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Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests

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Abstract

Dead wood is considered important in forest conservation, but patterns of fungal diversity on dead wood have rarely been quantified. We investigated the relative importance of coarse (diameter >10 cm) and fine woody debris (1–10 cm) for fungi in broadleaf forests in southern Sweden. The numbers of species per unit wood volume and per forest area were significantly higher for fine than for coarse woody debris for both ascomycetes and basidiomycetes. When the number of species was plotted against the number of records, coarse woody debris was more species rich than fine woody debris for a given number of basidiomycete records. Of the ascomycetes, 75% were found exclusively on fine woody debris (the corresponding proportion for basidiomycetes is 30%), 2% were found exclusively on coarse woody debris (basidiomycetes 26%), and 23% of the species were found on both diameter classes (basidiomycetes 44%). We conclude that fine woody debris is important for diversity of wood-inhabiting fungi, especially ascomycetes, in this forest type. However, coarse woody debris must also be provided to insure the occurrence of many species of basidiomycetes.

Keywords: Fungi; Coarse woody debris; Fine woody debris; Species richness; Species density

1. Introduction

A very large number of organisms are dependent on decaying wood for nutrients or habitat (Samuelsson et al., 1994; Ohlson et al., 1997; McComb and Lindenmayer, 1999; Boddy, 2001; Siitonen, 2001). Fungi are a crucial part of this biodiversity, and one of the main groups decomposing wood on dead or living trees world-wide (Dix and Webster, 1995). They also play a key role for the diversity of other organisms associated with dead wood, e.g. saproxylic insects (Batra, 1967; Wheeler and Blackwell, 1984; Wilding et al., 1989; Blackwell and Jones, 1997). Wood-inhabiting fungi are here defined as all fungi with fruitbodies on decaying wood. They are not necessarily wood decayers and may have other (primary) ecological roles as parasites or symbionts (Dix and Webster, 1995; Nordén et al., 1999).

The amount of dead wood has decreased drastically in Swedish forests since the middle of the 19th century following intense forestry (Linder and Östlund, 1998; Nilsson et al., 2001), and its associated biota has therefore become threatened (Berg et al., 1994; Gärdenfors, 2000) especially in the temperate broadleaf forest of southern Sweden (Berg et al., 1994; Rydin et al., 1997). Temperate broadleaf forest is one of the most severely disturbed and endangered biomes world-wide (Hannah et al., 1995), and has declined considerably in Sweden (Löfgren and Andersson, 2000; Nilsson et al., 2001). Most work on the importance of dead wood for fungi has been performed in boreal, coniferous forest (Jonsson and Kruys, 2001). In this study, we investigated the importance of dead wood for fungal diversity in the more southerly distributed broadleaf forest. We chose woodland dominated by the oaks *Quercus robur* L. and *Q. petraea* Liebl., since these have been reported to play key roles for biodiversity in the temperate broadleaf forests of Europe (Berg et al., 1994; Nilsson et al., 2001, Butler et al., 2001).

Several studies suggest that the occurrence of coarse woody debris (CWD, diameter >10 cm) is critical for diversity of wood-inhabiting fungi (Samuelsson et al.,

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1994; Bader et al., 1995; Bredesen et al., 1997; Jonsson and Kruys, 2001; Nilsson et al., 2001). For instance, the importance of CWD for fungi was investigated in a study of old-growth spruce swamp forests, in which the amount of CWD was correlated with species richness of polypores (Ohlson et al., 1997).

Recently, the interest in thinning and harvesting of tops and branches for production of biofuel has increased (Lundborg, 1998; Johansson, 2000; Malinen et al., 2001; Skogsstyrelsen, 2001; Fung et al., 2002). Thinning of younger trees around old oak trees, a recommended conservation management method in previous oak-pasture land (Read et al., 2001), is a potential source of biofuel subject to a current surge of interest in Sweden. Biofuel is an renewable energy source that gives no net contribution of the green-house gas CO_2 to the atmosphere, in contrast to fossil-fuels. Since harvest for biofuel may strongly reduce the amount of Fine Woody Debris (FWD; diameter 1–10 cm) in forests, the importance of FWD for biodiversity needs to be evaluated and related to the importance of CWD. As we show below, FWD potentially represents a considerable portion of the total volume of dead wood in temperate broadleaf forest, especially in managed woodlands. The objective of our study was to compare the importance of CWD and FWD for species richness of wood-inhabiting fungi and to help evaluate whether biofuel harvesting negatively affects fungal diversity. In addition, to our knowledge this is the first quantitative study of both basidiomycetes and ascomycetes fructifying on CWD and FWD in broadleaf forests.

2. Materials and methods

2.1. Study sites

Twenty-five sites in southern Sweden were surveyed (Fig. 1). The forest was located on relatively level, mesic ground. All sites had been oak wood-pasture earlier, but were abandoned between about 1930 and 1960. At present, they are mostly dominated by *Q. robur* and *Q. petraea* (25–75% by volume). The oldest oaks at each site are on average 100–160 years old. Younger trees of many species, mainly *Betula pendula* Roth, *Fraxinus excelsior* L., *Populus tremula* L., *Acer platanoides* L., *Tilia cordata* Mill., *Fagus silvatica* L., and *Salix caprea* L., have invaded the sites and now form dense stands around the oaks (80–95% canopy cover). In 10 of the sites Norwegian spruce [*Picea abies* (L.)H. Karst.] has invaded and now make up a significant part of the canopy. The 25 sites are either key habitats (18; Gustafsson, 1999) or nature reserves (7), with high conservation values and relatively high concentrations of CWD compared with production forest in southern Sweden (Table 1). Each site consists of two juxtaposed squares (assigned for other purposes), each covering 1 ha. The fieldwork was carried out during the fall in 2000 and during the spring in 2001.

2.2. Data collection

CWD was surveyed in four 10×100 m transects (4000 m^2) running across each square (two per site). The

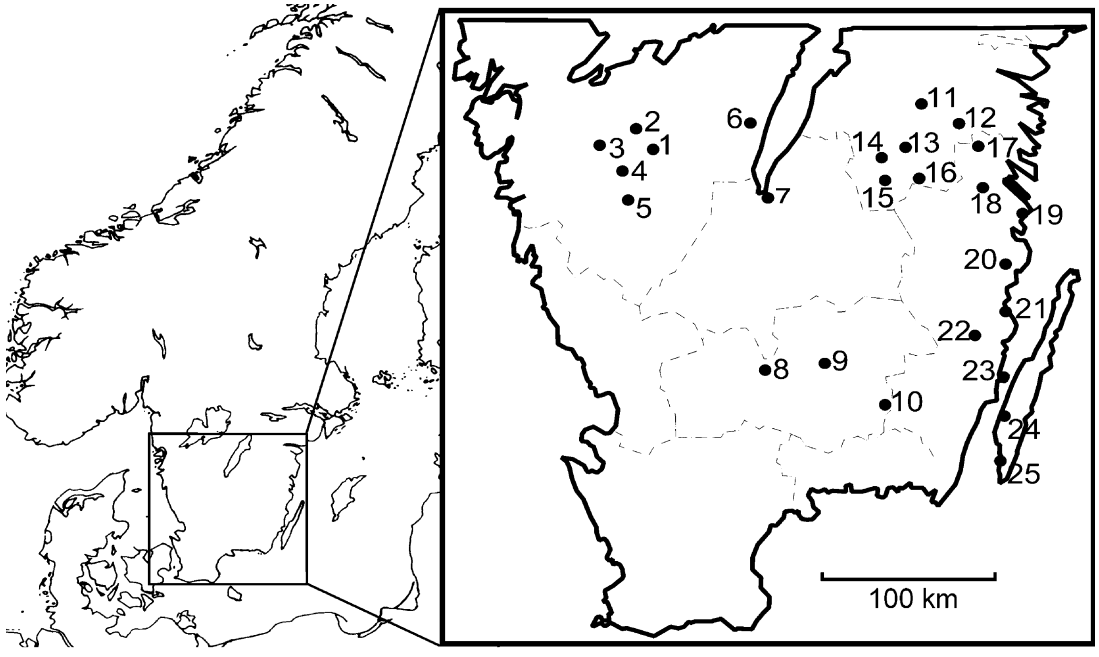

Fig. 1. Locations of the investigated forest stands in southern Sweden: 1. Skölvene, 2. Karla, 3. Östadkulle, 4. Sandviksås, 5. Rya åsar, 6. Strakaskogen, 7. Bondberget, 8. Långhult, 9. Bokhultet, 10. Kråksjöby, 11. Stavsäter, 12. Åtvidaberg, 13. Fagerhult, 14. Aspernäs, 15. Norra Vi, 16. Fröåsa, 17. Ulvsdal, 18. Hallingeberg, 19. Ytterhult, 20. Fårbo, 21. Emsfors, 22. Getebro, 23. Lindö, 24. Vickleby, 25. Albrunna.

Table 1
Characteristics of the studied sites

Site[a]	Protection status[b]	Size (ha)	Basal area of living trees (m^2/ha)			CWD density[c]	CWD volume (m^3/ha)			FWD volume (m^3/ha)		
			Coniferous	Oak	Other broadl.		Coniferous	Oak	Other broadl.	Coniferous	Oak	Other broadl.
1	WKH	7.0	1.2	18.2	9.0	32.5	0.0	2.3	7.6	0.0	0.4	13.1
2	WKH	4.0	0.3	13.1	6.7	32.0	0.0	0.9	6.4	1.8	2.8	3.6
3	WKH	4.2	1.6	15.1	14.4	34.8	0.1	1.0	1.2	0.0	0.5	14.2
4	WKH	9.0	15.1	10.2	5.5	54.5	0.2	5.4	3.4	0.5	3.9	2.4
5	NR	60.0	1.3	22.8	7.9	33.9	2.8	5.9	8.1	1.3	0.5	7.9
6	WKH	11.0	5.5	4.2	19.9	58.1	0.0	1.4	3.3	0.2	3.6	7.3
7	NR	104	1.1	11.6	0.0	54.9	0.0	9.9	9.2	0.2	1.8	5.7
8	WKH	22.3	0.2	11.8	15.8	34.4	0.1	1.5	0.4	1.6	2.2	4.4
9	NR	150	5.7	16.2	12.3	68.0	2.5	10.1	18.0	0.0	0.9	2.4
10	WKH	6.0	2.3	20.3	13.3	21.9	0.0	1.1	5.6	0.7	0.8	2.4
11	NR	18.0	0.0	6.0	15.6	48.1	0.3	0.8	11.1	1.3	0.8	13.8
12	WKH	7.0	4.5	17.2	16.5	81.6	0.7	5.7	15.2	0.0	0.9	17.0
13	WKH	20.0	3.5	7.2	16.1	61.8	0.4	0.7	2.7	0.4	0.6	25.2
14	WKH	28.0	2.6	14.0	13.0	46.6	0.0	5.9	8.5	0.3	1.3	6.6
15	WKH	8.0	4.9	18.8	5.9	21.0	0.3	8.1	3.3	0.0	1.6	3.2
16	WKH	6.0	11.0	15.8	7.5	26.1	0.2	1.7	5.0	1.5	2.2	2.1
17	WKH	12.0	1.4	10.1	13.0	32.7	0.0	8.6	1.8	0.0	1.3	10.0
18	WKH	6.5	0.5	18.3	7.1	44.2	0.3	6.2	2.7	0.6	3.7	8.0
19	WKH	15.0	3.5	14.4	5.5	39.3	0.7	4.1	3.1	4.9	2.2	4.2
20	WKH	17.0	8.7	17.1	5.4	90.1	9.2	18.9	3.7	2.2	4.3	5.3
21	WKH	8.4	0.3	10.6	15.8	55.8	0.0	6.9	10.5	0.0	1.8	7.9
22	NR	15.0	10.2	16.8	7.1	43.4	3.2	2.4	1.9	3.4	3.1	7.0
23	NR	13.0	2.7	8.5	10.4	62.5	0.0	1.6	4.2	1.3	1.9	7.7
24	NR	6.5	0.0	26.5	4.3	44.8	0.3	2.5	14.9	0.3	3.3	8.9
25	NR	25.0	0.0	11.9	17.2	65.5	0.0	11.5	1.8	0.0	1.4	17.1
Mean		23.3	3.5	14.3	10.6	47.5	0.9	5.0	6.1	0.9	1.9	8.3
S.D.		33.9	4.0	5.3	5.1	17.7	2.0	4.4	4.8	1.2	1.2	5.7

[a] Numbers refer to Fig. 1.
[b] WKH, Woodland Key Habitat; NR, Nature Reserve.
[c] Numbers of objects per ha.

transects were separated by at least 10 m. Only parts of dead woody objects inside the transects were included. Top and bottom diameter of the dead wood objects (down to 10 cm) were measured and the volume was calculated from the formula for a frustum of a cone.

Because FWD measurements are more time-consuming, we surveyed a smaller area of each CWD-transect for this fraction. Each transect was divided into four 25-m sections. The FWD was surveyed in 2×2.5 m squares placed randomly, one in each section, along the central axis of the transect. The total volume of CWD and FWD per ha was extrapolated from the respective measurements.

Fungi were inventoried along three of the four transects, each 2×100 m, thus covering a total area of 600 m^2 per square, or 1200 m^2 per site. The fungi transects coincided with the squares used for the FWD measurement, but covered a larger area. All dead wood within the transects (up to 2 m above ground, excluding branches of living trees not reaching the ground) was surveyed for fungi. In each 100 m transect the same four 25-m sections (see above) were used, and each species was recorded only once per 25-m section, i.e. presence–absence. Some species with prominent and easily identified fruitbodies were not collected but only recorded by field observation. Each "species hit" was based on either a collected fruitbody or field observation in one section, and is herewith denoted as one record.

Fungi were surveyed during the most favourable seasons for fruitbody production for the respective groups, viz. spring for ascomycetes and fall for basidiomycetes. Of the ascomycetes, pyrenomycetes with a stroma or fruitbody of a diameter of 1 mm or more and discomycetes with fruitbodies of a diameter of 5 mm or more were collected or recorded in the field. Of the basidiomycetes, all species with agaricoid, polyporoid, stereoid and corticioid fruitbodies including the two heterobasidiomycetes *Eichleriella deglubens* (Berk. and Broome) D.A. Reid and *Tulasnella violea* (Quél.) Bourdot and Galzin were recorded or collected. Date, location, transect number, section number along transect, and tree species were noted for each record and collection. The diameter of the dead wood object collected from was measured at the site of the fruitbody. The

collected fungi were identified by standard laboratory techniques.

2.3. Statistical analyses

Ascomycetes and basidiomycetes were treated separately in most analyses, due to indications that these two groups have different ecological requirements (e.g. diameter of dead wood). Unless otherwise stated, sites were sample units in statistical tests.

Average species accumulation curves were produced by random re-sampling among samples using EstimateS 5 (Colwell, 1997; Gotelli and Colwell, 2001). One hundred re-samplings were run and the average number of species represented by 1, 2... up to the total number of samples were calculated. We constructed average species accumulation curves to compare species density on CWD and FWD, for both ascomycetes and basidiomycetes. As explanatory variables (x-axis) we used the cumulative volume of dead wood or the cumulative forest area surveyed. Finally, we produced average species accumulation curves showing species richness (as defined by Gotelli and Colwell, 2001), i.e. where the x-axis represented the number of records of ascomycetes and basidiomycetes. communities. Following Hughes et al. (2001) we did not include confidence envelopes constructed from the variance among the resamples, since they can only be used to compare the observed richness among samples and is not a measure of confidence about the actual richness in the communities. To judge trends, we compared curves visually.

The significance of differences in species density and species richness between CWD and FWD was tested by Wilcoxon matched-pairs signed ranks test (two-tailed test, site was sample unit). Within each site, species accumulation curves for CWD and FWD were compared (geographical matching). Average species accumulation curves for CWD and FWD were constructed for each site using EstimateS 5. As sample units the 24 surveyed sections at each site were used. If species accumulation curves cross or approach each other or if both curves are still steeply increasing, this means that estimation of differences between them are sensitive to sampling effort. We checked all curve pairs, but there were no such cases, except for comparison of species richness of ascomycets (see below). We therefore decided that no site had to be omitted from any test for this reason.

For area the cumulative section area was used as the explanatory variable (x-axis). In the test, total numbers of species per 1200 m^2 sampling area per site ($n = 25$) were used. For wood volume the mean wood volume per section times the number of sections (1, 2, ...24) was used as explanatory variable (x-axis). The test variable, which was estimated from the average species accumulation curve and thus not an actual species count, was compared between sites at 0.5 m^3. Sites with less than 0.5 m^3 of either CWD or FWD were excluded from the test (eight excluded; $n = 17$).

For species richness, the number of records was used as explanatory variable (x-axis). For basidiomycetes, the curves were compared at 20 records. Sites with less than 20 records on either CWD or FWD were excluded from the test (four excluded; $n = 21$). The number of records on CWD of ascomycetes was too few in most sites to judge if the curves met the criteria mentioned above (not crossing or approaching), and no statistical test was performed.

To analyse species composition, the fungi were classified in six groups according to their fruit-body type: agarics, polypores, stereoids, corticioids, stromatic pyrenomycetes and one group containing the non-stromatic ascomycetes. In general these groups, according to current systematics, represent polyphyletic assemblages of fungi with similar ecological function or "life-forms" rather than taxonomic units. Agarics are basidiomycetes with a stem and cap and with the hymenophore in the shape of gills on the underside of the cap. Polypores are basidiomycetes with a hymenophore in the shape of tubes on the underside of the fruitbody. Stereoids are basidiomycetes with a smooth hymenophore on a firm resupinate or effused-reflexed fruitbody, and the circumscription of this group follows Jahn (1971). Corticioids are basidiomycetes with smooth to odontioid hymenophore on a soft, resupinate fruitbody. Stromatic pyrenomycetes are ascomycetes with a large stroma (mainly Xylariales). Non-stromatic ascomycetes include mainly pyrenomycetes and a few discomycetes. For the six groups, we compared the proportion of records on CWD and FWD. A χ^2-test was applied to test differences in frequency between CWD and FWD for the life-form groups. We used Spearman rank correlation test to investigate relationships between the number of species and the volume of CWD and FWD.

3. Results

In total, we made 1361 records of 102 ascomycete species and 2488 records of 309 basidiomycete species. The five most common species were *Hypoxylon fuscum* (Pers.: Fr.) Fr. (197 records), *Diatrypella verruciformis* (Ehrh.: Fr) Nitschke (131), *Diatrypella quercina* (Pers.: Fr.) Cooke (105), *Bertia moriformis* (Tode: Fr.) De Not. (100) and *Stereum rugosum* Pers.: Fr. (99), whereas 133 species were found just once, i.e. in one section.

The mean volume of CWD at our sites was 12.0 m^3/ha (range = 2.2–31.9; S.D. = 7.8 m^3/ha; $n = 25$). The sites contained a similar amount of fine woody debris; the mean volume was 11.2 m^3/ha (range = 4.0–26.2; S.D. = 5.1 m^3/ha; $n = 25$).

3.1. Distribution of ascomycetes and basidiomycetes on CWD and FWD

In total, 411 species were encountered and of these 170 species were found exclusively on FWD, 81 exclusively on CWD, and 160 species were found on both CWD and FWD. As much as 75% of the ascomycetes (77 of 102 species) were found exclusively on FWD, only 2% (two species) occurred exclusively on CWD, and 23% (23 species) were found on both FWD and CWD (Fig. 2 A). In contrast to the ascomycetes, the proportion of species of basidiomycetes was much lower on FWD: 30% (93 species) were found exclusively on FWD, 26% (79 species) occurred exclusively on CWD and 44% (137 species) were found on both FWD and CWD (Fig. 2B).

There were 18 different trees and bushes in the CWD fraction, all of which were also present as FWD. In addition, eight woody species not present as CWD occurred as FWD. These eight woody species held only 2.7% of the fungal records on FWD (in total 27 species, six were exclusive to the eight woody species). The contribution of this confounding factor was judged as small, and all analyses were run on the total data set.

3.2. Species density

In Fig. 3, species density for ascomycetes (A) and basidiomycetes (B) on CWD and FWD are given in relation to the cumulative increase in dead wood-volume, based on site ($n = 25$; dots in Fig. 3).

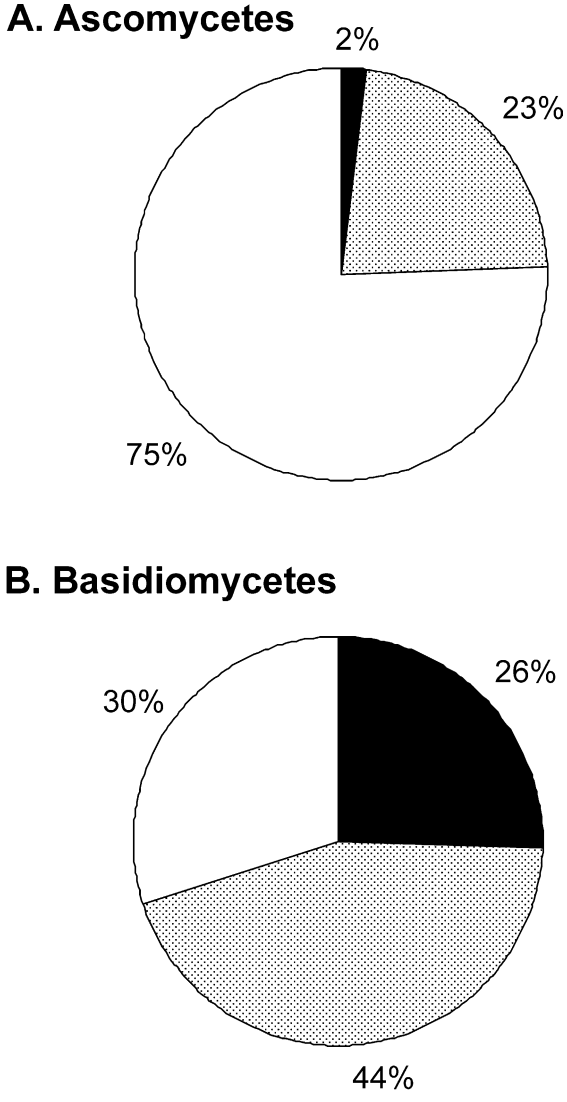

Fig. 2. The proportion of species found exclusively on CWD (black), exclusively on FWD (white) or on both CWD and FWD (stippled) for ascomycetes and basidiomycetes.

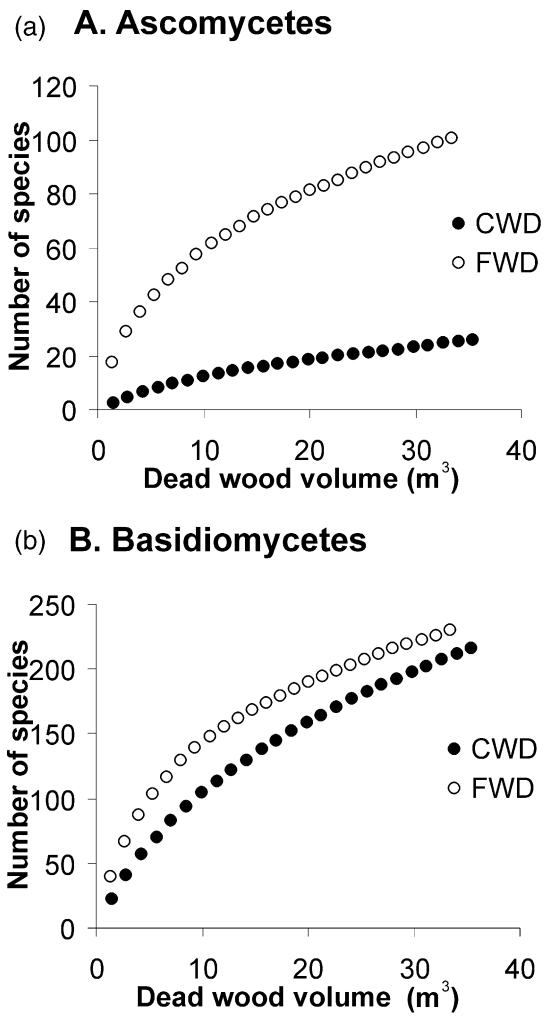

Fig. 3. Average species accumulation curves showing species density as mean number of species plotted against mean cumulative dead wood-volume (calculated as the mean wood volume per site times the number of sites), for (A) ascomycetes and (B) basidiomycetes on CWD and FWD (the dots represent sites). The curves were constructed through random re-sampling using EstimateS 5 (see text).

Comparing the species density curves for ascomycetes (Fig. 3A) with the corresponding curves for basidiomycetes (Fig. 3B), it is clear that there is a much wider gap between the CWD and FWD curves for ascomycetes than for basidiomycetes, indicating that FWD is especially important for species density of ascomycetes in temperate broadleaf forest. The Wilcoxon matched-pairs signed ranks test showed that species density was significantly higher on FWD than on CWD at 0.5 m^3 of dead wood for both ascomycetes ($Z=-3.62$, $n=17$ sites, $P<0.001$) and basidiomycetes ($Z=-2.44$, $n=17$ sites, $P=0.015$).

When the explanatory variable (x-axis) was cumulative area of sites, the pooled average species accumulation curves were similar to those for wood volume (Fig. 4). Also here, the Wilcoxon matched-pairs signed ranks tests showed significantly higher species density on FWD than CWD for ascomycetes ($Z=-4.38$, $n=25$ sites, $P<0.001$) and for basidiomycetes ($Z=-3.06$, $n=25$, $P=0.002$).

The tendency for the average species accumulation curves pooled for all sites as in Figs. 3B and 4B (basidiomycetes) to converge was never seen in the site-specific curves (used for testing), but was only encountered at the landscape scale.

3.3. Species richness

For ascomycetes, the number of records on CWD and FWD differed considerably, and no difference in species richness between CWD and FWD was apparent when comparing equal numbers of records, i.e. at 100 in Fig 5 A. The average species accumulation curves for species richness of basidiomycetes on CWD and FWD showed the opposite of what was found for species density, i.e.

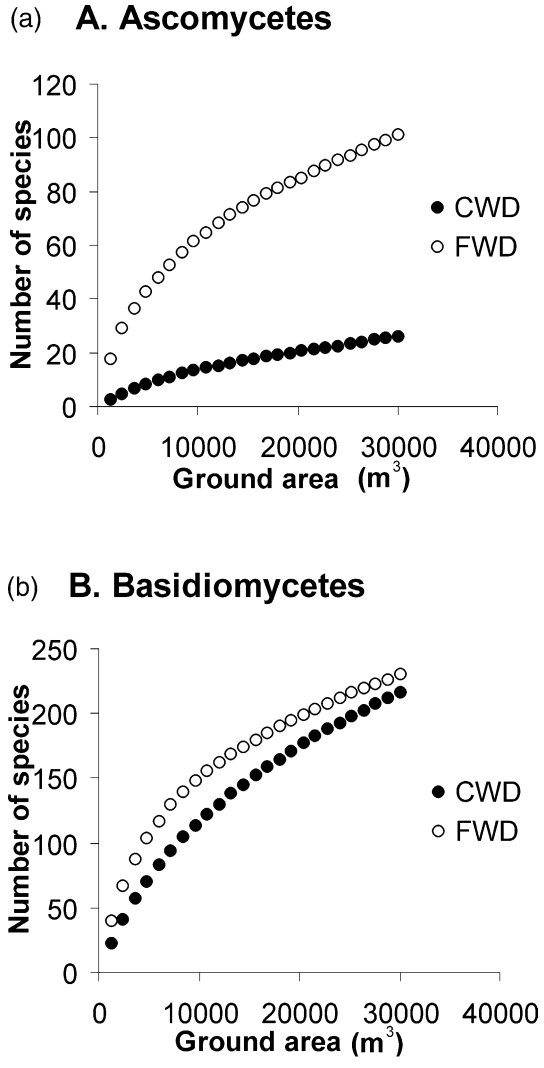

Fig. 4. Average species accumulation curves showing species density as mean number of species plotted against cumulative forest ground area for (A) ascomycetes and (B) basidiomycetes on CWD and FWD (the dots represent sites). The curves were constructed through random re-sampling using EstimateS 5 (see text).

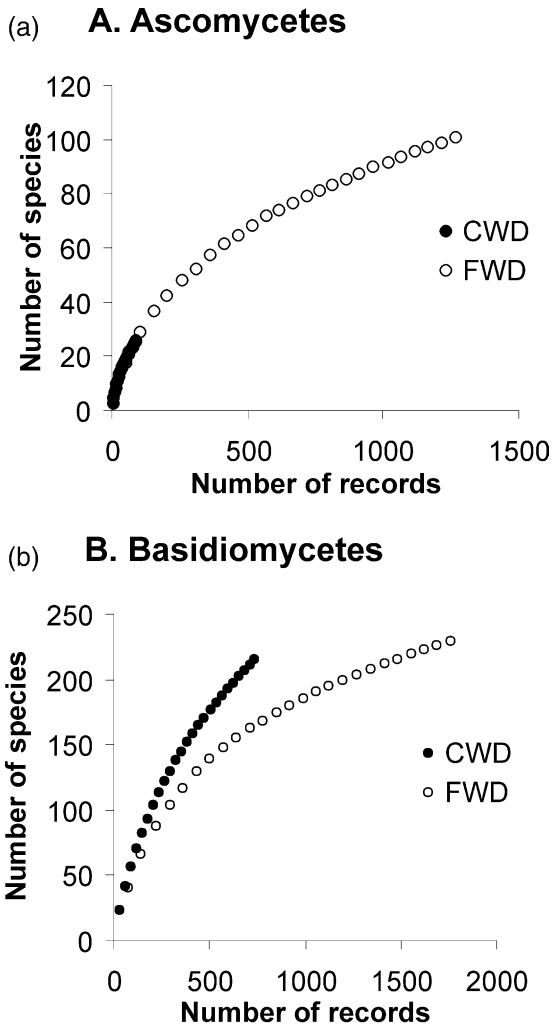

Fig. 5. Average species accumulation curve showing species richness as mean number of species plotted against mean number of records on CWD and FWD for (A) ascomycetes and (B) basidiomycetes (the dots represent sites). The curves were constructed through random re-sampling using EstimateS 5 (see text).

Table 2
The number of records on CWD and FWD and the total number of records for six fungal life-form groups

	Number of records on FWD	Number of records on CWD	Total	Expected number of records on FWD	Expected number of records on CWD
Agarics	80	122	202	158.6	43.45
Polypores	177	185	362	284.3	77.69
Stereoids	279	107	386	303.2	82.84
Corticioids	1219	322	1541	1210.3	330.7
Stromatoids	381	55	436	342.4	93.57
Non-stromatic ascomycetes	887	35	922	724.1	197.9
Total	3023	826	3849		

The expected numbers on CWD and FWD were calculated by multiplying the total number of records for each life-form group by the total number of records for each diameter class, and dividing by the total number of records. A χ^2-test, and indicated that the frequency of the life-form groups differed significantly between CWD and FWD ($P<0.001$).

higher species richness on CWD than on FWD (Fig. 5B).

The Wilcoxon matched-pairs signed ranks test showed no significant differences in species richness between basidiomycetes on CWD and FWD at 20 records ($Z=-1.32$, $n=21$ sites, $P=0.19$).

3.4. Occurrence of the fungal life-forms

When the fungal life-form groups were compared we found that different groups occurred in different proportions on CWD and FWD (Table 2 and Fig. 6). The four basidiomycete life-form groups had lower proportions on FWD than the two ascomycete life-form groups (see also above). Among the basidiomycete life-form groups, the agarics had the lowest proportion on FWD and the corticioids the highest. There was a less marked difference between the two ascomycete life-form groups. The large stromatic pyrenomycetes seemed to have slightly lower proportion on FWD than the non-stromatic ascomycetes (Fig. 6).

3.5. Red List species

We found three ascomycete species included in the Swedish Red List (Gärdenfors, 2000) on FWD and no Red List ascomycetes on CWD. In total, 11 Red List basidiomycetes were found, five only on CWD, four only on FWD and two on both CWD and FWD.

3.6. Species richness in relation to dead wood volume

The number of ascomycetes was not correlated to either FWD ($r_s=0.33$, $P=0.11$, $n=25$ sites) or CWD volume ($r_s=-0.23$, $P=0.27$, $n=25$ sites). The same applied for the number of basidiomycetes versus FWD ($r_s=0.26$, $P=0.21$, $n=25$ sites) or CWD ($r_s=-0.10$, $P=0.63$, $n=25$ sites). However, the total number of species, ascomycetes and basidiomycetes combined, was significantly correlated with FWD volume ($r_s=0.41$, $P=0.040$, $n=25$ sites), but not with CWD volume ($r_s=-0.091$, $P=0.67$, $n=25$ sites).

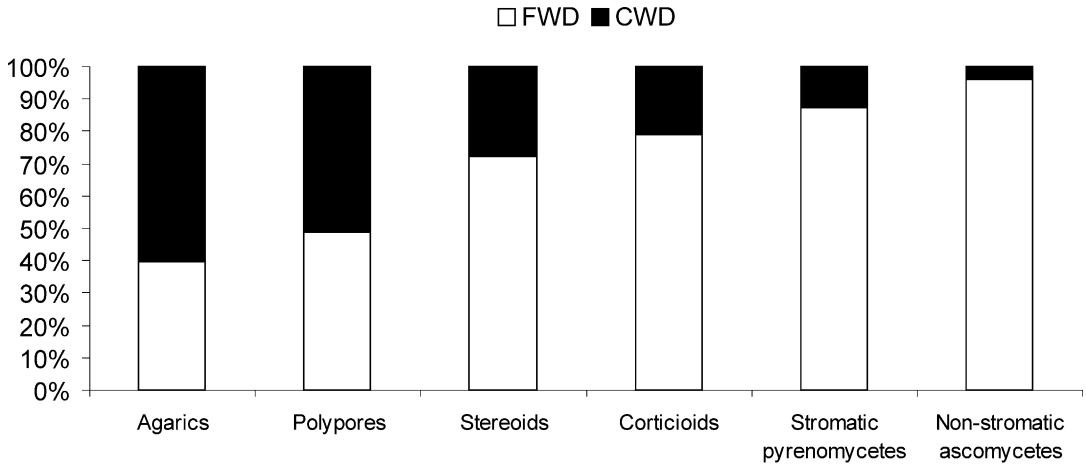

Fig. 6. The proportion of records on CWD and FWD for six fungal life-form groups (see Table 2 for sample sizes).

4. Discussion

In this study, fungi were identified by the presence of their fruitbodies. There were probably fungi present as mycelia that did not fructify on the dead wood during the survey period and therefore, some species were likely missed. Mycelia may be identified by molecular methods, but such methods are time-consuming, expensive, and not currently available for most species. Fruitbody inventory is presently the main method that can be used in larger field surveys, and should provide data suitable for comparisons between CWD and FWD. Furthermore, some wood-inhabiting fungi occur as mycelia in substrates (e.g. branches of certain trees) on which they do not fructify (Petrini, 1996), probably because some cue for fructification is lacking but growth is possible. Such occurrences will not, in general, contribute to dispersal or long-term population persistence, but are not discriminated against by molecular methods.

We compared species density in two ways, as the number of species per dead wood volume, and as the number of species per forest area. These two measures are relevant for harvesting of forest-fuel, and for evaluation and management of biodiversity in specific areas such as nature reserves (for discussion of species richness, see below). We found that FWD is more important than CWD for species density of wood-inhabiting fungi at 25 sites with similar average volumes of FWD and CWD. For basidiomycetes, the average species accumulation curves for CWD and FWD might converge and cross if more sites were sampled; this would mean that CWD is more important than FWD on a landscape level. The importance of FWD for fungal diversity is furthermore indicated by the fact that total species richness was significantly correlated with FWD volume among sites, but not with CWD volume among sites.

The relative importance of FWD for species density of wood-inhabiting fungi is probably even higher in managed "production" forest (with less CWD), that cover at least 90% of the total Swedish woodland area, than in the conservation stands investigated in this study. At our sites, the CWD volume was on average 12 m^3/ha. Managed woodlands in southern Sweden hold, on average, less then half this amount (Fridman and Walheim, 2000). Species density per forest area would of course be higher in a natural forest with much larger amount of CWD than in our stands, and the relative importance of FWD for fungal diversity would then be lower, at least regarding basidiomycetes. Virgin temperate forest containing more CWD than our study sites is, however, very rare in Europe and other parts of the world (Hannah et al., 1995; Peterken, 1996; Nilsson et al., 2002).

The level of CWD is generally low in production forest, but the FWD production might be relatively high there. Therefore, the difference is greater for CWD than for FWD between natural and managed forest. Probably for this reason, FWD has been neglected in previous research, and only CWD has been studied (Bader et al., 1995; Nilsson et al., 2001; but for a small set of fungi in coniferous forest, see Kruys and Jonsson 1999). The increased interest in biofuel harvesting poses a new threat to fungal diversity that motivates studies also of FWD and its associated mycoflora.

In this study, a wide perspective on fungal forest diversity emerge, as both ascomycetes and basidiomycetes of several wood-inhabiting groups were surveyed. Overall, 75% of the ascomycete species, 50% of the Red List species, and 30% of the basidiomycete species were found exclusively on FWD.

The dead wood dynamics of temperate broadleaf forest probably differ from boreal coniferous forest, e.g. in the production of much FWD through natural pruning of branches which is largely mediated by fungi, often ascomycetes (von Butin and Kowalski, 1983). This should be true especially for the relatively dense, closed forest that we studied, where trees successively shed lower branches. It is known that several fungi, especially ascomycetes, in this biome are adapted to live in branches of broadleaf trees and other FWD (Kowalski and Kehr, 1996; Rayner and Boddy, 1997). FWD (in this case hazel, *Corylus avellana* L.) has been shown to be a very species rich substratum for wood-inhabiting fungi (Nordén and Paltto, 2001), but our study is the first to quantify the difference in frequency of ascomycetes and basidiomycetes on wood of different diameter.

Apart from clear results for ascomycetes and basidiomycetes, differentiation was found between fungal life-form groups. Some basidiomycetes are adaptated to CWD, while others can fructify also on thinner stems. Differences in internal milieu between CWD and FWD include differences in climatic stability, moisture content, and CO_2 concentration (see Dix and Webster, 1995; Rayner and Boddy, 1997). Species adapted to CWD and FWD not only occupy different volumes of dead wood, but also tend to have different fruitbody morphology, e.g. large and perennial fruitbodies are mostly found on CWD, which is larger and has longer degradation time than FWD (Söderström, 1988). Further, larger logs contain more core-wood which supports a specialised flora of polypores with conk-shaped fruit-bodies (Rayner and Boddy, 1997).

The eight additional tree species in the FWD fraction held a small proportion of the fungal records on FWD, so this hardly explains the higher species density of FWD. The proportion of dead wood volume from different tree species do, however, differ between CWD and FWD. For example, hazel *C. avellana*, has a larger proportion of dead wood volume in the FWD fraction than in the CWD fraction. The magnitude to which this affects the result is hard to assess, but it is possible that

the conclusions drawn here may have limited generality for forests which differ much in tree species composition from the forests in this study.

CWD hold more species than FWD when compared at equal numbers of dead wood objects, because of greater volume of CWD. Some authors have hypothesized that for a given volume of dead wood, large trees can host more species than the same volume of thinner trees (Nilsson et al., 2001). Our results show the contrary result, several FWD objects held more species than a few CWD objects when both measure up to approximately the same volume. One reason might be that the number of different situations defined by various abiotic factors, such as temperature and moisture climate should be higher for FWD than for CWD since FWD is spread over a larger ground area. In addition, many small FWD objects, with large total surface area, spread over a large part of each surveyed transect, offer more opportunities for spore establishment than a few large CWD objects.

Species density (number of species per area) is the measure most often given in the ecological literature when the diversity of species is compared between sites, e.g. for conservation evaluation (Gotelli and Colwell, 2001). However, when evaluating the importance of CWD and FWD irrespective of area, species richness, i.e. the number of species per individuals (here records), is an appropriate measure (Gotelli and Colwell, 2001). When we compared species richness on FWD and CWD at equal numbers of records, the average species accumulation curves indicated that CWD was more species rich for basidiomycetes (i.e. the opposite from the result for species density). However, when tested on the basis of sites there was no significant difference. For ascomycetes, the number of records on CWD was too low to allow even a tentative graphical interpretation of the results. Additional sampling of ascomycets on CWD is needed to address this question. For basidiomycetes the curves might indicate that a larger species pool of basidiomycetes is available for CWD than for FWD. Large diameter logs may also contain more niches than thin logs (see above), thus promoting species richness.

5. Conservation implications

In conclusion, both CWD and FWD should be provided in forest ecosystems. Since FWD is an important resource for fungi in temperate broadleaf forest, thinning of young trees and harvesting of fine diameter wood from felled trees for biofuel may negatively affect fungal diversity in this forest type, if such harvest becomes a common practice. Measures that eliminate FWD would lead to decreased fungal diversity, especially of ascomycetes, a species rich group which has previously been neglected in conservation work. We further believe that dense, self-thinning succession forest should be allowed in the landscape, since such stands are richer in FWD than either grazed pasture or old-growth forest, and may promote fungal and other biodiversity.

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