Available online at www.sciencedirect.com

SCIENCE DIRECT®

Forest Ecology and Management 201 (2004) 105–117

Forest Ecology and Management

www.elsevier.com/locate/foreco

Does size matter?
On the importance of various dead wood fractions for fungal diversity in Danish beech forests

Jacob Heilmann-Clausen*, Morten Christensen

Danish Centre for Forest, Landscape and Planning, Royal Veterinary and Agricultural University,
Rolighedsvej 23, DK-1958 Frederiksberg C, Denmark

Received 18 July 2003; received in revised form 13 May 2004; accepted 8 June 2004

Abstract

The importance of different fractions of coarse wood debris (cwd) for species diversity of wood-inhabiting fungi was investigated in near-natural Danish beech stands. Species number per tree increased significantly with increasing tree size, pointing out large trees to be most valuable for fungal diversity if single samples are compared. Rarefaction curves, evaluating the importance of different cwd fractions in a cumulative space, revealed a different and more complex picture. Rarefaction curves based on wood volume showed small trees and branches to host more species per volume unit than larger trees and logs, respectively, while snags were the most species-poor fraction. Surface-based curves showed species density to be rather similar among cwd types, though species density still decreased slightly with tree size. These results are interpreted to reflect a combination of two factors: firstly, small diameter cwd represent a larger surface area per volume and hence more space for fungal sporocarps, than large diameter cwd. This ‘surface area factor’ explains the high degree of similarity of the surface-based rarefaction curves. Secondly, a collection of small diameter cwd involves more separate units than an equal volume of large diameter cwd, and represents thereby more individual cases of fungal infection and, most likely, more variation in environmental conditions. The effect of this ‘number of item factor’ is reflected in the slightly increasing species density per surface area with decreasing tree size. Richness patterns of red-listed and non-red-listed species were found to be strikingly similar across cwd types, and a general preference for large logs among red-listed species was hence absent. An individual look at the most frequent encountered red-listed species revealed substrate preference patterns to occur in three of six species, of which one, the heart-rot agent *Ischnoderma resinosum*, preferred large logs. Based on these results, it would be obvious to conclude that local fungal species diversity is most efficiently increased in managed forests if small diameter cwd is prioritised for natural decay. However, small diameter wood appear to be unable to support heart-rot agents and other species depending on a long and diverse infection history and thus the integrity of saproxylic communities may be seriously undermined if only small diameter cwd is left for decay. Therefore, we strongly recommend

---

* Corresponding author. Tel.: +45 35281743; fax: +45 35282671.
E-mail address: jhc@kvl.dk (J. Heilmann-Clausen).

doi:10.1016/j.foreco.2004.07.010

that whole, naturally dead trees, representing the full range of cwd habitats, are prioritised for natural decay in managed forests whenever possible.

Keywords: Biodiversity; Coarse woody debris; Conservation; *Fagus sylvatica*; Fungi; Rarefaction

---

1. Introduction

Management and restoration of native biodiversity is increasingly accepted as an important goal in sustainable forestry (e.g. MCPFE, 1998). In this respect, organisms associated with coarse woody debris (cwd) represent an important but problematic group. Siitonen (2001) reported that at least 4000 of 19,000 estimated forest dwelling species in Finland depend on dead wood, and Berg et al. (1994) found various types of decaying wood to constitute the most important habitats for threatened cryptogams and invertebrates in Sweden. Maintenance of cwd-associated biodiversity requires that wood, representing a possible economic income, is left for natural decay, and this could lead to the assumption that cwd-associated biodiversity is best protected in forest reserves. Managed forests may represent important stepping-stones for exchange of genes and species between reserves, and their role in the management of cwd-associated biodiversity should not be neglected (cf. Hansen et al., 1991; Niemelä, 1997; Ehnström, 2001). Accordingly, it is important to develop cwd management practices for managed forests that combine an optimal protection of biodiversity with minimal economic drawbacks. For this goal to be achieved, it is necessary to know the economic value as well as the conservation potential of different cwd fractions. Whereas economic values are usually easily obtainable from price indices familiar to forest managers, there are fewer available data on conservation value.

A number of studies have claimed that large logs are particularly important for fungal biodiversity (Bader et al., 1995; Renvall, 1995; Høiland and Bendiksen, 1996; Bredesen et al., 1997; Kruys et al., 1999; Sippola and Renvall, 1999), and similar claims have been put forward with respect to bryophytes (Söderström, 1988; Andersson and Hytteborn, 1991) and saproxylic insects (Grove et al., 2002; Similä et al., 2003). Most of these claims are difficult to verify, since it is often impossible to evaluate to which degree the reports reflect simple, positive species-area relationship predictions of increasing species numbers with increasing habitat size (e.g. Begon et al., 1990). Through the use of rarefaction curves species diversity of different habitat types can be compared in a more neutral space (Gotelli and Colwell, 2001). Some studies using this technique have shown that smaller cwd fractions in fact may be much more important than hitherto expected for both fungal (Kruys and Jonsson, 1999) and insect biodiversity (Schiegg, 2001). Rarefaction curves can be constructed in two alternative ways, using either the number of samples or the number of individuals sampled as basis for comparisons (Gotelli and Colwell, 2001). In studies of wood-inhabiting organisms on individual trees, the situation is complicated as trees are three-dimensional, discrete entities. This means that at least four relevant measures can be used for comparisons, i.e. number of individuals, number of samples, wood volume and surface area, making uncritical use of rarefaction curves dubious.

In this study, we use rarefaction curves based on these four measures to analyse the importance of various cwd fractions for fungal diversity in a range of near-natural beech stands, distinguishing among whole trees of different size classes, and different tree parts, i.e. logs, branches and stumps. Separate analyses are presented for red-listed as well as non-red-listed species, as the first group is often considered to be critically dependent on the presence of large decaying logs. The main questions addressed in the paper are:

(a) Are the defined and investigated cwd fractions all equally important for fungal diversity?
(b) How should rarefaction curves be scaled in comparisons of different cwd habitats?
(c) Does red-listed species differ in their habitat preferences compared to non-red-listed species?

The practical implications of the results are assessed and discussed in a sustainable forestry context.

2. Materials and methods

2.1. Study objects

The data presented here derive from two different studies in unmanaged beech forests in Denmark; both were carried out jointly by the authors. Study 1, including 110 dead beech trees distributed across nine localities, was carried out in 1997 and 1998. Study 2 was carried out in 2000 and 2001 and included 200 dead beech trees distributed across five localities, of which two were included in study 1. The 12 localities represent a range of the most common types of beech forests in Denmark.

In both studies, the trees were selected randomly from a predefined size class/decay class matrix, with the aim to get a comparable range of size and decay classes represented for each locality. Five decay classes (defined according to Heilmann-Clausen, 2001) and four size classes (diameter at breast height (dbh) = 20–49, 50–79, 80–109 and 110–139 cm) were distinguished.

2.2. Data collection

A number of environmental variables were recorded for each tree and each locality, but only the importance of tree size is covered in detail here. Wood volumes and surface areas were estimated using formulas for truncated cones:

$$\text{volume}\,(\text{cm}^3) = \frac{1}{2}[\pi l(r^2 + rR + R^2)]$$
$$\text{area}\,(\text{cm}^2) = p(R + r)h$$

where l is the length of the wood piece (cm), h is the length of its side, r is the radius (cm) at the narrow end and R is the radius (cm) at the broad end. Radii were measured at each end of all branches until the 10 cm size limit and in all branching points. The logs were measured at each end and at intervals of 2 m along the length.

The trees, including snags and branches with a diameter exceeding 10 cm, were inventoried for fungal sporocarps at three separate occasions (late summer, mid-autumn and late autumn). In the second study, the mycota was inventoried independently on the snag, the log, and larger branches with diameter exceeding 10 cm. Both studies included all groups of macromycetes (sporocarps larger than 1 mm), except fully resupinate corticoid fungi, non-stromatic pyrenomycetes and inoperculate discomycetes with sporocarps regularly smaller than 10 mm.

2.3. Data analysis

Basic relations between tree sizes and recorded species numbers were evaluated using Kendall rank correlation. Non-parametric correlation was favoured over parametric correlation, because of inequality in variances. Kendall rank correlation was favoured over Spearman rank correlation since the latter method is less efficient in the presence of many tied ranks (Legendre and Legendre, 1999).

The importance of various tree parts and tree size classes for fungal species diversity was investigated by comparison of Coleman rarefaction curves (Coleman et al., 1982; Gotelli and Colwell, 2001), calculated using EstimateS (Colwell, 2001). Comparisons of species diversity between substrate types were made by comparing: (a) equal number of sampled individuals; (b) equal numbers of sample items; (c) equal wood volumes; and (d) equal surface areas. As the unit for recording of species was trees or tree parts wood volumes and surface areas were standardised based on average values for each substrate type. Average numbers of sampled individuals with increasing sample size were calculated using EstimateS (Colwell, 2001). Following the terminology of Gotelli and Colwell (2001), we use the term species richness narrowly for relations between numbers of species and numbers of individuals, while the term species density is used for relations between species numbers and sample items, wood volumes and surface areas.

The species were divided into two groups, viz. species occurring in the Danish Red Data Book (Stoltze and Pihl, 1998), in the following referred to as red-listed species and the remaining species referred to as non-red-listed species. For the six most frequent red-listed species (more than six occurrences) *G*-tests (Fowler and Cohen, 1992) were applied to search for selectivity patterns with respect to the defined substrate types. The test was performed for each red-listed species, by testing its occurrence pattern across substrate types against the total number of occurrences of non-red-listed species.

2.4. Comparability of datasets

Tree size is not the only factor affecting fungal diversity and the presence of red-listed species on decaying wood. Several other factors, including tree decay stage, death cause, microclimatic conditions and forest history are known to influence local diversity (e.g. Bader et al., 1995; Renvall, 1995; Heilmann-Clausen and Christensen, 2003). It is therefore tricky to consider the effect of size variables isolated without paying attention to other relevant variables, especially when data from different localities and studies are pooled, as in the present study. A more detailed analysis of the same datasets (Heilmann-Clausen and Christensen, in press) found no significant effect of study year on species richness per tree, while both tree decay stage and locality were identified as important factors. This, potentially, is a problem as the representation of tree size classes is not equal among the included localities (Table 1), partly due to natural differences in size distributions across localities and partly due to differences in the sampling protocols of the two studies. Especially, the smallest and largest size class is under-represented in some localities, which would suggest these to act more unstable than intermediate sized trees in the analyses. However, we found no relation between average species richness and average tree size per locality, after controlling for the effect of individual tree size ($\tau = 0.23$, $P = 0.30$), for which reason we find our comparisons of different sized trees justified. However, it is clear that a more balanced study design should be preferred in future studies.

3. Results

3.1. The importance of size

A total of 5428 fungal occurrences were recorded, representing 348 fungal species of which 27 are red-listed (Table 2). The number of observed species per tree varied between 1 and 46 with a median of 16. Red-listed species were observed on 110 (34%) of the study trees. The highest number of red-listed species observed on a single tree was three.

Recorded species numbers per tree was highly correlated with dbh, wood volume and surface area ($\tau = 0.42^{***}$, 0.51^{***} and 0.54^{***}; $P < 0.0001$ in all cases). Still it is clear that the variation in species numbers with increasing tree size is considerable, with an asymptotic trend (Fig. 1). Comparisons of individual-based rarefaction curves show that species richness was virtually identical between tree size classes within the comparable range (Fig. 2a). The curves for red-listed species show a similar degree

Table 1
Number of dead trees investigated for fungal sporocarps at each locality and their distribution on tree size classes

Locality	Diameter at breast height				
	20–49 cm	50–79 cm	80–109 cm	>110 cm	Total
Møns Klinteskov[a]	31	13	6	0	50
Suserup Skov[a,b]	12	15	25	18	70
Strødam[a,b]	10	14	33	13	70
Gråsten Dyrehave[b]	0	2	4	1	7
Knagerne[a]	3	11	11	0	25
Velling Skov[a]	12	8	5	0	25
Farum Lillevang[b]	0	2	5	3	10
Moesgård Skovene[b]	0	3	3	4	10
Fussingø Indskove[b]	0	2	4	1	7
Lellige Skovhusvænge[b]	0	2	6	1	9
Nørreskoven ved Farum[b]	0	1	6	3	10
Stenderup Midtskov[b]	0	1	11	5	17
Total	68	74	119	49	310

[a] Indicates that the locality was included in study 2, carried out in 2000 and 2001.

[b] Indicates that the locality was included in study 1, carried out in 1997 and 1998.

Table 2
Red-listed fungal species recorded, sorted by number of occurrences

Species	Red-list status[a]	Number of occurrences	Minimum dbh of occupied trees (cm)
Nemania chestersii	Rare	31	21
Camarops tubulina[b]	Critically threatened	15	60
Pluteus umbrosus	Rare	13	70
Ischnoderma resinosum[b]	Vulnerable	11	74
Pluteus luctuosus	Rare	11	43
Micromphale brassicolens	Vulnerable	10	23
Mycena picta	Rare	7	51
Catinella olivacea	Rare	5	70
Pleurotus cornucopiae[c]	Rare	5	107
Ceriporiopsis gilvescens	Vulnerable	4	75
Pluteus hispidulus	Rare	4	46
Kavinia himantia	Critically threatened	3	23
Lentaria epichnoa	Rare	3	59
Omphalina epichysium	Critically threatened	3	80
Aurantioporus alborubescens[b]	Vulnerable	2	90
Entoloma tjallingiorum	Rare	2	38
Flammulaster limulatoides	Rare	2	75
Flammulaster muricatus	Critically threatened	2	36
Lentinellus vulpinus[d]	Critically threatened	2	111
Spongipellis delectans[e]	Critically threatened	2	70
Volvariella bombycina[c]	Rare	2	104
Conocybe utriformis	Rare	1	81
Coprinus alopecia	Rare	1	69
Coprinus echinosporus	Rare	1	85
Galerina heimansii	Rare	1	100
Nemania carbonacea	Rare	1	115
Stromatoscypha fimbriata	Rare	1	95
Volvariella caesiotincta	Vulnerable	1	65

Species in bold face are known or suspected heart-rot agents.

[a] According to Stoltze and Pihl (1998).

[b] According to own observations.

[c] According to Hansen and Knudsen (1992).

[d] According to Hallingbäck (1994).

[e] According to Ryvarden and Gilbertson (1994).

of similarity between tree size classes except for the smallest size class, which show a tendency to be less species rich (Fig. 2b).

Sample-based rarefaction curves show that the three larger dbh classes did not deviate significantly in species density, whereas trees of the smallest dbh class were significantly less species dense (Fig. 3a). When equal volumes are compared, a very different picture is seen with the smallest dbh class showing the highest species density, decreasing towards the largest dbh class (Fig. 3b). The same tendency, but weaker, is evident from comparisons based on surface areas (Fig. 3c), reflecting the relatively bigger surface area of small trees compared to large trees.

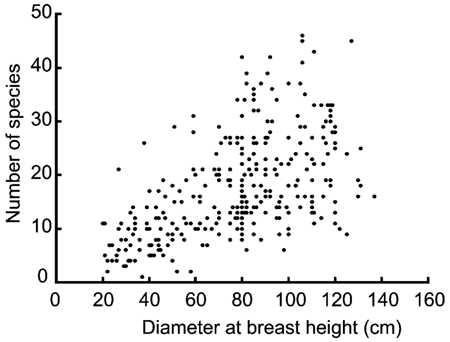

Fig. 1. The relation between tree diameter at breast height (dbh) and number of fungal species recorded per tree. A positive relation between dbh and species diversity is evident, but with substantial and increasing variation with increasing dbh.

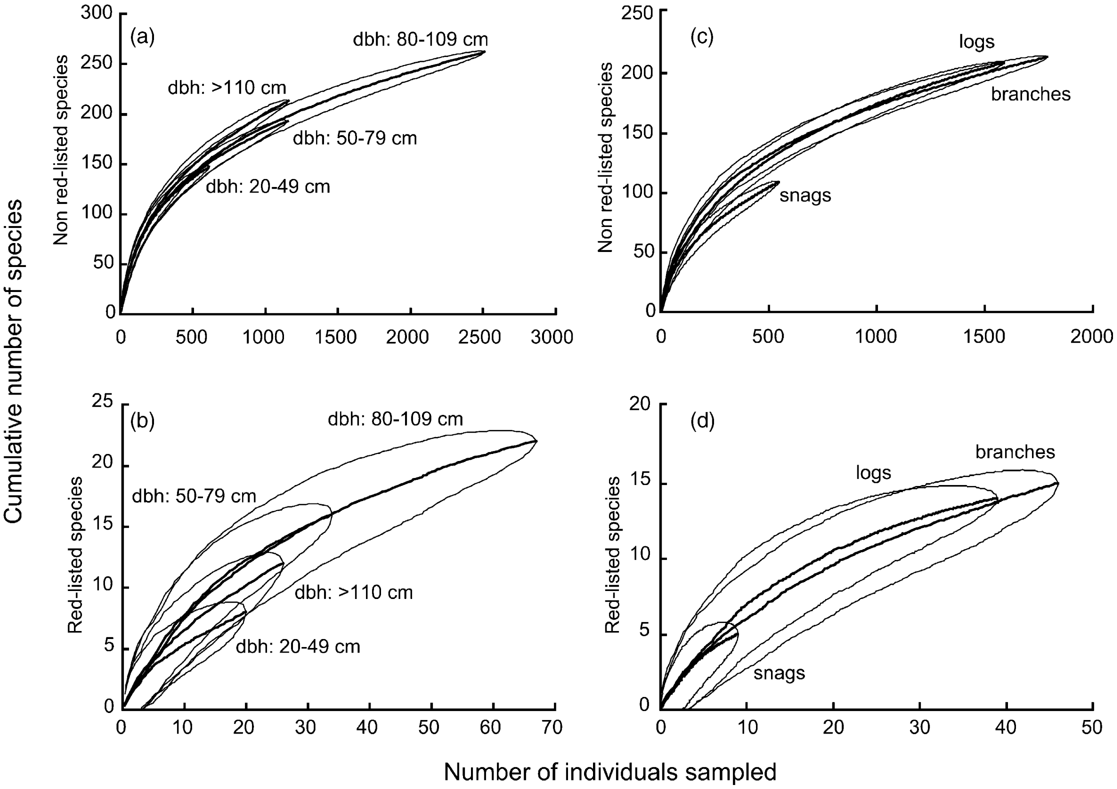

Fig. 2. Coleman rarefaction curves for non-red-listed (a and c) and red-listed fungi (b and d) in relation to tree size classes (a and b) and tree parts (c and d). Thin lines indicate 95% confidence intervals around the means for each substrate class. Note that the axes are differently scaled. The curves for red-listed and non-red-listed species are quite similar indicating that the two groups do not differ substantially in their habitat preferences. However, the smallest trees tend to be slightly less species rich for red-listed species than expected from the curves based on non-red-listed species.

Of the 27 red-listed species, a majority, including all known heart-rot agents, were recorded only on trees with a dbh exceeding 70 cm (Table 2), but the overall occurrence pattern of red-listed species across dbh classes did not deviate from the pattern shown by non-red-listed species (*G*-test, $P = 0.60$). Of the six most frequent red-listed species three were not recorded on trees in the smallest dbh class, but only *Ischnoderma resinosum* showed a significant preference for large trees (*G*-test, $P = 0.05$). *Micromphale brassicolens*, on the other hand, was over-represented on small trees (*G*-test, $P = 0.0006$) (Fig. 4a).

3.2. Importance of different tree parts

For 200 trees, the snag, log, and branch portions were investigated independently. Of these 127 had snags, yielding a total of 546 records of 109 fungal species. All trees possessed logs, yielding a total of 1587 records of 209 species, while branches occurred on 178 trees, yielding a total of 1790 records of 214 species.

Individual-based rarefaction curves show that logs and branches had very equal species richness, while snags were significantly poorer (Fig. 2c). The curves for red-listed species show the same trend (Fig. 2d), but due to the low total number of red-listed individuals recorded on snags it is impossible to discern whether snags were less species rich for this group.

Comparisons of sample-based rarefaction curves show that logs and branches had almost similar species density, while snags were significantly less species dense (Fig. 3d). When equal volumes are compared, the picture is only changed slightly. Branches now

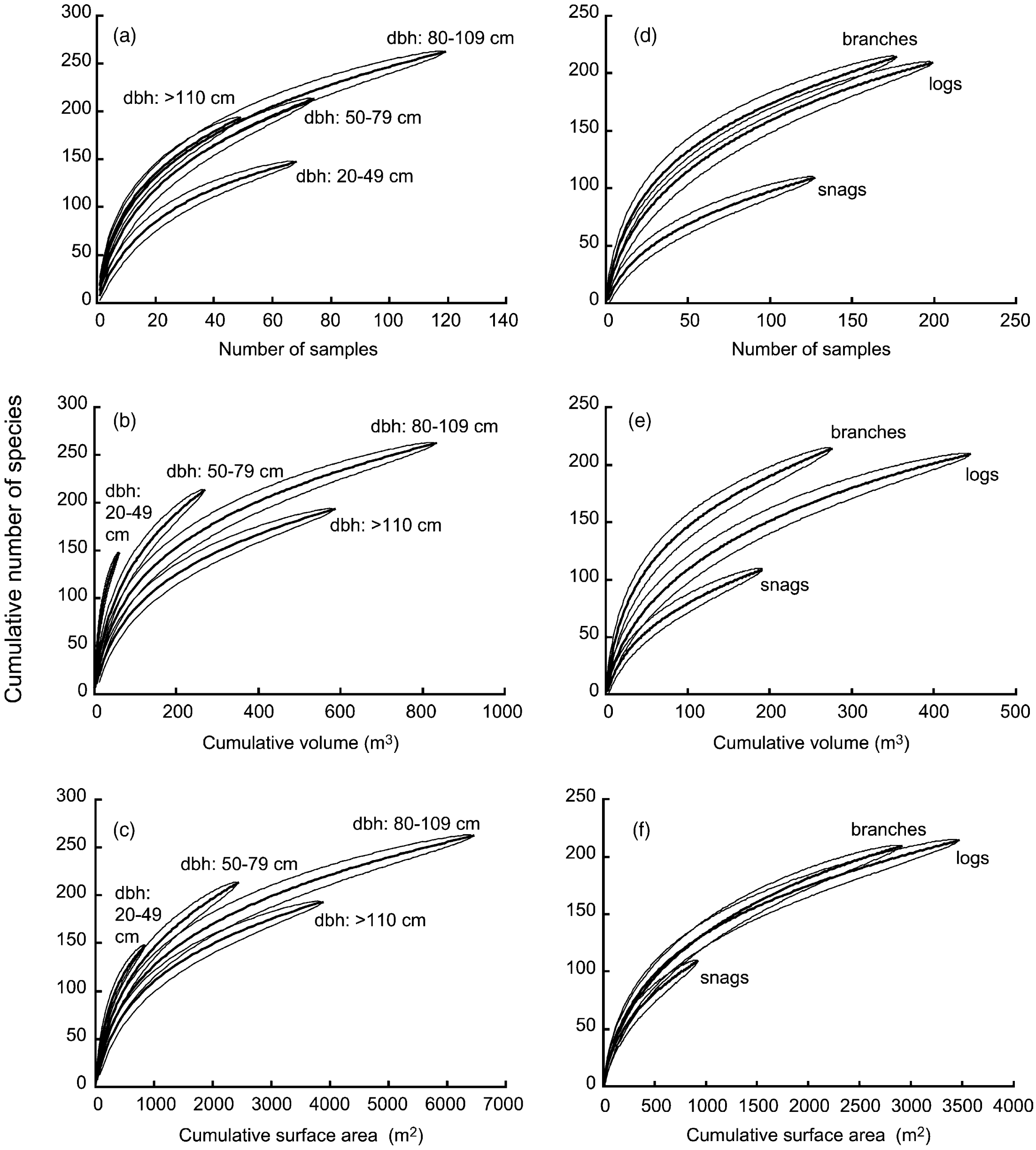

Fig. 3. Coleman rarefaction curves for non-red-listed fungi based on number of samples (a and d), cumulative volume (b and e) and surface area (c and f) in relation to tree size classes (a–c) and tree parts (d–f). Thin lines indicate 95% confidence intervals around the means for each substrate class. Note that the axes are differently scaled. The surface-based curves are in both cases rather similar indicating that cumulative surface area is the best predictor of cumulative species richness across substrate types.

appear to be significantly more species rich than logs, reflecting their lower average wood volume, while logs still appear to be significantly richer than snags (Fig. 3e). Finally, the comparison based on surface areas show all tree parts to have very similar density, with snags showing only a slightly lower trend (Fig. 3f).

The general occurrence pattern of red-listed species with respect to tree parts did not deviate significantly from the pattern for non-red-listed species (*G*-test,

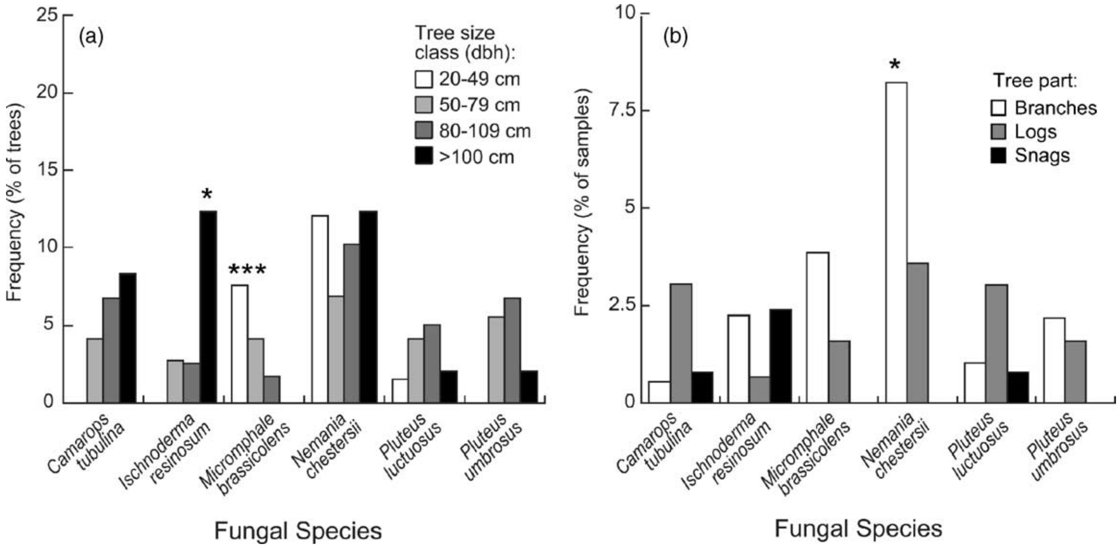

Fig. 4. Frequency of the six most frequent red-listed species on trees of different size classes (a) and on different tree parts (b). Frequency patterns deviating significantly (*G*-test) from the general occurrence patterns of non-red-listed species are indicated; $^{*}P < 0.05$, $^{***}P < 0.001$. Note that the axes are differently scaled.

$P = 0.55$), and of the six most frequent species only one showed significant preference patterns. Thus, *Nemania chestersii* was over-represented on branches (*G*-test, $P = 0.05$), while *Camarops tubulina* showed a non-significant preference for logs (*G*-test, $P = 0.10$) (Fig. 4b).

4. Discussion

4.1. Different measures — different diversity patterns

Like several previous studies (e.g. Bader et al., 1995; Renvall, 1995; Høiland and Bendiksen, 1996; Kruys et al., 1999; Heilmann-Clausen and Christensen, 2003), we found fungal species numbers per tree to be strongly and positively correlated with tree size variables. Of the investigated size measures, dbh performed only marginally poorer than wood volume and surface area, implying that all measures could be used interchangeable. Comparisons of rarefaction curves, however, revealed a very different and disturbingly complex picture.

Thus, individual-based rarefaction curves showed species diversity to be virtually similar among the defined tree size classes. Sample-based curves showed the smallest trees to host significantly fewer species than trees in the larger dbh classes. Finally, area- and volume-based curves showed the opposite picture, as the smallest trees hosted most species both per surface area and wood volume.

In accordance with our results, Kruys and Jonsson (1999) found spruce logs with diameter <10 cm to host more cryptogam species per volume unit than logs with diameter >10 cm. Similarly, Schiegg (2001), found beech limbs (diameter <10 cm) to host more saproxylic insect species (both common and red-listed) compared to beech trunks (diameter >20 cm). The trend of increasing species diversity per volume unit with decreasing tree size thus seems to be a general feature, which can be explained by considering two simple factors. Firstly, small diameter cwd has a bigger surface area and may hence support more fungal sporocarps (or attract more insects) per volume unit, compared to large diameter cwd (Kruys and Jonsson, 1999). We will denote this as the surface area factor. Secondly, small diameter cwd involves many more individual wood pieces per volume unit compared to large diameter cwd. Thereby, assemblages of small cwd will tend to have higher species density per volume unit due to the stochastic nature of colonization processes as long as many wood-inhabiting organisms are able to live in small cwd. The similarity of the individual-based rarefaction curves clearly shows that this premise is satisfied in the present case. In addition, more separate units are likely to cover more variation in edaphic conditions, microclimate, decay histories etc. and does thereby represent higher micro-habitat diversity per volume unit (Kruys and Jonsson, 1999; Schiegg, 2001). We will denote these two phenomena combined as the number of item factor.

The present study indicates that both factors contribute to the higher species density on small cwd. Thus, the area-based rarefaction curves show that a selection of smaller trees hosted more species per surface area compared to larger trees, indicating an effect of the number of item factor. Yet, the differences in species density between the tree size classes are significantly more distinct when volume-based rarefaction curves are compared, indicating a direct importance of the surface area factor.

Comparisons of rarefaction curves for the different tree parts support the importance of the surface area factor. Thus, the volume-based curves show that branches hosted significantly more species per volume unit compared to logs, while the surface-based curves show that the two habitat types were equally species dense per surface area. The similarity of the surface-based rarefaction curves indicate that habitat diversity is equal among the two tree parts, or indeed that it is higher in logs if stochastic colonization processes have major impact on community assembly as the branch fraction involves many more individual wood pieces per surface area compared to logs (data not shown).

Snags had the lowest species density in all comparisons, and the individual-based rarefaction curves showed species diversity in its narrow sense to be lower in this habitat type. This probably reflects stressful conditions in snags, due to strongly fluctuating microclimatic conditions and common desiccation events during dry periods (Renvall, 1995), which may be restrictive to some species. It may also play a role that the overall coverage of variation in environmental conditions and hence habitat diversity tend to be lower for snags compared to logs and branches. This is both because snags have a very limited horizontal distribution, but also because well-decayed snags are rare. Wood decay will normally cause beech snags to fall 10–20 years after tree dead. It is our experience that such fallen, partly decayed snags often host very diverse and characteristic fungal communities. It can therefore not be concluded that snags are relatively worthless fungal habitats, but rather that they have a decay development that differs considerably from that of logs and branches (cf. Yatskov et al., 2003).

4.2. Choosing an appropriate scale for comparisons

The discussion above pinpoints the importance of choosing an appropriate scale for rarefaction curves, and, more specific, to use size variables carefully when estimating the value of different cwd types for biodiversity. Sample-based rarefaction curves, and focus on species numbers per tree, point out large trees to be most valuable for species diversity, while focus on surface areas and especially wood volume show small diameter cwd items to be most valuable. Finally individual-based rarefaction curves show all of the evaluated habitat types, except snags, to be equally species rich. Which measures should then be used?

For practical conservation purposes we agree with Gotelli and Colwell (2001) that species density is generally most interesting, because it relates to the number of species on a scale of direct relevance for management. This qualifies number of samples, cumulative wood volume and surface area as relevant measures for comparison and formulation of practical conservation tools.

Guidelines for sustainable forestry often focus on the number of trees or snags left for natural decay per hectare of forest land (e.g. Skov- og Naturstyrelsen, 1995; Anon., 2000) and also in scientific evaluations of habitat quality number of samples has been used as the only basis for comparisons of rarefaction curves (e.g. Rolstad et al., 2004). The present study shows that this is inadequate, because species density per sample differs markedly depending on tree size or dead wood fraction, and we strongly recommend that direct emphasis is given to actual wood volumes or surface areas. In the present case cumulative surface area appeared to be the best predictor of fungal species density across habitat types and can hence be argued to be the preferable measure in a conservation context. However, wood volume gives a better expression of the resources available for fungal growth, and is a very relevant measure familiar to forest managers. In addition, wood volumes can be calculated with sufficient precision from dbh and height measurements of retained trees and can be included in dynamic models for species diversity over time if size-dependent decay rates are known. Therefore, wood volume will generally be the most relevant measure for management of wood-inhabiting organisms, and forms a good basis for comparisons of rarefaction curves involving different sized cwd. When data is available, we recommend that also surface areas are considered in order to evaluate the realised species density of different substrate types or different localities for fungi and other organisms utilising the wood surface. Finally, individual-based rarefaction curves could be used in order to compare species richness, in its narrow sense, among sites or habitat types.

4.3. Does size matter for red-listed species?

According to *G*-test statistics red-listed species did not appear to have any distinct preference for particular tree size classes or tree parts. Analyses of individual-based rarefaction curves showed the same pattern, apart from a weak tendency of the smallest tree size class to be slightly less species rich for red-listed species compared to larger trees. Due to the low number of records of red-listed species in this class, it is difficult to evaluate the significance of this difference, but generally our data do not support the often-stated view that large logs are particularly important for red-listed fungal species as a group (e.g. Bader et al., 1995; Renvall, 1995; Høiland and Bendiksen, 1996; Bredesen et al., 1997; Kruys et al., 1999; Sippola and Renvall, 1999).

Before drawing more definite conclusions, we find it useful to review different arguments for dependency on large logs among cwd-associated fungi, paying attention to our rather sparse data on selectivity patterns of specific red-listed species. Bader et al. (1995), Renvall (1995) and Stokland and Kauserud (2004) proposed that large logs, apart from a positive species-area effect, are able to maintain more stable microclimatic conditions required by some specialised species. Renvall (1995) added that large logs might benefit certain slow-growing specialist species simply because they decay slower than small logs, and hence function as substrates for a longer period. Finally, Stokland and Kauserud (2004) suggested that small logs may have insufficient nutrition to supply for some specialist species.

In this study, we found only one red-listed heart-rot agent on trees with a dbh below 70 cm (Table 2), and of the more frequent red-listed species the single species that showed a preference for large trees, viz. *I. resinosum*, is a heart-rot agent, while the four species that show no such trends are secondary invading saprotrophs (cf. Heilmann-Clausen, 2001; Heilmann-Clausen and Christensen, 2003). These results urge us to suggest an alternative hypothesis for explaining possible differences in fungal diversity linked to tree size, relating to fungal infection biology. Living trees are typically infected by hundreds of fungal individuals (e.g. Müller and Halleksala, 2000) representing various functional groups, including latent decay agents, wound parasites and heart-rot formers (Boddy, 2001). Especially members of the latter group, which infect living trees preferably through wounds, may cause the death of the tree, either through pathogenic activity, or because their decay makes the tree liable to break in storm. Tree wounds are formed by a range of processes including natural pruning, animal activity, frost, heat and storm damage and forestry activities each giving rise to different infection conditions and hence, potentially, to different fungal infections (cf. Rayner and Boddy, 1986). The probability of wounding and accomplishing fungal infection increases with time, and some wound types and their associated fungal and faunal communities appear to be restricted to large or old trees (cf. Ranius and Jansson, 2000; Yee et al., 2001; Parsons et al., 2003). We therefore suggest tree size to be important primarily for fungi infecting living trees, because large trees, due to their higher age, represent a longer and potentially more diverse infection history and a bigger volume of heartwood. Subsequently, heart-rot agents depending on old trees may open up more or less specific decay pathways benefiting specialised successor species (Niemelä et al., 1995; Renvall, 1995; Komonen, 2003). According to Heilmann-Clausen and Christensen (2003) *I. resinosum* appear to play such a key role in beech forest.

Of the four remaining frequent red-listed species recorded in this study, *Pluteus luctuosus* and *Pluteus umbrosus* showed no selectivity patterns with respect to defined tree size classes or tree parts, *N. chestersii* was slightly over-represented on branches while *M.*

brassicolens showed a preference for small trees. The latter species is a litter and wood saprotroph associated with calcareous soils (Hansen and Knudsen, 1992), and its preference for small diameter cwd-units is therefore not unexpected. The high frequency of *N. chestersii* on branches comes as a surprise, as we have earlier supposed this species to prefer large logs (Læssøe et al., 2000). For this, and the two *Pluteus* species, the present rarity seems to relate to other, to us unknown, factors than the specific lack of large logs. Indeed, we believe that for many purely saprotrophic wood-inhabiting fungi tree size per se is of subordinate importance, and eventual rarity of such species should, as long as nothing else is proven, be ascribed to the general lack of cwd of all types in the modern landscape, rather than to a specific lack of large decaying trees. In dry, continental climates the situation may be different and tree size may indeed be more important per se, with large wood volumes buffering against extensive desiccation, which may be critical to some specialist species (cf. Lindblad, 2001).

4.4. Implications for management

Our results show that large logs are not the only important cwd fraction for fungal species diversity in Danish beech forests. In contrast, smaller trees and branches appear to be more species dense cwd habitats supporting considerably higher number of species per volume unit than large logs. This could imply that small trees and branches should be the primary cwd fractions left for natural decay in managed forest, since these fractions represent the highest species density per volume unit and hence combines economic and ecologic value in an optimal way. There are, however, several complicating factors, suggesting such an approach to be problematic.

Firstly, it should be emphasized that smaller cwd fractions generally decay much faster than large logs (Stone et al., 1998; Mackensen and Bauhus, 1999; Tarasov and Birdsey, 2001), and hence represent a habitat for cwd-associated organisms for a considerably shorter period. Thus, maintenance of a specified amount of cwd per area unit requires the average annual amount of wood left for decay to be substantially bigger, if small cwd fractions are prioritised. This may be impractical in practice, and will easily lead to continuity breaks in local cwd amounts over time and hence impose negative effects on species requiring a stable, local representation of cwd in all stages of decay (cf. Stokland, 2001).

Secondly, our study is based on unmanaged forests, which differ considerably from managed forests with respect to tree architecture, mortality patterns and size/age relations. This may have important implications for fungi depending on special cwd habitats, infection strategies or old rather than large trees. Accordingly, it is probable that cwd of smaller dimensions is less valuable for fungal biodiversity in managed forests, compared to the situation in unmanaged forests (cf. Stokland and Kauserud, 2004).

Thirdly, it should be emphasized that preferences for certain cwd habitats seems to be common feature for many organisms associated with dead wood. In this study three of six investigated red-listed species showed significant habitat preferences. Other, more detailed studies have shown that species composition of saproxylic organisms may differ fundamentally and functionally between different dead wood habitats (Sippola and Renvall, 1999; Jonsell and Weslien, 2003; Similä et al., 2003; Nordén et al., 2004) even though this is not necessarily reflected in species density patterns.

With these reservations in mind, we find our results significant enough to suggest some general guidelines for cwd management, primarily valid for beech forests of Denmark and surrounding regions, but probably with a wider applicability for other deciduous tree species.

There is little doubt that the cheapest and most efficient way to increase saproxylic diversity locally in managed forests is to increase the amounts of small diameter dead wood, especially branches and small trees, which give good “value for money” with respect to species density (Kruys and Jonsson, 1999; Schiegg, 2001; Nordén et al., 2004; this study). In Denmark, designating of fixed firewood collection and manufacturing free zones would be an obvious initiative, as these activities have increased dramatically here since the 1970s, leaving many forest areas devoid of small diameter cwd fractions. However, if only small diameter dead wood is left for decay, there is an obvious risk that heart-rot agents and dependent species will disappear from managed forests, which may seriously undermine the integrity of saproxylic communities.

We believe that cwd-associated biodiversity will benefit most if measures are taken to increase the density of whole trees left for natural decay in managed forests. A whole dead tree above a certain size represents the full natural range of cwd habitats including log, stump (commonly) and branches of different dimensions, and is accordingly more likely to sustain many functional species groups compared to a similar volume of small diameter dead wood. If our hypothesis, that a long infection history is crucial for the establishment of specialist heart-rot agents, holds true, it can further be deduced that it is important to prioritise natural dead trees of advanced age, rather than artificially or wind-felled healthy trees. In this respect, even slow-growing suppressed trees as well as low quality trees misshaped, e.g. by marginal growth conditions may offer big biodiversity value. Today, such trees are often deliberately removed from managed forests with a marginal economic benefit. Near-natural forestry relying on natural thinning dynamics will, following the considerations above, have a good potential for restoring diversity of saproxylic communities, especially if scattered low quality trees are allowed to grow to maximum age and to decay naturally after their death.

Acknowledgements

We wish to thank various local forest authorities for the allowance to make the fungal inventories. In particular we wish to thank the Foundation of Sorø Akademi and the Strødam Committee for allowing us to work in the strict forest reserves Suserup Skov and Strødam. Two anonymous referees are thanked for valuable comments to an earlier version of the manuscript. The study was supported by the EU fifth framework program (grant no QLKS-CT-1999-01349) and by the Danish Research Councils.

References

Andersson, L.I., Hytteborn, H., 1991. Bryophytes and decaying wood: a comparison between managed and natural forests. Holarctic Ecol. 14, 121–130.

Anon., 2000. Swedish Standard for FSC-Certification of Forestry, Swedish FSC Council.

Bader, P., Jansson, S., Jonsson, B.G., 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biol. Conserv. 72, 355–362.

Begon, M., Harper, J.L., Townsend, C.R., 1990. Ecology: Individuals, Populations and Communities, second ed. Blackwell Scientific Publications, Boston.

Berg, Å., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M., Weslien, J., 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. Conserv. Biol. 8, 718–731.

Boddy, L., 2001. Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. Ecol. Bull. 49, 43–56.

Bredesen, B., Haugan, R., Aanderaa, R., Lindblad, I., Økland, B., Røsok, Ø., 1997. Vedlevende sopp som indikatorarter på kontinuitet i østnorske granskoger. Blyttia 54, 131–140.

Coleman, B.D., Mares, M.A., Willig, M.R., Hsieh, Y.-H., 1982. Randomness, area, and species richness. Ecology 63, 1121–1133.

Colwell, R.K., 2001. EstimateS: statistical estimation of species richness and shared species from samples, version 6. User's Guide and application published at: http://viceroy.eeb.uconn.edu/estimates.

Ehnström, B., 2001. Leaving dead wood for insects in boreal forests — suggestions for the future. Scand. J. For. Res. Suppl. 3, 91–98.

Fowler, J., Cohen, L., 1992. Practical Statistics for Field Biology, Wiley, Chichester.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4, 379–391.

Grove, S.J., Meggs, J., Goodwin, A., 2002. A Review of Biodiversity Conservation Issues Relating to Coarse Woody Debris Management in the Wet Eucalypt Production Forests of Tasmania, Forestry Tasmania, Hobart.

Hallingbäck, T., 1994. Ekologisk Katalog over Storsvampar. Summary: the macrofungi of Sweden. SNV Report No. 4313, Uppsala.

Hansen, L., Knudsen, H. (Eds.), 1992. Nordic Macromycetes. Polyporales, Boletales, Agaricales, Russulales, vol. 2. Nordsvamp, Copenhagen.

Hansen, A.J., Spies, T.A., Swanson, F.J., Ohmann, J.L., 1991. Conserving biodiversity in managed forests — lessons from natural forests. Bioscience 41, 382–392.

Heilmann-Clausen, J., 2001. A gradient analysis of communities of macrofungi and slime moulds on decaying beech logs. Mycol. Res. 105, 575–596.

Heilmann-Clausen, J., Christensen, M., 2003. Fungal diversity on decaying beech logs — implications for sustainable forestry. Biodivers. Conserv. 12, 953–973.

Heilmann-Clausen, J., Christensen, M. Wood-inhabiting macrofungi in Danish beech-forests — conflicting diversity patterns and their implications in a conservation perspective. Biol. Conserv., in press.

Høiland, K., Bendiksen, E., 1996. Biodiversity of wood-inhabiting fungi in a boreal coniferous forest in Sør-Trøndelag County, Central Norway. Nord. J. Bot. 16, 643–659.

Jonsell, M., Weslien, J., 2003. Felled or standing retained wood — it makes a difference for saproxylic beetles. For. Ecol. Manage. 175, 425–435.

Komonen, A., 2003. Hotspots of insect diversity in boreal forests. Conserv. Biol. 17, 976–981.

Kruys, N., Fries, C., Jonsson, B.G., Lämås, T., Ståhl, G., 1999. Wood-inhabiting cryptogams on dead Norway spruce (*Picea abies*) in managed Swedish boreal forests. Can. J. For. Res. 29, 178–186.

Kruys, N., Jonsson, B.G., 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. Can. J. For. Res. 29, 1295–1299.

Læssøe, T., Heilmann-Clausen, J., Christensen, M., 2000. Slægterne *Nemania*, *Euepixylon* og *Kretzschmaria* i Danmark. Svampe 42, 17–29.

Legendre, P., Legendre, L., 1999. Numerical ecology, second English edition. Dev. Environ. Model. 20, 1–853.

Lindblad, I., 2001. Diversity of poroid and some corticoid wood-inhabiting fungi along the rainfall gradient in tropical forests, Costa Rica. J. Trop. Ecol. 17, 353–369.

Mackensen, J., Bauhus, J., 1999. The decay of coarse woody debris. National Carbon Accounting System. Technical Report No. 6, Australian Greenhouse Office, Canberra.

MCPFE, 1998. Third Ministerial Conference on the Protection of Forests in Europe, Lisbon, Portugal, 2–4 June 1998.

Müller, M.M., Halleksala, A.-M., 2000. Fungal diversity in Norway spruce: a case study. Mycol. Res. 104, 1139–1145.

Niemelä, J., 1997. Invertebrates and boreal forest management. Conserv. Biol. 11, 601–610.

Niemelä, T., Renvall, P., Pentillä, R., 1995. Interactions of fungi at late stages of wood decomposition. Ann. Bot. Fenn. 32, 141–152.

Nordén, B., Ryberg, M., Gotmark, F., Olausson, B., 2004. Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. Biol. Conserv. 117, 1–10.

Parsons, S., Lewis, K.J., Psyllakis, J.M., 2003. Relationships between roosting habitat of bats and decay of aspen in the sub-boreal forests of British Columbia. For. Ecol. Manage. 177, 559–570.

Ranius, T., Jansson, N., 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. Biol. Conserv. 95, 85–94.

Rayner, A.D.M., Boddy, L., 1986. Population structure and the infection biology of wood-decay fungi in living trees. Adv. Plant Pathol. 5, 119–160.

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

Rolstad, J., Sætersdal, M., Gjerde, I., Storaunet, K.O., 2004. Wood-decaying fungi in boreal forests: are species richness and abundances influenced by small-scale spatiotemporal distribution of dead wood? Biol. Conserv. 117, 539–555.

Ryvarden, L., Gilbertson, R.L., 1994. European Polypores: Part 2. Synopsis Fungorum 6, Fungiflora, Oslo.

Schiegg, K., 2001. Saproxylic insect diversity of beech: limbs are richer than trunks. For. Ecol. Manage. 149, 295–304.

Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol. Bull. 49, 11–41.

Similä, M., Kouki, J., Martikainen, P., 2003. Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. For. Ecol. Manage. 174, 365–381.

Sippola, A.-L., Renvall, P., 1999. Wood-decomposing fungi and seed-tree cutting: a 40-year perspective. For. Ecol. Manage. 115, 183–201.

Skov- og Naturstyrelsen, 1995. Generelle retningslinier for drift af statsskovene, kap. 16. ''Farlige'' træer og efterladen af dødt ved. http://www.skovognatur.dk/skov/netpub/strategioversigt/kap16.htm.

Söderström, L., 1988. Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in northern Sweden. Nord. J. Bot. 8, 89–97.

Stokland, J.N., 2001. The coarse woody debris profile: an archive of recent forest history and an important biodiversity indicator. Ecol. Bull. 49, 71–83.

Stokland, J.N., Kauserud, H., 2004. *Phellinus nigrolimitatus* — a wood-decomposing fungus highly influenced by forestry. For. Ecol. Manage. 187, 333–343.

Stoltze, M., Pihl, S., 1998. Rødliste 1997 over Planter og Dyr i Danmark, Miljø- og Energiministeriet, Copenhagen, Denmark.

Stone, J.N., MacKinnon, A., Parminter, J.V., Lertzman, K.P., 1998. Coarse woody debris decomposition documented over 65 years on southern Vancouver Island. Can. J. For. Res. 28, 788–793.

Tarasov, M.E., Birdsey, R.A., 2001. Decay rate and potential storage of coarse woody debris in the Leningrad Region. Ecol. Bull. 49, 137–147.

Yatskov, M., Harmon, M.E., Krankina, O.N., 2003. A chronosequence of wood decomposition in the boreal forests of Russia. Can. J. For. Res. 33, 1211–1226.

Yee, M., Yuan, Z.-Q., Mohammed, C., 2001. Not just waste wood: decaying logs as key habitats in Tasmania's wet sclerophyll *Eucalyptus obliqua* production forests: the ecology of large and small logs compared. Tasforests 13, 119–128.