Landscape and Urban Planning 201 (2020) 103855

Contents lists available at ScienceDirect

Landscape and Urban Planning

journal homepage: www.elsevier.com/locate/landurbplan

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

Aku Korhonen[a,*], Juha Siitonen[a], D. Johan Kotze[b], Auli Immonen[a], Leena Hamberg[a]

[a] Natural Resources Institute Finland (Luke), Finland
[b] Ecosystems and Environment Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, Finland

ABSTRACT

Urban forests are usually not intensively managed and may provide suitable environments for species threatened by production forestry. Thus, urban forests could have the potential of enhancing biodiversity both within cities and at a larger landscape scale. In this study, we investigated stand structures of boreal urban forests to assess them in terms of naturalness and biodiversity conservation potential. We sampled two types of urban spruce-dominated stands: random urban stands as representatives of average urban forests, and valuable urban stands known to host high polypore richness and assumed to represent urban biodiversity hotspots. Urban forests were compared to rural forests with different levels of naturalness. Living and dead trees and cut stumps were measured from all studied stands. Urban forests had generally diverse living tree structures with abundant large-diameter trees. Random urban forests had more dead wood (median 10.1 m^3 ha^{-1}) than production forests (2.7 m^3 ha^{-1}) but still considerably less than protected, former production forests (53.9 m^3 ha^{-1}) or semi-natural forests (115.6 m^3 ha^{-1}). On the other hand, valuable urban forests had relatively high median volume of dead wood (88.2 m^3 ha^{-1}). We conclude that the combination of diverse stand composition and the presence of old-growth characteristics in boreal urban forests form a strong baseline from which their biodiversity value can be further developed, e.g. by leaving more fallen or cut trees to form dead wood. We propose that urban forests could become significant habitats for biodiversity conservation in the future.

1. Introduction

Direct and indirect effects of urbanization extend beyond the city core, potentially affecting substantial areas of forested land (Loeb, 2011). For example, in Central European countries, about one fifth of the total forested area is situated within 2 km from urban clusters (Gulsrud et al., 2018). In highly forested Nordic countries, the relative share of urban forest is only about 1%, but still, the area of forests within 5 km from city edges in Sweden was estimated to be roughly as much as the permanently protected productive forest area in the country (Hedblom & Söderström, 2008; Statistics Sweden, 2019), ca. 1 M ha.

The characteristics of urban forests compared to production and natural forests, and their potential in protecting biodiversity are poorly understood. Forested areas within and around urban settlement are subjected to stress factors such as fragmentation, edge effects and trampling (e.g. Harper et al., 2005; Hamberg, Lehvävirta, Malmivaara-Lämsä, Rita, & Kotze, 2008; Malmivaara-Lämsä, Hamberg & Haapamäki et al., 2008), aerial pollution and high nitrogen deposition (e.g. Lovett et al., 2000; Bettez & Groffman, 2013), and invasions by non-native species including pests and pathogens (e.g. Poland & McCullough, 2006). These effects are generally considered harmful to indigenous nature, and therefore urban forests are often perceived as degraded habitats.

However, the management of urban forests tends to be less production-oriented, less intensive, and smaller in scale than in rural production forests. Management practices are guided by the needs and preferences of the public, and typical management goals include the maintenance of forest continuity, aesthetics, safety, accessibility and resilience against environmental stressors (Konijnendijk, 2001; Gundersen et al., 2005; Ordóñez & Duinker, 2013). People tend to prefer urban forest stands with old trees, moderate tree species diversity and canopy stratification, and managed undergrowth that permits good visual penetration (Gundersen & Frivold, 2008; Edwards et al., 2012a, 2012b). Although lightly managed stands are usually preferred over unmanaged stands, public attitudes towards strong management actions such as clearcuttings are negative. Ecologically important natural forest structures such as dead and decaying trees can be divisive in terms of public preferences. Negative attitudes towards dead wood have been reported especially in the Nordic region (Gundersen & Frivold, 2008; Edwards et al., 2012b), but public acceptance of dead wood can be increased by education and increased awareness of their ecological benefits (Gundersen, Stange, Kaltenborn, & Vistad, 2017).

Preservation of biodiversity is increasingly recognized as a distinct goal in the management guidelines for urban forests (Gundersen et al., 2005; Saukkonen, Holstein, Siuruainen, Ylikotila, & Virtanen, 2013),

* Corresponding author at: Natural Resources Institute Finland (Luke), PO Box 2 (Latokartanonkaari 9), FI-00791 Helsinki, Finland.
E-mail addresses: akuolavikorhonen@gmail.com (A. Korhonen), juha.siitonen@luke.fi (J. Siitonen), johan.kotze@helsinki.fi (D.J. Kotze), auli.immonen@luke.fi (A. Immonen), leena.hamberg@luke.fi (L. Hamberg).

https://doi.org/10.1016/j.landurbplan.2020.103855
Received 12 December 2019; Received in revised form 18 May 2020; Accepted 19 May 2020
Available online 29 May 2020

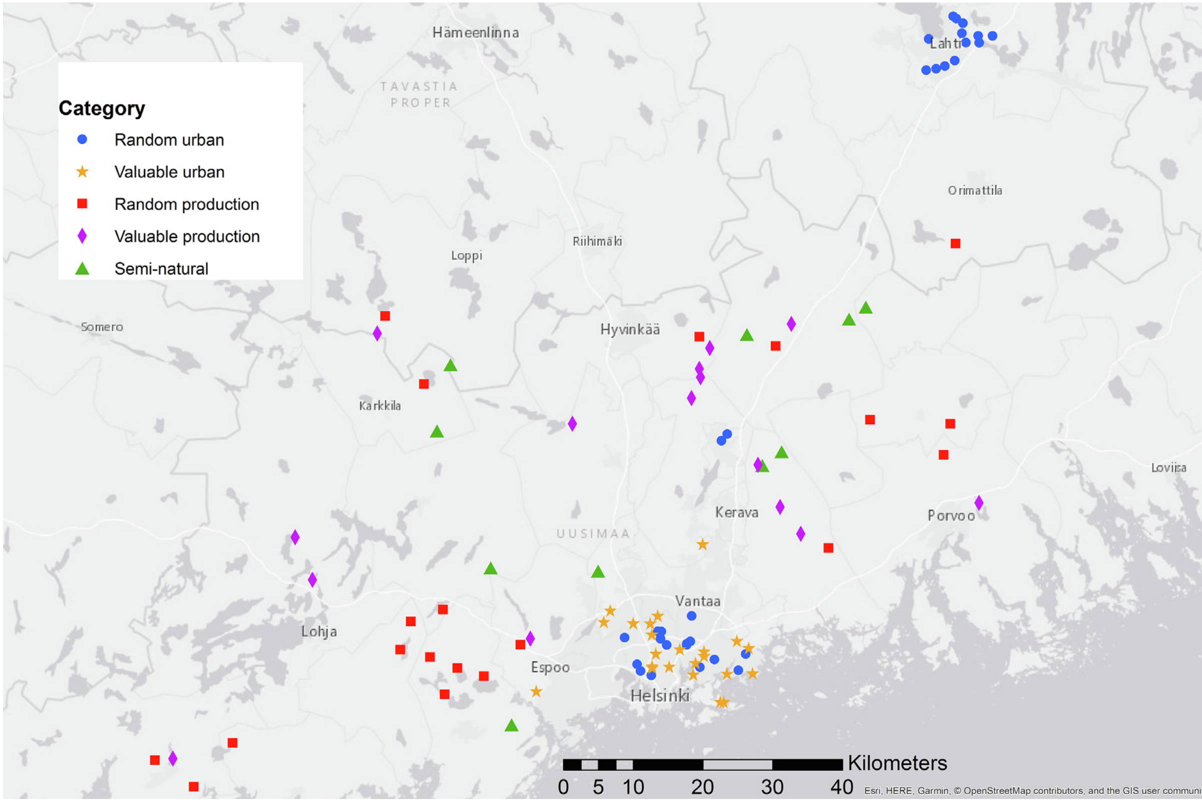

Fig. 1. Locations of study sites in the Tavastia-Uusimaa region, southern Finland.

and urban green areas can host significant biodiversity when compared to surrounding areas where habitats are degraded by rural forms of land-use (Alvey, 2006; Ives et al., 2016). If urban forests could be managed to preserve habitat quality for threatened species, they could have significant potential in contributing to biodiversity conservation by complementing protected areas. Indications to support this view have emerged, for instance, in the Helsinki metropolitan area, southern Finland. Helsinki and the surrounding cities have become nationally significant areas for the occurrence of two forest species under EU-level protection (Habitats Directive 92/43/EEC): the Siberian flying squirrel (*Pteromys volans*) (Lammi & Routasuo, 2018) and the green shield-moss (*Buxbaumia viridis*) (Manninen, 2017). In addition, inventories of wood-decaying polypore fungi in the city of Helsinki (e.g. Savola, 2012, 2015, 2016) have revealed species richness that is comparable to the protected area network surrounding the metropolitan area (Savola & Kolehmainen, 2015).

In order to evaluate habitat quality of urban forests, quantitative data about stand characteristics in urban forests is needed. Few such studies exist (but see Lehvävirta & Rita, 2002; Pregitzer et al., 2019), while the structure of urban forests as compared to similar forest types in both commercially managed and naturally developed settings has not been explored previously. Such data could be valuable to inform urban forestry and land-use planning for promoting biodiversity conservation in urban forests.

We studied stand characteristics, including the volume and composition of both living stand and dead wood, in urban Norway spruce (*Picea abies*) dominated forests in southern Finland. Following the definition of urban forest by Lehvävirta (2007), we only included sites with spontaneous understory vegetation, and excluded built parks and horticulturally managed areas. We sampled two categories of urban forests: (1) a random sample of urban forest stands representative of the general urban forest landscape, and (2) a selection of urban forest sites with high polypore species richness representative of urban biodiversity hotspots (see Materials and methods). Urban forests were compared to rural forests of similar vegetation type and development class, including three forest categories: (3) random production forests, (4) valuable production forests with some former management, but which have been recently protected because of their high nature values, and (5) semi-natural forests with little or no recent history of forest management. The purpose of the comparisons was to assess the position of urban forests along the naturalness gradient.

We hypothesized that urban forests would contain more mature, large-diameter trees, and a wider variety of tree species and sizes than production forests. We also expected that there would be a lower intensity of tree cutting, and hence a larger amount and greater diversity of dead wood in urban forests than in production forests, but still less so than in semi-natural forests. Therefore, urban forests may represent valuable habitat refugia for species that have become threatened due to intensive forest use.

2. Materials and methods

2.1. Study area and site selection

Norway spruce is the natural climax tree species in mesic upland forests of boreal Fennoscandia and the dominant tree species in most of the urban and rural landscapes in southern Finland (Mäkisara, Katila, Peräsaari, & Tomppo, 2016). We focused on spruce-dominated stands and set the following criteria for site selection: 1) vegetation type of the stand was herb-rich to mesic heathland forest, corresponding to the *Oxalis-Myrtillus* type (OMT) or *Myrtillus* type (MT) (Cajander, 1926), 2) dominating tree species was Norway spruce, and 3) the age of dominating trees was at least 60 years. The study area covered the Tavastia-Uusimaa region in southern Finland. Five different forest categories were included in the study: (1) randomly selected urban forests, (2) valuable urban forests, (3) randomly selected production forests, (4) valuable production forests and (5) semi-natural forests (Fig. 1, Table 1). Following the urban–rural spatial classification (nationwide

Table 1
Characteristics of the study sites. Sites were classified to vegetation types either as MT (less fertile) or OMT (more fertile) according to their understory vegetation, and to hemiboreal (more southern) and southern boreal (more northern) (Ahti, Hämet-Ahti., & Jalas, 1968) based on their location. Proportions of built and forested area within a 100 m radius from the sample plot center were calculated with Corine Land Cover 2018 dataset provided by the Finnish Environment Institute (syke.fi/opendata).

Characteristics	Forest category				
	Random urban ($n = 31$)	Valuable urban ($n = 23$)	Random production ($n = 20$)	Valuable production ($n = 15$)	Semi-natural ($n = 10$)
OMT sites, frequency (%)	39	57	35	47	50
Hemiboreal sites, frequency (%)	52	78	55	13	10
Built area, median (%) (min–max)	42 (0–93)	0 (0–23)	0 (0–28)	0 (0–13)	0 (0–0)
Forested area, median (%) (min–max)	58 (7–100)	98 (47–100)	86 (44–100)	90 (59–100)	100 (98–100)

geographic dataset with 250 × 250 m grid cells) by the Finnish Environment Institute (2018), urban forest sites were sampled within the core urban zone. All other forest sites were situated at least 2.5 km away from the nearest edge of the core urban zone. See Korhonen, Siitonen, Kotze, Immonen, and Hamberg (2020) for exact site locations and further site specific data.

We studied 31 random urban forest sites which were assumed to represent average urban forest biodiversity. The sites were located in the cities of Helsinki (60°10′N 24°56′E, population about 650 000, 16 sites) in the hemiboreal zone, and Lahti (60°59′N 25°39′E, population about 120 000, 13 sites) and Järvenpää (60°28.5′N 25°05.5′E, population about 43 000, 2 sites) in the southern boreal zone (Official Statistics of Finland, 2019). The sites were chosen randomly from forest stand data obtained from the cities.

In addition to the random urban forests, we selected a set of valuable urban forests (23 sites) from the Helsinki metropolitan area to gain more specific information about urban forests with high biodiversity value. The selection of sites was based on publicly available polypore species inventory reports commissioned by the cities (Savola & Wikholm, 2005; Kinnunen, 2006; Savola, 2012, 2015, 2016). These reports were used to identify and locate suitable urban forest sites where high polypore species diversity and at least some old-growth indicator species (Kotiranta & Niemelä, 1996) had been observed. The sites were reported to be rich in dead wood, but no quantitative data in this regard were available before this study. Four of the selected valuable urban forest sites have been established as protected areas after 2011.

Twenty mature production forest stands were randomly selected from the Finnish National Forest Inventory sample plots in southern Finland (Finnish Forest Research Institute Metla, 2012). We assumed that these sites represented production forests irrespective of the actual intensity of management, which varies from stand to stand depending on the activity and interests of forest owners.

A total of 15 valuable production forests were sampled. These sites represented former production forests that were under permanent or provisional protection within the Forest Biodiversity Program for Southern Finland (METSO). The METSO program started in 2008, and protected sites comprise former production forests where natural-like characteristics have developed to varying degrees. Their value for biodiversity conservation is evaluated based on ecological selection criteria emphasizing the age, structural diversity and amount of dead wood of the stand (Syrjänen et al., 2016). We presumed that these stands, here referred to as valuable production forests, represent biodiversity hotspots within the production forest matrix.

Due to the long history of forest use in southern Finland, virgin stands representative of truly natural forest were not available in the study area. Instead, we selected 10 late-successional semi-natural stands located within larger protected areas as the best available representatives of natural forest.

2.2. Sample plots

A sample plot of 20 m × 100 m (0.2 ha) was established in each stand within the snow-free periods of 2012–2018. Each plot was divided into five 20 m × 20 m (0.04 ha) cells. The sample plot was placed approximately in the middle of the stand at a random direction. If a straight 20 × 100 m plot could not be fitted into the stand, one or two of the cells were placed parallel to the others so that the area and unity of the sample plot was retained. At three sites including one random urban, one valuable urban, and one production forest, a complete 0.2 ha plot could not be fitted in any configuration. Instead, a smaller 0.16 ha plot (four cells) was used.

2.3. Measurements of stand characteristics

Living trees with at least 5 cm diameter at breast height (DBH, breast height at 1.3 m) were measured and identified to species. Trees were inventoried cell by cell until at least 100 trees were recorded. The number of cells needed to achieve at least 100 measured trees varied from two to five depending on the density of living trees on the plot. To increase the representativeness of the sample across the plot area, cells were inventoried in the order first, third, fifth, second and fourth.

All dead standing or fallen trunks with DBH ≥ 10 cm and other pieces of dead wood with basal diameter ≥10 cm and length ≥1.3 m were measured in the sample plot. A dead tree was included in the plot if the rooting point was inside the plot. Fallen trees originating from the plot but extending outside were measured entirely, while fallen trees projecting onto the plot from outside were not measured. For other pieces of dead wood (fallen branches, cut bolts, logging-residue tops etc.), the location of the basal end determined whether they belonged to the plot. DBH or basal diameter and height (length) were measured for snags (standing dead trees with missing top), pieces of logs, cut bolts, and fallen or cut tops. Top diameter and height were measured for cut stumps. For entire dead trees, only DBH was measured. Tree species and decay class were recorded for all dead wood objects. A commonly used decay classification from Renvall (1995) with five levels (1 to 5 from least to most decayed) was applied.

2.4. Data preparation

Variables for comparing living tree structure among forest categories were calculated based on the sample of measured trees. Stand volume (m^3 ha^{-1}), stem number per ha, and quadratic mean diameter of stems at breast height (QM-DBH; cm) (Curtis & Marshall, 2000) were included as the basic descriptive variables of stand density and dominant tree size. Diversity of the living stand was assessed using the number of tree species and a diversity index that combines the variability in tree species and sizes (calculation explained below). In addition, we examined the abundance of large trees, as they have special importance as providers of stand structural diversity, and reservoirs for recruitment of large-diameter dead wood (Nilsson et al., 2002). For the dominant tree species, i.e. spruce, we included trees with DBH ≥ 40 cm. For admixed canopy-forming tree species, i.e. Scots pine (*Pinus sylvestris*), birches (*Betula pendula* and *B. pubescens*) and aspen (*Populus tremula*), we included trees with DBH ≥ 30 cm. We measured the structure of the understory in terms of the number of small-diameter (5–9 cm in DBH) spruce and broadleaf trees (here referring to all angiosperm trees).

Variables for comparing dead wood structure included volumes (m^3 ha^{-1}) of dead spruce, birch, other broadleaf trees and pine, and the diversity of dead wood (calculation explained below). Downed spruce logs are usually the most common type of dead wood in spruce-dominated stands. In addition, provide the preferred substrate for many threatened dead-wood dependent species (Renvall, 1995; Tikkanen, Martikainen, Hyvärinen, Junninen, & Kouki, 2006; Hottola, Ovaskainen, & Hanski, 2009). Therefore, we investigated the number of medium to large diameter (DBH ≥ 20 cm) downed spruce trunks, as well as their future reservoirs represented by dead but still standing spruce trees (DBH ≥ 20 cm). Furthermore, we examined the volume of dead wood at mid to advanced stages of decay (decay classes 3–4, including all tree species) as an indicator of dead wood continuity, encompassing dead wood approximately 20 to 60 years old (Rinne-Garmston et al., 2019).

The total cross-sectional area (m^2 ha^{-1}) of cut stumps was used as an indicator of the intensity of past logging (Siitonen, Hottola, & Immonen, 2009). We omitted the oldest and most decayed stumps (decay class 5) due to difficulty in determining the original diameter.

Volumes of the measured living and dead tree objects were calculated using the KPL program (Heinonen, 1994). Volume equations based on tree species and DBH (Laasasenaho, 1982) were applied for calculating the volume of entire trees. The volume of pieces of dead trees was calculated based on the basal diameter and length of each piece by means of taper curve functions (Laasasenaho, 1982). Cut stumps were not included in the volumes of dead wood. Heights of entire trees required for volume calculations were estimated from previously collected sample tree data from the study region and similar forest types (*Picea abies*, 1625 measured trees; *Betula pubescens*, 386; *Pinus sylvestris*, 238; *Betula pendula*, 144; *Populus tremula*, 97; *Alnus incana*, 77; *Alnus glutinosa*, 37; *Sorbus aucuparia*, 34; other broadleaf trees, 76).

Diversity of the living stand and the dead wood in each plot was summarized by calculating indices that combine the variability in species composition and tree size, as well as in quality and decay class (Renvall, 1995) for dead wood observed in each plot. Indices were calculated as the number of observed combinations in terms of tree species, size categories, quality categories and decay classes. For the calculation of a living stand diversity index, all tree species except birches (*Betula pendula* and *B. pubescens*) were considered separately. Variability in living tree size was measured as the number of size categories, using DBH intervals 5–9 cm, 10–19 cm, 20–29 cm, … and ≥ 50 cm. For the calculation of a dead wood diversity index, broadleaf tree species other than birches (*B. pendula* and *B. pubescens* combined), aspen (*Populus tremula*), grey alder (*Alnus incana*) and black alder (*A. glutinosa*) were combined to a single category. Size categories used for dead wood were 10–19 cm, 20–29 cm, … and ≥ 50 cm. Quality categories of dead wood were (1) entire dead standing trees, (2) snags (broken and cut, height ≥ 1.3 m) and (3) downed logs. Cut and natural stumps (height < 1.3 m) were omitted from the calculation of dead wood diversity index.

2.5. Models for stand characteristics

We tested differences between the random urban forests and other forest categories by using generalized linear models (GLMs) in R v.3.5.1 (R Core Team, 2018). In the models, forest category was used as an explanatory variable (factor with five levels: [1] random urban, [2] valuable urban, [3] random production, [4] valuable production, and [5] semi-natural). For analyzing differences in dead spruce trunks between forest categories, random urban and random production forests had to be excluded due to insufficient data points (only few observations with standing dead spruce trees and downed spruce logs), and therefore, valuable urban forests were used as the baseline instead.

We considered vegetation type (site fertility) and latitude as potential confounding factors that affect living stand structure, because forest productivity is expected to increase with fertility and decrease towards the north (Solantie, 2005). Vegetation type, indicating site fertility, was included as a factor with two levels: [1] MT and [2] OMT. Latitude was included as a continuous variable scaled between 0 and 10.3 where one unit represents 10 km of latitudinal difference. Inventory area of living trees (0.08, 0.12, 0.16 or 0.2 ha, based on the number of inventoried plot cells) was furthermore included as a covariate for modelling the number of tree species and the living stand diversity index. This was done to account for the effect of inventory area on the probability of encountering tree species with scattered distribution patterns. With regard to dead wood composition, the effects of environmental variability (site fertility and latitude) were considered negligible and were not included in the dead wood models.

Total volume of the living stand, QM-DBH, diversity of the living stand and the diversity of dead wood, and the cross-sectional area of cut stumps were modelled with simple linear models. To meet the assumption of normally distributed residuals, the cross-sectional area of cut stumps was square root transformed. The number of species was modelled by GLM following a Poisson distribution with a log-link function. The number of stems was modelled by GLM following a negative binomial distribution with a log-link function using the *MASS* v7.3–50 library (Venables & Ripley, 2002). Counts and volumes including abundant zeros (number of large- and small-diameter trees, numbers of downed and dead standing spruce trunks, volumes of dead wood) were modelled by GLM following a Tweedie distribution (Dunn & Smyth, 2005, 2008) with a log-link function. Variance power parameters for a Tweedie distribution were estimated using the *tweedie* v.2.3 library (Dunn, 2017). Presence-absence data (large aspens and dead pines) were modelled by GLM following a binomial distribution and a probit-link function. Residual plots (residuals vs. fitted values) were inspected after each model to check for potential outliers, linearity between the (transformed) expectation and predictors, and for homogeneity of residuals across predicted values. We also checked for approximate normality of residuals (Q-Q plots) to verify the fit of the response distribution for non-binomial models.

As the urban forests in Lahti were spatially segregated from other study sites, we tested differences between the random urban forests of Lahti and those of Helsinki and Järvenpää to investigate possible regional effects. Tests were conducted with the same modelling approach as described above, with region as a bivariate factor variable, and vegetation type as a covariate in models of living stand characteristics.

3. Results

3.1. Living stand

Both random and valuable urban forests had generally lower volumes of spruce (*Picea abies*) and larger volumes of birch (*Betula pendula* and *B. pubescens*) compared to other forest categories (Appendix A). Birch was the most common and abundant admixed tree species in random and valuable urban forests. Other common tree species occurring in at least half of the random and valuable urban sample plots were rowan (*Sorbus aucuparia*), pine (*Pinus sylvestris*), aspen (*Populus tremula*) and goat willow (*Salix caprea*).

Random urban forests contained more large spruces than random production forests and valuable production forests. Large birches were also more abundant in random urban forests than in random production forests. The prevalence of large-diameter trees in random urban forests was also shown in higher QM-DBH values and, less markedly, in a

Table 2
Generalized linear model results for differences in living stand characteristics between the random urban forest category (intercept) and the other forest categories. Coefficients with standard errors (Coeff. ± SE) and p values are presented. Statistically significant differences ($p < 0.05$) are in bold and indicative differences ($0.05 \leq p < 0.10$) are underlined. Frequencies of sites (Fr.) where the variables have values larger than zero are expressed as percentages. See Fig. 2 for model predictions. Results regarding the effects of vegetation type, latitude and inventory area are presented in the text.

Variable	Random urban			Valuable urban			Random production			Valuable production			Semi-natural		
	$n = 31$			$n = 23$			$n = 20$			$n = 15$			$n = 10$		
	Fr.	Intercept ± SE	p	Fr.	Coeff. ± SE	p	Fr.	Coeff. ± SE	p	Fr.	Coeff. ± SE	p	Fr.	Coeff. ± SE	p
Stand volume ($m^3\ ha^{-1}$)	100	441.6 ± 20.2	< 0.001	100	−39.1 ± 21.5	0.072	100	**−43.3 ± 20.8**	**0.04**	100	−41.5 ± 22.0	0.063	100	7.7 ± 25.3	0.763
Stems (number per ha)	100	6.39 ± 0.09	< 0.001	100	0.19 ± 0.10	0.057	100	0.03 ± 0.10	0.786	100	**0.32 ± 0.10**	**0.002**	100	0.01 ± 0.12	0.905
QM-DBH[a] (cm)	100	36.7 ± 1.2	< 0.001	100	−0.5 ± 1.3	0.693	100	**−4.5 ± 1.3**	**< 0.001**	100	**−4.1 ± 1.3**	**0.003**	100	0.5 ± 1.5	0.745
Tree species number	100	1.99 ± 0.30	< 0.001	100	−0.14 ± 0.13	0.307	100	**−0.58 ± 0.15**	**< 0.001**	100	−0.16 ± 0.15	0.278	100	**−0.37 ± 0.17**	**0.033**
Diversity of living stand[b]	100	21.50 ± 2.07	< 0.001	100	−0.95 ± 0.99	0.340	100	**−6.40 ± 0.94**	**< 0.001**	100	**−2.79 ± 1.06**	**0.010**	100	**−5.88 ± 1.15**	**< 0.001**
Spruces ≥40 cm (number per ha)	97	4.09 ± 0.18	< 0.001	100	−0.14 ± 0.19	0.4	**95**	**−0.67 ± 0.21**	**0.002**	**87**	**−0.45 ± 0.21**	**0.035**	100	0.14 ± 0.20	0.503
Pines ≥30 cm (number per ha)	81	3.34 ± 0.32	< 0.001	78	0.14 ± 0.34	0.687	55	−0.21 ± 0.34	0.547	73	0.03 ± 0.36	0.924	50	−0.15 ± 0.42	0.722
Birches ≥30 cm (number per ha)	74	4.05 ± 0.23	< 0.001	91	−0.15 ± 0.23	0.504	**65**	**−1.34 ± 0.34**	**< 0.001**	67	−0.43 ± 0.30	0.16	50	−0.64 ± 0.39	0.106
Aspens ≥30 cm (presence–absence)	45	−0.02 ± 0.37	0.96	43	−0.22 ± 0.39	0.583	20	−0.79 ± 0.41	0.055	27	−0.57 ± 0.42	0.177	50	0.06 ± 0.46	0.889
Spruces 5–10 cm (number per ha)	77	3.85 ± 0.35	< 0.001	**96**	**0.89 ± 0.35**	**< 0.001**	90	0.52 ± 0.34	0.125	**100**	**1.20 ± 0.32**	**< 0.001**	**100**	**1.13 ± 0.36**	**0.002**
Broadleaf trees 5–10 cm (number per ha)	97	4.31 ± 0.33	< 0.001	100	0.39 ± 0.33	0.241	**70**	**−1.22 ± 0.40**	**0.003**	93	−0.06 ± 0.35	0.873	**50**	**−2.36 ± 0.63**	**< 0.001**

[a] Quadratic mean diameter at breast height.
[b] Measured by the diversity index; larger values indicate higher diversity of tree species and sizes.

larger volume of the living stand (Table 2, Fig. 2) when compared to random production forests and valuable production forests. Stand diversity was also higher in random urban forests than in random production forests and in valuable production forests. In general, these differences were less pronounced (and less significant) in relation to valuable production forests. Small-diameter broadleaf trees were more abundant and large aspens were more common in random urban than in random production forests, whereas valuable production forests did not differ significantly from random urban forests in these respects. However, valuable production forests had significantly more small-diameter spruces than random urban forests.

The number of stems, total volume and QM-DBH did not differ between random urban and semi-natural forests. Diversity of living stand, in terms of tree species number and the number of small-diameter broadleaf trees, was higher in urban forests whereas small-diameter spruce was more abundant in semi-natural forests.

Valuable urban forests differed from random urban forests only in terms of the number of small-diameter spruces, which was larger in valuable urban forests (Table 2, Fig. 2). This was also reflected in slightly larger total stem density in valuable urban forests (Fig. 2).

Vegetation type had a negligible effect on living stand structure with indicative significance for small spruces (-0.36 ± 0.21, $p = 0.095$). Latitude had significant negative effects on stand volume (-8.44 ± 2.69, $p = 0.002$), diversity of living stands (-0.34 ± 0.12, $p = 0.007$), and number of large birches (-0.18 ± 0.04, $p < 0.001$). The effects of inventory area on tree species number and diversity of living stand were non-significant ($p > 0.05$). Significant differences between random urban forests of Lahti and those of Helsinki and Järvenpää were identified only in the number of large birches ($p = 0.002$) which was lower in Lahti.

3.2. Dead wood

The total volume of dead wood excluding cut stumps ranged between 0 and 54.9 $m^3\ ha^{-1}$ (median = 10.1 $m^3\ ha^{-1}$) in random urban forests. Only one random urban site (in Järvenpää) had no measurable dead wood, and 16% of the sites had 20 $m^3\ ha^{-1}$ or more. Compared to other forests categories, the median volume of dead wood in random urban forests was higher than in random production forests (2.7 $m^3\ ha^{-1}$) but clearly lower than in valuable urban forests (88.3 $m^3\ ha^{-1}$), valuable production forests (53.9 $m^3\ ha^{-1}$) and semi-natural forests (115.6 $m^3\ ha^{-1}$) (Appendix B).

Spruce was generally the most dominant dead wood type, but its proportion in random urban forests was low compared to other forest categories (Table 3, Fig. 3, Appendix B). No dead spruce (with diameter of at least 10 cm) was found in 13% of the random urban sample plots and 10% of the random production forest sample plots, whereas all sites in other forests categories had at least some present.

Early decay classes (1–2) formed the largest fraction of the dead wood in all forest categories. Proportions of decay class 1–2 wood were highest in random urban forests and random production forests and lowest in valuable urban forests and semi-natural forests (Appendix B). The remaining portion of dead wood was mainly in decay classes 3–4. Wood in decay class 5 was scarce with median proportions below 1% in all except the semi-natural forests (1.5%).

Random urban forests had significantly less cut stumps and higher diversity of dead wood than random production forests while the opposite was true in relation to all other forest categories (Table 3, Fig. 3). The volume of dead spruce was significantly higher in random urban forests than in random production forests. However, this difference was smaller than differences in volumes of dead spruce between random urban forests and a) valuable urban forests, b) valuable production forests, and c) semi-natural forests, which had median volumes of dead spruce more than an order of magnitude higher than random urban forests (Appendix B). Decay class 3–4 dead wood was similarly much more abundant in valuable urban forests, valuable production forests

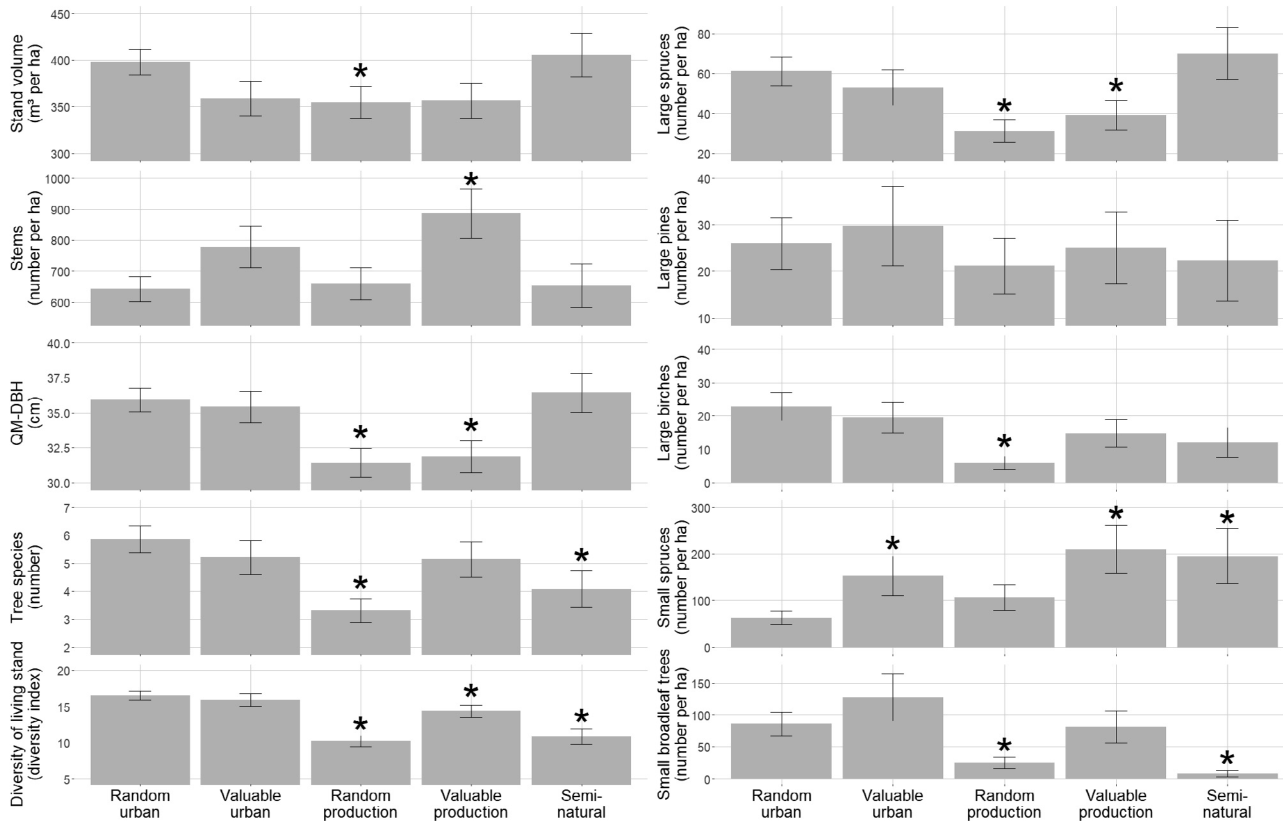

Fig. 2. Living stand characteristics in the random urban, valuable urban, random production, valuable production and semi-natural forests. Values represent predictions with standard errors from the GLMs for MT vegetation type and midpoint of the latitudinal range. Significant ($p < 0.05$) differences between random urban forests and other forest categories are indicated with asterisks. Differences between MT and OMT vegetation types were not significant ($p \geq 0.095$). Large spruces have a DBH ≥ 40 cm, large pines and birches a DBH ≥ 30 cm. Small trees have a DBH 5–9 cm. See Table 2 for model coefficients and further variable explanations.

and semi-natural forests than in random urban forests (Table 3, Fig. 3, Appendix B).

Differences in the volumes of dead broadleaf wood were less pronounced, but random urban forests had significantly higher volumes than random production forests. Compared to random urban forests, valuable urban and semi-natural forests tended to have higher volumes of dead birch (Table 3, Fig. 3), but overall the differences were small. Dead pine was relatively scarse in all forest categories, and no significant differences were found between the forest categories.

Standing and downed spruce trunks ≥20 cm in DBH were present in less than 40% of random urban and random production forest sample plots, and in 80–100% of sample plots in the other forest categories. Number of standing dead spruce trunks in valuable urban forests did not differ from those in valuable production forests, nor semi-natural forests, but downed trunks were less abundant in valuable urban forests than in semi-natural forests (Table 3, Fig. 4).

4. Discussion

Our results confirm the hypotheses that urban spruce-dominated stands in southern Finland have diverse stand composition and contain valuable structural elements, such as old and overmature trees. As expected, these elements were more abundant in urban forests than in managed production forests. Differences were similar but smaller when urban forests were compared to protected, former production forests. Compared to protected semi-natural stands, urban forests were equally rich in large-diameter trees but had greater stand diversity with more abundant broadleaf admixture particularly in the undergrowth. While the volume of dead wood in a typical urban stand was higher than in average production forests, it was still distinctly lower than in rural protected forests. Nevertheless, a sample of valuable urban forests revealed that high concentrations of dead wood already exist in urban areas sporadically. Furthermore, diverse tree species composition and the prevalence of large living trees in urban stands provide good prerequisites for the rapid development of diverse dead wood substrates, including large-diameter downed wood. In order to make use of this potential for increasing the biodiversity value of urban forests in the future, more permissive retention of dead trees is required.

4.1. Living stand

High stand diversity in urban forests was mainly attributed to greater abundance and species richness of broadleaf trees and the presence of large trees, which increased the range of tree size variation. The prevalence of large trees in urban forests is indicative of relatively long stand level continuity, which is consistent with the public's appreciation of old trees and stands (Gundersen & Frivold, 2008, Edwards et al. 2012a) as well as their aversion to strong, stand-replacing management actions (Edwards et al., 2012b). Long continuity of urban stands may also be important for biodiversity, as the reduction of old-growth forests and decreasing number of large trees are among the primary threats to forest species in Finland and Sweden (Berg et al., 1994; ArtDatabanken, 2015; Hyvärinen, Juslén, Kemppainen, Uddström, & Liukko, 2019). In production forest landscapes, the development of old-growth structures is effectively prevented by even-aged silviculture. In southern Finland, spruce stands are usually clear-cut when the average tree diameter reaches 26–32 cm (Äijälä, Koistinen, Sved, Vanhatalo, & Väisänen, 2019), which implies rotation times typically below 80 years (Hyytiäinen, Tahvonen, & Valsta, 2010). According to rough estimation based on tree size, the dominant canopy trees in urban forests were generally older than this, but tree stands had usually been managed to some extent by selective logging. Valuable

Table 3

Generalized linear model results for dead wood (DW) characteristics. Differences have been tested between random urban forests (intercept for rows 1–7) and other forest categories (see Fig. 3). For dead spruce trunks, differences have been tested between valuable urban forest (intercept for rows 8–9), valuable production and semi-natural forests (see Fig. 4). Coefficients with standard errors (Coeff. ± SE) and p values are presented. Statistically significant differences ($p < 0.05$) are in bold and indicative differences ($0.05 \le p < 0.10$) are underlined. Frequencies of sites (Fr.) where the variables have values larger than zero are expressed as percentages.

	Random urban (n = 31)			Valuable urban (n = 23)			Random production (n = 20)			Valuable production (n = 15)			Semi-natural (n = 10)		
Variable	Fr.	Intercept ± SE	p	Fr.	Coeff. ± SE	p	Fr.	Coeff. ± SE	p	Fr.	Coeff. ± SE	p	Fr.	Coeff. ± SE	p
Spruce DW ($m^3 ha^{-1}$)	87	2.05 ± 0.21	< 0.001	**100**	**2.26 ± 0.26**	**< 0.001**	**90**	**−0.76 ± 0.37**	**0.043**	**100**	**1.95 ± 0.29**	**< 0.001**	**100**	**2.70 ± 0.30**	**< 0.001**
Birch DW ($m^3 ha^{-1}$)	58	1.15 ± 0.38	0.003	78	0.91 ± 0.54	0.096	**40**	**−1.66 ± 0.74**	**0.028**	73	0.00 ± 0.67	0.999	90	1.03 ± 0.69	0.138
Other broadleaf DW ($m^3 ha^{-1}$)	74	0.50 ± 0.25	0.049	83	0.47 ± 0.36	0.197	**30**	**−2.30 ± 0.59**	**< 0.001**	73	0.37 ± 0.41	0.370	70	0.11 ± 0.50	0.824
Pine DW (pres–abs.)	35	−0.37 ± 0.23	0.107	30	−0.14 ± 0.36	0.697	20	−0.47 ± 0.39	0.234	60	0.63 ± 0.40	0.118	40	0.12 ± 0.46	0.797
Decay class 3–4 DW ($m^3 ha^{-1}$)	71	0.66 ± 0.32	0.045	**96**	**2.60 ± 0.41**	**< 0.001**	75	−0.71 ± 0.56	0.202	**100**	**1.67 ± 0.48**	**< 0.001**	**100**	**2.96 ± 0.48**	**< 0.001**
Diversity of DW[a]	97	7.52 ± 0.86	< 0.001	100	**11.74 ± 1.31**	**< 0.001**	95	**−3.62 ± 1.37**	**0.010**	100	**11.02 ± 1.50**	**< 0.001**	100	**17.58 ± 1.74**	**< 0.001**
Cut stumps ($m^2 ha^{-1}$)	100	2.64 ± 0.17	< 0.001	74	**−1.78 ± 0.26**	**< 0.001**	100	**0.65 ± 0.27**	**0.017**	93	**−1.23 ± 0.29**	**< 0.001**	80	**−1.61 ± 0.34**	**< 0.001**
Variable[b]				Fr.	Intercept ± SE	p				Fr.	Coeff. ± SE	p	Fr.	Coeff. ± SE	p
Spruce trunks DBH ≥19.5 cm															
- Standing (number per ha)	35	–	–	91	3.21 ± 0.20	< 0.001	20	–	–	80	−0.09 ± 0.32	0.784	80	0.11 ± 0.35	0.762
- Downed (number per ha)	39	–	–	100	3.49 ± 0.13	< 0.001	30	–	–	93	−0.43 ± 0.24	0.078	**100**	**0.67 ± 0.21**	**0.002**

[a] Measured by the diversity index; larger values indicate higher diversity of dead wood qualities (tree species and quality categories) and sizes.

[b] Random urban and random production forests had only few observations with dead standing and downed spruce trunks with DBH ≥20 cm. Therefore, comparisons were made between valuable urban forests, valuable production and semi-natural forests, using valuable urban forests as the baseline category.

urban forests were distinguished from random urban forests by a lower number of cut stumps, indicating less management and more natural-like stand structure at these sites.

Old and large broadleaf trees, in particular, have a special importance for conservation as they provide habitats for many threatened specialist species including, e.g. gastropods, insects and epiphytic lichens (Berg et al., 1994; Hyvärinen et al., 2019). In urban spruce stands, large broadleaf admixture trees were primarily birches and, to a lesser extent, aspens. Both were more common in urban stands than in production forests, although the abundance of birch differed significantly between the investigated regions. A lower abundance of birch in the city of Lahti may reflect regional differences in the history of urbanization and forest management.

In urban spruce stands, the understory was enriched with broadleaf trees, especially rowan, as has been found in previous studies (Lehvävirta & Rita, 2002; Malmivaara-Lämsä, Hamberg & Haapamäki et al., 2008; Hamberg, Malmivaara-Lämsä, Lehvävirta, & Kotze, 2009; Lehvävirta, Vilisics, Hamberg, Malmivaara-Lämsä, & Kotze, 2014). Factors associated with this abundance of broadleaf trees in urban forests include e.g. increased light penetration and windborne nutrient deposition due to fragmentation and thinning of tree stands, and the exclusion of large herbivores from urban areas.

Dense thickets of broadleaf trees can be considered problematic in terms of aesthetics or recreational value, and therefore, they are actively suppressed in urban forests (Tyrväinen, Silvennoinen, & Kolehmainen, 2003; Gundersen & Frivold, 2008; Gundersen, Clarke, Dramstad, & Fjellstad, 2016). This is perhaps the reason why we found small broadleaf trees to be most abundant in valuable urban forests, which had been allowed to develop with less maintenance than random urban forests. Analogous post-management development may also explain the abundance of small broadleaf trees in valuable production forests, although birch was more often the dominant species in these sites.

In connection with increased amounts of broadleaf tree saplings, an under-representation of spruce saplings in urban spruce stands has also been noted in previous studies (Lehvävirta & Rita, 2002; Hauru, Niemi, & Lehvävirta, 2012). A reduction in spruce regeneration has been associated with e.g. wear and tear due to trampling and changes in the microclimate due to edge effects (Lehvävirta & Rita, 2002), but results have been only indicative or contradictory (Malmivaara-Lämsä, Hamberg, Löfström, Vanha-Majamaa, & Niemelä, 2008; Hauru et al., 2012; Lehvävirta et al., 2014). In contrast to broadleaf tree species, which are quick to recover from disturbances by vegetative regeneration from roots and stumps (Zerbe, 2001; Hamberg, Malmivaara-Lämsä, Löfström, & Hantula, 2014), spruce regenerates only from seeds and is therefore more effectively suppressed by forest management. Accordingly, our results show greater abundance of small spruce in unmanaged rural forests (valuable production and semi-natural) as well as in valuable urban forests than in random urban forests. As discussed above, clearance of spruce undergrowth in urban forests may often lead to replacement with fast growing broadleaf thickets, which are more difficult to control.

4.2. Dead wood

The median amount of dead wood in random urban forests (10.1 $m^3 ha^{-1}$) was almost four times as high as in the random production forests included in this study (2.7 $m^3 ha^{-1}$), and about twice as high as the estimated average volume of dead wood (4.4 $m^3 ha^{-1}$) in forests of southern Finland (Natural Resources Institute Finland, 2019). Even so, the median volume was less than 10% of that in semi-natural forests (115.6 $m^3 ha^{-1}$), and < 20% of that in valuable production forests (53.9 $m^3 ha^{-1}$).

Our sampling of valuable urban forests confirmed that urban polypore hotspots in the Helsinki metropolitan area represent stands with exceptionally high volumes (88.3 $m^3 ha^{-1}$) and diversity of dead wood.

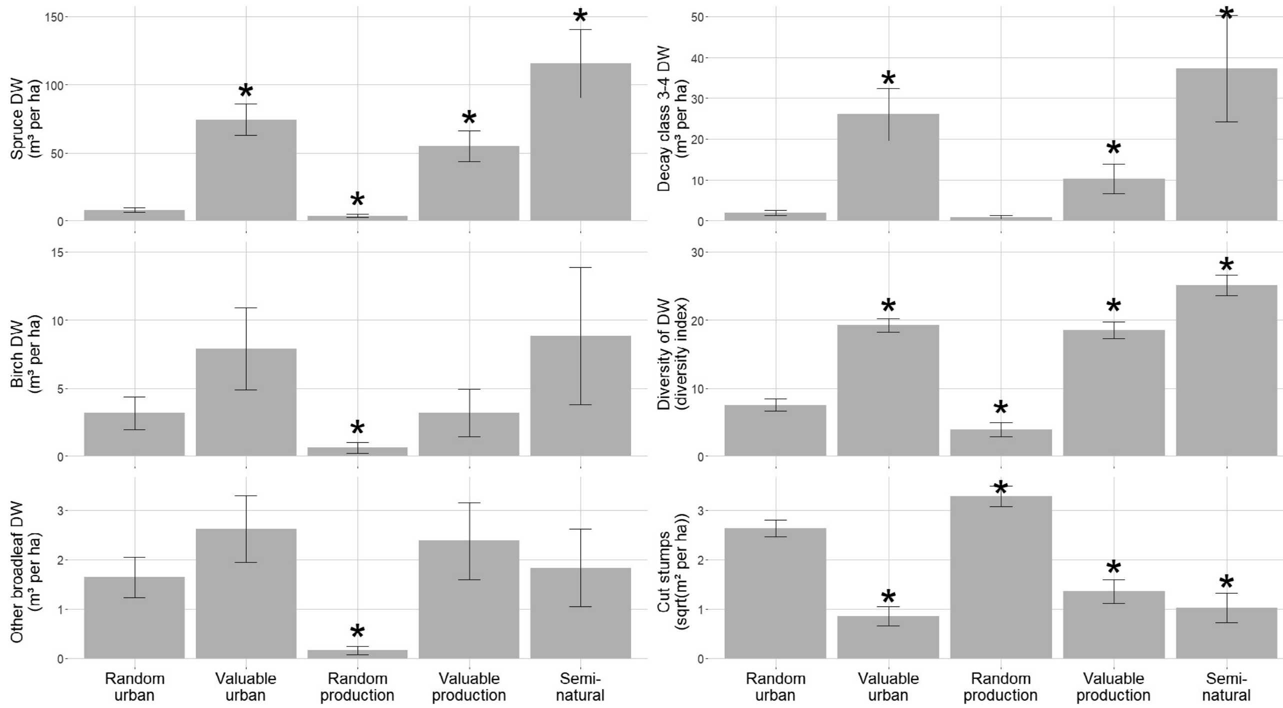

Fig. 3. Dead wood (DW) characteristics in the random urban, valuable urban, random production, valuable production and semi-natural forests. Values represent predictions with standard errors from the GLMs. Note that the modelled measure for cut stumps was the square root of cross-sectional area of stumps. Significant ($p < 0.05$) differences between random urban forests and other forest categories are indicated with asterisks. See Table 3 for model coefficients.

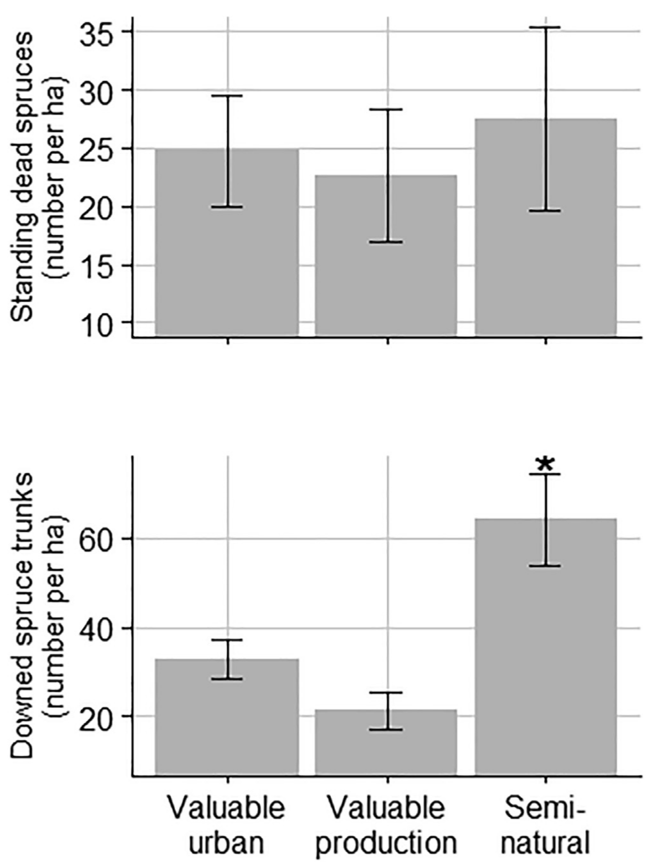

Fig. 4. Coarse spruce dead wood (entire trunks with DBH ≥ 20 cm) in valuable urban, valuable production and semi-natural forests. Values represent predictions with standard errors from the GLMs. Significant ($p < 0.05$) differences between valuable urban forests and other forest categories are indicated with asterisks. See Table 3 for model coefficients.

In terms of dead wood volumes, valuable urban forests were generally between valuable production and semi-natural forests. Based on the amount of wood in advanced stages of decay, valuable urban forests appeared to have a longer history of dead wood accumulation than valuable production forests. Large reserves of fresh dead wood, represented by standing dead spruce trees, indicate that continuity of coarse dead wood is secured in the near future too.

Large-diameter conifer logs are of special importance for dead-wood dependent biodiversity in boreal forests, as they are the most abundant dead wood substrate in old-growth spruce forests (Siitonen, Martikainen, Punttila, & Rauh, 2000), and the most important substrate type for red-listed polypore species (Renvall, 1995; Tikkanen et al., 2006; Hottola et al., 2009). Our findings suggest that in urban areas these substrates seem to be largely restricted to valuable urban forests, being scarce in the majority of the forest landscape; large-diameter spruce logs were not present in over 60% of random urban plots.

Large differences in dead wood structure that we observed between random and valuable urban forests reflect the variability of management regimes applied across the urban forested landscape. Corresponding differentiation between conventionally managed urban forests (12.1 m^3 ha^{-1} of dead wood) and minimally managed biodiversity forests (60.5 m^3 ha^{-1} of dead wood) has also been found in the city of Lahti (Kolu, 2019). Such heterogeneity is likely characteristic to most urban landscapes and potentially enforced by explicit management categorization of urban forested areas (see e.g. Rydberg & Falck, 2000; Nuotio, 2007): some sites are managed for recreation and some for biodiversity.

4.3. Implications for biodiversity conservation and urban forest management

The high degree of fragmentation in urban forested landscapes stresses the need of making use of all remaining forest area to improve ecological quality and carrying capacity of the urban environment. It has been speculated that the character of old urban spruce stands may change significantly in the future as the old canopy forming spruce trees die and are replaced increasingly by broadleaf trees (e.g. Hauru et al., 2012; Lehvävirta et al., 2014). Further studies will be needed to properly assess the validity of this scenario, but as the forest damages from wind throws, pest insects (*Ips typographus*) and fungal pathogens (*Heterobasidion parviporum*) are predicted to increase with climate change (Kellomäki, Peltola, Nuutinen, Korhonen, & Strandman, 2007), there will likely be pressure to replace old spruce stands with more mixed stand structures. This shift could potentially increase species diversity in urban spruce stands, but implications for conservation can vary.

For instance, increasing the number of large aspens could be beneficial for many threatened species (Kuusinen, 1996; Kouki, Arnold, & Martikainen, 2004; Tikkanen et al., 2006). While the continuity of old aspen trees is being widely threatened by intensive browsing by moose (*Alces alces*) populations in rural forests (Angelstam, Wikberg, Danilov, Faber, & Nygren, 2000; Kouki et al., 2004), large browsing animals are largely excluded from urban areas. In the future, urban forests could develop into valuable areas with regard to the continuity of aspen trees. Although urban conditions may prove unsuitable for some aspen-associated species, such as strict old-growth specialists or pollution-sensitive species (Hedenås & Ericson, 2004), many species specialized in utilizing dead aspen have been found to survive in exposed retention trees in clear-cut openings (Martikainen, Penttilä, Kotiranta, & Miettinen, 2000; Martikainen, 2001; Junninen, Penttilä, & Martikainen, 2007). These species (e.g. polypores *Funalia trogii* and *Perenniporia tenuis*, and many threatened beetle (Coleoptera) species) may well be able to tolerate urban stressors as well.

While many species will benefit from enrichment of the broadleaf component in urban forested landscapes (Äijälä et al. 2019), attention should also be paid to maintining areas with conditions more like those of natural old-growth spruce forests, e.g. continuity of old and senescent spruce trees and multilayered conifer dominated canopies. Continuous shade, wind shelter and stable moisture under evergreen canopies may be vital for old-growth specialists including species of epiphytic lichens (Gauslaa & Solhaug, 1996; Hedenås & Ericson, 2004) and litter-dwelling fungi (von Bonsdorff et al., 2014, 2019), even when they use broadleaf trees as their primary substrates or mycorrhizal partners.

Fragmentation and ensuing edge effects may limit the conservation potential of dead-wood dependent biodiversity as well. In Finnish woodland key habitats, which are often comparable in size with urban forest fragments (< 1 ha), small habitat patch size has been found to affect polypore species diversity negatively, and the effect was significant even when habitat quality (volume of dead wood) was taken into account (Ylisirniö, Mönkkönen, Hallikainen, Ranta-Maunus, & Kouki, 2016). This may be partly due to a drier microclimate resulting from edge effects (Malmivaara-Lämsä, Hamberg & Haapamäki et al., 2008), which has also been associated with lower incidence of some old-growth indicator polypores (Snäll & Jonsson, 2001; Siitonen, Lehtinen, & Siitonen, 2005).

Edge effects can be mitigated to some extent by controlling the tree structure in forest stands, especially near the edges (Matlack, 1993). For instance, Hamberg, Lehvävirta, and Kotze (2009) suggest that forest edges should be dense (225–250 m^3 ha^{-1} of trees) with at least 80% conifers, in order to maintain natural understory vegetation in fragmented urban spruce forests. Closed forest edges that block visibility to the urban matrix, have also been found to improve the sense of restorativeness that people perceive in urban forests (Hauru, Lehvävirta, Korpela, & Kotze, 2012).

In terms of dead wood volumes, several studies (reviewed in Müller & Bütler, 2010) have suggested threshold values of 20–30 m^3 ha^{-1} of coarse woody debris for maintaining diverse saproxylic communities in boreal coniferous forest landscapes. For natural forest specialist fungi, the threshold is probably higher (Siitonen, 2001; Nordén et al., 2018). As only 16% of random urban forests had at least 20 m^3 ha^{-1} of dead wood, it is evident that the retention of dead wood should be significantly increased in large parts of the urban forest landscape. Adequate concentrations of dead wood for maintaining red-listed polypore species seem to be found mainly in valuable urban forests. The spatial extent and distributions of these dead-wood rich stands in the urban landscape remains unknown, but their scarcity in our random sample of urban forests suggests that they are a minority. Small and isolated habitat fragments have a limited capacity to maintain temporal continuity of resources for saproxylic organisms due to locally fluctuating inputs and continuous depletion of dead wood (Aakala, 2011). Therefore, special attention should be paid to restoring habitat quality in larger forested areas remaining within and around urban areas, and to connect isolated dead-wood hotspots to each other (Jonsson, Kruys, & Ranius, 2005; Siitonen et al., 2005, Hottola et al., 2009).

Overall, the abundance of old and overmature trees in the urban spruce stands provide good prerequisites for natural recruitment of large-diameter dead wood, especially spruce. Public safety may also necessitate artificial felling of trees in urban areas, but not the removal of tree trunks once they are on the ground. The potential for using downed logs, e.g. for guiding recreational use and restricting off-path passage (see e.g. Lehvävirta, Rita, & Koivula, 2004; Hauru, Koskinen, Kotze, & Lehvävirta, 2014) is already recognized in practical management guidelines for urban forests, for instance, in the city of Helsinki (Saukkonen et al., 2013), but could be more extensively utilized.

As the urban forested landscape is highly fragmented, sheltered locations that are distant from paths and out of sight are scarce. Therefore, increasing the quantity of dead wood in urban forests means that the public will inevitably encounter dead wood more often. Maintenance of the recreational and restorative value of urban forests for wide audiences necessitates that the public can adapt to these visual and structural changes. Studies have already shown that the public is increasingly willing to accept logs as natural features in urban forests (Hauru et al., 2014), possibly due to increasing awareness of the ecological significance of dead wood (Gundersen & Frivold, 2011; Gundersen et al., 2017). Improving the public's acceptance of increased dead wood quantities may thus require effective communication of their ecological benefits. People's reactions to the addition of dead wood in urban forests – and their interactions with dead-wood rich environments – should be further investigated as previous studies have focused only on visual perceptions using either pictures (Tyrväinen et al., 2003; Gundersen & Frivold, 2011; Gundersen et al., 2017) or static observation points on site (Hauru et al., 2014).

Although nature conservation is already being taken into consideration in city-level land-use planning, the potential of urban forest areas in complementing protected area networks on a larger spatial scale has been less discussed. A shift to renewable resources in energy and commodity production will increase industrial demand for biomass (Staffas, Gustavsson, & McCormick, 2013) and probably lead to intensification of forest use in northern Europe (Kraxner & Nordström, 2015; Rytter et al., 2016). This development will challenge the advancements of forest biodiversity conservation in European boreal zone, where productive forest land is already in efficient use. In this context, urban forests could represent areas where biodiversity conservation could be implemented as a part of urban multi-use forestry with relatively low conflicts of interests. Our results suggest that urban forest stand structures have aspects that can promote biodiversity, but further research is needed to assess the role of urban stress factors such as fragmentation and wear as potentially limiting factors to biodiversity in urban forests.

CRediT authorship contribution statement

Aku Korhonen: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft. **Juha Siitonen:** Conceptualization, Methodology, Investigation, Writing - review & editing. **D. Johan Kotze:** Conceptualization, Investigation, Writing - review & editing. **Auli Immonen:** Data curation, Formal analysis.

Leena Hamberg: Conceptualization, Investigation, Writing - review & editing, Supervision.

Acknowledgements

This work was supported by Maj and Tor Nessling Foundation, Helsinki, Finland (grant no. 201800093); and Natural Resources Institute Finland (project no. 41007-00119000).

We are grateful to the cities of Helsinki, Lahti and Järvenpää for providing forest sites for the study; Suvi Kolu, Pentti Kananen, and Marju Prass for assistance in the field; and the anonymous reviewers for their constructive comments.

Appendix A. Species composition of the living stand

Frequency (Fr., percentage) and median volume ($m^3\ ha^{-1}$) of the most abundant tree species (according to measured volumes) are presented. Minimum and maximum values are shown in parentheses.

	Tree species										
	Spruce[a]	Birch		Pine		Aspen		Rowan		Goat willow	
Forest category	$m^3\ ha^{-1}$	Fr.	$m^3\ ha^{-1}$	Fr.	$m^3\ ha^{-1}$	Fr.	$m^3\ ha^{-1}$	Fr.	$m^3\ ha^{-1}$	Fr.	$m^3\ ha^{-1}$
Random urban	288.1 (139.0–542.4)	100	52.1 (0.2–184.9)	87	44.0 (0–105.2)	71	5.4 (0–120.6)	87	4.9 (0–27.4)	52	0.1 (0–13.9)
Valuable urban	272.1 (147.8–393.1)	100	46.0 (11.0–129.7)	78	36.9 (0–142.1)	65	4.7 (0–150.6)	100	6.3 (0.1–30.6)	30	0.0 (0–13.4)
Random production	335.0 (158.0–440.0)	90	16.0 (0–86.2)	65	8.1 (0–105.2)	20	0.0 (0–61.1)	20	0.0 (0–5.2)	20	0.0 (0–1.7)
Valuable production	292.5 (141.3–397.1)	100	19.5 (0.1–200.4)	73	28.6 (0–105.7)	53	0.7 (0–43.3)	80	1.9 (0–19.6)	53	1.3 (0–9.5)
Semi-natural	341.9 (274.3–413.4)	100	17.6 (2.1–92.0)	60	6.7 (0–154.5)	50	5.5 (0–21.7)	40	0.0 (0–1.0)	20	0.0 (0–4.3)

Appendix B. Volume and composition of dead wood

Frequency (Fr., percentage) and median volume ($m^3\ ha^{-1}$) of total dead wood (A), and dead wood partitioned by tree species (B) and decay class (C) in different forest categories are presented. Minimum and maximum values are shown in parentheses.

A	Total dead wood	
Forest category	Fr.	$m^3\ ha^{-1}$
Random urban	97	10.1 (0–54.9)
Valuable urban	100	88.3 (25.3–179.2)
Random production	95	2.7 (0–24.3)
Valuable production	100	53.9 (17.4–174.4)
Semi-natural	100	115.6 (59.4–226.8)

B	Species composition of dead wood					
Forest category	Spruce		Birch		Other broadleaf	
	Fr.	$m^3\ ha^{-1}$	Fr.	$m^3\ ha^{-1}$	Fr.	$m^3\ ha^{-1}$
Random urban	87	4.1 (0–38.9)	58	0.4 (0–49.6)	74	1.1 (0–7.6)
Valuable urban	100	73.4 (24.4–142.1)	78	2.1 (0–48.8)	61	1.0 (0–18.2)
Random production	90	1.1 (0–21.1)	40	0.0 (0–5.0)	30	0.0 (0–1.2)
Valuable production	100	42.8 (7.4–174.4)	73	0.6 (0–16.3)	73	0.7 (0–12.7)
Semi-natural	100	109.3 (36.0–211.6)	90	4.1 (0–45.6)	70	0.4 (0–7.5)

C	Decay class composition of dead wood			
Forest category	Decay classes 1–2		Decay classes 3–4	
	Fr.	$m^3\ ha^{-1}$	Fr.	$m^3\ ha^{-1}$
Random urban	94	9.4 (0–39.6)	71	0.7 (0–18.6)
Valuable urban	100	49.8 (21.4–126.7)	96	14.5 (0–104.7)
Random production	85	1.8 (0–13.6)	75	0.1 (0–10.2)
Valuable production	100	41.7 (11.9–143.9)	100	6.8 (1.9–30.5)
Semi-natural	100	75.6 (40.4–160.6)	100	21.9 (5.8–119.3)

References

Aakala, T. (2011). Temporal variability of deadwood volume and quality in boreal old-growth forests. *Silva Fennica, 45*(5), 969–981.

Ahti, T., Hämet-Ahti, L., & Jalas, J. (1968). Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici, 5*, 169–211.

Äijälä, O., Koistinen, A., Sved, J., Vanhatalo, K., & Väisänen, P. (Eds.) (2019). Metsänhoidon suositukset [Best Practices for Sustainable Forest Management]. Helsinki, Finland: Tapio (In Finnish).

Alvey, A. A. (2006). Promoting and preserving biodiversity in the urban forest. *Urban Forestry & Urban Greening, 5*(4), 195–201. https://doi.org/10.1016/j.ufug.2006.09.003.

Angelstam, P., Wikberg, P. E., Danilov, P., Faber, W. E., & Nygren, K. (2000). Effects of moose density on timber quality and biodiversity restoration in Sweden, Finland, and Russian Karelia. *Alces, 36*, 133–146.

ArtDatabanken (2015). Rödlistade arter i Sverige 2015 [The 2015 Swedish Red List]. Uppsala, Sweden: ArtDatabanken SLU (In Swedish with English summary).

Berg, Å., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M., & Weslien, J. (1994). Threatened plant, animal, and fungus species in Swedish forests: Distribution and habitat associations. *Conservation Biology, 8*(3), 718–731. https://doi.org/10.1046/j.1523-1739.1994.08030718.x.

Bettez, N. D., & Groffman, P. M. (2013). Nitrogen deposition in and near an urban ecosystem. *Environmental Science & Technology, 47*(11), 6047–6051. https://doi.org/10.1021/es400664b.

von Bonsdorff, T., Kytövuori, I., Vauras, J., Huhtinen, S., Halme, P., Rämä, T., ... Jakobsson, S. (2014). Sienet ja metsien luontoarvot [Indicator fungi]. *Norrlinia, 27*, 1–272 (In Finnish with English summaries).

von Bonsdorff, T., Niskanen, T., Kytövuori, I., Vauras, J., Liimatainen, K., Höijer, P., ... Huhtinen, S. (2019). Helttasienet ja tatit [Agaricoid and boletoid fungi]. In E. Hyvärinen, A. Juslén, E. Kemppainen, A. Uddström, & U.-. M. Liukko (Eds.). *Suomen lajien uhanalaisuus–punainen kirja 2019 [The 2019 Red List of Finnish Species]* (pp. 263–312). Helsinki, Finland: Ministry of the Environment & Finnish Environment Institute (In Finnish with English summary).

Cajander, A. K. (1926). The theory of forest types. *Acta Forestalia Fennica, 29*(3), 1–108.

Curtis, R. P., & Marshall, D. D. (2000). Why quadratic mean diameter? *Western Journal of Applied Forestry, 15*, 137–139. https://doi.org/10.1093/wjaf/15.3.137.

Dunn, P. K. (2017). Tweedie: Evaluation of Tweedie exponential family models. *R package version, 2*, 3.

Dunn, P. K., & Smyth, G. K. (2005). Series evaluation of tweedie exponential dispersion model densities. *Statistics and Computing, 15*, 267–280. https://doi.org/10.1007/s11222-005-4070-y.

Dunn, P. K., & Smyth, G. K. (2008). Evaluation of Tweedie exponential dispersion models using Fourier inversion. *Statistics and Computing, 18*(1), 73–86. https://doi.org/10.1007/s11222-007-9039-6.

Edwards, D. M., Jay, M., Jensen, F. S., Lucas, B., Marzano, M., Montagné, C., ... Weiss, G. (2012a). Public preferences across Europe for different forest stand types as sites for recreation. *Ecology and Society, 17*(1), https://doi.org/10.5751/ES-04520-170127.

Edwards, D., Jay, M., Jensen, F. S., Lucas, B., Marzano, M., Montagné, C., ... Weiss, G. (2012b). Public preferences for structural attributes of forests: Towards a pan-European perspective. *Forest Policy and Economics, 19*, 12–19. https://doi.org/10.1016/j.forpol.2011.07.006.

Finnish Environment Institute. (2018). YKR Urban-rural classification. Retrieved April 1, 2019 from https://www.syke.fi/openinformation.

Finnish Forest Research Institute Metla. (2012). National Forest Inventory data from 2012. Unpublished data.

Gauslaa, Y., & Solhaug, K. A. (1996). Differences in the susceptibility to light stress between epiphytic lichens of ancient and young boreal forest stands. *Functional Ecology, 10*, 344–354.

Gulsrud, N. M., Nielsen, A. B., Bastrup-Birk, A., Olafsson, A. S., Lier, M., Fischer, C., Zalkauskas, R., Hedblom, M., Sievänen, T., Nordh, H., Dahlgren, J., Kulbokas, G., Davies, C., & Polley, H. (2018). Urban Forests in a European Perspective: what can the National Forest Inventory tell us: Workshop for Practitioners and Researchers held on March 15, Brussels – Summary of workshop results. Department of Geosciences and Natural Resource Management, .University of Copenhagen, Frederiksberg, Denmark.

Gundersen, V., Clarke, N., Dramstad, W., & Fjellstad, W. (2016). Effects of bioenergy extraction on visual preferences in boreal forests: A review of surveys from Finland, Sweden and Norway. *Scandinavian Journal of Forest Research, 31*(3), 323–334.

Gundersen, V., & Frivold, L. H. (2008). Public preferences for forest structures: A review of quantitative surveys from Finland, Norway and Sweden. *Urban Forestry & Urban Greening, 7*(4), 241–258. https://doi.org/10.1016/j.ufug.2008.05.001.

Gundersen, V., & Frivold, L. H. (2011). Naturally dead and downed wood in Norwegian boreal forests: Public preferences and the effect of information. *Scandinavian Journal of Forest Research, 26*(2), 110–119. https://doi.org/10.1080/02827581.2010.536567.

Gundersen, V., Frivold, L. H., Löfström, I., Jørgensen, B. B., Falck, J., & Øyen, B. H. (2005). Urban woodland management–the case of 13 major Nordic cities. *Urban Forestry & Urban Greening, 3*(3–4), 189–202. https://doi.org/10.1016/j.ufug.2005.03.001.

Gundersen, V., Stange, E. E., Kaltenborn, B. P., & Vistad, O. I. (2017). Public visual preferences for dead wood in natural boreal forests: The effects of added information. *Landscape and Urban Planning, 158*, 12–24. https://doi.org/10.1016/j.landurbplan.2016.09.020.

Hamberg, L., Lehvävirta, S., & Kotze, D. J. (2009). Forest edge structure as a shaping factor of understorey vegetation in urban forests in Finland. *Forest Ecology and Management, 257*(2), 712–722. https://doi.org/10.1016/j.foreco.2008.10.003.

Hamberg, L., Lehvävirta, S., Malmivaara-Lämsä, M., Rita, H., & Kotze, D. J. (2008). The effects of habitat edges and trampling on understorey vegetation in urban forests in Helsinki, Finland. *Applied Vegetation Science, 11*(1), 83–98. https://doi.org/10.1111/j.1654-109X.2008.tb00207.x.

Hamberg, L., Malmivaara-Lämsä, M., Lehvävirta, S., & Kotze, D. J. (2009). The effects of soil fertility on the abundance of rowan (*Sorbus aucuparia* L.) in urban forests. *Plant Ecology, 204*(1), 21–32. https://doi.org/10.1007/s11258-008-9561-4.

Hamberg, L., Malmivaara-Lämsä, M., Löfström, I., & Hantula, J. (2014). Effects of a biocontrol agent *Chondrostereum purpureum* on sprouting of *Sorbus aucuparia* and *Populus tremula* after four growing seasons. *BioControl, 59*, 125–137. https://doi.org/10.1007/s10526-013-9550-y.

Harper, K. A., Macdonald, S. E., Burton, P. J., Chen, J., Brosofske, K. D., Saunders, S. C., ... Esseen, P. A. (2005). Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology, 19*(3), 768–782. https://doi.org/10.1111/j.1523-1739.2005.00045.x.

Hauru, K., Koskinen, S., Kotze, D. J., & Lehvävirta, S. (2014). The effects of decaying logs on the aesthetic experience and acceptability of urban forests–Implications for forest management. *Landscape and Urban Planning, 123*, 114–123. https://doi.org/10.1016/j.landurbplan.2013.12.014.

Hauru, K., Lehvävirta, S., Korpela, K., & Kotze, D. J. (2012). Closure of view to the urban matrix has positive effects on perceived restorativeness in urban forests in Helsinki, Finland. *Landscape and Urban Planning, 107*(4), 361–369. https://doi.org/10.1016/j.landurbplan.2012.07.002.

Hauru, K., Niemi, A., & Lehvävirta, S. (2012). Spatial distribution of saplings in heavily worn urban forests: Implications for regeneration and management. *Urban Forestry & Urban Greening, 11*(3), 279–289. https://doi.org/10.1016/j.ufug.2012.03.004.

Hedblom, M., & Söderström, B. (2008). Woodlands across Swedish urban gradients: Status, structure and management implications. *Landscape and Urban Planning, 84*(1), 62–73. https://doi.org/10.1016/j.landurbplan.2007.06.007.

Hedenås, H., & Ericson, L. (2004). Aspen lichens in agricultural and forest landscapes: The importance of habitat quality. *Ecography, 27*(4), 521–531. https://doi.org/10.1111/j.0906-7590.2004.03866.x.

Heinonen, J. (1994). Koealojen puu- ja puustotunnusten laskentaohjelma KPL. Käyttöohje [KPL programme for the computation of tree and stand characteristics. Users guide] (The Finnish Forest Research Institute Research Papers, 504). Retrieved from http://urn.fi/URN:ISBN:951-40-1369-7 (In Finnish).

Hottola, J., Ovaskainen, O., & Hanski, I. (2009). A unified measure of the number, volume and diversity of dead trees and the response of fungal communities. *Journal of Ecology, 97*(6), 1320–1328. https://doi.org/10.1111/j.1365-2745.2009.01583.x.

Hyvärinen, E., Juslén, A., Kemppainen, E., Uddström, A., & Liukko, U. M. (Eds.) (2019). Suomen lajien uhanalaisuus–punainen kirja 2019 [The 2019 Red List of Finnish Species]. Helsinki, Finland: Ministry of the Environment & Finnish Environment Institute (In Finnish with English summaries).

Ives, C. D., Lentini, P. E., Threlfall, C. G., Ikin, K., Shanahan, D. F., Garrard, G. E., ... Kendal, D. (2016). Cities are hotspots for threatened species. *Global Ecology and Biogeography, 25*(1), 117–126. https://doi.org/10.1111/geb.12404.

Jonsson, B. G., Kruys, N., & Ranius, T. (2005). Ecology of species living on dead wood–lessons for dead wood management. *Silva Fennica, 39*(2), 289–309.

Junninen, K., Penttilä, R., & Martikainen, P. (2007). Fallen retention aspen trees on clear-cuts can be important habitats for red-listed polypores: A case study in Finland. *Biodiversity and Conservation, 16*(2), 475–490. https://doi.org/10.1007/s10531-005-6227-6.

Kellomäki, S., Peltola, H., Nuutinen, T., Korhonen, K. T., & Strandman, H. (2007). Sensitivity of managed boreal forests in Finland to climate change, with implications for adaptive management. *Philosophical Transactions of the Royal Society B: Biological Sciences, 363*(1501), 2339–2349. https://doi.org/10.1098/rstb.2007.2204.

Kinnunen, J. (2006). *Espoon keskuspuiston länsiosan liito-orava- ja kääpäinventoinnit 2006 [Inventories of the flying squirrel and polypores in western parts of the Espoo central park] (Espoon ympäristökeskuksen monistesarja, 7/2006).* Espoo, Finland: City of Espoo Environment Centre (In Finnish).

Hyytiäinen, K., Tahvonen, O., & Valsta, L. (2010). Taloudellisesti optimaalisista harvennuksista ja kiertoajoista männylle ja kuuselle [Economically optimal thinnings and rotation times for *Pinus sylvelstris* and *Picea abies*] (Working Papers of the Finnish Forest Research Institute, 143). Retrieved from http://www.metla.fi/julkaisut/workingpapers/2010/mwp143.pdf (In Finnish).

Kolu, S. (2019). Lahopuun määrä ja laatu Lahden kaupunkimetsissä -indikaatiot monimuotoisuudelle [Quantity and quality of dead wood in urban forests of Lahti – indications for biodiversity] (Unpublished master's thesis). Helsinki, Finland: University of Helsinki, Faculty of Biological and Environmental Sciences. Retrieved from https://helda.helsinki.fi/handle/10138/300898 (In Finnish).

Konijnendijk, C. C. (2001). Urban Forestry in Europe. In M. Palo, J. Uusivuori, & G. Mery (Vol. Eds.), *World Forests, Markets and Policies. World Forests: vol. 3*, (pp. 413–424). New York, NY: Springer.

Korhonen, A., Siitonen, J., Kotze, D. J., Immonen, A., & Hamberg, L. (2020). Data for: Stand characteristics and dead wood in urban forests: Potential biodiversity hotspots in managed boreal landscapes. *Mendeley Data, v1*.

Kotiranta, H., & Niemelä, T. (1996). *Threatened polypores in Finland.* Ympäristöopas: Finnish Environment Institute & Edita10.

Kouki, J., Arnold, K., & Martikainen, P. (2004). Long-term persistence of aspen–a key host for many threatened species–is endangered in old-growth conservation areas in Finland. *Journal for Nature Conservation, 12*(1), 41–52. https://doi.org/10.1016/j.jnc.2003.08.002.

Kraxner, F., & Nordström, E. M. (2015). Bioenergy futures: A global outlook on the implications of land use for forest-based feedstock production. In E. Westholm, K. B. Lindahl, & F. Kraxner (Eds.). *The future use of nordic forests* (pp. 63–81). New York, NY: Springer.

Kuusinen, M. (1996). Epiphyte flora and diversity on basal trunks of six old-growth forest tree species in southern and middle boreal Finland. *Lichenologist, 28*, 443–463. https://doi.org/10.1006/lich.1996.0043.

Laasasenaho, J. (1982). Taper curve and volume functions for pine, spruce and birch. *Communicationes Instituti Forestalis Fenniae, 108*, 1–74.

Lammi, E. & Routasuo, P. (2018). Helsingin liito-oravakartoitus 2018 [Flying squirrel survey of Helsinki 2018] (Publications by the Urban Environment Division of the City of Helsinki, 2018:27). Retrieved from https://www.hel.fi/static/liitteet/kaupunkiymparisto/julkaisut/julkaisut/julkaisu-27-18.pdf (In Finnish with English summary).

Lehvävirta, S. (2007). Non-anthropogenic dynamic factors and regeneration of (hemi) boreal urban woodlands–synthesising urban and rural ecological knowledge. *Urban Forestry & Urban Greening, 6*(3), 119–134. https://doi.org/10.1016/j.ufug.2007.05.005.

Lehvävirta, S., & Rita, H. (2002). Natural regeneration of trees in urban woodlands. *Journal of Vegetation Science, 13*(1), 57–66. https://doi.org/10.1111/j.1654-1103.2002.tb02023.x.

Lehvävirta, S., Rita, H., & Koivula, M. (2004). Barriers against wear affect the spatial distribution of tree saplings in urban woodlands. *Urban Forestry & Urban Greening, 3*(1), 3–17. https://doi.org/10.1016/j.ufug.2003.10.001.

Lehvävirta, S., Vilisics, F., Hamberg, L., Malmivaara-Lämsä, M., & Kotze, D. J. (2014).

Fragmentation and recreational use affect tree regeneration in urban forests. *Urban Forestry & Urban Greening, 13*(4), 869–877. https://doi.org/10.1016/j.ufug.2014.10.003.

Loeb, R. E. (2011). What and where are old growth urban forests? *Old growth urban forests* (pp. 1–14). New York, NY: Springer.

Lovett, G. M., Traynor, M. M., Pouyat, R. V., Carreiro, M. M., Zhu, W. X., & Baxter, J. W. (2000). Atmospheric deposition to oak forests along an urban− rural gradient. *Environmental Science & Technology, 34*(20), 4294–4300. https://doi.org/10.1021/es001077q.

Mäkisara, K., Katila, M., Peräsaari, J., & Tomppo, E. (2016). The Multi-Source National Forest Inventory of Finland–methods and results 2013 (Natural Resources and Bioeconomy Studies, 10/2016). Retrieved from http://urn.fi/URN:ISBN:978-952-326-186-0.

Malmivaara-Lämsä, M., Hamberg, L., Haapamäki, E., Liski, J., Kotze, D. J., Lehvävirta, S., & Fritze, H. (2008). Edge effects and trampling in boreal urban forest fragments–impacts on the soil microbial community. *Soil Biology and Biochemistry, 40*(7), 1612–1621. https://doi.org/10.1016/j.soilbio.2008.01.013.

Malmivaara-Lämsä, M., Hamberg, L., Löfström, I., Vanha-Majamaa, I., & Niemelä, J. (2008). Trampling tolerance of understorey vegetation in different hemiboreal urban forest site types in Finland. *Urban Ecosystems, 11*(1), 1–16. https://doi.org/10.1007/s11252-007-0046-3.

Manninen, O. (2017). Helsingin lahokaviosammalselvitys 2017 [The green shield-moss survey of Helsinki 2017] (Publications by the Urban Environment Division of the City of Helsinki, 2017:8). Retrieved from https://www.hel.fi/static/liitteet/kaupunkiymparisto/julkaisut/julkaisut/julkaisu-08-17.pdf (In Finnish with English summary).

Martikainen, P. (2001). Conservation of threatened saproxylic beetles: Significance of retained aspen *Populus tremula* on clearcut areas. *Ecological Bulletins, 49*, 205–218.

Martikainen, P., Penttilä, R., Kotiranta, H., & Miettinen, O. (2000). New records of *Funalia trogii*, *Perenniporia tenuis* and *Polyporus pseudobetulinus* from Finland, with notes on their habitat requirements and conservation implications. *Karstenia, 40*(1–2), 79–92.

Matlack, G. R. (1993). Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation, 66*(3), 185–194.

Müller, J., & Bütler, R. (2010). A review of habitat thresholds for dead wood: A baseline for management recommendations in European forests. *European Journal of Forest Research, 129*(6), 981–992. https://doi.org/10.1007/s10342-010-0400-5.

Natural Resources Institute Finland. (2019). Mean volume of decayed and other dead trees on forest land (m3/ha). Retrieved April 1, 2019 from http://statdb.luke.fi/PXWeb/pxweb/en/LUKE/LUKE__04%20Metsa__06%20Metsavarat/2.06_Kuolleen_puuston_keskitilavuus_metsam.px/table/tableViewLayout1/?rxid=dc711a9e-de6d-454b-82c2-74ff79a3a5e0.

Nilsson, S. G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J. M., Linder, P., ... Ranius, T. (2002). Densities of large living and dead trees in old-growth temperate and boreal forests. *Forest Ecology and Management, 161*, 189–204. https://doi.org/10.1016/S0378-1127(01)00480-7.

Nordén, J., Åström, J., Josefsson, T., Blumentrath, S., Ovaskainen, O., Sverdrup-Thygeson, A., & Nordén, B. (2018). At which spatial and temporal scales can fungi indicate habitat connectivity?. *Ecological Indicators, 91*, 138–148. https://doi.org/10.1016/j.ecolind.2018.03.062.

Nuotio, A-K. (ed.) (2007). Viheralueiden hoitoluokitus [Management categorization of urban green areas] (Viherympäristöliitto ry julkaisu, 36). Helsinki, Finland: The Finnish Association of Landscape Industries (In Finnish).

Official Statistics of Finland (2019). Preliminary population structure by area, 2019M01. Retrieved February 28, 2019 from http://pxnet2.stat.fi/PXWeb/pxweb/en/StatFin/StatFin__vrm__vamuu/statfin_vamuu_pxt_11lj.px/table/tableViewLayout1/.

Ordóñez, C., & Duinker, P. N. (2013). An analysis of urban forest management plans in Canada: Implications for urban forest management. *Landscape and Urban Planning, 116*, 36–47. https://doi.org/10.1016/j.landurbplan.2013.04.007.

Poland, T. M., & McCullough, D. G. (2006). Emerald ash borer: Invasion of the urban forest and the threat to North America's ash resource. *Journal of Forestry, 104*(3), 118–124. https://doi.org/10.1093/jof/104.3.118.

Pregitzer, C. C., Charlop-Powers, S., Bibbo, S., Forgione, H. M., Gunther, B., Hallett, R. A., & Bradford, M. A. (2019). A city-scale assessment reveals that native forest types and overstory species dominate New York City forests. *Ecological Applications, 29*(1), e01819. https://doi.org/10.1002/eap.1819.

Core Team, R. (2018). *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing Retrieved from https://www.R-project.org/.

Renvall, P. (1995). Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. *Karstenia, 35*, 1–51.

Rinne-Garmston, K., Peltoniemi, K., Chen, J., Peltoniemi, M., Fritze, H., & Mäkipää, R. (2019). Carbon flux from decomposing wood and its dependency on temperature, wood N2 fixation rate, moisture and fungal composition in a Norway spruce forest. *Global Change Biology, 25*(5), 1852–1867. https://doi.org/10.1111/gcb.14594.

Rydberg, D., & Falck, J. (2000). Urban forestry in Sweden from a silvicultural perspective: A review. *Landscape and Urban Planning, 47*(1–2), 1–18. https://doi.org/10.1016/S0169-2046(99)00068-7.

Rytter, L., Ingerslev, M., Kilpeläinen, A., Torssonen, P., Lazdina, D., Löf, M., ... Stener, L. G. (2016). Increased forest biomass production in the Nordic and Baltic countries–a review on current and future opportunities. *Silva Fennica, 50*(5), 1660.

Saukkonen, T., Holstein, M., Siuruainen, A., Ylikotila, T., & Virtanen, T. (2013). Luonnonhoidon työohje–Metsät [Management guidelines for urban nature–Forests] (Publications by City of Helsinki Public Works Department, 2013:9). Retrieved from https://www.hel.fi/static/hkr/julkaisut/2013/luonnonhoidon_ohje_2013_web.pdf (In Finnish).

Savola, K. (2012). Helsingin metsien kääpäselvitys 2011 [The polypore survey of the forests in Helsinki 2011] (Publications by City of Helsinki Environment Centre, 5/2012). Retrieved from https://www.hel.fi/static/ymk/julkaisut/julkaisu-05-12.pdf (In Finnish).

Savola, K. (2015). Helsingin metsien kääpäselvityksen täydennys 2014 [The polypore survey of the forests in Helsinki – supplement 2014] (Publications by City of Helsinki Environment Centre, 1/2015). Retrieved from https://www.hel.fi/static/ymk/julkaisut/julkaisu-01-15.pdf (In Finnish).

Savola, K. (2016). Helsingin Haltialan metsien kääpäselvitys 2015 [The polypore survey of the forests in Haltiala, Helsinki 2015] (Publications by City of Helsinki Environment Centre, 3/2016). Retrieved from https://www.hel.fi/static/ymk/julkaisut/julkaisu-03-16.pdf (In Finnish).

Savola, K., & Kolehmainen, K. (2015). Pääkaupunkiseudun Viherkehän suojelualueiden käävät [Polypores in the Green Belt protected areas of the Helsinki Metropolitan Area] (Metsähallituksen luonnonsuojelujulkaisuja A 220). Retrieved from https://julkaisut.metsa.fi/assets/pdf/lp/Asarja/a220.pdf (In Finnish).

Savola, K., & Wikholm, M. (2005). *Vantaan kääpätutkimus 2003/2004 [Polypore survey in Vantaa 2003/2004].* Vantaa, Finland: City of Vantaa Environment Centre (In Finnish).

Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins, 49*, 11–41.

Siitonen, J., Hottola, J., & Immonen, A. (2009). Differences in stand characteristics between brook-side key habitats and managed forests in southern Finland. *Silva Fennica, 43*(1), 21–37.

Siitonen, J., Martikainen, P., Punttila, P., & Rauh, J. (2000). Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest Ecology and Management, 128*(3), 211–225. https://doi.org/10.1016/S0378-1127(99)00148-6.

Siitonen, P., Lehtinen, A., & Siitonen, M. (2005). Effects of forest edges on the distribution, abundance, and regional persistence of wood-rotting fungi. *Conservation Biology, 19*(1), 250–260. https://doi.org/10.1111/j.1523-1739.2005.00232.x.

Snäll, T., & Jonsson, B. G. (2001). Edge effects on six polyporous fungi used as old-growth indicators in Swedish boreal forest. *Ecological Bulletins, 49*, 255–262.

Solantie, R. (2005). Productivity of boreal forests in relation to climate and vegetation zones. *Boreal Environment Research, 10*, 275–297.

Staffas, L., Gustavsson, M., & McCormick, K. (2013). Strategies and policies for the bioeconomy and bio-based economy: An analysis of official national approaches. *Sustainability, 5*(6), 2751–2769. https://doi.org/10.3390/su5062751.

Statistics Sweden. (2019). Skyddad natur 2018-12-31 [Protected nature 2018]. Retrieved from https://www.scb.se/contentassets/0581e8801be54a20983ef7afd0281214/mi0603_2018a01_sm_mi41sm1901.pdf.

Syrjänen, K., Hakalisto, S., Mikkola, J., Musta, I., Nissinen, M., Savolainen, R., Seppälä, J., Seppälä, M., Siitonen, J. & Valkeapää, A. 2016. Identification of forest ecosystems valuable in terms of biodiversity. Scientific selection criteria of the Forest Biodiversity Programme for Southern Finland (METSO) 2016–2025 (Reports of the Ministry of the Environment, 17/2016). Retrieved from http://urn.fi/URN:ISBN:978-952-11-4606-0 (In Finnish with English summary).

Tikkanen, O. P., Martikainen, P., Hyvärinen, E., Junninen, K., & Kouki, J. (2006). Red-listed boreal forest species of Finland: Associations with forest structure, tree species, and decaying wood. *Annales Zoologici Fennici, 43*, 373–383.

Tyrväinen, L., Silvennoinen, H., & Kolehmainen, O. (2003). Ecological and aesthetic values in urban forest management. *Urban Forestry & Urban Greening, 1*(3), 135–149. https://doi.org/10.1078/1618-8667-00014.

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). New York, NY: Springer.

Ylisirniö, A. L., Mönkkönen, M., Hallikainen, V., Ranta-Maunus, T., & Kouki, J. (2016). Woodland key habitats in preserving polypore diversity in boreal forests: Effects of patch size, stand structure and microclimate. *Forest Ecology and Management, 373*, 138–148. https://doi.org/10.1016/j.foreco.2016.04.042.

Zerbe, S. (2001). On the ecology of *Sorbus aucuparia* (Rosaceae) with special regard to germination, establishment and growth. *Polish Botanical Journal, 46*, 229–239.