

# Quality of substrate and forest structure determine macrofungal richness along a gradient of management intensity in beech forests

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## ABSTRACT

The richness of saproxyllic species is commonly found to be compromised in managed forests. However, it is often less clear if this reflects local scarcity of high quality deadwood objects or changes to the overall forest structure. Further, anthropogenic and natural drivers working at the landscape scale may have a strong impact. Hence, it is difficult to give detailed advice on how to conserve biodiversity in a cost-effective manner. Here we explored macrofungal richness on deadwood across a gradient of forest management intensity in Danish *Fagus sylvatica* forests. We aimed to disentangle the importance of habitat quality per se from the effects of variables recorded at the forest stand and landscape scales. Data was collected from 40 beech stands, each representing one of four broad management types: conventionally managed, near-to-nature managed, recently unmanaged and long unmanaged. Stands were aggregated within six larger forest clusters, to account for variation at the landscape scale. Fungal species were recorded as fruitbodies on deadwood at five decay stages. We found that the four management types showed strong differences in fungal richness, deadwood volume and forest structure, with long unmanaged stands having notably higher structural complexity and species richness. Fungal species richness and presence of red-listed fungi appeared to be mainly driven by deadwood volume, tree species and decay stage, but some stand-level variables such as canopy gaps, basal area and stand age were also of importance. Lying coarse deadwood had the highest species richness while standing coarse woody debris and fine deadwood had lower species density. Saproxyllic fungal richness on individual deadwood objects was largely affected by resource quality and size, which is often limited in managed forests. Our results indicate that the best measure to increase fungal species richness, especially in managed stands, is to increase the amount of large diameter deadwood.

## 1. Introduction

According to recent forest statistics, European forests on average contain 11.5 m<sup>3</sup>/ha of deadwood combined across all management types (FOREST EUROPE, 2015). This is a low amount compared to the reference values reported from unmanaged old-growth forests in the temperate zone (average 130–150 m<sup>3</sup>/ha, Christensen et al., 2005; Burrascano et al., 2013) and well below the threshold values of 20–50 m<sup>3</sup>/ha reported by Müller and Bütler (2010) as minimum values for sustaining viable communities of saproxyllic species. In Denmark, the amount of deadwood is as low as 5.7–6.5 m<sup>3</sup>/ha in the two most widespread beech forest types of the EU Habitats Directive (beech on mor and beech on mull) (Nygaard et al., 2019), making living

conditions for saproxyllic organisms truly marginal.

Timber extraction leaves forests with few deadwood habitats supporting presence of saproxyllic fungi (Jonsson et al., 2005), hence putting them at the heart of the conflict between forestry and conservation of biodiversity. Saproxyllic fungi are key components of forest biodiversity and ecosystem functioning. They are fundamental to decomposition and recycling of nutrients, and instrumental in the creation of habitats for other saproxyllic organisms (Stokland et al., 2012; Heilmann-Clausen et al., 2014). Therefore, they are considered important indicators of decomposer diversity related to deadwood (Halme et al., 2017).

Deadwood occurs in various shapes and sizes, from big fallen logs of mature trees, over snags to fine woody debris, each supporting different

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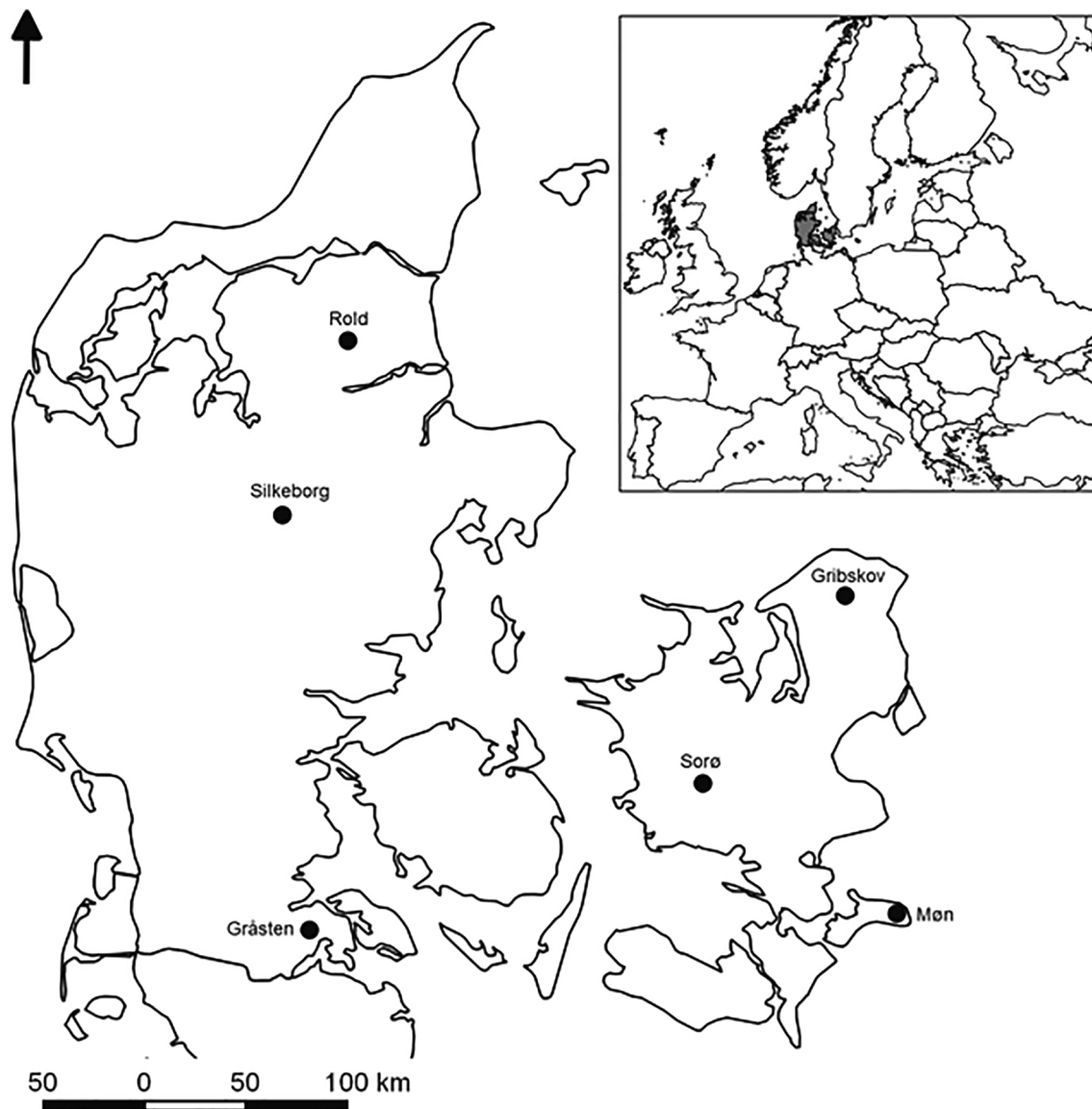


Fig. 1. Positions of the six forest clusters in Denmark.

fungus communities (Abrego and Salcedo 2013). It is generally observed that saproxylic fungi of conservation concern prefer larger logs and other types of coarse woody debris (CWD), probably because they represent stable and continuous availability of resources (e.g. Heilmann-Clausen and Christensen 2004; Bässler et al., 2010). On the other hand, fine woody debris (FWD) is known to support high fungal diversity, especially when comparing with equal volumes of CWD, due to larger surface area and higher number of individual deadwood objects per volume unit (Kruys and Jonsson, 1999; Nordén et al. 2004; Pasanen et al. 2019). In managed stands, where CWD is scarce, FWD makes up most of the deadwood available for saproxylic organisms, making it a potentially important refuge (Küffer and Senn-Irlet, 2005; Juutilainen et al., 2014).

Other deadwood properties than size are also important in determining fungal diversity. Many species are specialists of certain decay stages, tree species and decay pathways (Berglund et al., 2011; Heilmann-Clausen et al., 2005; Abrego and Salcedo, 2013; Ottoson et al., 2014). Microclimatic conditions affect species survival and interspecific competition, and hence shape fungal community composition and decay rate in deadwood (Boddy 2000; Bässler et al. 2010; Pouska et al. 2016). Finally, landscape scale factors, both

anthropogenic and natural, influence fungal communities at both local and regional scales. This, intensive land use and habitat fragmentation has been shown to affect not only habitat abundance but also the composition of the species pool of saproxylic fungi, favoring generalist species to the benefit of specialists (Nordén et al., 2013; Heilmann-Clausen et al., 2014). Complex interactions between drivers of fungal diversity imply that the most cost-efficient strategies to mitigate negative effects of forestry on biodiversity are far from straightforward. Protection of strict forest reserves in carefully selected areas is required to conserve the most demanding species (Junninen et al. 2005; Abrego et al., 2015) but is also costly (Petersen et al., 2015) and often restricted by private ownership of land. Hence, it is important to investigate to how conservation of saproxylic fungi can be integrated in managed forests, and to identify specific habitats that should be prioritized in these efforts.

In this study, we explored saproxylic fungal species richness in 40 beech stands along a gradient in forest management intensity in Denmark. To account for potential regional differences in fungal diversity, we used a nested study design where the gradient in management intensity was represented across six study areas (clusters) in a balanced way. Fungal species richness was analyzed at deadwood

object level measured on transects, by including predictor variables at three different spatial grain sizes: deadwood object, forest stand and landscape scale; the latter treated as a random effect. Hereby, we aimed to disentangle the importance of substrate quality per se, from the effect of stand scale variables, at the same time controlling for landscape scale differences related to forest history, regional climate and other factors affecting the regional species pools. While larger amounts of CWD are characteristic of unmanaged forests, FWD and cut stumps may act as refuges for saproxylic fungi in managed forests. Hence these substrates were included in the study and the fungal richness associated with these substrates was compared with the fungal richness on CWD in the same study areas.

Overall, we expected (1) substrate quality to be the most important determinant of fungal species richness on deadwood object level, and (2) stand-scale variables related to tree age and stand structure to be relatively more important for the incidence of red-listed species than for overall species richness (cf. Heilmann-Clausen and Christensen 2005; Flensted et al., 2016). Finally, we expected (3) a clear distinction between species pools and their respective sizes on various deadwood types, with lying CWD being the substrate supporting most species of fungi, including red-listed taxa.

## 2. Methodology

### 2.1. Study sites

The study covered 40 forest stands dominated by European beech (*Fagus sylvatica* L.) aggregated in six forest clusters across Denmark (Fig. 1). The stands were selected to represent a gradient in forest management intensity of four broadly defined categories: (i) conventionally managed shelter-wood stands, with dominant trees 70–100 years old, structurally simple with one dominant tree layer and no or little CWD (ii) managed stands, dominant trees 80–150 years old, more structurally complex with multiple layers and with presence of some CWD, often subject to near-to-nature management, (iii) recently unmanaged (unmanaged < 30 years) stands with dominant trees older than 100 years and iv) long unmanaged stands (unmanaged > 50 years) with dominant trees older than 200 years. Each of the four management classes were represented by one stand in each cluster, except for the Gribskov cluster, which was studied more intensively and included 20 stands, equally distributed across the four management classes. The forest clusters were chosen based on the following criteria: (1) presence of protected unmanaged old-growth remnants covering at least 10 ha in size, (2) large overall forest size with substantial areas of semi-natural forest types remaining, and (3) complementarity in coverage of geographical and climate variation in Denmark. The stands were a mixture of state and private property. The size of stands ranged between 3.01 and 6.5 ha, and were delimited to avoid external forest edges and larger wetland areas. *Fagus sylvatica* L. was the dominant tree species (> 60% of basal area) in all areas, with overstorey trees older than 70 years (for stand level descriptions, see Appendix A, Table A1). Part of the dataset was earlier analyzed by Lelli et al. (2018), focussing on multitaxa diversity following a different analytical approach.

### 2.2. Data collection

Deadwood and saproxylic fungi were surveyed during field visits in 2015 (Gribskov), and 2017 (other areas) along ten 50 m long transects per stand. Transect start points were placed randomly in GIS, with a minimum distance of 50 m. Thereafter compass angles were manually added on field maps to avoid overlapping transect bands. Deadwood was classified into four substrata types: lying CWD, standing CWD, cut stumps and FWD, using a diameter of 10 cm as a threshold to differentiate FWD (diameter 5–10 cm) from CWD (diameter > 10 cm), cf. Kruys and Jonsson (1999) and Nordin et al., (2004). Lying CWD was recorded along all transects based on the line-intersect method (Bate

et al., 2009). Standing CWD (diameter > 10 cm, Kruys and Jonsson, 1999; Nordin et al., 2004) and cut stumps (diameter > 10 cm) were surveyed if their centers were situated within a 5 m broad belt along either side of all transects, i.e. rectangular belt transects of 50 × 10 m; total area for a whole stand 0.5 ha (10 transects of 50 m × 10 m). FWD was investigated on the first 10 m of each transect (or in a 10 × 10 m plot for standing FWD and cut stumps, which were very infrequent). Start and end diameter as well as length were recorded for each deadwood object to calculate deadwood volume, and the tree species and decay stage were assessed based on the five-level classification system of Heilmann-Clausen and Christensen (2003).

Fruiting bodies of macrofungi (see full species list in Appendix B) including polypores, agarics, pileate corticioids, selected resupinate corticioids, i.e., species from the genera *Coniophora*, *Phlebia* and *Steccherinum*, larger discomycetes (cup fungi) (fruit bodies > 5 mm in diameter) and stromatic pyrenomycetes were recorded on all recorded deadwood objects during two consecutive field campaigns (in the early fruiting season (late August–September) and late season (October–November), respectively). Fungi were identified in the field or collected for identification in the laboratory. The conservation concern of recorded fungal species was based on their status as threatened (IUCN categories VU, EN and CR), near-threatened (NT) or data deficient (DD) in the national red-list (Moeslund et al., 2019).

Stand age was noted from forest maps provided by the forest owners (mainly the Danish state), while management types were based on data in Graae and Buchwald (1997) or personal communication with the local forest managers. In all stands, forest development phases (FDPs) were mapped based on Emborg et al. (2000). FDPs are spatial patterns of the forest cycle, which shift between developmental phases: innovation, degradation, early biostatic, late biostatic and degradation (more details on FDPs in Table 1). We applied two modifications when mapping FDPs: first, the threshold between early and late biostatic trees were set at different diameter at breast height (DBH) values (70–75–80 cm), depending on stand productivity determined by edaphic conditions in each forest area (Appendix A, Table A2). Second, small areas (up to 0.13 ha) with high enough water table to hinder tree establishment were mapped separately as wetlands (for more details on the different variables, see Table 1).

### 2.3. Data analyses

All statistical analyses were performed in RStudio software (version 1.1.463, RStudio Team, 2015). We performed a Generalized Mixed Effect Model (GLMM) and a Generalized Linear Model (GLM) to predict: (a) total fungal species richness and (b) red-listed fungal species richness. To assess relative importance of various deadwood substrate types and decay stages for total fungal richness, we constructed species accumulation and rarefaction curves and performed indicator species analyses.

#### 2.3.1. ANOVAs: differences between the management types

We compared different forest structural variables across the four management types by one-way and two-way ANOVAs (R package “stats”, function “aov”, R Core Team, 2019), followed by Tukey’s post hoc tests (R package “multcomp”, function “glht” Hothorn et al., 2008). Where ANOVA assumptions of equal variances were not met, we used one-way Welsh ANOVA (R package “lattice”, function “oneway”, Sarkar, 2008), followed by Games-Howell tests (R package “lattice”, function “oneway”).

#### 2.3.2. Modelling of species richness

Before setting up species richness models, the data distribution of response variables was checked by histograms and Shapiro-Wilk’s normality test (package “stats”, function “shapiro.test”). The relationships between predictor variables were checked by conducting Spearman rank-based correlation plots among different variables in the

**Table 1**  
Full list of predictor variables included in the mixed models. Levels: Cluster (C); Stand (S); Deadwood object (DO); Transect (T). Innovation, aggradation, early biostatic, late biostatic and degradation are forest developmental phases, which are spatial patterns of the forest cycle cf. [Emborg et al. \(2000\)](#). Application of each variable was indicated based on whether the variable was used as a predictor (fixed) variable or as a random effect in the analysis. Variance Inflation Factor (VIF) indicate the value at the first variable correlation control, before the modeling, and applies only for continuous variables.

Parameter	Description	Level	Range/structure	Application	VIF
Clusters	Aggregates of forest stands in geographically distinct regions, each containing stands with the studied management types	C	1–6	Random effect	–
Stand	Forest stand number	S	1–40	Random effect	–
Transect	Sampling unit for deadwood objects	T	10 transects per stand, size: 10 × 50 m	Random effect	–
Age	The year of stand establishment until 2019	S	77–350 years	Predictor	2.7
Basal area	Basal area of living trees with DBH > 10 cm	S	12.73–43.3 m <sup>2</sup>	Predictor	2.4
Cut stumps	Number of cut stumps, used as a proxy for management intensity	S	0–81	Predictor	3.5
Aggradation	Dominant trees are 3–25 m tall and are under rapid growth	S	0–30,748 m <sup>2</sup>	Predictor	8690.8
Early biostatic	Dominant trees > 25 m tall, with DBH < 80 cm (< 70 cm or < 75 cm in less productive stands)	S	3367–42,791 m <sup>2</sup>	Predictor	18302.5
Late biostatic	Mature and damage-prone trees with DBH > 80 cm (> 70 cm or > 75 cm in less productive stands)	S	0–43,359 m <sup>2</sup>	Predictor	8555.4
Innovation	Regeneration phase, tree height < 3 m. The innovation and degradation phases were summed and used as a “total gap area”	S	0–5019 m <sup>2</sup>	Predictor	279
Degradation	Canopy openings due to dead or dying trees. The innovation and degradation phases were summed and used as a “total gap area”	S	336–7974 m <sup>2</sup>	Predictor	698.5
Wetlands	Areas within a stand with high enough water table to hinder tree establishment, but can contain fallen deadwood	S	0–2353 m <sup>2</sup>	Predictor	1.4
Deadwood volume	Deadwood volume (m <sup>3</sup> ) square transformed	DI	0.000476–13.97 m <sup>3</sup> square transformed: 0.031–3.74 m <sup>3</sup>	Predictor	1.2
Decay stage	Deadwood decomposition level	DI	1–5	Predictor	–
Deadwood tree species	Main categories of tree species (> 10 trees within dataset) of deadwood species	DI	Coniferous; <i>Fagus sylvatica</i> L; <i>Prunus excelsior</i> L; <i>Quercus robur</i> L; other deciduous	Predictor	–
Deadwood type	Deadwood type according to position and/or size	DI	Lying CWD; standing CWD; cut stumps; fine woody debris (FWD)	Predictor	–

dataset (R packages “corrplot”, function “corrplot”, [Wei and Simko, 2017](#); and “Hmisc”, function “rcorr”, [Harrell, 2020](#)). Predictor variables were checked for multicollinearity before modelling by computing the variance inflation factor (VIF; R package “usdm”, function “vifcor”, [Naimi et al., 2014](#)) and excluded if a variable had a factor higher than four. The variable “early biostatic” was highly intercorrelated with late biostatic development phase, aggradation development phase as well as with gaps, as shown by high VIF (Table 1), and was therefore not used in the modelling to avoid multicollinearity introduced bias.

We modelled the influence of predictor variables on two response variables: (a) total fungal species richness and (b) incidence of red-listed species by multiple regression techniques. Both response variables were analyzed on the deadwood object level.

Total fungal richness was explored using generalized mixed effects models (GLMM, R package “glmmTMB”, function “glmmTMB”, [Brooks et al., 2017](#)), using maximum likelihood estimations, Laplace approximation and a Poisson error distribution ([Bolker et al., 2009](#)). Maximum likelihood estimation methods are prone to suffer from small-sample bias in case of rare event modeling ([Leitgöb, 2013](#)), which was evident in the data for red-listed species (only 53 positive records). To make robust estimations for incidence of red-listed species, we hence fitted competing mixed effect models based on maximum (R package “glmmTMB”, function “glmmTMB”) and penalized likelihood (R package “MASS”, function “glmmpQL”, [Venables and Ripley, 2002](#)), as well as maximum likelihood generalized linear models (GLM) (R package “mixlm”, function “glm”, [Liland, 2019](#)) and penalized GLM (R package “brglm”, function “brglm”, [Kosmidis, 2019](#)). In all cases a logistic link function was used. Firth’s penalized regression ([Firth, 1993](#); R package “brglm”, function “brglm”), showed almost no differences in parameter estimates when compared to maximum likelihood GLM (R package “mixlm”, function “glm”). However, penalized deviance implied that Firth’s penalized regression had the best fit, and hence this modelling approach was chosen (Appendix C, Table C1).

For both response variables, models were initially run with 12 predictor variables, three of which were categorical (Table 1). Deadwood volumes were root-squared to account for a non-linear relationship with fungal species richness, to make variance constant and to have normally distributed residuals. For each categorical variable, one category was chosen as a reference point, e.g. fungal richness at decay stage 1 was chosen as a reference and richness on the other decay stages was compared to decay stage 1. Instead of using the four broad forest management classes in the models, we focused directly on the environmental and structural variables recorded at site level. This was done to put focus directly on the structural attributes that we expected to affect fungal species richness, rather than highlighting effects of management per se, which was in reality more heterogeneous than the broad classes encompass. The management classes were used mainly to secure a balanced representation of the management gradient within each forest cluster. However some descriptive statistics for the four classes are presented, to provide insight into differences and overlaps in key figures between these.

We included three nested random factors (automatically estimating interaction variance) in the initial models: cluster number, stand number and transect number, in order to account for the pseudo-replicated sampling design and spatial autocorrelation within and among stands. Likelihood ratio tests (R package “lmerTest”, function “lmerTest”, [Zeileis and Hothorn, 2002](#)) were performed to assess the fit of random effects. In the models for red listed species incidence, the among group variance of random factors was close to 0 when fitting either one of the GLMMs, Hence, random factors were excluded from the final model.

The models were checked a second time for multicollinearity by using VIF tests with a cut-off value of four (package “performance”, function “check\_multicollinearity”, [Lüdtke et al., 2020](#)), however, multicollinearity issues were not detected. In the total fungal species richness model, we reduced the full model by backwards stepwise elimination (package “stats”, function “drop1”) until only significant

( $p > 0.05$ ) and close to significant variables remained. For the red-listed model, the variable selection was done manually based on  $p$ -value ( $p < 0.5$ ), since neither drop1 nor ANOVA are advised when using bias reduced GLM (Kosmidis, 2019).

The goodness-of-fit of the total fungal richness models was evaluated by creating quantile residual simulations, Q-Q plots and dispersion plots (R package “DHARMa”, functions “simulateResiduals”, “testDispersion” and “testZeroInflation”, Hartig, 2020). For the red-listed fungal model, we plotted binned residuals to assess how well the data fits model assumptions and area under the ROC curve (R package “pROC”, function “roc”; Robin et al., 2011) to assess the predictive power of the red-listed fungal model. Due to very low incidence of red-listed fungi and unbalanced deadwood volume distribution, only 48% of the residuals were inside the error bounds (R package “performance”, function “binned\_residuals”), indicating a weak predicting power of the model.

We used incidence rate ratios (IRR) for the Poisson model for fungal species richness and log-odds ratio (OR) for the logistic model of red-listed species incidence to present parameter estimates (R package “sjPlot”, function “tab\_model”, Lüdtke, 2020). IRR and OR estimates the modelled change in species number and red-listed species incidence per change of unit of each predictor variable, keeping all other variables at their mean value (Rita and Komonen, 2008). The reference point was one which indicated no effect, and values above one indicated positive effect, while values below one indicated a negative effect. This allowed us to simplify the variable effect size comparison, also for categorical variables, where it is important to enable quantitative ecological interpretations (Rita and Komonen, 2008).

### 2.3.3. Importance of various deadwood properties for fungal communities and species pool

To investigate differences in cumulative fungal species richness across deadwood substrate types (lying CWD, standing CWD, cut stumps or FWD) as well as decay stages, we ran individual and sample-based species accumulation curves (SAC; R package “vegan”, function “specaccum”, Oksanen et al., 2019). Hurlbert's (1971) analytical formulas were applied for individual based accumulation curves, with individuals being pooled together via rarefaction. For sample-based SAC, the method of Gotelli and Colwell (2001) was used, where SAC mean values were calculated via randomized permutations of data to obtain random site order. We applied several non-parametric richness estimators (Chao2, Jackknife and Bootstrap, R package “vegan”, function “specpool”) to evaluate the extrapolated species richness (Colwell and Coddington, 1994).

To identify species significantly associated with one of the studied deadwood substrate types, certain tree species (*Fagus sylvatica*, *Fraxinus excelsior*, *Quercus robur*, other deciduous or conifers) and decay stages, we performed Indicator Species Analysis (R package “indicspecies”, function “multipatt”, De Cáceres and Legendre, 2009). As the dataset consisted of presence-absence values at deadwood object level, the obtained indicator values express frequency and specificity, rather than species dominance on particular deadwood type. Pearson's *phi* coefficient of association, with accounting for unequal group size as suggested by Tichý and Chytrý (2006) was used as the statistical index that measures the correlation between two binary vectors (De Cáceres et al., 2010). Evaluation of *phi* values was done by permutation tests (9999 permutations).

## 3. Results

In total, 2519 deadwood objects were surveyed, unevenly distributed across the four defined deadwood types. Lying CWD was represented by 646 objects, standing CWD by 173 objects, lying FWD by 219 objects and cut stumps by 1478 objects. The majority of deadwood objects (1943) was of *Fagus sylvatica*, while *Fraxinus excelsior*, *Quercus robur*, other deciduous trees and coniferous trees were represented by

128, 121, 131 and 196 deadwood objects respectively.

In total 12,072 records of 250 fungal species were registered on the surveyed deadwood objects. The mean species number per deadwood object was 2.29 ( $SD = 2.91$ ), with a median value of two. The highest number of species recorded on a single object was 27, while 562 objects had no fungi recorded. Of the recorded species, 18 were red-listed in Denmark, with a total of 53 records. The Silkeborg and Sorø clusters had the highest average species richness per stand (58.5,  $SD = 11.4$  and  $SD = 14.7$ , respectively), while the Møn cluster had the lowest average species richness per stand (39,  $SD = 3.3$ ).

### 3.1. Differences in forest structural elements and fungal richness between forest management types

Based on ANOVA tests, long unmanaged forest stands had the highest species richness at stand level for both total fungi ( $p = 0.0375$ ) and red-listed fungi ( $p < 0.0001$ ) (Fig. 2a–b). Six stand structural variables showed significant differences between management types based on ANOVA and Welsh ANOVA tests (Fig. 2c–h). Long unmanaged stands showed the highest structural richness and the smallest impact of management. This was most clearly expressed for basal area ( $F = 5.9$ ,  $p = 0.002$ ), late biostatic development phase ( $F = 7.2$ ,  $p < 0.0001$ ), age ( $F = 13.45$ ,  $p < 0.001$ ), volume of cut stumps ( $F = 6.5$ ,  $p < 0.0001$ ), lying CWD ( $F = 13.3$ ,  $p = 0.001$ ) and standing CWD ( $F = 9.3$ ,  $p < 0.0001$ ). The two actively managed stand categories were not significantly different from each other and in most cases not different from the recently unmanaged stands either. Total area of gaps and FWD volume did not show significant differences between the management types.

### 3.2. Main drivers of total fungal richness at deadwood object level

Based on the GLMM, fungal species richness was most strongly affected by the properties of individual deadwood objects. Thus, species richness increased with deadwood volume, and peaked on decay stage 2, *Fagus* and lying deadwood respectively (Table 2; see Appendix C, Table C2 for the full list of tested variables in GLMMs). Among the stand level variables, stand age, gap area and basal area had smaller, but significant impact on species richness. Effects were positive for the two former variables, and negative for the latter. The resulting model explained 56% of variation in species richness.

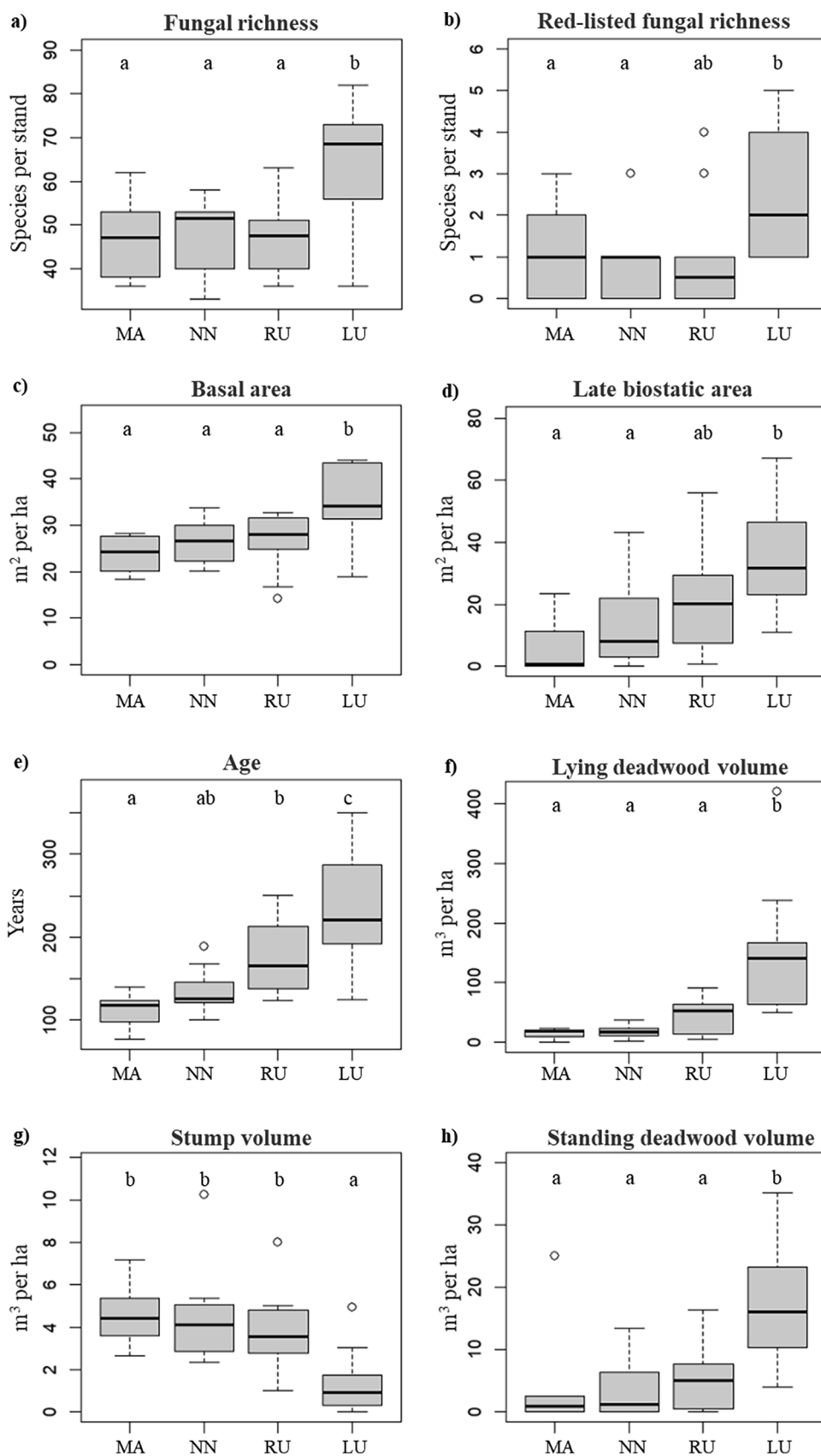
### 3.3. Main drivers of red-listed fungal incidence

As red-listed species had a very low incidence rate (2.1%) and classifies as “rare events”, the initial red-listed models were checked for complete and semi-separation and infinite maximum likelihood estimates, however, such issues were not detected.

Based on the GLM, resource size (i.e. high deadwood volume) was the most important driver of red-listed fungal incidence within forest stands, but the stand level variables- gap area and stand age, also contributed positively, with the latter variable being only marginally significant (Table 3 for main variables, Appendix C, Table C3 for full GLM). The model explained only 5% of the red-listed incidence, reflecting the low number of positive incidences in the dataset, and a high level of stochasticity.

### 3.4. Accumulated species richness across deadwood substrate types

Sample-based accumulation curves for fungal species richness showed similar trends for standing CWD and FWD, while lying CWD and cut stumps had higher and lower accumulated species richness respectively, when comparing the same number of sampled deadwood objects (Fig. 3a). Individual-based rarefaction (Fig. 3b) showed roughly similar patterns but indicated the total species pool to be significantly lower on FWD and standing CWD compared to cut stumps, a result that



**Fig. 2.** Boxplots of total fungal (a) and red-listed fungal (b) richness and main structural differences at stand level (c-h) among the four management types (MA: managed, NN: near-to-nature managed, RU: recently unmanaged, LU: long unmanaged). Thick horizontal lines show the mean values for each management type. Different letters above the box plots indicate significant difference between means, based on Games-Howell and Tukey tests.

was supported by the calculated species richness estimators (Table 4). For decay stage, accumulation and rarefaction curves (Fig. 3c and d) largely confirmed the results from the GLMM model, and indicated to deadwood in decay stage 2 to support the largest total pool of fruiting macrofungi within the groups covered, while decay stage 1 and 5 supported fewest species in total. Due to the low number of deadwood objects representing other tree species than *Fagus sylvatica* accumulation and rarefaction curves were not constructed to compare species pools among tree species.

### 3.5. Species preferences for deadwood substrate type, decay stage and tree species

Based on Indicator Species Analysis, deadwood type was the variable most strongly selecting for different fungal species. Thus 83 of the 250 recorded species showed a significant preference for one of the four substrate types (Appendix D, Table D1), while 75 and 64 species showed preference for decay stage (Appendix D, Table D2) and tree species (Appendix D, Table D3) respectively. Of the species showing a significant substrate type preference, the majority (59 species) showed preference for lying CWD, while only nine, seven and eight species, showed preference for standing CWD, cut stumps and FWD respectively. Five species had a Pearson's phi coefficient > 0.2, indicating a strong substrate preference. Four of these were associated with lying CWD, while the fifth species was associated with cut stumps (Appendix D, Table D1). Lying CWD was also the most important substrate type for red-listed fungal species, with higher numbers of species and occurrences than other substrates (Table 5). However, cut stumps showed a relatively high number of red-listed occurrences, mainly due to the presence of two species, *Mycena picta* and *Psathyrella maculata*. Of the species showing preference for decay stages, 21, 19 and 23 species were associated with decay stages 1, 2 and 3, respectively, while only 10 and 2 species showed preference for decay stage 4 and 5. Of species with a strong preference (i.e. a phi coefficient higher than 0.2), four species were associated with decay stage 1 and 2 with decay stage 2 (Appendix D, Table D2). Finally, 19, 13, 13 and 11 species showed preference for *Fagus sylvatica*, *Quercus robur*, other deciduous trees and *Fraxinus excelsior* respectively, while only eight species showed a preference for coniferous trees. Thirteen species had a Pearson's phi coefficient > 0.2. Four of those species were associated with a *Fagus sylvatica*, three with *Quercus robur*, two with *Fraxinus excelsior*, and another four with other deciduous trees (Appendix D, Table D3). The highest number of red-listed species (nine) was present on deadwood in decay stage 4, followed by stage 5 and 3. Most (14) red-listed species were found on *Fagus sylvatica*, while no other tree species supported more than two red-listed species (Table 5).

## 4. Discussion

We identified lying CWD as the most important substrate type supporting macrofungal richness, based on all metrics. While standing CWD, cut stumps and FWD had few selective or red-listed species associated, the accumulated and total predicted species richness was approximately half of that recorded on lying CWD. Deciduous trees, especially *Fagus sylvatica* was the preferred substrate for both total and red-listed fungal species. Overall, decay stage two and four had the highest total fungal richness, while red-listed species preferred more decayed wood (stage four and five). Variables recorded at stand level, relating to stand structure and stand age had much smaller, yet significant effects. Thus, on the smallest scale, fungal species richness was found mostly to depend on substrate quality, with deadwood volume being the single most important predictor. Incidence of red-listed species proved difficult to predict, due to the low number of presences in the dataset, but the relative amount of variation explained by stand level variables (as expressed by the Z statistics) were far higher than for overall species richness.

**Table 2**

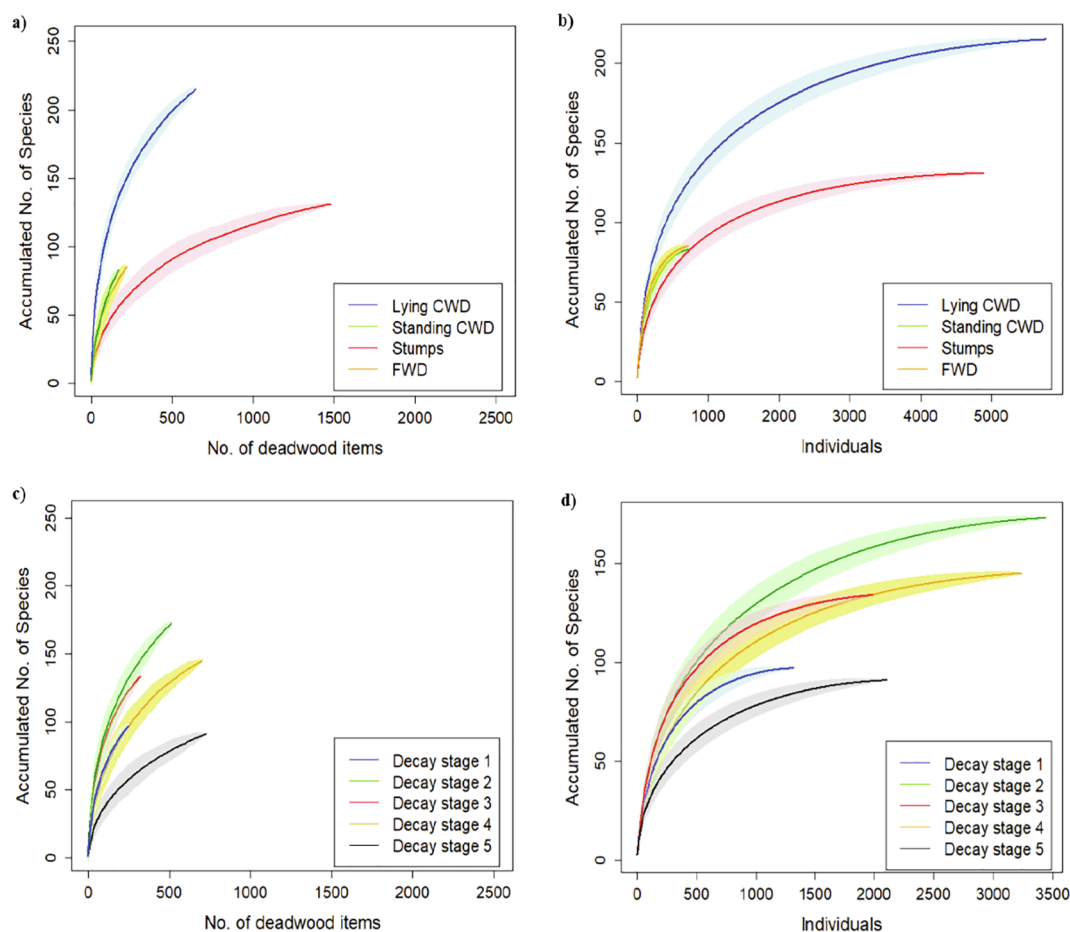
GLMM variable effects on fungal species richness on deadwood object level. The results are expressed in IRR values, where the reference point is one, indicating no effect on species richness, and values above one indicate a positive effect, while values below one indicate a negative effect on species richness. For categorical variables, a "reference" category was selected to allow comparisons with the other categories within the variable. Deadwood types: FWD – fine woody debris; Lying CWD – lying coarse woody debris; Standing CWD – standing coarse woody debris. Random effects:  $\sigma^2$  – residual or unexplained variability;  $\tau_{00}$  – variance explained by different combinations of random factors; ICC – intra-class correlation between individuals within groups; N – number of individual groups within each random effect; Marginal  $R^2$  – explained variance without accounting for random effects (as in GLM); Conditional  $R^2$  – explained variance with accounting for random effects, as calculated by Nakagawa and Schielzeth (2012).

GLMM for total fungal species richness				
Predictors	Incidence Rate Ratios	std. Error	Z stat.	p
(Intercept)	0.28	0.21	−5.96	< 0.001
<b>Deadwood object level variables:</b>				
Deadwood volume	2.08	0.03	27.86	< 0.001
Decay stage 1	Reference			
Decay stage 2	1.42	0.06	5.93	< 0.001
Decay stage 3	1.32	0.06	5	< 0.001
Decay stage 4	1.12	0.06	2.08	0.038
Decay stage 5	0.81	0.06	−3.44	0.001
Coniferous deadwood	Reference			
Deciduous deadwood	2.84	0.14	7.62	< 0.001
<i>Fagus</i> deadwood	3.82	0.11	12.62	< 0.001
<i>Fraxinus</i> deadwood	2.72	0.13	7.55	< 0.001
<i>Quercus</i> deadwood	2.19	0.13	5.93	< 0.001
FWD	Reference			
Lying CWD	1.74	0.07	8.36	< 0.001
Standing CWD	0.79	0.09	−2.8	0.005
Cut stumps	1.3	0.07	3.97	< 0.001
<b>Stand level variables:</b>				
Gaps (m <sup>2</sup> /ha)	1.01	0.01	2.15	0.032
Basal area (m <sup>2</sup> /ha)	0.99	0.01	−1.96	0.05
Stand age	1	0	2.43	0.015
<b>Random Effects</b>				
$\sigma^2$	0.39	ICC		0.17
$\tau_{00}$ cluster	0.01	N cluster		6
$\tau_{00}$ cluster:stand	0.03	N stand		40
$\tau_{00}$ cluster:stand:transect	0.05	N transect		399
Observations	2519			
Marginal $R^2$ /Conditional $R^2$	0.467/0.559			

**Table 3**

Firth bias adjusted GLM variable effects on red-listed species on deadwood object level. The results are expressed in odds ratios, where the reference point is one indicating no effect, and values above one indicate increased odds of species occurrence and values below one indicate decreased odds of species occurrence.  $R^2$  as calculated by Tjur (2009).

GLM for red-listed fungal species richness				
Predictors	Odds Ratios	Std. Error	Z stat.	p
(Intercept)	0	0.42	−13.02	< 0.001
<b>Deadwood object level variables:</b>				
Deadwood volume sq. (m <sup>3</sup> /object)	3.47	0.17	6.97	< 0.001
<b>Stand level variables:</b>				
Gaps (m <sup>2</sup> /ha)	1.05	0.01	2.33	0.022
Stand age	1.00	0.00	1.82	0.08
Observations	2519			
$R^2$	0.05			



**Fig. 3.** Sample-based species accumulation curve (a) and individual-based rarefaction curve (b) for total fungal species richness in relation to deadwood substrate types as classified in this study; and Sample-based species accumulation curve (c) and individual-based rarefaction curve (d) for total fungal species richness in relation to decay stages of deadwood. Deadwood types: FWD – fine woody debris; Lying CWD – lying coarse woody debris; Standing CWD – standing coarse woody debris.

**Table 4**

Species richness estimators for total species richness for each deadwood type and decay stages. Species – actual species count; chao – chao 1 estimate; jack1 – first order jackknife estimate; jack2 – second order jackknife estimate; boot – bootstrap estimate. *n* indicates the number of surveyed deadwood objects in each substrate category. Deadwood types: FWD – fine woody debris; Lying CWD – lying coarse woody debris; Standing CWD – standing coarse woody debris.

Substrate	Species	chao	jack1	jack2	boot	n
All	250	291 ± 14.1	307 ± 7.8	324.0	277 ± 4.6	2519
Lying CWD	215	281 ± 22.1	278 ± 8.8	310.8	244 ± 4.7	646
Standing CWD	83	144 ± 26.9	123 ± 7.7	149.5	100 ± 4.2	173
Stumps	131	164 ± 14.1	168 ± 6.1	184.0	148 ± 3.5	1478
FWD	85	126 ± 18.4	120 ± 7.3	139.7	100 ± 4.5	222
Decay stage	Species	chao	jack1	jack2	boot	n
Decay stage 1	97	132 ± 16.1	132 ± 6.5	150	113 ± 3.9	250
Decay stage 2	134	168 ± 13.7	175 ± 7.1	191	153 ± 4.4	326
Decay stage 3	173	244 ± 24.5	234 ± 8.4	269	200 ± 4.7	515
Decay stage 4	145	182 ± 14	192 ± 7.4	209	167 ± 4.5	702
Decay stage 5	91	132 ± 18.5	126 ± 6.5	146	106 ± 3.8	726

#### 4.1. Importance of deadwood quality

The relative and absolute importance of various deadwood variables for fungal richness found in this study is in good agreement with previous knowledge. Deadwood size has repeatedly been reported as one of the main drivers affecting saproxylic fungal diversity. This reflects that larger deadwood objects provide more resources to sustain fungal individuals and species (e.g. Schmit, 2005). Additionally, decay rate decreases with increasing deadwood dimensions (Přivětivý et al., 2016),

allowing more time for slow-colonizing species to establish (Jönsson et al., 2008; Stokland et al., 2012). Finally, larger deadwood provides a more stable microclimate (Pouska et al., 2016) and an increased probability of microhabitat occurrence (e.g. rot holes, cavities, etc.), which allows the establishment of specialized fungal species with narrow niches (Heilmann-Clausen and Christensen, 2004; Ódor et al., 2006).

The finding that lying CWD hosted the highest number of fungal species compared to other deadwood types is in agreement with

**Table 5**

A list of red-listed fungal species recorded in this study, and number of occurrences and species count per deadwood type, decay stages and deadwood tree species, as well as their red-list status according to Moeslund et al. (2019). The numbers for each species indicate how many positive incidences were recorded on different deadwood objects; total occurrences refer to the total amount of deadwood objects with red-listed occurrences. Decay stage and tree species indicate which stages and tree species a particular red-listed fungal species had been recorded on. Deadwood types: lying coarse woody debris, standing coarse woody debris, cut stumps, fine woody debris. Tree species: Dec. – various deciduous, Fag. – *Fagus sylvatica*, Que. – *Quercus robur*, Frax. – *Fraxinus excelsior*, Con. – various coniferous species.

Species	Deadwood type				Decay stages	Tree species	Red-list status
	Lying CWD	Standing CWD	Cut stumps	FWD			
<i>Arrhenia epichysium</i>	2	–	–	–	4	Dec.	EN
<i>Clitocybe truncicola</i>	1	–	–	–	5	Fag.	DD
<i>Crepidotus applanatus</i>	4	–	–	–	4–5	Fag.	VU
<i>Flammulaster muricatus</i>	2	–	–	–	4–5	Fag.	EN
<i>Galerina ampullaceocystis</i>	1	–	1	–	3, 5	Fag.	DD
<i>Galerina heimansii</i>	1	–	–	–	3	Que.	VU
<i>Hemimycena tortuosa</i>	–	1	–	–	1	Frax.	DD
<i>Hydropus scabripes</i>	–	–	1	–	5	Fag.	EN
<i>Leucoglyphana sororia</i>	1	–	–	–	3	Con.	DD
<i>Mycena picta</i>	1	1	7	–	3–5	Fag.	VU
<i>Ossicaulis lignatilis</i>	1	1	–	–	2	Fag.	VU
<i>Porotheleum fimbriatum</i>	1	–	–	–	4	Fag.	EN
<i>Psathyrella fagetophila</i>	–	1	–	1	1–2	Fag.	DD
<i>Psathyrella maculate</i>	3	–	5	–	3–4	Fag.	VU
<i>Psathyrella pseudocasca</i>	5	1	–	–	1–4	Fag.	DD
<i>Psathyrella rostellata</i>	2	–	–	–	4	Dec.	VU
<i>Psathyrella spintrigeroides</i>	9	–	–	–	2–5	Fag. Que.	EN
<i>Simocybe sumptuosa</i>	–	–	1	–	5	Fag.	VU
Total occurrences	33	4	15	1			
Total no. of species	14	5	5	1			

previous studies (Heilmann-Clausen and Christensen, 2004; Abrego and Salcedo, 2011; Pasanen et al. 2019), although the difference was surprisingly large when aggregated across substrate objects using rarefaction curves. Standing CWD was by far the poorest substrate for saproxylic fungi, which probably reflects lower water availability limiting fungal fruiting (Pouska et al., 2016). Yet, standing CWD provides important habitats for other aspects of biodiversity, not least insects and woodpeckers (Czeszczewik et al., 2013; Dufour-Pelletier and Tremblay 2020), but also for specialized fungi, which may only utilize the resource after the trunk has fallen to the ground (Niemelä et al., 2002).

FWD in our study was a rather poor refuge for macrofungi supporting only half the species pool associated with lying CWD, based on species accumulation curves and overall richness predictors. This result is different from other studies (e.g. Nordén et al., 2004; Küffer and Senn-Irlet, 2005) that reported FWD to provide important habitats sustaining a high number of fungal species. In contrast to these studies, we defined macrofungi more narrowly and excluded certain species rich groups, e.g. most corticoid fungi and *Ascomycota* with small fruitbodies, of which many prefer smaller substrate dimensions (Nordén et al., 2004; Abrego and Salcedo, 2011). This delimitation was made deliberately to put emphasis on the part of the fungal community that is most sensitive to forestry based on previous studies (Juutilainen et al., 2014; Runnel and Lohmus, 2017). Thus, our results do not imply that FWD is a species poor substrate for saproxylic fungi overall, but only for the species groups assessed here.

Overall, the signal for deadwood tree species was strong (Table 2), reflecting that saproxylic fungi are specialized in their host tree selection. Like several previous studies (Küffer and Senn-Irlet 2005; Purahong et al., 2018; Pasanen et al. 2019) we found that deciduous tree species hosted significantly higher numbers of fungal species than conifers, both per deadwood object and in terms of selective species based on indicator species analysis (Appendix D; Table D3). The low species richness on coniferous deadwood may be explained by the low pH, low nitrogen contents and high amounts of extractives, which seem to cause not only a slower decay rate, but also a more restricted species pool, compared to deciduous hosts with less acidic wood (Heilmann-

Clausen et al. 2016; Kahl et al., 2017). It could also reflect that conifers are mainly introduced in Denmark, and hence may support fewer associated species compared to native hosts (cf. Brändle and Brandl 2001). In conclusion, the strong positive effect of *Fagus* deadwood (and other deciduous trees) on species richness supports the notion by Heilmann-Clausen et al., (2005), that locally abundant host species support the highest richness of associated biota (Brändle and Brandl, 2001).

While overall richness of saproxylic fungi peaked on deadwood in intermediate decay stages, as found in numerous studies, we found no significant response to decay stage in the models for red-listed fungi, in contrast to several other studies (e.g. Pouska et al., 2011; Heilmann-Clausen and Christensen, 2005). This seems to reflect the low number of positive occurrences of red-listed species in this transect-based dataset, and a more individualistic approach focusing on single-species occurrence patterns revealed deadwood in late decay stages to support the highest number of red-listed taxa (Table 5).

#### 4.2. Importance of stand structure and age

Even though deadwood object variables explained most of the variation in overall species richness and red-listed species incidence, stand structural variables also contributed. The modeled incidence rate ratios (Table 2) showed that deadwood in older and partly open stands with evident gap phases supported more species and had more records of red-listed species compared to similar objects in younger or more closed stands. Effects of sun exposure on fungi are generally reported as negative, typically based on rather steep forest edge or substrate type mediated effects (Pouska et al., 2016). The positive effect of canopy gaps in our study suggests that a dense and closed canopy may restrict fungal richness on decaying wood, while gaps with more moderately increased light influx, higher ground temperatures and more variable moisture levels appear to benefit species richness, and not least the presence of red-listed taxa. Brazee et al. (2014) and Pasanen et al. (2019) found similar results in experimental gap-cutting studies, indicating sun-exposure to increase fungal richness more generally. However, we consider the effect to be context specific and most likely

restricted to rather cool and humid climates, where drought stress is not so severe that fungal growth and survival is halted.

#### 4.3. Recommendations for management

It is generally acknowledged that forest reserves are strongly beneficial for saproxylic species, due to presence of favorable deadwood habitat conditions (Burrascano et al., 2008) allowing slow-colonizing and demanding species sensitive to management activities to establish or persist (e.g. Junninen and Komonen 2011). However, as shown by Vandekerckhove et al. (2009) the development of structural and compositional characteristics of old growth forests is often a slow process when new reserves are created in formerly managed forests. Hence, recent forest reserves may lack the structural complexity needed to support biodiversity associated with these features (Schall et al., 2018), as also highlighted in this study, where far the biggest structural differences were found, not between unmanaged forest reserves and managed stands generally, but specifically between long unmanaged stands and all other stand types (Fig. 2). In this context, integrative forest management offers an opportunity to increase deadwood actively, and increase associated biodiversity as shown by Dörfler et al. (2018). Our study showed that lying deciduous CWD provided most resources for saproxylic macrofungi, and hence such substrates should be prioritized in managed stands when possible. This is relevant during timber harvesting, where low quality logs and larger branches can be left for natural decay. However, it is even more important to allow or even promote natural death of trees to allow a fuller range of deadwood microhabitats (Larrieu and Cabanettes, 2012). Naturally dying trees may in addition deliver standing CWD, supporting beetles and birds such as woodpeckers (Czeszczewik et al., 2013) before they fall over. If possible, tree species diversity should be promoted in the deadwood pool, favoring locally abundant species, rather than introduced species, which in this study were found to be poorly able to support saproxylic fungi.

To overcome extinction bottlenecks when creating new forest reserves in managed forest landscapes, the option to speed up habitat creation by active veteranization, deadwood enrichment and creation of canopy gaps can be considered (Brazee et al., 2014; Sandström et al., 2019), under consideration of the associated costs.

#### Author contribution statement

The study was designed by HHB, CR and JHC. Fungal data collection was conducted by TL, RRH, JHC while AA and GGB mapped forest development phases. AA, GGB and JHC wrote the manuscript, with feedback and contributions from all authors.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118512>.

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