications are referred to in the text by their roman numerals.

Table of contributions

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conceptualization</td>
<td>AK, JS, JK, LH</td>
<td>AK, RP, JS, LH</td>
<td>AK, LH</td>
</tr>
<tr>
<td>Methodology</td>
<td>AK, JS, LH, AI</td>
<td>AK, RP, JS, LH</td>
<td>AK, LH</td>
</tr>
<tr>
<td>Data collection</td>
<td>AK, JS, JK, LH</td>
<td>AK, RP</td>
<td>AK</td>
</tr>
<tr>
<td>Formal analysis</td>
<td>AK</td>
<td>AK</td>
<td>AK</td>
</tr>
<tr>
<td>Writing - Original Draft</td>
<td>AK</td>
<td>AK</td>
<td>AK</td>
</tr>
<tr>
<td>Writing - Review &amp; Editing</td>
<td>AK, JS, JK, AI, LH</td>
<td>AK, RP, JS, OM, AI, LH</td>
<td>AK, OM, JK, LH</td>
</tr>
</tbody>
</table>

AK = Aku Korhonen, AI = Auli Immonen, JK = Johan Kotze, JS = Juha Siitonen, LH = Leena Hamberg, OM = Otto Miettinen, RP = Reijo Penttilä

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1 INTRODUCTION

1.1 URBAN FORESTS

Urbanization, i.e., concentration of population in cities and associated expansion and intensification of built areas, often happens at the expense of forests and other natural areas. Yet, fragments of the original forest cover are usually retained within and at the outskirts of cities as urban green spaces and recreational areas. Secondary forests may also develop spontaneously or by active reforestation in vacant lots and former agricultural land. These forested urban areas with natural forest vegetation, collectively referred to as urban forests, are the focus of this thesis. Although urban forests cover only a small fraction of the total forest cover in the boreal Nordic region (ca. 1%, Gulsrud et al., 2018), urban forests can constitute significant habitat areas regionally. For instance, urban areas within 75 km from the city center of Helsinki (Finland) contain 246.7 km² (4.6%) of productive forest land (Appendix A).

The distinction between urban and non-urban forests is not clean-cut and better understood as a gradient involving proximity to urban centers and associated changes related to urbanization (Kowarik, 2005). Forests in urbanized landscapes become increasingly fragmented and isolated toward urban cores with increasing proportion of edge environment and increasing intensity of urban-associated environmental disturbances. On the other hand, the use, the ownership and management regimes of forests change from rural to urban areas as well. European urban forests are largely municipally owned and managed with emphasis to societal needs such as recreation, in contrast with more production-oriented forestry dominating in rural areas (Rydberg & Falck, 2000; Kowarik, 2005; Konijnendijk, 1999; Ottitsch & Krott, 2005; Gulsrud et al., 2018). In the Nordic countries, urban foresters and planners are usually trained as forestry professionals, and management regimes applied in urban forests are largely adapted from silvicultural systems originally designed for production forestry (Gundersen et al., 2005). However, larger urban centers, such as Stockholm (Barthel et al., 2005) and Helsinki (Saukkonen, 2011), have relatively long histories of distinctively urban forest management. Compared to production forestry, urban forest management tends to be less intensive and smaller in scale. Due to the lower incentive to harvest wood (Gundersen et al., 2005) and public’s preference for mature stands and trees (Gundersen & Frivold, 2008; Edwards et al., 2012), urban forests harbor more veteran trees than rural forests (Gulsrud et al., 2018). Small-scaled management regimes also provide opportunities for fine-tuned consideration of biodiversity values.

Along with other urban natural remnants such as meadows, shrublands, swamps, streams, ponds and coastal areas, urban forests provide valuable habitat areas that can maintain native biodiversity within cities. Access and exposure to nature is increasingly recognized as an important factor contributing to the health and well-being of urban residents (Taylor & Hochuli, 2015; Soga & Gaston, 2016).
1.2 EFFECTS OF URBANIZATION ON BIODIVERSITY

Urbanization is a major driver of habitat destruction and a significant threat to biodiversity globally (IPBES, 2019). In addition to biodiversity loss due to the reduction and fragmentation of habitat area, urbanization tends to cause net declines of species diversity and populations also in the remnant habitat. However, responses vary among taxa and depend on the spatial scale at which biodiversity is assessed (Faeth, Bang, & Saari, 2011; Piano et al., 2020). Urbanization changes the abiotic conditions in the retained habitat fragments, e.g., by increasing temperatures (Oke, 1973), nutrient deposition (Bettez & Groffman, 2013) and wear (Hamberg et al., 2008). As a result, habitat quality may deteriorate, which has cascading effects on the diversity and composition of the local biota (Grimm et al., 2008). These environmental stressors emanate from the urban matrix towards habitat interiors, and their effects are usually strongest near habitat edges (Matlack 1993a, 1993b; Hamberg et al., 2008; Noreika & Kotze, 2012).

Despite the net negative effects of urbanization, urban forests can still retain significant biodiversity values, such as populations of threatened species (Ives et al., 2016; Soanes et al., 2019). Encouraging examples from the study area of this thesis (Helsinki metropolitan area, Finland) include the rapid expansion of Siberian flying squirrel (Pteromys volans), assessed as vulnerable species in Finland, into the urbanized forest landscape (Lammi & Routasuo, 2019) and numerous reports of species-rich assemblages of wood-inhabiting polypore fungi existing in urban and recreational forests (Savola & Wikholm, 2005; Savola, 2012, 2015). Similarly, forested green space corridors of Greater Stockholm (Sweden) have provided refuge for some red-listed bird species that are declining in rural areas (Mörtberg & Wallentinus, 2000), and urban parks in Rome (Italy) were identified as hotspots of monumental trees hosting threatened saproxylic beetles (Carpaneto et al., 2010). Indeed, the value of urban natural areas should be assessed in relation to the surrounding rural habitats that may suffer from different forms of habitat degradation, such as intensive agricultural use (cf. Turrini & Knop, 2015). The value of urban forests for biodiversity conservation may be minor for cities surrounded by high amounts of relatively undisturbed forests, but it could be significant for cities surrounded by intensively used and ecologically impoverished landscapes (Kowarik, 2011).

In boreal Fennoscandia, intensively managed stands predominate over large parts of the productive forest land. Logging has led to dramatic reductions in the cover of natural old-growth forest and in the availability of deadwood. Compared to the estimated natural levels of deadwood (ca. 100 m³ ha⁻¹ in mesic spruce-dominated forests southern and middle boreal zones), average amounts of deadwood in managed forest landscapes (< 10 m³ ha⁻¹) have been reduced by more than 90% (Siitonen, 2001). Widespread reduction of available resources in this magnitude coupled with the fragmentation of the remaining natural-like forest area has greatly diminished the carrying capacity for wood-inhabiting species richness in Fennoscandia (Jonsson, Kryus, & Ranius, 2005). Therefore, the potential of urban forests in supplementing current biodiversity conservation efforts is certainly worth investigating (Lonsdale,
INTRODUCTION

Pautasso, & Holdenrieder, 2008; Svensson et al., 2019). In this regard, it is important to understand whether species of conservation concern are limited by the lack of suitable habitat that could be feasibly restored in urbanized areas (See Le Roux et al., 2014), or whether urbanization limits conservation opportunities regardless.

1.3 DEADWOOD AND WOOD-INHABITING FUNGI

In terms of biodiversity, the focus of this thesis is on fungi inhabiting deadwood. The term refers to all fungal species growing naturally on dead woody material, comprising a taxonomically and ecologically heterogeneous assemblage of species. In boreal forests, wood-decaying fungi play a significant role in ecosystem functioning by releasing carbon and nutrients locked in woody plant debris, and by creating dynamic microhabitats for other wildlife in the process (Lonsdale et al., 2008). In addition to wood-decomposing saprotrophs, decaying wood hosts saprobic fungi without lignocellulose degrading capabilities as well as pathogenic, parasitic, endophytic, mycorrhizal and lichenized species (Ottosson et al., 2015). In Article III, wood-inhabiting fungi were studied with a broad taxonomic range (kingdom Fungi) by using molecular methods of species detection and identification targeting DNA present in the deadwood. Article II focuses more restrictively on wood-inhabiting polyporoid fungi that were studied by surveying fruiting-bodies, i.e, the spore-producing reproductive structures. Polyporoid fungi, or polypores, represent a polyphyletic assemblage of non-boletoid Basidiomycota characterized by poroid hymenophores (Niemelä, 2016), which are easy to observe and identify. Wood-inhabiting polypores are often used as an indicator group of forest naturalness and conservation value (Nitare, 2000; Niemelä, 2016) and as a target group of biodiversity studies, especially in Fennoscandia (Junninen & Komonen, 2011).

The indicator value of polypores as biodiversity surrogates (see Halme, Holec, & Heilmann-Clausen, 2017) stems from their tight association with deadwood and, consequently, their sensitivity to factors affecting the availability and continuity of deadwood (Junninnen & Komonen, 2011, Lassauce et al., 2011). The ecological role of polypores as the primary decomposers of woody material implies that their diversity can have cascading effects on many biotic interactions and ecosystem functions, e.g., by affecting species successions in decaying wood, and the rates of carbon and nutrient cycling in the forest (Niemelä, Renvall, & Penttilä, 1995; Lindner et al., 2011; Dickie, Fukami, Wilkie, Allen, & Buchanan, 2012; Birkemoe, Jacobsen, Sverdrup-Thygeson, Biedermann, 2018). In the latest Red List assessment of Finnish species, over 40% of the assessed polypore species were red-listed, mostly due to deficient availability of deadwood, old trees and old forests (Kotiranta et al., 2019). Previous studies have indicated that maintaining red-listed polypore species may require deadwood volumes of 20–40 m³ ha⁻¹ at the stand scale (Penttilä et al., 2004; Hottola, Ovaskainen, & Hanski, 2009), and that this dependency may be further modulated by old forest connectivity (Nordén et al., 2013, 2018). However, it remains poorly understood how strictly these species are specialized to specific old-growth forest conditions, and to what extent they are able to use deadwood substrates in other habitat conditions (Kouki et al., 2001), such as human-altered and highly fragmented urban forests.
1.4 WOOD-INHABITING FUNGI UNDER URBANIZATION

In urbanized landscapes, potential habitat areas for wood-inhabiting fungi consists of a patchwork of discrete forest fragments of varying size and quality. While the most important factor explaining stand-scale diversity of wood-inhabiting fungi is the quantity and diversity of locally available deadwood (e.g., Hottola et al., 2009), colonization-extinction dynamics of species are also affected by larger-scale spatio-temporal aspects of deadwood resource availability (Hanski, 2005). Responses to habitat fragmentation can vary across species depending on their dispersal ability (Jönsson, Edman, Jonsson, 2008) and the degree of specialization in resource use (Nordén et al., 2013; Abrego et al., 2017; Moor et al., 2020). While these landscape-scale effects have been relatively well studied in terms of boreal wood-inhabiting fungi (e.g., Penttilä et al., 2006; Jönsson et al., 2008; Laaksonen et al., 2008; Stokland & Larsson, 2011; Nordén et al., 2018; Moor et al., 2020), studies considering environmental filters imposed by the quality of habitat matrix, such as urbanization, are still very few (see Meyer, Rusterholz, & Baur, 2021).

Changes in deadwood substrate quality in urbanized environments represent possible mechanisms that could make wood-inhabiting fungi sensitive to urbanization. Hypothesized alterations of wood characteristics include lower wood moisture due to edge effects (Murcia, 1995; Crockatt & Bebber, 2015; Meyer et al., 2021), as well as direct disturbance on deadwood substrates. Thus, urbanization may shift conditions in woody substrates in ways that benefit some species and hinder others. Old-forest specialist species, which tend to be sensitive to habitat fragmentation (e.g., Nordén et al., 2013) and edge effects (Siitonen, Lehtinen, & Siitonen, 2005; Ruete, Snäll, & Jönsson, 2016), could be expected to be the losers also in urban environments. Possible winners are likely to include species with relatively flexible habitat requirements and good dispersal abilities. Higher average temperatures in cities, could also benefit some species that are at the northern edge of their distribution.

Patterns of wood-inhabiting fungal species richness and composition provide a practical viewpoint for assessing ecological trends related to urbanization. The optimal research approach would be to analyze patterns of species occurrences species by species, but due to the inherent rarity of most polypore species (Berglund & Jonsson, 2003; Ylläsjärvi, Berglund, & Kuuluvainen, 2011), data limitations often restrict these analyses to a small fraction of observed species. More general ecological signals can still be traced from patterns of species richness, which represent stacked occurrence patterns of all species present in the landscape. In this thesis, both collective (stacked) species occurrence patterns as well as some individual species occurrence patterns have been analyzed. In addition to overall species richness patterns, more specific attention is given to the collective occurrence patterns of spruce-associated red-listed species to see if this species group is vulnerable to urbanization.
AIMS OF THIS STUDY

The general aim of this study was to gain insight into the potential of urban forests for preserving biodiversity in the boreal zone, with special focus on fungi inhabiting dead spruce. Firstly, I studied the structural features and deadwood abundance of forest stands to place urban forests along a naturalness continuum (Article I). Secondly, I studied whether urbanization affects wood-inhabiting polypore fungi beyond the general effects related to forest habitat connectivity and availability of deadwood (Article II). Thirdly, I studied how urbanization changes the characteristics of a deadwood substrate and how wood-inhabiting fungal communities respond to those changes (Article III). To address the aspect of biodiversity conservation potential in urban forests more specifically, I focused on spruce-associated, red-listed fungi. The conceptual framework of this thesis is summarized in Fig. 1 and the associated hypotheses in Table 1.

Figure 1  Conceptual framework of this study depicting the studied phenomena and their connections. Roman numerals indicate articles where each topic is addressed.
Table 1. *Study questions and hypotheses.*

<table>
<thead>
<tr>
<th>Art.</th>
<th>Questions</th>
<th>Hypotheses</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>How do urban forest compare with rural managed and protected forests in terms of forest stand characteristics?</td>
<td>Urban forests have more diverse tree species composition, more large-diameter trees and more deadwood than managed rural forests.</td>
</tr>
<tr>
<td></td>
<td>What are the characteristics of urban polypore hotspots? How do they compare with urban forest stands in general, and with protected rural forests?</td>
<td>Urban polypore hotspots are clearly distinct from random urban forests stands in terms of deadwood volume but not necessarily in terms of living stand structure.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Quantities of large-diameter deadwood in urban deadwood hotspots is comparable with protected rural forests.</td>
</tr>
<tr>
<td>II</td>
<td>Is polypore diversity affected by urbanization?</td>
<td>Urbanization has a distinct effect on polypores that cannot be explained by accounting for forest habitat connectivity and deadwood availability alone.</td>
</tr>
<tr>
<td></td>
<td>Which species (groups) benefit or suffer from urbanization?</td>
<td>Urbanization has a negative effect on red-listed spruce-associated polypores, which tend to be old-forest specialists.</td>
</tr>
<tr>
<td></td>
<td>Does urbanization affect fungal growth conditions in deadwood?</td>
<td>Deadwood in urban forests is more exposed to desiccation and temperature fluctuations than deadwood in continuous semi-natural forest landscapes.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Epiphyte cover on deadwood is reduced in urban forests which exacerbates wood desiccation and temperature fluctuations.</td>
</tr>
<tr>
<td>III</td>
<td>Are urban-associated environmental changes relevant in explaining fungal community composition in deadwood?</td>
<td>Fungal community composition reflects wood moisture and temperature conditions.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Red-listed spruce-associated fungi are adapted to stable old-forest conditions and are less prevalent in substrates with lower moisture and higher temperature variation.</td>
</tr>
</tbody>
</table>
2 MATERIAL AND METHODS

Three independent datasets were collected for this study. The first dataset, addressing forest stand structure and deadwood (Article I), was based on field-measurements of living and dead trees. The second dataset, focusing on polypore diversity (Article II), was collected by field inventory of coarse woody debris and polypore fruiting-bodies growing on deadwood. This data was appended with landscape variables acquired from GIS datasets. The third dataset, focusing on the relationships between wood-inhabiting fungi and the quality of deadwood (Article III), consisted of fungal community data acquired with molecular methods and associated field measurements of environmental variables. Key methods applied in data collection, processing and analysis are summarized in Table 2 with further overview in the following sections.

Table 2. Key methods applied in data collection, data processing and analyses.

<table>
<thead>
<tr>
<th>Purpose</th>
<th>Method</th>
<th>Art.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Collection of data on forest stand structure</td>
<td>Measurement of living and dead trees in sample plots</td>
<td>I</td>
</tr>
<tr>
<td>Computation of tree and stand volumes</td>
<td>Tree volume calculations based on taper curve and volume functions</td>
<td>I, II</td>
</tr>
<tr>
<td>Collection of data on polypore species occurrences</td>
<td>Survey of polypore fruiting-bodies and concurrent measurement of deadwood in inventory plots</td>
<td>II</td>
</tr>
<tr>
<td>Collection of data on wood-inhabiting fungal communities</td>
<td>Metabarcoding of fungal communities from wood samples</td>
<td>III</td>
</tr>
<tr>
<td>Testing differences in between forest categories</td>
<td>Generalized linear models</td>
<td>I</td>
</tr>
<tr>
<td>Analysis of polypore species richness in forest stands</td>
<td>Generalized additive models</td>
<td>II</td>
</tr>
<tr>
<td>Analysis of species niches</td>
<td>Joint species distribution models</td>
<td>II, III</td>
</tr>
<tr>
<td>Exploring associations between fungal community composition and environmental variables</td>
<td>Non-metric multidimensional scaling and environmental variable fitting</td>
<td>III</td>
</tr>
<tr>
<td>Analysis of causal linkages between the environment, tree trunk variables and wood-inhabiting fungi</td>
<td>Path analysis</td>
<td>III</td>
</tr>
</tbody>
</table>

2.1 STUDY AREA AND FOREST SITES

This study was conducted in the province of Southern Finland. Landscapes in the region range from rural to highly urbanized. The province covers only 10% of the country but contains over 40% of the Finnish population (StatFin, 2021). The largest urban conglomeration in the area is the Helsinki metropolitan area with a combined population of 1.2 million (StatFin, 2021). By European standards, the density of urban development in the Helsinki metropolitan area is relatively low (Kasanko et al., 2006).
Residential areas are mostly discontinuous and a lot of forested areas remain between built-up areas. In bioclimatic classification, southwestern parts of the study region and the southern coast belong to the hemiboreal zone which transitions into the southern boreal zone toward north and east (Ahti, Hämet-Ahti, & Jalas, 1968).

Study sites represented mature spruce-dominated forest stands with herb-rich to mesic forest vegetation, Norway spruce (*Picea abies* (L.) H. Karst.) as the dominant tree species, and the age of dominant trees at least 60 years. Norway spruce is the natural climax tree species in mesic upland sites and the dominant tree species in most of the urban and rural landscapes in the study area (Mäkisara, Katila, Peräsaari, & Tomppo, 2019). Urban forests, as they are defined in this study, represent similar vegetation types that occur in rural forest landscapes. Furthermore, urban forests in the boreal parts of the Nordic region are usually dominated by native tree species (Gundersen et al., 2005). Alien tree species, which can be major constituents of urban forests in more southern latitudes (Pregitzer et al., 2019; Kowarik et al., 2019), have very little foothold in the Nordic boreal zone (Chytrý et al., 2009; Kjær, Lobo, & Myking, 2014). Accordingly, the potential range of forest structural features is similar across urban and rural forest landscapes, with differences arising primarily from forest management history and variability in local abiotic environmental conditions.

Upon urbanization, habitat loss, fragmentation and transformation usually occur concurrently and their effects on ecosystems can be interdependent (Bartlett et al., 2016; Liu et al., 2016) and difficult to disentangle (Smith et al., 2009). A minimum requirement for solving this issue is explicit quantification of individual habitat factors that are significant in shaping biodiversity alongside urbanization (Beninde, Veith, & Hochkirch, 2015). In addition, separating the relative contributions of different factors necessitates finding independent gradients, which can be practically challenging as individual drivers are often intercorrelated (Fenoglio et al., 2021). To overcome this problem, sampling of the study sites was stratified among forest categories representing different levels of urbanization and management intensity (Fig. 2, Table 3).

Study sites in Article II were a subset of those in Article I (except for two new random urban sites), and sites in Article III were a subset of those in Article II.
**Figure 2** Sampling was distributed across gradients of urbanization and management intensity by targeting forest sites across categories representing different landscape settings (urban and non-urban) and management levels. The ellipses depict the presumed range of variation in the degree of urbanization and management intensity between forests in each category.

**Table 3.** Sampling intensity across forests categories.

<table>
<thead>
<tr>
<th>Art.</th>
<th>Forest category</th>
<th>Number of study sites</th>
<th>Number of surveyed deadwood units</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>Random urban</td>
<td>31</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Valuable urban</td>
<td>23</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Random production</td>
<td>20</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Valuable production</td>
<td>15</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Semi-natural</td>
<td>10</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td><strong>99</strong></td>
<td>-</td>
</tr>
<tr>
<td>II</td>
<td>Urban</td>
<td>41</td>
<td>741</td>
</tr>
<tr>
<td></td>
<td>Production</td>
<td>31</td>
<td>682</td>
</tr>
<tr>
<td></td>
<td>Semi-natural</td>
<td>9</td>
<td>594</td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td><strong>81</strong></td>
<td><strong>2017</strong></td>
</tr>
<tr>
<td>III</td>
<td>Urban</td>
<td>24</td>
<td>66</td>
</tr>
<tr>
<td></td>
<td>Semi-natural</td>
<td>8</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td><strong>32</strong></td>
<td><strong>90</strong></td>
</tr>
</tbody>
</table>
2.2 MEASUREMENT OF FOREST STAND CHARACTERISTICS

Forest stand characteristics (Article I), i.e., quantities of living and dead trees in different size and quality classes, were measured by using 0.2 ha sample plots (Fig. 3), following a system used by Siitonen, Hottola and Immonen (2009). A plot area of 0.2 ha was considered adequate for a representative sampling of the stand (at least 100 measured living trees) and small enough to fit within most forest stands which could be less than 0.5 ha in urban areas. Living trees with diameter $\geq 5$ cm at breast height (1.3 m) were measured. Dead trees with diameter $\geq 10$ cm and other deadwood objects with basal diameter $\geq 10$ cm and length $\geq 1.3$ m were measured. The logging history of the stand was assessed by measuring cut stumps $< 1.3$ m in height but with diameter $\geq 10$ cm at cut surface. Both living trees and deadwood objects were identified to species. Deadwood objects were further assigned to decay and quality classes following the system applied in the Finnish National Forest Inventory (Table 4; Renvall, 1995; Siitonen et al., 2009).

Figure 3  Spatial scales of data collection within and around a study site. The aerial view shows one of the study sites in Maunula, Helsinki. Forest stand characteristics studied in Article I were measured on a 0.2 ha plot, consisting of five connected 20 $\times$ 20 m squares pictured in blue. For Article II, coarse woody debris and polypores were inventoried within a study plot (ca. 1 ha) pictured in yellow, encompassing the whole forest stand. Local habitat connectivity of the forest stand was quantified by calculating the proportion of mature ($\geq 60$ y old) forest within 200 m radius, depicted in pink. The degree of urbanization around the forest stand was quantified by the density of resident human population. The value was extracted from population grid data with 1 $\times$ 1 km cell resolution (in white). Downed spruce trunks, studied in Article III (pictured with orange $\pi$-symbols) were situated within the polypore inventory area or its immediate surroundings. One to four trunks were selected from one site depending on the availability of suitable trunks.
Table 4. Quality and decay classification of deadwood objects and associated measurements.

<table>
<thead>
<tr>
<th>Quality class</th>
<th>Measurements</th>
</tr>
</thead>
<tbody>
<tr>
<td>Entire dead standing trees</td>
<td>diameter at breast height, 1.3 m (DBH)</td>
</tr>
<tr>
<td>Broken snags with ≥ 1/3 of the upper part of the stem broken off, height ≥ 1.3 m</td>
<td>DBH, height</td>
</tr>
<tr>
<td>Fallen tops</td>
<td>diameter at base, height</td>
</tr>
<tr>
<td>Uprooted trees</td>
<td>DBH</td>
</tr>
<tr>
<td>Broken logs</td>
<td>DBH</td>
</tr>
<tr>
<td>Cut stumps</td>
<td>diameter at cut surface, height</td>
</tr>
<tr>
<td>Cut bolts</td>
<td>diameter at base, height</td>
</tr>
<tr>
<td>Logging-residue tops</td>
<td>diameter at base, height</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Decay class</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>hard, a knife penetrates by pushing only a few mm into the wood</td>
</tr>
<tr>
<td>2</td>
<td>relatively hard, knife penetrates 1–2 cm</td>
</tr>
<tr>
<td>3</td>
<td>relatively soft, knife penetrates 3–5 cm</td>
</tr>
<tr>
<td>4</td>
<td>soft throughout</td>
</tr>
<tr>
<td>5</td>
<td>very soft, can be moulded by hand</td>
</tr>
</tbody>
</table>

2.3 VOLUME CALCULATIONS FOR LIVING TREES AND DEADWOOD

Due to the practical difficulty of getting reliable measurements of tree height in the field, only diameter at breast height (1.3 m) was measured for entire trees (Table 4). The missing tree heights, required for volume calculations, were instead estimated from previously collected sample tree data. This data, collected earlier from this study region, consisted of complete measurements of trees of different species and sizes from similar site types. Volumes of both living trees (Article I) and deadwood (Articles I–II) were calculated by KPL program (Heinonen, 1994) with the taper curve and volume functions of Laasasenaho (1982) using the information from sample tree data.

2.4 POLYPORE FRUITING-BODY INVENTORIES

The diversity of wood-inhabiting fungal communities at the scales of forest stands and individual deadwood units was studied in Article II by inventorying fruiting-bodies of spruce-associated polypore fungi. Surveys were conducted following a protocol applied in the inventories for the Forest Biodiversity Program for Southern Finland (METSO) that includes simultaneous measurement of surveyed deadwood. The dataset analyzed in Article II was collated from earlier METSO inventories (years 2009–2015; 28 sites, 1010 deadwood units) in rural forests and from new inventories (years 2018–2019; 53 sites, 1007 deadwood units) in urban and rural forests. Inventory
plots were delimited according to the natural boundaries of the forest stand (Fig. 3), and their sizes varied from 0.2 ha to 4.9 ha (mean 1.2 ha). In this study, the survey of polypore fruiting bodies was limited to coarse woody debris (Ø ≥ 15 cm) of spruce in decay classes 2, 3 and 4 (Table 4). Deadwood in the earliest (decay class 1) and the last (decay class 5) stages of decay rarely host polypore fruiting-bodies and were not included in the survey. Inventories were done once in each stand between September and November.

2.5 MOLECULAR ANALYSIS OF FUNGAL COMMUNITIES

To gain insight into the wood-inhabiting fungal communities residing as vegetative states inside decaying spruce trunk, fungi were identified with DNA metabarcoding from wood samples (Article III). Detection of fungi was based on PCR amplification and massively parallel sequencing of the Internal Transcribed Spacer 2 (ITS2) barcode region from DNA extracted from wood samples. ITS region of the nuclear rDNA has relatively good taxonomic resolution power with short, < 700 read lengths (Tedersoo et al., 2015), and it is commonly used as a barcode marker in metabarcoding studies of wood-inhabiting fungi (e.g., Ottosson et al., 2015; Mäkipää et al., 2017). Curated sequence databases, such as UNITE (Abarenkov et al., 2010), have relatively good coverage for North European fungal diversity and enable the mapping of recovered ITS2 sequence clusters to taxonomic groups, i.e., species or higher taxa. In practice, ITS2 region was amplified by using primers gITS7 (Ihrmark et al., 2012) and ITS4 (White et al., 1990), and the fragments were sequenced with Illumina MiSeq v3 2 × 300 bp paired-end system.

Fungal communities were analyzed from four wood samples from each trunk (Fig. 4) yielding four community samples per tree. After passing through quality filtering steps (described in Article III) ITS2 sequence data were grouped into operational taxonomic units (OTUs) which represent hypothesized species. A single-linkage clustering approach (Swarm v2; Mahé et al., 2015) was applied to accommodate different ranges of intraspecific ITS2 sequence variation from species to species (Nilsson et al., 2008, 2019). Initial clustering was done with high-resolution settings which retain much intraspecific sequence variation as separate OTUs. These raw OTUs were then identified to taxonomic groups. Raw OTUs were further post-clustered based on taxonomic identity or sequence similarity depending on how precisely and reliably OTUs had been identified. The principle followed in post-clustering is described in detail in the supplements of Article III.
2.6 PROPERTIES OF DECAYING SPRUCE TRUNKS

Wood-inhabiting fungi experience the external environment primarily through the properties of the woody substrate that they inhabit. For instance, moisture and temperature of the wood are sensitive to the external environment, and both variables are also relevant for biological activity in the wood (Zabel & Morrell, 2020). However, moisture and temperature conditions inside the woody substrate are also modulated by structural characteristics of the deadwood unit, such as diameter (or volume), stage of decay and ground contact, as well as epiphytic vegetation growing on the wood (Pouska, Macek, & Zíbarová, 2016; Chang et al., 2019). To gain a more focused view on the effects of urbanization on the properties of the deadwood, Article III focused on a specific substrate type: downed spruce trunks within a limited range of diameters (ca. 20–40 cm) and decay stages (primarily decay class 3; Table 4).

To investigate how the internal conditions of the wood were related to the external environment, while accounting for the structural characteristics of the substrate, properties of the downed spruce trunks were measured following the scheme depicted
in Fig. 4 B. Spruce trunks were selected from forest stands in two different landscape settings: urban and (rural) semi-natural. Detailed variable definitions and methods used for measurements are explained in the methods section of Article III.

2.7 STATISTICAL ANALYSES

2.7.1 COMPARISON OF FOREST STAND CHARACTERISTICS

In Article I, differences in stand characteristics between forest categories were tested using generalized linear models. Forest category was included in the models as the focal explanatory variable to test whether random urban forests (used as the reference level) differed significantly from other forest categories. Because site fertility classes and latitudinal location could not be fully balanced among all forest categories, vegetation type (indicative of soil fertility) and latitude (indicative of bioclimatic setting) were also included in the models as controlling variables (Fig. 5 A).

2.7.2 POLYPORE SPECIES RICHNESS IN FOREST STANDS AND OCCUPANCY OF DEADWOOD UNITS

In Article II, polypore species richness in forest stands was analyzed with generalized additive models (Wood, 2017). Polypore species richness was analyzed in terms of 1) total number of polypore species and 2) number of red-listed species (Fig. 5 B). The purpose of the analysis was to test whether urbanization (measured as human population density) had significant role in explaining polypore species richness after accounting for other relevant habitat variables. Based on earlier knowledge on the ecology of boreal polypores (e.g., Junninen & Komonen, 2011 and references therein), local volume of deadwood and habitat connectivity (proportion of mature forest within 200 m radius) were expected to be important predictors of polypore species richness. Furthermore, their effects were presumed to be interconnected so that the effect of deadwood volume would be partly dependent on the surrounding habitat structure. For instance, increasing deadwood volume in a forest stand surrounded by large amount of similar habitat was expected to increase local species richness more than similar resource input in an isolated forest stand. This effect was expected, especially for specialized and red-listed species, because species colonizations and extinctions in the focal stand are affected by the resource abundance and species pools of the near surrounding landscape (e.g., Jönsson et al. 2008; Moor et al., 2020).

In practice, this interaction was included in the models as a single multivariate smooth term (tensor product; Wood, 2006) capturing the joint effect of deadwood volume and local habitat connectivity (Fig. 5 B). Human population density (log-transformed) was included in the models as simple linear term. For total species richness, cumulative heat sum was added as a simple linear term to control for differences in survey timing and interannual variation in weather condition. For red-listed species richness, heat sum was not significant and was omitted. Instead, forest naturalness (true if site was semi-natural, false otherwise) was included as a control variable to account for greater representation of red-listed species in semi-natural forests due to longer habitat continuity (Lindblad, 1998; Penttilä et al. 2004; Berglund
et al., 2011; Nordén et al., 2018). Area of the polypore inventory plot was included as an offsetting variable to account for variable plot sizes.

The models described above were further extended to individual deadwood units to analyze how urbanization affected polypore occupancy at the substrate level (Fig. 5 C). Models included the same explanatory variables as described above with additional variables (decay class and volume) describing the quality of deadwood units. Models were estimated for the presence–absence of fruiting-bodies. First the model was estimated considering presence–absence of any polypore species (total occupancy), and secondly, focusing on red-listed species only.

When modeling the number of red-listed species at the stand scale, only species of the latest Finnish Rest list assessment (Kotiranta et al., 2019) were considered (see Article II). A more inclusive circumscription of red-listed species was used for substrate-scale occupancy model to ensure adequate number of positive observations. For this purpose, Red lists of neighboring regions (Estonia, Norway, Sweden, Leningrad region of Russia) were considered as well (See Appendix B). The same broader circumscription of red-listed species was applied in Article III.

2.7.3 EXPLORING ASSOCIATIONS BETWEEN FUNGAL COMMUNITY COMPOSITION AND ENVIRONMENTAL VARIABLES AT THE SUBSTRATE-LEVEL

Associations between fungal community composition in decaying spruce trunks and trunk properties (Article III) were analyzed using ordination. Non-metric multidimensional scaling (NMDS) was used to arrange sampling units (tree trunks) across a multidimensional space based on species composition of fungal communities (OTU presence–absence). Measured environmental variables and properties of the tree trunks were then fitted onto this ordination to analyze how the ordering of fungal community composition corresponded with the environmental gradients represented by the measured variables.

2.7.4 TESTING LINKAGES BETWEEN LANDSCAPE SETTING, TREE TRUNK VARIABLES AND THE OCCURRENCE OF RED-LISTED SPECIES IN TREE TRUNKS

In Article III, hypothesized causal linkages between tree trunk characteristics, the external environment and wood-inhabiting fungi were tested and refined with path analysis. The purpose of this analysis was to pinpoint the most plausible mechanisms by which the effects of urbanization are mediated to wood-inhabiting fungi. In the path analysis, hypothesized pairwise linkages between variables (Fig. 6) were tested. Furthermore, conditional independence of the variables was checked by tests of directed separation (Shipley, 2000), i.e., whether other linkages than those defined in the hypothesized path diagram were implied by the data.
A
Generalized linear model for stand variables (Article I)

- Forest category
- Vegetation type
- Latitude

B
Polypore species richness in a forest stand

- Offset [Inventory area]
- Heat sum or Naturalness
- Human population density
te[DW volume × Forest cover]

Generalized additive model for polypore species richness in forest stands (Article II)

C
Occupancy of DW unit

- Decay class of the DW unit
- Volume of the DW unit
- Human population density
- te[DW volume × Forest cover]
- Heat sum or Naturalness

Generalized additive mixed model for fruiting-body occupancy of DW units (Appendix B)

D
Joint species distribution model for fruiting-body occurrences on DW units (Article II)

- Presence-absence of a polypore species on a DW unit
- Decay class of the DW unit
- Volume of the DW unit
- Interaction
- Stand DW volume
- Forest cover
- Naturalness
- Heat sum
- Human population density

Random effects:
- Site
- DW unit

E
Joint species distribution model for DNA level species abundances in wood samples from decaying spruce trunks (Article III)

- ITS2 sequence count of a fungal species
- Decay class
- Epiphyte cover
- Naturalness
- Sequencing depth

Random effects:
- Site
- Tree trunk
- Sample
MATERIAL AND METHODS

Figure 5  (On previous page) Summary of model structures. Response variables are presented on the left side and explanatory variables on the right side of the arrows. DW = deadwood. Forest cover = proportion of mature forest around inventory plot. te() = tensor product smooth function. In the additive models (B and C), heat sum was used as a control variable for modelling total species richness and the overall occupancy of DW units, whereas forest naturalness was used for respective models focusing on red-listed species. See the referenced articles for detailed model specifications.

Figure 6  Hypothesized causal linkages between the landscape setting, properties of the tree trunk and the fungal community. Wood moisture and temperature conditions were hypothesized to be less stable in urban forests but also dependent on the properties of the tree trunk. Red-listed fungi were expected to be more prevalent in semi-natural forests, but potential associations with tree trunk characteristics (depicted with a dashed arrow) were investigated exploratively.

2.7.5 HABITAT MODELLING WITH JOINT SPECIES DISTRIBUTION MODELS

Joint species distribution models were estimated in order to understand how individual species respond to urbanization (Article II) and conditions in the woody substrate (Article III). Models were estimated with Hierarchical Modelling of Species Communities (HMSC). With this analysis approach, it was possible to account for the nested sampling design (sites > deadwood units > DNA samples).

In Article II, joint species distribution modelling was used for assessing the importance of urbanization (measured as human population density) in explaining polypore species occurrences. This was done by fitting two model variants: one with human population density (Fig. 5 D) and the other without it. The predictive powers of these model variants were then compared to see whether accounting for urbanization provided any improvement in predicting polypore species occurrences. In Article III, the model was used for inferring fungal species niches in relation to substrate characteristics (Fig. 5 E).
3 RESULTS AND DISCUSSION

3.1 URBAN FORESTS ALONG THE NATURALNESS CONTINUUM

3.1.1 URBAN FORESTS ARE CHARACTERIZED BY A DISTINCTIVE COMBINATION OF STAND STRUCTURAL FEATURES

In Article I, stand characteristics were compared across urban and rural forest categories representing different management levels of the same spruce-dominated forest type to map the position of urban forests in relation to rural commercially managed and natural-like forests. The results showed that urban forests featured a distinctive combination of stand characteristics. Urban stands were characterized by large size of the dominant trees (spruces, *Picea abies*), abundance of large broadleaf trees (mostly birches, *Betula* spp.) and relatively high diversity of the living stand. High stand diversity in urban forests reflected the variety of tree species present in the stands as well as the wide range of tree sizes. Overall, urban forests were most clearly distinguished from production forests while protected forests (i.e., semi-natural forests and former production forests) were structurally closer to urban forests (Fig. 7A).

![Figure 7](image)

**Figure 7** Latent variable ordination of (A) living stand and (B) deadwood characteristics. Points represent centroids for sites in each forest category, and they are surrounded by corresponding 95% standard error confidence ellipses. Arrows depict the direction and strength of correlation between analyzed stand variables and the ordination plane. The depicted ordinations were produced with data from Article I and methods described in Appendix C.

The characteristics of urban forests reflect the reduced intensity of forest management regimes as well as urban environmental conditions. Mature stands with large trees are generally preferred by the public (Edwards *et al.*, 2012), and accordingly, urban forestry in the Nordic region has been shifting away from conventional clearcutting systems towards more sparing harvesting (Gundersen *et al.*, 2005). In part, the abundance of large-diameter trees may also be explained by increased tree growth rates enabled by urban heat, nutrient loading and reduced light.
RESULTS AND DISCUSSION

competition near edges (O’Brien, Ettinger, & HilleRisLambers, 2012; Pretzsch et al. 2017). The abundance of broadleaf tree admixture may as well be actively favored in urban spruce-dominated stands to increase visual and biological diversity, but broadleaf trees are also promoted by the absence of large browsing animals such as moose (*Alces alces*; Olsson et al., 2011) and by increased soil fertility (Hamberg et al., 2009).

The abundance of broadleaf tree species was especially evident in the small-diameter class of trees, where the proliferation of rowans (*Sorbus aucuparia*) has sometimes been considered a nuisance (Hamberg et al., 2009). Reciprocally, small-diameter spruce trees were relatively scarce in urban stands. Similar patterns have also been reported in earlier studies focusing on tree saplings in urban spruce-dominated forests, where edge effects and wear from intense recreational use have been suggested as possible causes for poor regeneration of conifers (Lehvävirta & Rita, 2002; Hauru, Niemi, & Lehvävirta, 2012; Lehvävirta et al., 2014). Accordingly, shortage of young spruce trees was not as evident in valuable urban forests that were often situated in less densely populated areas than randomly sampled urban stands (Fig. 8 A).

![Logging intensity in random and valuable urban forests in relation to resident population density (A) and correlations between logging intensity and deadwood volume (B–D). Data for panel A is derived from Article I and II, and data for panels B–D from Article I. Some sites with exceptionally high values in deadwood volume are left outside of the plotted range in panels C–D.

3.1.2 URBAN SPRUCE FORESTS HAVE LOW AMOUNTS OF LARGE CONIFEROUS DEADWOOD

Volumes of deadwood in urban forests were overall larger than those in production forests, but the accumulation of deadwood had been clearly restricted by active removal of felled trees. This was especially evident in the quantities of large-diameter dead spruce (Fig. 8 B) which is the most abundant type of deadwood in natural spruce-dominated stands (Siitonen et al., 2000). As a result, the deadwood profile of random urban forests was closer to production forests than rural protected forests (Fig. 7 B).

Broadleaf deadwood was less associated with management intensity than coniferous deadwood (Fig. 8 B–C), and volumes of broadleaf deadwood in urban
forests did not differ significantly from those in protected rural forests. In conifer-dominated forests in southern Finland, the volumes of broadleaf deadwood are, however, naturally modest (Siitonen et al., 2000). In urbanized settings, even conifer-dominated forests may still provide opportunities for the accumulation of rich reserves of broadleaf deadwood due to the abundance of short-lived ruderal trees such as rowan and goat willow (Salix caprea) (Faliński, 1998; Zerbe, 2001). Deadwood produced by these species is relatively small-sized (Hämäläinen, Tahvanainen, & Junninen, 2018), so it may be perceived as less of an obstruction and safety hazard than deadwood produced by taller canopy trees.

Valuable urban forests, representing urban deadwood hotspots in the Helsinki metropolitan area, were comparable with rural protected forests in deadwood abundance (Fig. 7 B). Compared to random urban forests, these hotspots had accumulated exceptionally high quantities of dead spruce (Fig. 8 B). Evidently, more liberal retention of deadwood in these sites was related to the fact that they were dispersed further into the peri-urban regions than random urban forests (Fig. 8 A). Indeed, more intensive management can be expected near dense human population (cf. Hedblom & Söderström, 2008). However, in the Helsinki metropolitan area, valuable urban stands were not entirely excluded from densely populated areas, and management intensity across these sites was consistently low regardless of the degree of urbanization (Fig. 8 A).

### 3.2 EFFECTS OF URBANIZATION ON WOOD-INHABITING FUNGI

#### 3.2.1 LANDSCAPE SCALE PATTERNS OF FUNGAL DIVERSITY

After accounting for other habitat variability, i.e., abundance of deadwood and forest habitat connectivity, the effects of urbanization on spruce-associated polypore fungi were resolved mainly as negligible or negative (Article II). Urbanization had a marginally significant negative effect on species richness of red-listed polypore species while total species richness was not significantly affected. However, it should be noted that small changes in species occurrence frequencies are more easily manifested at the stand scale for rare species, which red-listed polypores are, even when the underlying process is affecting a broader range of species. Indeed, a more general negative effect of urbanization was suggested by a slight but significant reduction in the overall occurrence of polypore fruiting-bodies on deadwood (Appendix B). Significant species-specific responses to urbanization were resolved only for a few species. Notably, negatively responding species included *Fomitopsis pinicola* and *Trichaptum abietinum* that are few of the most abundant and common polypore species across the whole study region. Thus, urbanization appears to have negative consequences even for species with relatively loose habitat requirements.

To further understand fungal diversity patterns across urbanized landscapes, it is important to acknowledge that urbanization is inherently coupled with simultaneous fragmentation of forest habitat area (Liu et al., 2016). The expected outcomes of these processes, individually and synergistically, are illustrated in Fig. 9 for different scenarios representing plausible combinations of human population density and forest
landscape integrity. Although total polypore species richness is little affected by urbanization in the habitat matrix, species richness in urban forests can be expected to decline due to forest fragmentation alone (Nordén et al., 2013; Ramiadantsoa, Hanski, & Ovaskainen, 2018). The decline in species richness appears to be strongest already at low to moderate levels of forest fragmentation, after which, the remaining set of species is relatively robust to further forest fragmentation. For red-listed species, the negative effects of forest fragmentation and urbanization are compounded, resulting in low expected occurrence probability (species richness < 1 per ha) in highly urbanized landscapes, even for stands with large amounts of deadwood.

Another viewpoint to fungal diversity in urban deadwood was provided by the DNA based study on large intermediately decayed spruce trunks (Article III). Comparison of fungal communities in this substrate type between urban and semi-natural settings showed that most of the analyzed species, were relatively less abundant in samples from urban forests. Therefore, community dominance in urban spruce trunks seemed to be concentrated on a narrower and slightly shifted set of fungal species, as compared to similar substrates in semi-natural forests. Reduced abundance of red-listed species, suggested by fruiting-body data (Fig. 9), was also evident in DNA level analyses (Fig. 10 A). However, relative contributions of urban-associated changes in substrate quality (e.g. wood microclimate) and landscape-level processes (See the urban–semi-natural gradient in Fig. 10 A) could not be disentangled with regard to the DNA-level data.

Taken together, the results indicate that urbanization leads to simplification of species assemblages inhabiting decaying spruce. While this process appears to be driven largely by habitat fragmentation (Fig. 9), urbanization in the landscape matrix has a further aggravating effect especially for red-listed species. Similar trends have also been reported from a temperate forest setting, where species richness of early-colonizing fungal communities in fine woody debris of oak was found to decrease along a rural-urban gradient (Meyer et al., 2021).

### 3.2.2 URBAN EFFECTS ON DEADWOOD CHARACTERISTICS

Although diversity patterns of wood-inhabiting fungi along a rural–urban gradient can be largely explained by accounting for deadwood resource availability and forest fragmentation, results from Article II showed that some unexplained variation could still be captured by accounting for human population density. These residual effects were assumed to involve urban-associated phenomena such as urban heat island (Oke, 1973), intensification of microclimatic edge effects (Murcia, 1995; Harper et al., 2005) and direct human disturbances from recreational activity. Due to these factors, deadwood in urbanized environments was hypothesized to be more susceptible to desiccation, temperature instability, and erosion of epiphyte cover on wood surface, and thus representing altered habitat conditions for wood-inhabiting fungi (see e.g., Boddy & Heilmann-Clausen, 2008; Crockatt & Bebber, 2015; Pouska et al., 2016; Chang et al., 2019). In Article III, these hypotheses (Table 1, Fig. 6) were tested and further explored with data from intermediately decayed spruce trunks in urban and semi-natural forest environments.
Occupancy of deadwood units

Species richness in forest stands

Human population density

Proportion of mature forest within 200 m

Any polypore species

Red-listed species

Total species richness

Red-listed species

Proportion of mature forest within 200 m

1 2 3

0.90 0.95 0.94

0.92 0.93 0.94

0.90 0.95 0.94

0.90 0.95 0.94

0.30 0.35 0.40

0.20 0.25 0.30

0.15 0.20 0.25

0.05 0.10 0.15

20 24 28

20 24 28

20 24 28

20 24 28

2 2 2

2 2 2
RESULTS AND DISCUSSION

Figure 9  (On previous page) Effects of urbanization and forest habitat loss on polypore species richness and occupancy on deadwood units. Model predictions ± SE represent expected polypore fruiting-body occupancy on individual deadwood units and species richness of in 1 ha forest patches. For all predictions, the environmental setting was assumed to be a deadwood rich (40 m³ ha⁻¹) but not pristine (e.g., not semi-natural) forest stand. For the occupancy predictions, deadwood unit was assumed to be a 1 m³ spruce log in decay class 3. On the top row, human population density is changed while keeping forest fragmentation at an intermediate level (proportion of mature forest at 50%). On the middle row, the surrounding forest landscape is changed while keeping urbanization at an intermediate level (human population density at 500 per km²). On the bottom row, the scenarios of the two upper rows are combined, illustrating the expected change under simultaneously increasing urbanization and forest fragmentation from the least altered (1) to the most urbanized and fragmented forest landscape (3). Other controlling variables included in the models were set to mean values. Predictions of species richness are based on generalized additive models from Article II and predictions of occupancy are based on generalized additive mixed models estimated with data from Article II (see Appendix B). Note that red-listed species in the stand-scale model (right panel) encompass the Finnish red-list only whereas the substrate-scale occupancy model (left panel) includes additional species from the red-lists of neighboring regions: Estonia, Norway, Sweden and Leningrad region of Russia.

Results from Article III confirmed that urban spruce trunks were drier, had less epiphyte cover, and hosted fewer red-listed species than similar trunks in semi-natural forests (Fig. 10 A). However, significant linkages between epiphyte cover and wood temperature variability and moisture were not identified. Species turnover in fungal community composition between urban and semi-natural spruce trunks was aligned with a wood-microclimatic gradient but not with epiphyte cover (Fig. 10 B). Thus, both epiphyte cover and the measured aspects of wood-microclimatic variation appear to convey some ecologically relevant signals, but independently of each other. After accounting for the landscape setting, epiphyte cover was the only substrate-level variable that showed independent influence on the occurrence of red-listed species (Fig. 10 A), although the proportion of explained variance was very low ($R^2 = 0.03$, Article III).

Overall, the apparent lack congruence between wood-microclimatic variables and epiphyte cover could be interpreted to mean that the effects of epiphyte cover on wood-inhabiting fungi are not mediated through wood moisture and temperature conditions. Hypothetical alternative mechanisms could include physical insulation of the woody substrate from fungal spore rain (Dynesius, Gibb, & Hjältén, 2010) or bioactive leachates from epiphytic vegetation (Chang et al., 2019). On the other hand, due to the coarse resolution of wood-microclimatic measurements in this study, dynamic effects between epiphyte cover and wood microclimate at fine spatial and temporal scales could not be captured. Such effects could matter especially for species primarily utilizing the outer, i.e., more exposed, layers of the woody substrate (Kubartová et al., 2012; Chang et al., 2019).
Figure 10  Associations between the environment, tree trunk characteristics and fungal communities. Path model (A) depicts significant interconnections ($p < 0.05$ depicted with solid arrows, $0.05 \leq p < 0.10$ depicted with dashed arrows) between environmental variables and their connections to the occurrence of red-listed fungi. Associations ($p < 0.05$) of environmental variables with the fungal community composition are depicted as vectors fitted to NMDS ordination (B). The urban–semi-natural distinction in landscape setting, which was treated as a binary variable, was assumed to involve several intercorrelated environmental gradients summarized in panel A. Figure is adapted from Article III.

3.2.3 FUNGAL WINNERS IN URBAN DEADWOOD

Both fruiting-body-based (Article II) and DNA-based analyses (Article III) indicated that fungal species responding positively to urbanization are few. Models based on fruiting-body occurrences indicated positive responses (with associated increase in predictive power) only for one polypore species, *Postia stiptica* (Article II). Models based on DNA data indicated positive responses for three additional taxa, *Dacrymyces stillatus*, *Heterobasidion parviporum* and Helotiales OTU0016. The inferred preferences of *D. stillatus* and Helotiales OUT0016 for urban forests coincided with evasion of moss-covered substrates (Article III), suggesting that these species might be adapted to exposed and disturbed substrates. *H. parviporum* and *P. stiptica* are wood-decayers capable of infecting living trees, and both species are also well adapted to utilizing cut stumps as substrates for growth and fruiting-body production (Piri, 1996; Niemelä, 2016). Logging activities as well as damages on tree roots from trampling may have contributed to their prevalence in urban forests. Vegetative transmission of *H. parviporum* through root connections (Piri, 1996) could also benefit from altered urban soil conditions such as increased alkalinity (Hamberg *et al.*, 2009) and from reduced amounts of antagonistic soil microbes (Brüna *et al.*, 2019).

Based on DNA level frequency and abundance, *H. parviporum* was one of the most prevalent decomposers of downed spruce trunks in urban forests (Article III). The species was detected in almost every second studied trunk (48%) in urban forests, while respective frequency in semi-natural forests was 33%. The other dominant
RESULTS AND DISCUSSION

Wood-decaying basidiomycete, *Fomitopsis pinicola*, had slightly opposing trend with frequency of 44% in urban and 50% in semi-natural forests. High frequency and dominance of *H. parviporum* in large urban spruce trunks is notable since this substrate type is also particularly important for many spruce-associated red-listed species (Tikkanen et al., 2006). From this perspective, possible priority effects (Ottosson et al., 2014; Hiscox et al., 2015; Norberg et al., 2019) from early-colonizing *H. parviporum* to later decay succession could have significant implications for the conservation value of dead spruce in urban forests. Negative species-to-species associations have been previously been indicated between *H. parviporum* and some saproxylic beetles (Abrahamsson, Lindbladh, & Rönnberg, 2008). However, identification of possible long-term legacy effects from *H. parviporum* on late-successional wood-inhabiting communities would warrant further studies.

### 3.3 CONCLUSIONS

During the past decades, biodiversity values have become increasingly important in guiding urban forestry in the Nordic region (Gundersen et al., 2005). However, it has been rarely investigated how these trends have been manifested concretely in stand structures and biodiversity potential in urban forests in relation to surrounding rural areas (but see e.g., Hedblom & Söderström, 2008). In this thesis, I have shed light on this matter from the viewpoint of deadwood and wood-inhabiting fungi and provide new insights about the role of urbanization in shaping fungal assemblages.

Based on the living tree structure, urban spruce-dominated forests in southern Finland provide more opportunities for the accumulation of broadleaf and large-diameter (Ø > 30 cm) deadwood qualities than typical production forests. Diversified tree species composition can enable a larger variety of wood-inhabiting species to occur than would otherwise be expected in conifer dominated stands (See Hämäläinen, Tahvanainen, & Junninen, 2018). Some of the broadleaf tree species, such as *Alnus incana*, *Populus tremula*, *Salix caprea* and *Sorbus aucuparia*, rarely form pure stands and their prominence as admixed tree species in urban conifer-dominated stands could be significant for the regional persistence of species specifically associated with them (Huuskonen et al., 2021). As the projected climate change scenarios for southern Finland predict deteriorating growing conditions and increased risk of damages for Norway spruce (Venäläinen et al., 2020), it is probable that the share of broadleaf trees in urban forests will still increase in the future.

Provided that adequate deadwood resources are present, urban forests can host species-rich assemblages of polypores, albeit the most fragmentation-sensitive species may have limited ability to persist in urban forest landscapes. Deducing from the results in Article II, the occurrences of spruce-associated red-listed polypores become unlikely when the cover of mature forest drops below 40–50% in the near surrounding landscape (200 m radius), even when local deadwood abundance is high. These results are in line with the view that land sparing, instead of interspersed natural and urban land, is crucial for sustaining ecosystem services (Stott et al., 2015) and biodiversity (Beninde et al., 2015). Thus, if the preservation of threatened species is set as a target in urban planning, maintaining the integrity of the remaining large forest habitat areas
should be given a high priority. In large intact forest areas, where deadwood is more removed from the immediate vicinity of the urban matrix, the added negative effects related to urbanization are also likely to be less severe.

From the perspective of species conservation, the prevalence of large-diameter trees in urban forests is intriguing because many threatened wood-inhabiting species seem to be largely confined to large logs (Tikkanen et al., 2006), and scarcity of large trees is considered to be a significant threat factor for Finnish forest species nationally (Hyvärinen et al., 2019). In this respect, urban forests have two assets over production forests: prolonged lifespans of trees which allows more individuals to reach large proportions, and lower emphasis on wood production which may allow more liberal retention of large trees as deadwood. Yet, large amounts of coarse woody debris may still be viewed by many as a hindrance to forest recreational use and a contradiction to the general public’s visual preferences (Tyrvääinen, Silvennoinen, & Kolehmainen, 2003; Gundersen & Frivold, 2011). Accordingly, deadwood is most often confined to less frequented areas. However, increasing the average volume of coarse woody debris to ecologically justified levels, e.g., 20 m³ ha⁻¹ (a suggested minimum level for maintaining diverse saproxylic communities, Junninen & Komonen, 2011) would imply more extensive and visible presence of deadwood across the whole urban forest landscape. Acceptability of such changes in the appearance of urban forests necessitates effective communication of the ecological benefits to the urban residents (Gundersen et al., 2017).

Overall, the role of urbanization as an added environmental filter for wood-inhabiting biota was found to be relatively minor in relation to other variables defining habitat quality for wood-inhabiting fungi. In this study, effects related specifically to urbanization were detected in reduced occurrence of polypore fruiting-bodies and reduced species richness of red-listed polypores. However, specific mechanisms underlying these patterns remain to be clarified. As urban deadwood was found to be drier, and fungal fruiting-body formation in deadwood may be water-limited (Moore et al., 2008), the dynamics of wood moisture balance in urban conditions could be worth investigating more thoroughly. In highly urbanized settings, deadwood may also be subjected to novel kinds of disturbances such as trampling and accelerated mechanical fragmentation. Further research regarding these and other factors contributing to the urban deadwood dynamics would be useful for guiding the management of deadwood associated biodiversity in forest under intensifying urban development.
APPENDICES

APPENDIX A. THE PROPORTION OF PRODUCTIVE FOREST LAND LOCATED WITHIN URBAN ZONES AROUND HELSINKI.

The proportion of productive forest land located under urban zones within 75 km from Helsinki city center was calculated with a GIS analysis in QGIS Desktop 3.16.10. The input datasets were Land class 2019 GeoTIFF published and distributed by Natural Resources Institute Finland and YKR Urban-Rural classification 2018 SHP published and distributed by Finnish Environment Institute. Only productive forest land (land class 1) was considered in forest cover and urban zones were considered to include inner urban and outer urban areas. Areas were measured within a radius of 75 km from the city center of Helsinki (6672208, 385786, ETRS-TM35FIN).

Total productive forest area was 5409 km² and forest area within the urban zones was 246.7 km² (Supplementary Fig. A1). The share of productive forest land within urban zones was therefore 4.6%.

Supplementary Fig. A1 Productive forest land (black area) within 75 km from Helsinki city center. Inner urban areas are shaded with red and outer urban areas with yellow. Classification of areas is based on YKR Urban-Rural classification 2018 by Finnish Environment Institute.
APPENDIX B. GENERALIZED ADDITIVE MIXED MODELS FOR POLYPORE FRUITING-BODY OCCUPANCY.

Generalized additive mixed models were fitted to the data from Article II to answer whether urbanization affected the overall occupancy of deadwood units, i.e., whether a deadwood unit hosted living polypore fruiting-bodies or not. Generalized additive mixed models were estimated separately for the presence-absence of fruiting-bodies of (1) any polypore species and (2) red-listed species (Supplementary Table B1). Decay class and volume were included as substrate-level explanatory variables. Stand-level explanatory variables and their formulations were the same as in the additive models used in Article II. Site was included as random factor to account for non-independence of deadwood units inventoried in the same stands, and the day of the inventory (day of the year) was included to account for variability in inventory timing. Statistical output from these analyses is presented in Supplementary Tables B2 and B3.

Supplementary Table B1. Red-listed species according to national assessments of Estonia (EE, 2021), Finland (FI, 2019), Norway (NO, 2021) and Sweden (SE, 2020) and regional assessment of Leningrad region of Russia (LE, 2018). Fruiting-body observations (Article II) are reported separately for urban forests, production forests (which include non-protected and recently protected production forests) and semi-natural forests. Red-list categories are near-threatened (NT), vulnerable (VU), endangered (EN), critically endangered (CR) and regionally extinct (RE).

<table>
<thead>
<tr>
<th>Species</th>
<th>Red List status</th>
<th>Fruiting-body observations</th>
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<tr>
<td></td>
<td>Urban stands (n = 741)</td>
<td>(Former) production stands (n = 682)</td>
</tr>
<tr>
<td>Amylocystis lapponica</td>
<td>NTFI, VU_NO, SE, CRLE</td>
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<td>Anomoloma albolutecens</td>
<td>NTFI, EN_NO, NO, CRLE, SE</td>
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<tr>
<td>Antrodia piceata</td>
<td>VUFI, LE, SE, ENFI, NO</td>
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</tr>
<tr>
<td>Antrodiella citrinella</td>
<td>NTFI, NO, CRE</td>
<td>2</td>
</tr>
<tr>
<td>Fibroporia gossypium</td>
<td>VUFI, VU</td>
<td>2</td>
</tr>
<tr>
<td>Fomitopsis rosea</td>
<td>NTFI, FL, NO, SE</td>
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</tr>
<tr>
<td>Leptoporus mollis coll</td>
<td>NTNO, SE</td>
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<tr>
<td>Osteina undosa</td>
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<tr>
<td>Perenniporia subacida</td>
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<td>Phellinus viticola</td>
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<td>Physisporinus vitreus</td>
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<td>Postia floriformis</td>
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<td>Steccerinum collabens</td>
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**Supplementary Table B2. Model summary for occupancy of deadwood units by any polypore species.**

Family: binomial  
Link function: logit  

Formula:  
‘Presence of any polypore fruiting-bodies’ ~ ‘Decay class’ + log(‘Volume of deadwood unit’) +  
te(‘Deadwood volume of the stand’, ‘Mature forest cover within 200 m radius’) + log(‘Resident population density’) + ‘Day of the year’ + s(Site, bs = “re”)  

| Parametric coefficients: | Estimate | Std. Error | z value | Pr(>|z|) |
|--------------------------|----------|------------|---------|----------|
| (Intercept)              | 3.14826  | 0.35356    | 8.904   | <2e-16   *** |
| ‘Decay class 3’          | -0.41501 | 0.19517    | -2.126  | 0.0335   *  |
| ‘Decay class 4’          | -1.63777 | 0.19372    | -8.454  | <2e-16   *** |
| log(‘Volume of deadwood unit’) | 1.69015 | 0.19210    | 8.798   | <2e-16   *** |
| log(‘Resident population density’) | -0.17541 | 0.08174    | -2.146  | 0.0319   *  |
| ‘Day of the year’        | 0.13606  | 0.06502    | 2.093   | 0.0364   *  |

Approximate significance of smooth terms:  

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<th>Ref.df</th>
<th>Chi.sq</th>
<th>p-value</th>
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<td>s(Site)</td>
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<td>78.000</td>
<td>44.806</td>
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Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1  

R-sq.(adj) = 0.143  
Deviance explained = 19%  
UBRE = -0.3649  
Scale est. = 1  
n = 2017
**Supplementary Table B3.** Model summary for occupancy of deadwood units by red-listed or species.

Family: binomial
Link function: logit

Formula:
‘Presence of red-listed species’ ~ ‘Decay class’ + log(‘Volume of deadwood unit’) + te(‘Deadwood volume of the stand’, ‘Mature forest cover within 200 m radius’) + log(‘Resident population density’) + Naturalness + ‘Day of the year’ + s(Site, bs = "re")

Parametric coefficients:

| Estimate | Std. Error | z value | Pr(>|z|) |
|----------|------------|---------|----------|
| (Intercept) | -1.00345 | 0.27205 | -3.689 | 0.000226 ** |
| ‘Decay class 3’ | 0.35271 | 0.12395 | 2.846 | 0.004432 *** |
| ‘Decay class 4’ | -0.07259 | 0.15593 | -0.466 | 0.641547 |
| log(‘Volume of deadwood unit’) | 1.03537 | 0.15313 | 6.761 | 1.37e-11 *** |
| log(‘Resident population density’) | -0.06093 | 0.07252 | -0.840 | 0.400830 |
| ‘Natural 1’ | 1.33261 | 0.37790 | 3.526 | 0.000421 *** |
| ‘Day of the year’ | -0.06749 | 0.05956 | -1.133 | 0.257207 |

Approximate significance of smooth terms:

<table>
<thead>
<tr>
<th>edf</th>
<th>Ref.df</th>
<th>Chi.sq</th>
<th>p-value</th>
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<tbody>
<tr>
<td>te(‘Deadwood volume of the stand’, ‘Mature forest cover’)</td>
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<td>3.002</td>
<td>2.55</td>
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<td>s(Site)</td>
<td>21.048</td>
<td>77.000</td>
<td>51.66</td>
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Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) = 0.162  Deviance explained = 14.9%
UBRE = 0.023198  Scale est. = 1  n = 2017

**APPENDIX C. LATENT VARIABLE ORDINATION OF STAND CHARACTERISTICS.**

For visual presentation, the relationships between forest categories studied in Article I were summarized with Bayesian latent variable ordination (Fig. 7). Analyses were performed with the R package BORAL v.1.7 (Hui, 2016). The ordination of living stand composition was based on stem numbers of rowans (*Sorbus aucuparia*), large pines (*Pinus sylvestris*) (DBH ≥ 30 cm), birches (*Betula*) in DBH categories 10–29 cm and ≥ 30 cm, and spruces in DBH categories 5–9, 10–19, 20–29, 30–39 cm, and ≥ 40 cm. The ordination of deadwood composition was based on volumes categorized by quality classes: standing dead trees, snags, broken downed trunks, uprooted downed trunks and cut stumps. Data were modelled following a Tweedie distribution and a log-link function. Consistent with the GLMs estimated in Article I, site type and latitude were included as covariates in models of the living stand composition in order to remove their effects from the residual latent variables used for constructing the ordination.
REFERENCES


Noreika, N., & Kotze, D. J. (2012). Forest edge contrasts have a predictable effect on the spatial distribution of carabid beetles in urban forests. Journal of Insect Conservation, 16(6), 867–881.


