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Urban forests host rich polypore assemblages in a Nordic metropolitan area

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HIGHLIGHTS

- Polypore species richness was dependent mainly on the abundance of dead wood.
- Both forest fragmentation and dense human population decreased red-listed species occurrences.
- Accounting for urbanization was not important in predicting individual species occurrences.

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ABSTRACT

Urban forests are often remnants of former larger forested areas, and traditionally considered as degraded habitats due to negative effects of urbanization. However, recent studies have shown that urban forests managed for recreational purposes can be structurally close to natural forests and may provide habitat features, such as dead wood, that are scarce in intensively managed forest landscapes. In this study, we assessed how urbanization affects polypore species richness and the number of red-listed polypore species in forest stands, and the occurrences of polypore species on individual units of dead wood. Spruce-inhabiting polypore assemblages and their associations to urbanization, local habitat connectivity and dead-wood abundance were investigated in southern Finland. The effects of urbanization on polypore species richness and individual species were largely negligible when other environmental variability was accounted for. Several red-listed polypore species were found in dead-wood hotspots of urban forests, though urbanization had a marginally significant negative effect on their richness. The main driver of total species richness was dead-wood abundance while the number of red-listed species was also strongly dependent on local habitat connectivity, implying that a high degree of fragmentation can decrease their occurrence in urban forests. We conclude that the highest potential for providing habitats for threatened species in the urban context lies in large peri-urban recreational forests which have been preserved for recreational purposes around many cities. On the other hand, overall polypore diversity can be increased simply by increasing dead-wood abundance, irrespective of landscape context.

1. Introduction

Urban forests are often remnants of previously larger, contiguous forested areas. They have traditionally been considered as low-value habitats due to negative effects of urbanization (e.g. Cavin, 2013). However, as urban forests are managed primarily for recreational purposes and not for wood production, they can be structurally close to natural forests and maintain important habitat features, such as dead wood, that are scarce in intensively managed forest landscapes (Hedblom & Söderström, 2008; Korhonen, Siitonen, Kotze, Immonen, & Hamberg, 2020). Urban forests may therefore provide important habitats for different taxa in human-modified landscapes (Alvey, 2006; Croci, Butet, Georges, Aguejdad, & Clergeau, 2008; Ives et al., 2016; Soanes et al., 2019).

Forested urban greenspaces and recreational forests are usually set aside from wood production and offer more freedom for biodiversity-oriented management than commercially managed forests (Gundersen et al., 2005; Hedblom & Söderström, 2008). In the boreal zone of

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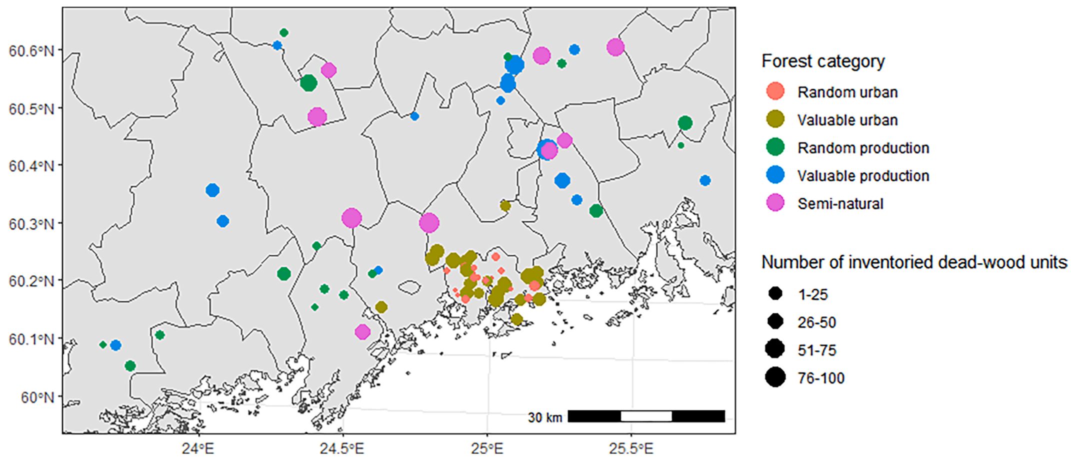

Fig. 1. Locations of studied forest stands in southern Finland. Forest stands sampled in the different forest categories are indicated by different colors. Size of the dot reflects the number of dead-wood units inventoried in the stand.

northern Europe, replenishment of dead wood is one of the key goals in ecological restoration of forests (Similä & Junninen, 2012). Dead wood is a vital resource for ca. 20–25% of forest species in the region, and the quantities of coarse woody debris have been reduced by over 90% from the levels found in natural forests because of intensive wood harvesting (Siitonen, 2001). Along with decreased amount of old forests and old trees, decreased amount of dead wood is among the leading causes of threat for forest species in Finland (Hyvärinen et al., 2019). Urban forests represent areas where dead wood could be retained with relatively low economic costs. However, only a few studies have addressed the potential effects of urbanization on dead-wood inhabiting species diversity (see Fattorini & Galassi, 2016; Meyer, Rusterholz, & Baur, 2021).

Among dead-wood dependent organisms, polypore fungi (a form group of Basidiomycota characterized by poroid hymenophores) play a key role in the decomposition process of the woody material in boreal forests (Niemelä, 2016). Diverse decay processes employed by different species also contribute to the diversity of dead-wood microhabitats and saproxylic diversity (Niemelä, Renvall, & Penttilä, 1995; Lindner et al., 2011; Dickie, Fukami, Wilkie, Allen, & Buchanan, 2012; Birkemoe et al., 2018). Because polypores are sensitive to dead-wood availability, they have often been targeted in biodiversity studies, and they are commonly used as indicators of conservation value in boreal forests (Kotiranta & Niemelä, 1996; Nitare, 2000). In the boreal zone, species richness of polypores generally correlates with local abundance and diversity of dead-wood substrates (e.g. Penttilä, Siitonen, & Kuusinen, 2004; Similä, Kouki, Mönkkönen, Sippola, & Huhta, 2006; Hottola, Ovaskainen, & Hanski, 2009). However, distribution and history of suitable habitats over larger regional scales also play a role in shaping polypore communities (e.g. Penttilä, Lindgren, Miettinen, Rita, & Hanski, 2006; Nordén et al., 2013).

In urbanized areas, forest fragments are situated within a heterogenous matrix. Environmental conditions in small forest fragments may thus be strongly affected by the proximity of adjacent built-up areas. Urban environmental stress factors include edge effects (Harper et al., 2005), trampling (Hamberg, Lehvävirta, Minna, Rita, & Kotze, 2008), aerial pollution and high nitrogen deposition (e.g. Lovett et al., 2000; Bettez & Groffman, 2013; Andrew et al., 2018), and their intensity is expected to increase along the rural-to-urban gradient (McDonnell & Pickett, 1990). These stress factors are known to alter forest vegetation, but their significance for wood-inhabiting fungal communities has not been studied. However, studies in rural forest landscapes have demonstrated that wood-inhabiting fungi can be sensitive to highly contrasting edges (Snäll & Jonsson, 2001; Selonen, Ahlroth, & Kotiaho, 2005; Siitonen, Lehtinen, & Siitonen, 2005; Ylisirniö, Mönkkönen, Hallikainen, Ranta-Maunus, & Kouki, 2016) that are also characteristic to urban forests in built-up landscapes.

In this study, we assess the significance of urbanization in shaping the species richness and species composition of spruce-associated polypores by using fruiting body inventory data from urban, peri-urban and rural forest stands in southern Finland. We analyzed urbanization as a landscape gradient quantified by resident human population density. To separate the effect of urbanization from other variability in habitat quality, we accounted for dead-wood abundance and local cover of mature forest. Our hypothesis was that urbanization has an added effect on polypore species communities that can be distinguished from the variability due to the effects of other habitat variables. Firstly, we looked for this effect in terms of (1) total species richness and (2) the number of red-listed species at the forest stand level. The effect of urbanization was disentangled from other stand-level variability with the use of generalized additive models. Secondly, we applied joint species distribution modeling to reveal species-specific responses to urbanization and other environmental variables down to the level of individual dead-wood units.

2. Material and methods

2.1. Study sites

Study sites were distributed in and around the Helsinki metropolitan area in southern Finland (Fig. 1). The Helsinki metropolitan area is the main urban conglomeration in this region, consisting of the cities of Helsinki (area 214 km^2, population density 3060 per km^2), Espoo (312 km^2, 930 per km^2) and Vantaa (240 km^2, 990 per km^2) with a combined population of ca. 1.2 million National Land Survey of Finland, 2020; Statistics Finland, 2020a). By European standards, a large proportion of green space remains between residential areas in the Helsinki metropolitan area (Kasanko et al., 2006). In the city of Helsinki, forests cover ca. 22% of the land area (Erävuori et al., 2019). The study area is situated at the southern edge of the Fennoscandian boreal zone (Ahti, Hämet-Ahti, & Jalas, 1968), and forests in the area are predominantly conifer-dominated.

Study sites were selected based on the following criteria: 1) vegetation type was herb-rich to mesic heathland forest, corresponding to the *Oxalis-Myrtillus* type (OMT) or *Myrtillus* type (MT) (Cajander, 1926), 2) the dominating tree species was Norway spruce (*Picea abies*), and 3) the age of dominating trees was at least 60 years.

To cover different degrees of urbanization and dead-wood resource abundance, we sampled forests in five different categories: randomly selected urban forests (n = 17), valuable urban forests (n = 24), randomly selected production forests (n = 16), valuable production

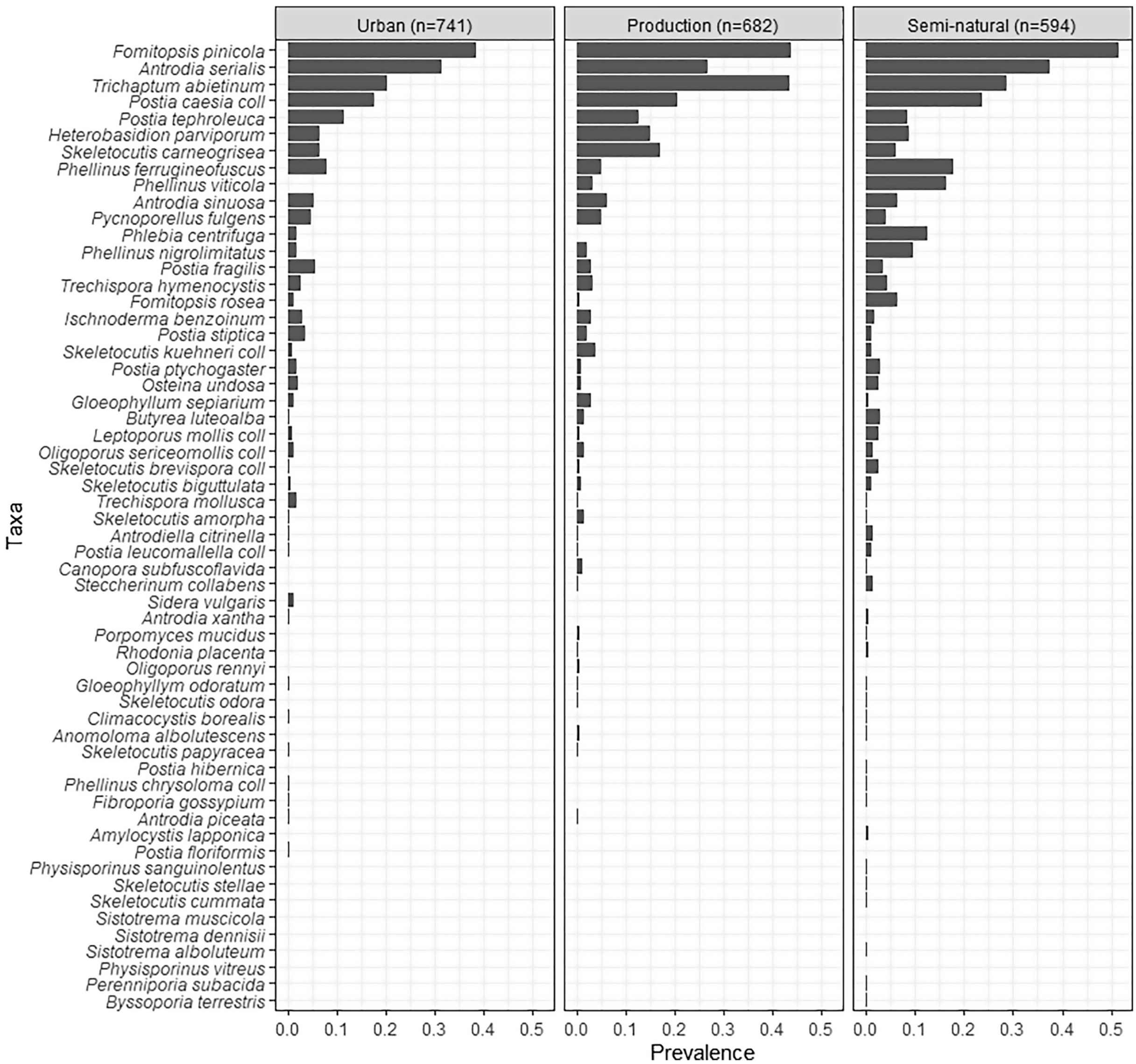

Fig. 2. Species prevalence (proportion of dead-wood units occupied by polypore species) in investigated forest categories. *N* denotes the number of inventoried dead-wood units in each category. Data from random urban (number of studied dead-wood units, $n = 73$) and valuable urban ($n = 668$) forests and from random production ($n = 238$) and valuable production ($n = 444$) forests have been pooled.

Table 1
Generalized additive model results concerning polypore species richness at the stand level. Models followed Poisson distribution with a log-link function. Deviance explained, parameter estimates with standard errors in transformed scale and *p* values are given. *P* values with < 0.05 significance level are in bold and those with $0.05 \leq p < 0.10$ significance level are underlined. ($n = 81$).

	Deviance explained (%)	Parametric coefficients								Smooth term
		Intercept		Human population density		Heat sum		Naturalness[a]		Dead-wood abundance (m^3 ha^{-1}) and mature forest cover within 200 m radius[b]
		Est. ± SE	*p*	Est. ± SE	*p*	Est. ± SE	*p*	Est. ± SE	*p*	*p*
Total species richness	79.8	2.33 ± 0.06	<0.001	−0.01 ± 0.03	0.600	0.11 ± 0.04	**0.003**	–	–	**<0.001**
Number of red-listed species	57.6	−0.66 ± 0.30	0.027	−0.26 ± 0.15	0.091	–	–	0.34 ± 0.59	0.563	**0.002**

[a] Forest naturalness was included as a two-level factor indicating whether a site was semi-natural (1) or not (0).
[b] The effects of dead-wood abundance and surrounding mature forest cover were modelled conjointly with a tensor product smooth. See Fig. 3 for graphical results.

forests ($n = 15$) and semi-natural forests ($n = 9$). Randomly selected urban and production forests were sampled from forest stand data obtained from the city of Helsinki and National Forest Inventory data, respectively. Furthermore, we also included valuable urban sites across the Helsinki metropolitan area (cities of Helsinki, Vantaa and Espoo) that were known to be rich in dead wood. These sites were necessary to

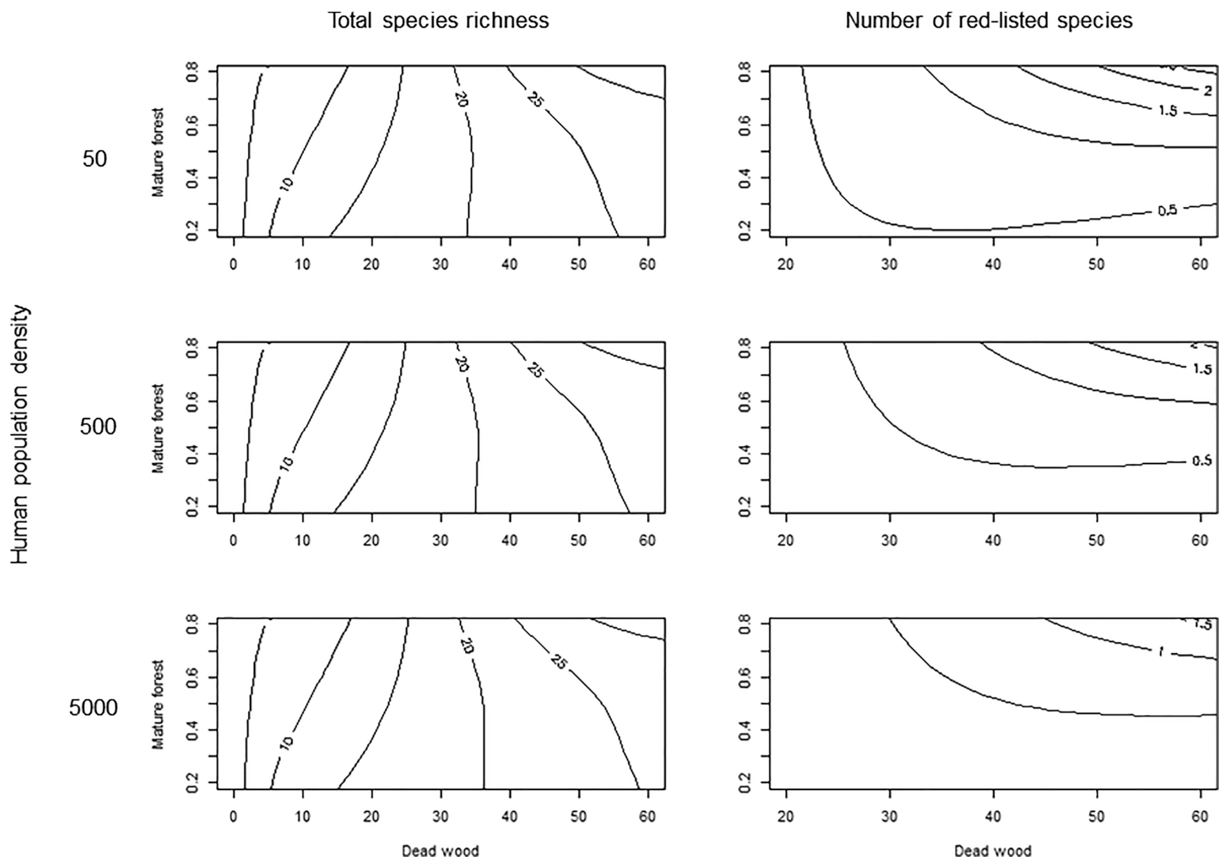

Fig. 3. Predicted total polypore species richness (left column) and number of red-listed polypore species (right column) as contours within 1 ha, across gradients of dead-wood abundance in m^3 ha^{-1} (Dead wood), proportion of surrounding mature forest cover within 200 m radius (Mature forest) and urbanization as human population density per km^2 from 50 to 5000 (rows from top to bottom). Heat sum, included in the model for total species richness, was set to mean value (1562). Predictions for red-listed species richness are for forests that are assumed to have recent management history, i.e. not considered as semi-natural.

distinguish the effects of dead-wood abundance from the effect of urbanization on polypore species diversity. These sites were chosen based on forest site type characterizations in polypore species inventory reports commissioned by the cities (Savola & Wikholm, 2005; Kinnunen, 2006; Savola 2015). Valuable production forests were selected from sites included in the Forest Biodiversity Programme for Southern Finland (METSO). These sites were either permanently or provisionally protected under the METSO programme which started in 2008, and they represent former production forests where natural-like characteristics, such as dead wood, have developed to varying degrees (Syrjänen et al., 2016). Furthermore, nine semi-natural stands were selected from the best available representatives of natural-like old spruce forests with large amounts of dead wood. These stands were situated within rural protected areas and had no visible signs of forest management or only minimal signs of past selective logging.

2.2. Inventory plots and polypore survey

Inventory plots were delimited and recorded in GPS tracks by following natural boundaries of each forest stand, so that the forest vegetation type and stand structure within the plot remained homogenous. Stand boundaries were set at forest edges or at transition zones where tree stand composition or the type of field layer vegetation changed. Therefore, inventory area varied from stand to stand between 0.23 and 4.9 ha (mean 1.2 ha). In semi-natural forest sites, that often have large stands with unclear boundaries, inventory plots of ca. 1 ha were located within the stands in random places to keep the sampling effort within reasonable limits.

Polypore fruiting bodies were surveyed once in each stand during September-November of 2009, 2010, 2013–2015 and 2018–2019. Within the inventory plots, all pieces of dead Norway spruce (*Picea abies*), that were at least 15 cm in basal diameter and 1.3 m long and in middle stages of decay (classes 2–4; Renvall, 1995), were surveyed. Wood in the earliest and latest stages of decay, i.e. classes 1 and 5, supports polypore fruiting infrequently (Renvall, 1995) and was not included in the inventories. Dead wood units on the edges of the inventory plot were included only if the basal part of the unit was inside the inventory plot. All surveyed dead wood units were inspected for living fruiting bodies of polypore fungi (Niemelä, 2016) and one corticioid indicator species *Phlebia centrifuga* (hereafter included under the collective term polypores). Occurrences were recorded as presence–absence data on the level of individual dead-wood units (data available in Korhonen et al. (2021)).

2.3. Dead-wood measurement and volume calculation

Each surveyed dead-wood unit was measured for volume calculation and assigned to a decay class following Renvall's (1995) classification that is based on knife penetration into the wood. Plots depicting volume and decay class distribution of surveyed dead-wood units in forest category groups are provided in Appendix A Fig. A1.

Diameter at breast height (DBH, 1.3 m) was measured for entire fallen trees. Basal diameter and height (length) were measured for snags (standing dead trees with missing tops), pieces of logs, cut bolts, and fallen or cut tops. Volumes of dead wood units were calculated using the KPL program (Heinonen, 1994). Volume equations based on DBH and length (Laasasenaho, 1982) were applied for calculating the volume of entire dead trees. The volume of pieces of dead trees was calculated

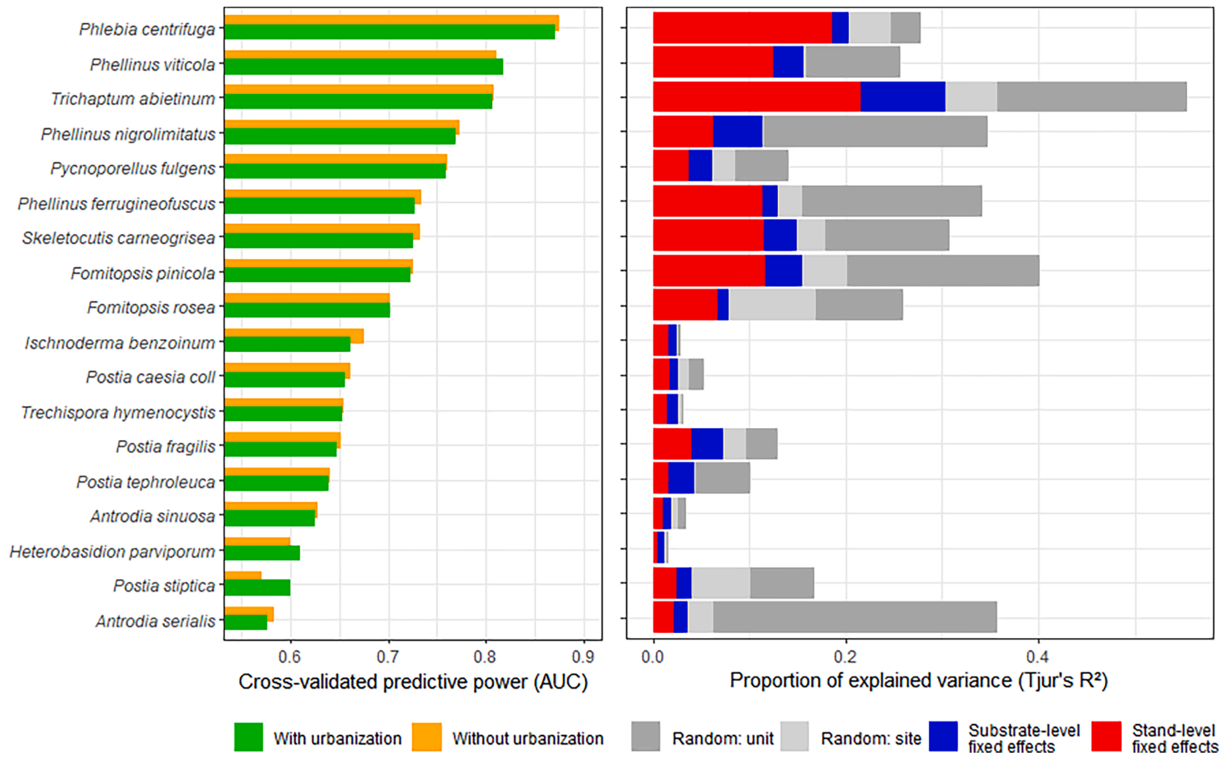

Fig. 4. Predictive power of the joint species distribution models with and without accounting for urbanization (left panel) and variance partitioning of the full model among measured environmental explanatory variables and random effects (right panel). Predictive power is based on four-fold cross-validation where data was partitioned over forest stands so that random effects were excluded. Therefore, predictive power was solely based on inference with fixed effects, i.e. measured environmental variability. Variance (Tjur's R^2) explained by the full joint species distribution model was partitioned among grouped environmental variables (fixed effects) and random effects. Fixed effects have been grouped into substrate-level variables (decay class, volume) and stand-level variables (dead-wood abundance, surrounding forest cover, naturalness, heat sum and urbanization). Total length of the bar indicates how much of variance was explained by the model for each species in total. Length of the colored sections indicate how much of the explained variation is attributed to measured environmental variability (fixed effects: red and blue) and how much to unmeasured variability captured by the random effects (grey). In the calculation of variance partitioning, covariances among variables have been accounted for within each group but not for between groups (Ovaskainen and Abrego 2020). Old-forest indicator species are denoted with an asterisk.

based on the basal diameter and length of each piece by means of taper curve functions (Laasasenaho, 1982). Heights of entire trees required for volume calculations were estimated from previously collected sample tree data from similar forest types in the study region (1625 measured Norway spruce trees).

2.4. Stand-level environmental variables

We used resident human population density to measure the degree of urbanization (see e.g. Kuussaari et al., 2021). Higher human population density is generally associated with increased land cover alteration and intensity of land use (McDonnell et al., 1997). Values of population density were extracted from 1 km × 1 km population grid data (Statistics Finland, 2020b) from the year 2018 and assigned to inventory plots based on their location on the grid. For analyses, values were log-transformed in order to make them more normally and evenly distributed across study sites.

Local abundance of dead wood was measured as the pooled volume of dead-wood units within the inventory plot, calculated per hectare ($m^3\ ha^{-1}$). The amount of potential habitat in the near neighborhood of the inventory plot was calculated as the proportion (0–1) of mature, i.e. at least 60 y old forest within a 200 m radius from the center of the inventory plot. Spatial data of forest stand age estimates was attained from multi-source national forest inventory maps (Mäkisara et al., 2019). Graphical representation of the spatial scales of data collection are provided in Appendix B Fig. B1. Distributions of stand-level environmental variables among forest categories and variable intercorrelations are provided in Appendix C Figs. C1 and C2.

To account for variation in weather conditions between inventory sites and years (Abrego, Halme, Purhonen, & Ovaskainen, 2016), we calculated the cumulative heat sum for each inventory plot from the beginning of the year to the inventory date, measured at the nearest weather station (Finnish Meteorological Institute, 2020). Heat sum was defined as the sum of the positive differences between diurnal mean temperatures and 5 °C.

2.5. Polypore data and species richness

In total, the data consisted of 4604 fruiting body observations belonging to 58 taxa (Fig. 2), distributed on 2017 dead-wood units in 81 forest stands. In taxonomic nomenclature, we followed Kotiranta et al. (2020) but considered some recently revised species complexes collectively. Those included *Leptoporus mollis* coll. (including *L. erubescens* (Fr.) Bourdot & Galzin and *L. mollis* s.str. (Pers.: Fr.) Quél.), *Oligoporus sericeomollis* coll. (including *O. romellii* (M.Pieri & B.Rivoire) Niemelä and *O. sericeomollis* s.str. (Romell) Jülich), *Phellinus chrysoloma* coll. (including *Ph. abietis* (P. Karst.) Jahn and *Ph. chrysoloma* s.str. (Fr.) Donk), *Postia caesia* coll. (see Miettinen, Vlasák, Rivoire, & Spirin, 2018), *Po. leucomallella* coll. (*Po. calvenda* nom. Prov. and *Po. rufescens* nom. Prov.), *Skeletocutis brevispora* coll. (*S. brevispora* s.str. Niemelä and *S. delicata* Miettinen & Niemelä) and *Skeletocutis kuehneri* coll. (*S. exilis* Miettinen & Niemelä and *S. kuehneri* A. David).

We quantified species richness in forest stands with two measures: total number of all observed species and the number of red-listed species. Species assessed as at least near threatened (IUCN classification; Kotiranta et al., 2019) were included in the red-listed species. Observed

Table 2
Species niches based on standardized model coefficients (posterior means) from the joint species distribution model. Red color indicates positive and blue negative effect of an explanatory variable on the probability of occurrence of an investigated species. Darker colors indicate 95% posterior probability and lighter colors 90% posterior probability for coefficients deviating from 0 (white cells indicate non-significant effects). Coefficient explanations: interaction is between dead-wood abundance and mature forest cover, naturalness refers to forest management history, i.e. semi-natural stand (1) or not (0), urbanization is human population density (log-transformed). Old-forest indicator species (Niemelä 2016) are denoted with an asterisk. (For interpretation of the references to color in this table legend, the reader is referred to the web version of this article.)

	Intercept	Decay class 3	Decay class 4	Substrate volume	Dead-wood abundance	Mature forest cover	Interaction	Naturalness	Heat sum	**Urbanization**
Antrodia serialis	-0.698	0.402	-0.171	0.590	0.001	0.252	-0.010	0.283	-0.040	0.000
Antrodia sinuosa	-1.136	0.412	0.378	0.424	0.006	0.782	-0.021	0.256	0.032	-0.001
Fomitopsis pinicola	1.177	-0.140	-0.883	1.234	0.009	0.516	-0.027	0.470	-0.071	-0.001
*Fomitopsis rosea**	-4.517	0.041	-0.627	1.077	-0.004	1.312	0.003	0.298	-0.073	0.001
Heterobasidion parviporum	-0.606	-0.106	-0.309	0.645	-0.005	0.131	-0.018	0.309	-0.086	>-0.001
Ischnoderma benzoinum	-1.658	0.263	-0.034	0.941	0.001	1.095	-0.016	0.047	0.031	-0.001
*Phellinus ferrugineofuscus**	-3.104	-0.468	-1.751	0.470	-0.001	1.349	-0.007	0.410	-0.039	0.001
*Phellinus nigrolimitatus**	-4.263	0.865	0.928	-0.170	0.001	1.639	0.021	0.102	-0.100	0.000
*Phellinus viticola**	-1.861	0.312	0.125	-0.226	0.002	1.797	0.015	0.365	-0.207	-0.001
*Phlebia centrifuga**	-4.605	-0.355	-1.567	1.619	0.001	2.154	-0.001	0.782	0.022	0.001
Postia caesia coll	0.193	-0.161	-0.798	0.505	0.008	0.938	-0.037	0.357	-0.024	-0.001
Postia fragilis	-2.785	0.466	0.534	0.388	0.005	1.238	-0.021	0.042	0.073	<0.001
Postia stiptica	-2.237	0.030	-0.185	0.251	0.006	0.613	-0.025	0.026	0.104	<0.001
Postia tephroleuca	-0.882	0.172	-0.368	0.533	0.009	0.576	-0.038	0.183	-0.010	0.000
*Pycnoporellus fulgens**	-0.737	0.592	0.290	1.276	0.006	0.256	-0.019	0.301	0.054	-0.001
Skeletocutis carneogrisea	-0.393	-0.626	-2.104	0.904	-0.007	0.607	-0.027	0.241	0.036	-0.001
Trechispora hymenocystis	-1.657	0.413	0.878	-0.039	0.007	0.521	-0.017	0.258	-0.007	-0.001
Trichaptum abietinum	2.035	-1.403	-3.259	0.920	-0.001	-0.479	-0.036	0.603	-0.139	-0.001

red-listed species included *Amylocystis lapponica* (near threatened), *Anomoloma albolutescens* (near threatened), *Antrodia piceata* (vulnerable), *Antrodiella citrinella* (near threatened), *Fomitopsis rosea* (near threatened), *Perenniporia subacida* (near threatened), *Skeletocutis brevispora* coll. (including *Sk. brevispora* s.str. and *Sk. delicata*, both near threatened), *Sk. cummata* A. Korhonen & Miettinen (vulnerable, assessed with misapplied name *Sk. ochroalba* Niemelä), *Sk. odora* (near threatened), *Sk. stellae* (vulnerable) and *Steccherinum collabens* (near threatened). Observations of *Sidera vulgaris* (near threatened) were excluded from the analyses because its distribution covers only the southernmost part of the study area (Niemelä, 2016). The complete list of species with information about Red List status, causes of threat, old-forest indicator status (Niemelä, 2016) and numbers of observations are provided in Appendix D Table D1.

2.6. Analyses of stand-level species richness

To study the effects of urbanization on stand-level species richness, we estimated generalized additive models that allow fitting of curvilinear relationships between response and explanatory variables. Models were estimated with R (v.4.0.2; R core team, 2020) package *mgcv* v.1.8–33 (Wood, 2017). Models following Poisson distribution with a log-link function were initially fitted with all environmental variables, i.e. human population density (inhabitants per 1 km^2, log-transformed) describing urban–rural gradient, local dead-wood abundance (m^3 ha^{-1}), surrounding mature forest cover (proportion within 200 m radius) and heat sum (centered and scaled to unit standard deviation). In addition, we included a categorical control variable indicative of management history of the site (semi-natural stand or not) in the model for red-listed species. This variable was added to account for potential overrepresentation of red-listed species in semi-natural sites due to longer historical habitat continuity (Penttilä et al. 2004; Berglund, Hottola, Penttilä, & Siitonen, 2011; Nordén et al., 2018). Inventory area (log-transformed) was included as an offset term to account for differences between the sizes of studied areas. After estimating the initial models, we reduced model complexity for red-listed species by excluding heat sum that had a statistically insignificant effect. Other explanatory variables were kept in the models regardless of statistical significance.

The effects of dead-wood abundance and mature forest cover were assumed to be interconnected, so that the positive effect of dead-wood abundance would be greater in a plot that has more mature forest in the surroundings compared to one that has less. To take this potential interaction into account, the effect of dead-wood abundance and mature forest cover was modelled jointly with a tensor product smooth (Wood, 2006). Population density (log-transformed) and heat sum were included in the models as linear terms.

2.7. Analysis of species-specific responses to urbanization

To examine the significance of substrate-level and landscape-level environmental predictors in explaining species composition in more detail, we fitted joint species distribution models with Hierarchical Modeling of Species Communities (implemented with R package *Hmsc* v.3.0–6; Tikhonov et al., 2020). The response variable in the models was species presence or absence on a dead-wood unit that was modelled with a binomial distribution with a probit-link function. We included species with a minimum of 40 occurrences (representing 91% of all fruiting body observations) amounting to 18 species in total. Those species included six old-forest indicator species (Niemelä, 2016), one of which was also red-listed (*Fomitopsis rosea*).

To evaluate the significance of urbanization in explaining species occurrences specifically, we fitted two different model variants, one with and one without accounting for human population density while including all other relevant environmental variables in both models. Models were estimated at the level of individual dead-wood units, and environmental variables included in the models were volume (m^3, log-transformed) and decay class (three categories) for each dead-wood unit, stand-level dead-wood abundance (m^3 ha^{-1} calculated without the volume of the focal dead-wood unit), mature forest cover (within a 200 m radius around the stand), interaction between the last two, heat sum and forest naturalness (semi-natural or not). We included two random factors reflecting the nested sampling design: the dead-wood unit and the inventory plot. The dead-wood unit as a random factor takes into account the fact that more than one polypore species may have been recorded from the same growth substrate and the plot-level random factor that several polypore observations were recorded within the same stand instead of totally random sampling. In addition, we included information on the phylogenetic relationships with a taxonomy-based tree (Ovaskainen & Abrego, 2020) following the classifications of Justo et al. (2017) for Polyporales and Niemelä (2016) for other groups. The applied taxonomy is provided in Appendix E Table E1.

We fitted the models with two Markov Chain Monte Carlo (MCMC) chains, each of which consisted of 150,000 iterations, out of which we discarded the first 50,000 as burn-in and thinned the remaining by 100 to yield in total 2000 posterior samples. We assessed the convergence of the MCMC chains by examining the distribution of the potential scale reduction factor over the parameters that measure the responses of the species to the fixed effects included in the model. Model performance was evaluated by calculating Tjur's R^2 (also known as the coefficient of discrimination; Tjur, 2009) and area under the receiver operating characteristics curve (AUC; Pearce & Ferrier, 2000). Predictive power was calculated by four-fold cross-validation. Sampling units were divided into four folds over inventory plots which eliminated the effects of both random factors (dead-wood unit and inventory plot), and therefore, predictions were based solely on fixed effects.

3. Results

3.1. Stand-level species richness

After accounting for other environmental variability, the effect of urbanization (human population density) was insignificant for total species richness ($p = 0.596$) but marginally significant and negative for the number of red-listed species ($p = 0.091$) (Table 1). Red-listed species were observed in 42% of valuable urban forests, 25% of random production forests, 40% of valuable production forests and in all semi-natural forests. None were observed in random urban forests. Red-listed species observed in valuable urban forests included *Antrodia piceata, Antrodiella citrinella, Fomitopsis rosea, Skeletocutis brevispora* s.str. and *S. delicata*, and *Sidera vulgaris* which was not included in the analyses.

Looking more closely at the effects of dead-wood abundance and the surrounding forests landscape (Fig. 3), both total species richness and the number of red-listed species were consistently increased by dead-wood abundance. Highest species richness was expected in stands with highest dead-wood abundances and the largest amount of mature forest in the surroundings. However, with low dead-wood abundances more species were expected in stands with a lower amount of mature forest. The occurrence of red-listed species was strongly related to the amount of mature forest in the surroundings. No red-listed species were expected to occur in a stand (of 1 ha) below dead-wood abundances of ca. 30 m^3 ha^{-1} and surrounding mature forest cover of ca. 50%, even when human population density was low (Fig. 3). Increasing population density further decreased the occurrence of red-listed species. In addition to habitat characteristics, heat sum was positively associated to total species richness ($p = 0.003$).

3.2. Species-specific responses

Accounting for urbanization (human population density) generally didn't affect the capability to predict polypore species occurrences. Mean cross-validated predictive power averaged over all 18 included species was 0.70 in AUC and 0.06 in Tjur's R^2 for both model variants, one accounting for urbanization and the other not. Differences in predictive power for individual species were generally negligible between the models (Fig. 4). Urbanization improved predictive power notably (41% relative increase in AUC) only for *Postia stiptica*, but the predictive power for that species remained poor (AUC = 0.60). AUC > 0.70, indicating useful predictive capability (Berglund, O'Hara, & Jonsson, 2009), was achieved for nine species: *Phlebia centrifuga, Phellinus viticola, Trichaptum abietinum, Phe. nigrolimitatus, Pycnoporellus fulgens, Phe. ferrugineofuscus, Skeletocutis carneogrisea, Fomitopsis pinicola* and *Fomitopsis rosea* with both model variants, i.e. both models had good predictive capability, but the effect of urbanization was negligible.

For half of the species, more variance was explained by the random effects, that capture the effects of unaccounted variability, than by fixed effects representing measured environmental variability (Fig. 4). Stand-level fixed effects, accounting for the effects of dead-wood abundance, surrounding mature forest cover, urbanization and heat sum, explained on average more variation (35.8%) than stand-level random effects (11.6%). However, the largest proportion of the explained variance was attributed to substrate-level effects, 18.5% being explained by fixed effects, i.e. volume and decay class, and 34.0% by random effects.

The estimated effect size of urbanization on species occurrence was generally small but statistically significant for four species with minimum 95% posterior probability and two additional species with minimum 90% posterior probability (Table 2). The effect was positive for *Postia fragilis* and *Po. stiptica* and negative for *Fomitopsis pinicola, Heterobasidion parviporum, Phellinus viticola* and *Trichaptum abietinum*. Other model coefficients, when compared between the two model variants, were very close to each other (Appendix E Table E2), indicating that they were not seriously affected by the inclusion or exclusion of urbanization in the model. Overall, the largest effect sizes were attributed to the surrounding cover of mature forest with a positive effect for all species except *T. abietinum*. The effect sizes of local dead-wood abundance and its interaction with mature forest cover were small, but for most non-indicator species, the interaction was significantly negative. For old-forest indicator species, this interaction term was not significant or marginally positive. Niche specialization in terms of decay class varied among species but most showed positive responses to increasing volume of the dead-wood unit, except for *Ph. viticola*.

4. Discussion

4.1. Urbanization

Our results suggest that the urbanization gradient (McDonnell & Pickett, 1990) itself has only minor importance in explaining patterns of spruce (*Picea abies*) associated polypore species diversity in the context of a Nordic metropolitan area. After accounting for the effects of local habitat quality, i.e. dead-wood abundance and mature forest cover in the near surroundings, the effects of urbanization on total species richness was negligible. Similarly, species specific habitat models, comprising 18 of the most abundant species and including six old-forest indicators, revealed only minimal effects related to urbanization at the species-level.

However, even after accounting for other habitat variables and forest management history, the richness of red-listed species was negatively affected by urbanization, albeit with marginal statistical significance. Negative effects of urbanization on wood-inhabiting species have also been demonstrated by Meyer et al. (2021) who showed that abundances of several saproxylic insect groups and species richness of fungi in fine woody debris decreased along a gradient from rural to urban forest environments. In densely populated urbanized landscapes, with high proportions of non-vegetated built surfaces, forest patches can be susceptible to severe and deeply penetrating edge effects (Noreika & Kotze, 2012). Associated increases in temperature and humidity fluctuations (Crockatt, 2012; Ylisirniö et al., 2016) have been associated with reduced fungal species richness in dead spruce (Pouska, Macek, Zíbarová, & Ostrow, 2017). Red-listed species in our data were mostly represented by old-forest specialists (Niemelä, 2016; Kotiranta et al., 2019) that may be specifically adapted to interior forest conditions (cf. Ruete, Snäll, & Jönsson, 2016). Therefore, these species could be particularly vulnerable to urban-associated environmental changes.

Secondly, the observed trend of lower occurrence of red-listed species in more densely populated areas might be related to forest management history and isolation of urban forests at a larger spatial scale than what was accounted for in our analyses. In the city of Helsinki for example, old forests were relatively rare in the 1950s (Saukkonen, 2011), meaning that habitat availability for old-forest species in urban landscapes has probably been lower in recent history compared to the present day. Consequently, habitat patches in urban forests may be, on average, further away from colonization sources of red-listed species than rural forests. Furthermore, the high degree of habitat fragmentation in urban landscapes can make it difficult for rare and specialized species to colonize urban forests due to poor dispersal ability (Jönsson, Edman, & Jonsson, 2008) and competitive exclusion by prevalent generalist species that are more competitive when resources are sparsely distributed (Nordén et al., 2013; Moor et al., 2020). However, forest fragmentation is not a uniquely urban phenomenon, as rural land conversion and forestry use can result in habitat fragmentation as well.

Our results show that the effects of surrounding forest landscape, reflecting the connectivity of the focal forest stand, were particularly strong for the number of red-listed species even when dead-wood abundance in the stand was high. This effect may be related to increasing edge effects as discussed above, as surrounding forest area is reduced. In addition, the cover of mature forest may carry information about the unmeasured dead-wood resource availability around the inventory plot. For red-listed species, resource availability on this extended spatial scale could be particularly important, as their colonization success has been found to be sensitive to the loss of local substrate connectivity (Penttilä et al., 2006; Nordén et al., 2013; Moor et al., 2020). In highly fragmented stands, even high local dead-wood abundances may not guarantee the continuity of suitable dead-wood substrates for red-listed species that tend to be highly specialized in resource use (Nordén et al., 2013).

The effect of forest fragmentation on total polypore species richness in forest stands depended on dead-wood abundance. Highest species richness was expected in dead-wood rich stands in intact forest landscapes, which is consistent with the importance of habitat connectivity for old-forest specialist species, as discussed above. However, when dead-wood abundance was low, slightly higher species richness was expected in fragmented forest landscapes. This trend may be related to larger prevalence of edge-specialist species (cf. Lövei, Magura, Tóthmérész, & Ködöböcz, 2006) or larger variability in habitat microsites in fragmented forests, which could have increased species richness especially when the total number of species was low. Nevertheless, species-specific habitat models indicated that surrounding mature forest cover had a relatively strong positive effect on the occurrence of almost every one of the analyzed species, suggesting that even common generalist species occurred more frequently in larger intact forest areas.

4.2. Dead-wood abundance

Our results are in line with the conclusions of several earlier studies (e.g. Penttilä et al. 2004, Similä et al. 2006) in that dead-wood abundance is a key aspect in determining the stand-level species richness of polypores. Larger amounts of dead-wood substrates can be expected to increase species richness through more comprehensive sampling from regional species pools and by supporting larger and more resilient populations of species (Carnicer, Brotons, Sol, & De Cáceres, 2008). Dead-wood quantity is also generally correlated with the diversity of dead wood (Similä et al. 2006), providing habitats for a larger variety of specialized species (Siitonen, 2001).

The threshold value for dead-wood abundance, ca. 30–40 m^3 ha^{-1} of coarse woody debris of spruce, below which the occurrence of spruce-associated red-listed polypore species becomes unlikely, was comparable to values of 20 m^3 ha^{-1} or higher and 29 m^3 ha^{-1} suggested by Penttilä et al. (2004) and by Nordén et al. (2018), respectively. In general, these values are well above those typical for managed urban forests in this study area (mean 3.3 m^3 ha^{-1} in random urban forests).

Furthermore, Nordén et al. (2018) suggested that when dead-wood abundance is high, old-forest specialist fungi can become abundant enough to influence non-indicator fungi through competitive interactions. Accordingly, our results also suggest that there was a slight but significant negative effect from the interaction between dead-wood abundance and surrounding mature forest cover on many common generalist species (but also two successor species, *Pycnoporellus fulgens* which is also considered an old-forest indicator (Niemelä, 2016), and *Skeletocutis carneogrisea*), indicating that high stand-level dead-wood abundance reduced their occurrence when the forest stand was also well connected. This effect was possibly due to increased competition with old-forest specialists (such as *Fomitopsis rosea*, *Phellinus* spp., *Phlebia centrifuga* as well as other species that could not be included in the joint species distribution model).

4.3. Conclusions and practical considerations

Our results suggest that urbanized forests are largely comparable to rural forests as habitats for boreal spruce-associated polypore species when accounting for variability in primary habitat characteristics, i.e. amount of dead wood and local forest connectivity. Overall, species richness of polypores can be increased by increasing local dead-wood abundance, while the effect of the surrounding landscape setting is only minor. The potential for increasing habitat for dead-wood dependent biodiversity in urban forests can be high due to low commercial production demands (Hedblom & Söderström, 2008) and high relative abundance of large-diameter trees (Gulsrud et al., 2018; Korhonen et al., 2020) that are necessary for the formation of ecologically valuable large-diameter dead-wood substrates (Tikkanen, Martikainen, Hyvärinen, Junninen, & Kouki, 2006; Berglund et al., 2011).

In terms of red-listed old-forest species, the best habitat potential lies in large forest patches that are most likely to be found in peri-urban areas. Larger forest areas could also provide more locations where dead-wood abundance could be increased significantly without compromising recreational value. This potential is available especially in many Nordic cities where extensive recreational forest areas have been retained around urban cores (Borges et al., 2017). Our results in the Helsinki metropolitan area also confirm that red-listed species already occur in the dead-wood hotspots of the urban forest landscape.

In conclusion, our results add to the increasing understanding of the potential value of urban forests in biodiversity conservation (Ives et al., 2016; Soanes et al., 2019). Optimally, urban forests could function as integral parts of regional ecological networks, in which they complement and connect natural and protected forest areas (see e.g. Jalkanen, Toivonen, & Moilanen, 2020). Realization of this potential will depend on cities' capacity to maintain urban forests under increasing population pressure and to improve their ecological condition, e.g. by increasing the quantity of dead wood.

CRediT authorship contribution statement

Aku Korhonen: Conceptualization, Methodology, Investigation, Formal analysis, Writing - review & editing. **Reijo Penttilä:** Conceptualization, Methodology, Investigation, Writing - review & editing. **Juha Siitonen:** Conceptualization, Methodology, Writing - review & editing. **Otto Miettinen:** Data curation, Supervision, Writing - review & editing. **Auli Immonen:** Data curation, Formal analysis. **Leena Hamberg:** Conceptualization, Supervision, Methodology, Writing - review & editing.

Appendix A. Volume and decay class distribution of surveyed dead-wood units in forest categories.

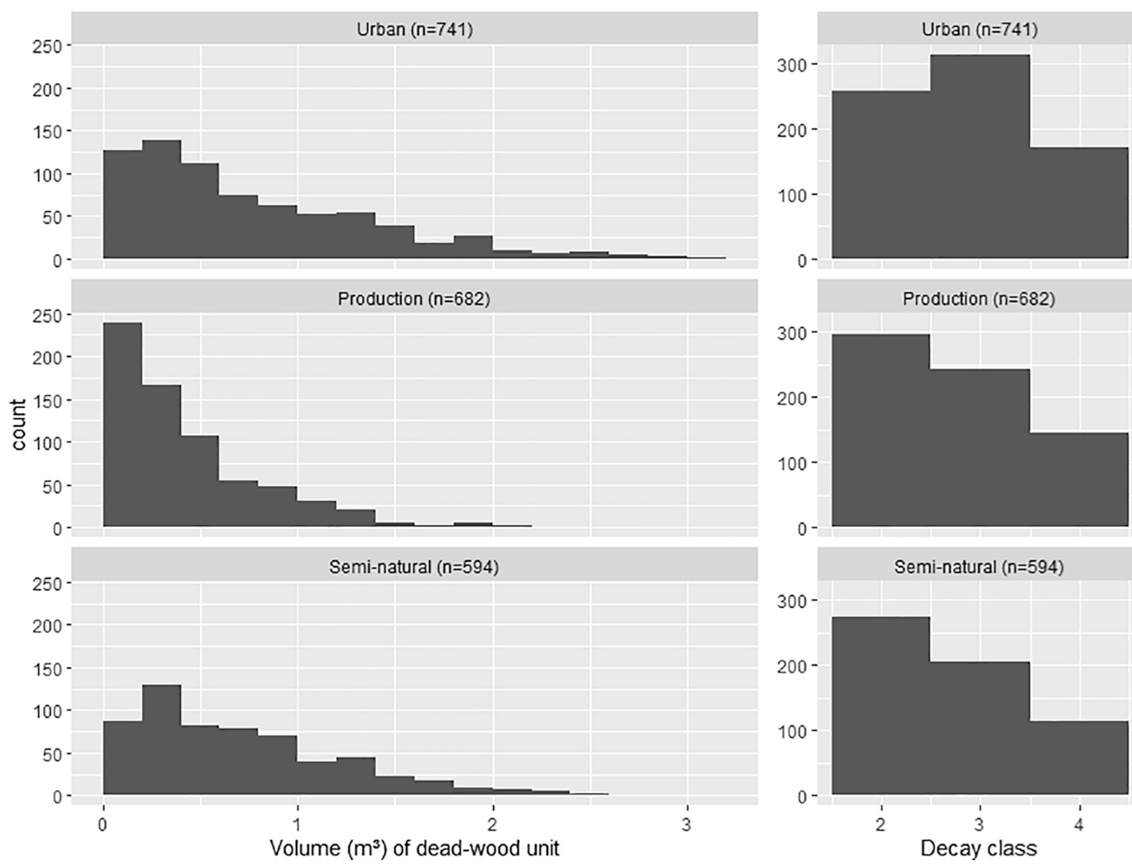

Fig. A1. Volume and decay class distribution of surveyed dead-wood units in forest categories. Data from random and valuable urban forests and from random and valuable production forests have been pooled. *N* denotes the number of surveyed dead-wood units in each category.

Appendix B. Schematic representation of a study plot and the spatial scales of data collection.

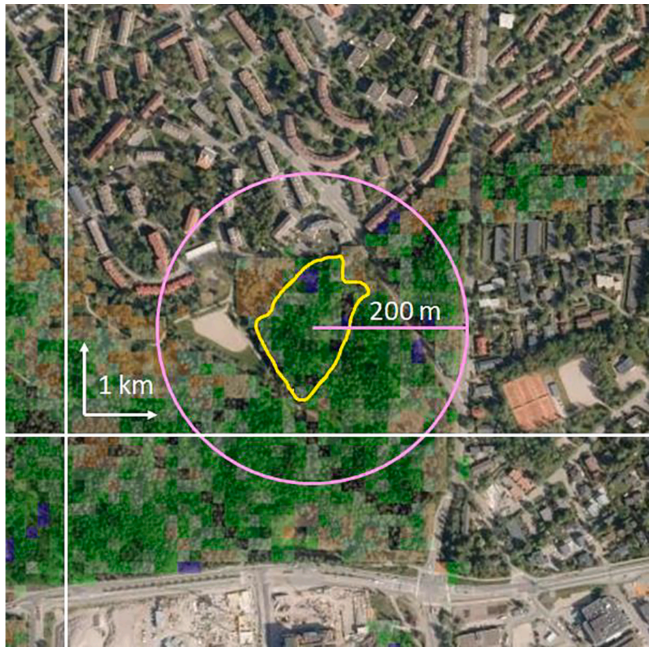

Fig. B1. Schematic representation of a study plot and the spatial scales of data collection. Polypores were inventoried in ca. 1 ha plots of mature spruce forests delimited by natural boundaries (shown in yellow). Proportion of mature forest (map pixels shaded with green and blue) was measured within 200 m radius from the inventory plot center (area inside the pink circle). Information about human population density was acquired from 1 km × 1 km grid data (white lines depicting grid boundaries). Background photo from National Land Survey of Finland aerial photographs database 01/2021.

Appendix C. Values of environmental variables among forest stands and forest categories.

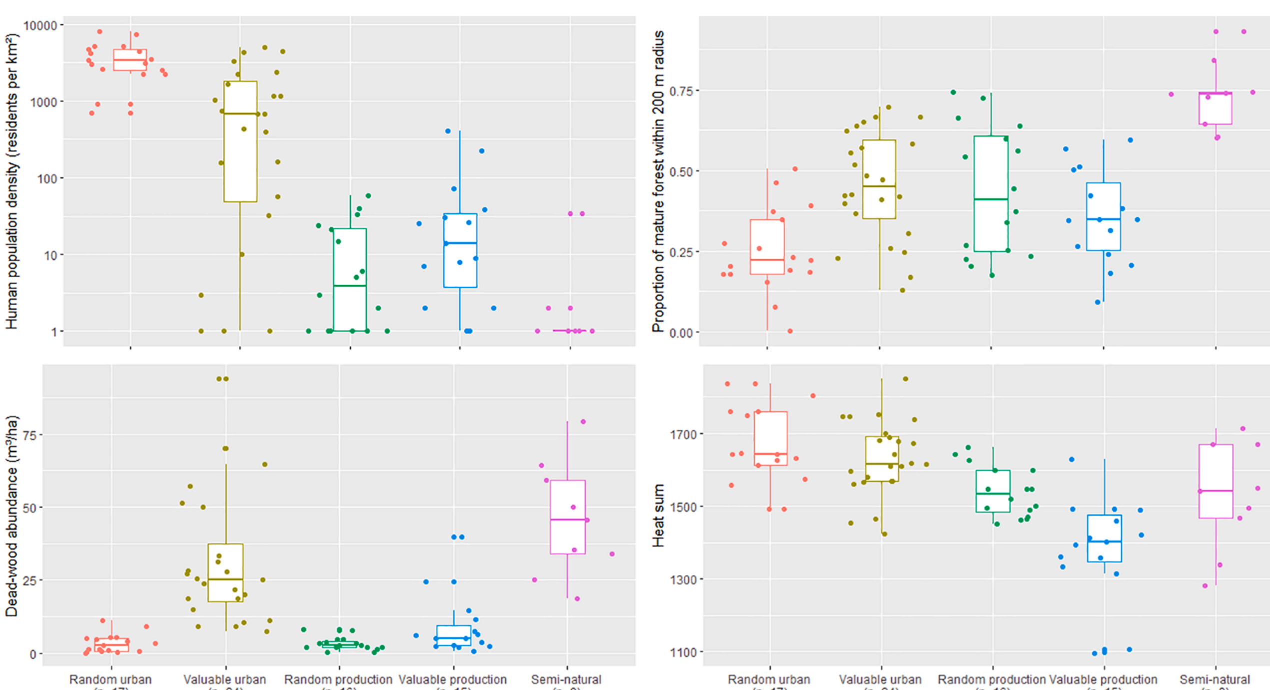

Fig. C1. Values of environmental variables among forest stands and forest categories. For each forest category, medians and first (Q1) and third (Q3) quartiles are indicated in boxplots with lines denoting range between Q1-1.5*interquartile range and Q3+1.5*interquartile range. Individual sites are overlaid as points. *N* denotes the number of inventoried stands in each forest category.

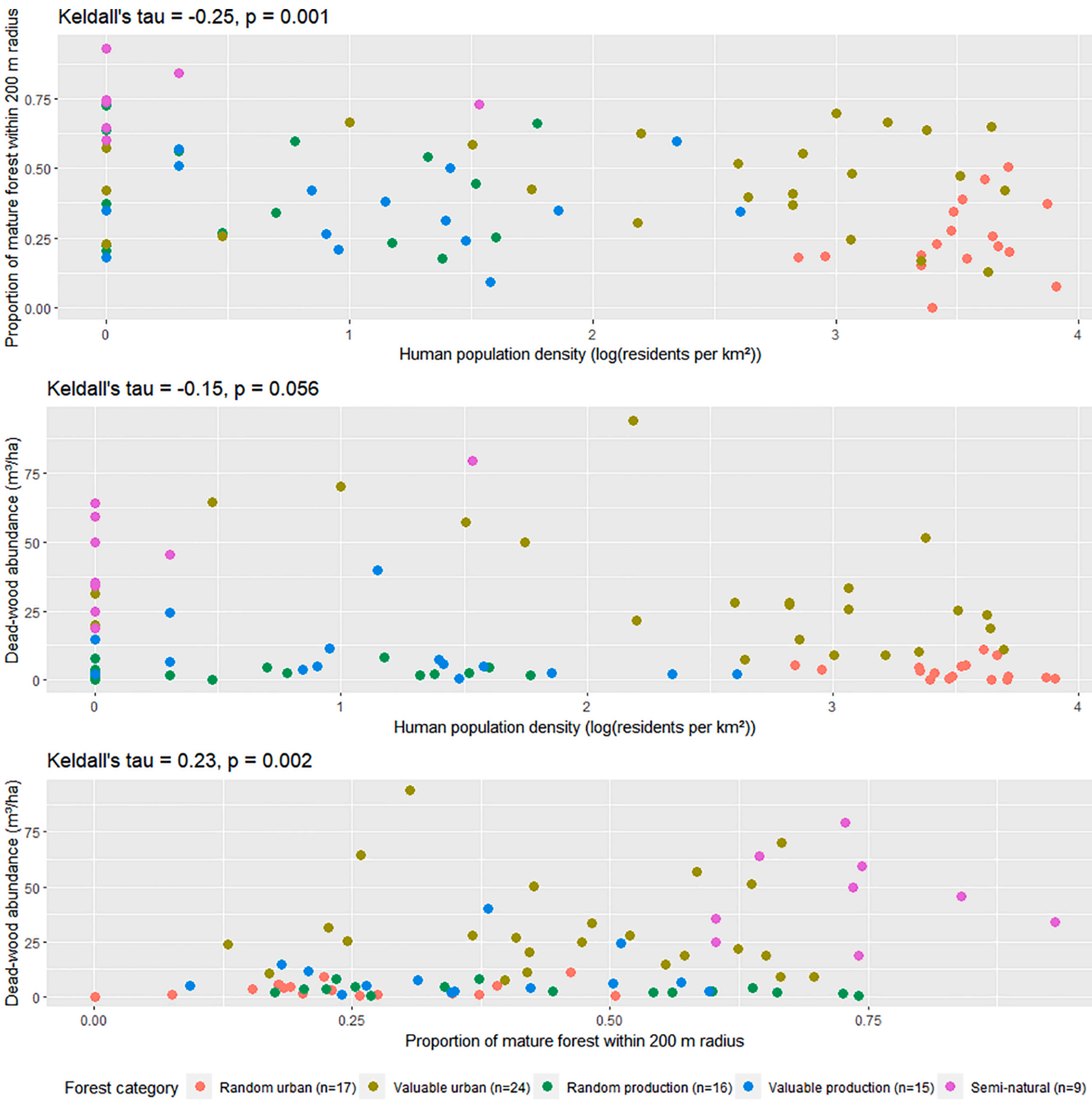

Fig. C2. Correlations between urbanization and mature forest cover (top) and dead-wood abundance (middle) and between mature forest cover and dead-wood abundance (bottom). Points depict study sites.

Appendix D. Observed polypore species.

Table D1
Observed polypore species. For each species, information is given about Finnish Red List (2019) status, causes of threat, old-forest indicator species status and the number of observations in different forest categories. Data from random and valuable urban forests and from random and valuable production forests have been pooled. *N* denotes the number of surveyed dead-wood units in each category.

	Finnish IUCN Red List status 2019[a]	Causes of threat[b]	Old-forest indicator status[c]	Urban (n = 741)	(Former) production (n = 682)	Semi-natural (n = 594)
Amylocystis lapponica	NT	Mv, Ml	virgin forest	0	0	3
Anomoloma albolutescens	NT	Ml		0	3	1
Antrodia piceata	VU	Mv, Ml		2	1	0
Antrodia serialis				233	182	222
Antrodia sinuosa				40	43	38
Antrodia xantha				3	0	4
Antrodiella citrinella	NT	Mv, Ml	virgin forest	2	2	9
Butyrea luteoalba				2	10	17
Byssoporia terrestris				0	0	1
Canopora subfuscoflavida				1	8	1
Climacocystis borealis				3	0	1
Fibroporia gossypium				2	0	1
Fomitopsis pinicola				286	299	307
Fomitopsis rosea	NT	Mv, Ml		10	4	38
Gloeophyllum sepiarium				8	21	3
Gloeophyllym odoratum				2	1	2
Heterobasidion parviporum				48	103	52
Ischnoderma benzoinum				21	19	11
Leptoporus mollis coll			old forest	7	4	15
Oligoporus rennyi				1	4	0
Oligoporus sericeomollis coll				8	9	8
Osteina undosa				15	5	15
Perenniporia subacida	NT	Ml, Mv	old forest	0	0	1
Phellinus chrysoloma coll			old forest	2	0	1
Phellinus ferrugineofuscus			old forest	60	34	106
Phellinus nigrolimitatus			old forest	14	14	58
Phellinus viticola			old forest	1	23	98
Phlebia centrifuga			virgin forest	13	0	75
Physisporinus sanguinolentus				1	0	1
Physisporinus vitreus				1	0	0
Porpomyces mucidus				1	4	1
Postia caesia coll				130	141	140
Postia floriformis				2	0	0
Postia fragilis				42	21	20
Postia hibernica				1	0	2
Postia leucomallella coll				3	1	6
Postia ptychogaster				14	6	17
Postia stiptica				27	14	6
Postia tephroleuca				85	87	50
Pycnoporellus fulgens			old forest	36	34	24
Rhodonia placenta			old forest	0	1	4
Sidera vulgaris	NT	Ml		8	0	0
Sistotrema alboluteum				0	0	1
Sistotrema dennisii				1	0	0
Sistotrema muscicola				1	0	0
Skeletocutis amorpha				4	6	6
Skeletocutis biguttulata				3	10	2
Skeletocutis brevispora coll	NT	Ml, Mv		2	4	15
Skeletocutis carneogrisea				49	116	37
Skeletocutis cummata	VU	Ml		0	0	1
Skeletocutis kuehneri coll				6	26	6
Skeletocutis odora	NT	Ml, Mv	old forest	0	2	2
Skeletocutis papyracea				2	1	0
Skeletocutis stellae	VU	Ml, Mv	virgin forest	0	0	1
Steccherinum collabens	NT	Mv, Ml	virgin forest	0	1	8
Trechispora hymenocystis				19	22	25
Trechispora mollusca				13	1	1
Trichaptum abietinum				150	296	170

[a] NT = near threatened, VU = vulnerable (Kotiranta et al., 2019).
[b] Ml = decreasing amounts of decaying wood, Mv = reduction of old-growth forests and the decreasing number of large trees (Kotiranta et al., 2019).
[c] Niemelä 2016.

Appendix E. Supporting information on species distribution modelling.

Table E1
Classification of taxa included in the joint species distribution models. All included taxa belong to the class Agaricomycetes (Basidiomycota).

Species	Genus[a]	Family[b]	Order
Antrodia serialis	*Antrodia serialis* clade[a]	Fomitopsidaceae	Polyporales
Antrodia sinuosa	*Amyloporia* clade[a]	*Amyloporia-Fibroporia* clade	Polyporales
Fomitopsis pinicola	*Fomitopsis*	Fomitopsidaceae	Polyporales
Fomitopsis rosea	*Rhodofomes*[a]	Fomitopsidaceae	Polyporales
Heterobasidion parviporum	*Heterobasidion*	Bondartzewiaceae	Russulales
Ischnoderma benzoinum	*Ischnoderma*	Ischnodermataceae	Polyporales
Phellinus ferrugineofuscus	*Phellinidium*[a]	Hymenochaetaceae	Hymenochaetales
Phellinus nigrolimitatus	*Phellopilus*[a]	Hymenochaetaceae	Hymenochaetales
Phellinus viticola	*Fuscoporia*[a]	Hymenochaetaceae	Hymenochaetales
Phlebia centrifuga	*Phlebia*	Meruliaceae	Polyporales
Postia caesia coll	*Postia*	Dacryobolaceae	Polyporales
Postia fragilis	*Postia*	Dacryobolaceae	Polyporales
Postia stiptica	*Postia*	Dacryobolaceae	Polyporales
Postia tephroleuca	*Postia*	Dacryobolaceae	Polyporales
Pycnoporellus fulgens	*Pycnoporellus*	Polyporales incertae sedis	Polyporales
Skeletocutis carneogrisea	*Skeletocutis*	Incrustoporiaceae	Polyporales
Trechispora hymenocystis	*Trechispora*	Hydnodontaceae	Trechisporales
Trichaptum abietinum	*Trichaptum*	Hymenochaetales incertae sedis	Hymenochaetales

[a] Genus-level classification of species follows Niemelä 2016. Note that *Antrodia* s.l., *Fomitopsis* s.l. and *Phellinus* s.l. are divided into more narrowly defined (monophyletic) genera or groups following Niemelä (2016) and Justo et al. (2017).
[b] Family-level classification of genera in Polyporales follows Justo et al. (2017).

Table E2
Standardized model coefficients (posterior means) from the joint species distribution models estimated with (upper values) and without (values below) urbanization (residend human population density). Red color indicates positive and blue negative effect of an explanatory variable on the probability of occurrence of an investigated species. Darker colors indicate 95% posterior probability and lighter colors 90% posterior probability for coefficients deviating from 0 (white cells indicate non-significant effects). Coefficient explanations: interaction is between dead-wood abundance and mature forest cover, naturalness refers to forest management history, i.e. semi-natural stand (1) or not (0), urbanization is human population density (log-transformed). (For interpretation of the references to color in this table legend, the reader is referred to the web version of this article.)

	Intercept	DC3	DC4	Vol	DW	Forest	DW*Forest	Naturalness	Heat sum	**Urbanization**
Antrodia serialis	-0.698	0.402	-0.171	0.590	0.001	0.252	-0.010	0.283	-0.040	0.000
	-0.702	0.402	-0.153	0.567	0.001	0.267	-0.012	0.345	0.000	NA
Antrodia sinuosa	-1.136	0.412	0.378	0.424	0.006	0.782	-0.021	0.256	0.032	-0.001
	-1.229	0.412	0.373	0.433	0.006	0.760	-0.020	0.211	-0.001	NA
Fomitopsis pinicola	1.177	-0.140	-0.883	1.234	0.009	0.516	-0.027	0.470	-0.071	-0.001
	1.259	-0.142	-0.869	1.210	0.011	0.600	-0.031	0.597	-0.001	NA
Fomitopsis rosea	-4.517	0.041	-0.627	1.077	-0.004	1.312	0.003	0.298	-0.073	0.001
	-4.518	0.028	-0.665	1.060	-0.005	1.385	0.004	0.353	0.001	NA
Heterobasidion parviporum	-0.606	-0.106	-0.309	0.645	-0.005	0.131	-0.018	0.309	-0.086	>0.001
	-0.436	-0.110	-0.308	0.634	-0.004	0.203	-0.020	0.404	-0.001	NA
Ischnoderma benzoinum	-1.658	0.263	-0.034	0.941	0.001	1.095	-0.016	0.047	0.031	-0.001
	-1.690	0.267	-0.030	0.955	0.001	1.080	-0.015	-0.015	0.000	NA
Phellinus ferrugineofuscus	-3.104	-0.468	-1.751	0.470	-0.001	1.349	-0.007	0.410	-0.039	0.001
	-3.061	-0.476	-1.769	0.465	0.000	1.372	-0.010	0.514	0.001	NA
Phellinus nigrolimitatus	-4.263	0.865	0.928	-0.170	0.001	1.639	0.021	0.102	-0.100	0.000
	-4.079	0.846	0.904	-0.204	0.001	1.688	0.021	0.194	-0.001	NA
Phellinus viticola	-1.861	0.312	0.125	-0.226	0.002	1.797	0.015	0.365	-0.207	-0.001
	-1.557	0.296	0.115	-0.258	0.002	1.998	0.011	0.591	-0.002	NA
Phlebia centrifuga	-4.605	-0.355	-1.567	1.619	0.001	2.154	-0.001	0.782	0.022	0.001
	-4.614	-0.352	-1.584	1.621	0.000	2.064	0.000	0.766	0.001	NA
Postia caesia coll	0.193	-0.161	-0.798	0.505	0.008	0.938	-0.037	0.357	-0.024	-0.001
	0.260	-0.162	-0.804	0.497	0.009	0.953	-0.037	0.386	-0.001	NA
Postia fragilis	-2.785	0.466	0.534	0.388	0.005	1.238	-0.021	0.042	0.073	<0.001
	-2.848	0.476	0.537	0.409	0.005	1.211	-0.019	-0.064	0.000	NA
Postia stiptica	-2.237	0.030	-0.185	0.251	0.006	0.613	-0.025	0.026	0.104	<0.001
	-2.483	0.047	-0.184	0.301	0.005	0.542	-0.023	-0.097	0.000	NA
Postia tephroleuca	-0.882	0.172	-0.368	0.533	0.009	0.576	-0.038	0.183	-0.010	0.000
	-0.848	0.166	-0.373	0.529	0.009	0.594	-0.037	0.171	0.000	NA
Pycnoporellus fulgens	-0.737	0.592	0.290	1.276	0.006	0.256	-0.019	0.301	0.054	-0.001
	-0.790	0.596	0.290	1.293	0.005	0.179	-0.017	0.229	-0.001	NA
Skeletocutis carneogrisea	-0.393	-0.626	-2.104	0.904	-0.007	0.607	-0.027	0.241	0.036	-0.001
	-0.467	-0.617	-2.091	0.930	-0.007	0.550	-0.027	0.181	0.000	NA
Trechispora hymenocystis	-1.657	0.413	0.878	-0.039	0.007	0.521	-0.017	0.258	-0.007	-0.001
	-1.641	0.412	0.873	-0.047	0.007	0.522	-0.017	0.272	-0.001	NA
Trichaptum abietinum	2.035	-1.403	-3.259	0.920	-0.001	-0.479	-0.036	0.603	-0.139	-0.001
	2.217	-1.406	-3.246	0.900	0.001	-0.303	-0.042	0.796	-0.001	NA

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