



## Fungal diversity on decaying beech logs – implications for sustainable forestry

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**Abstract.** An analysis of factors influencing the diversity of macrofungi fruiting on decaying beech logs at site level is presented. Variables related to log size and shape and decay stage were found to explain up to 56% of the variation in total species richness and 42% of the variation in the richness of threatened (red-listed) species. Inclusion of variables relating to the vernal flora and the degree of soil contact further increased the explained variation in total species richness to 71%, but these variables were non-significant with respect to red-listed species. However, inclusion of the variable *log type*, distinguishing uprooted logs, logs broken at root neck and logs broken 1–7 and 8–15 m above ground, increased the amount of explained variation in richness of red-listed species to 50%. Among the log size and shape variables, the number of bole forks was superior in describing the variation in both total and red-listed species richness. Accordingly, forked trees should preferably be selected for decay in order to improve biodiversity, since they support comparably higher species diversity than unforked logs and have limited economical value. The importance of log type for the richness of threatened species appears to be connected with the occurrence of certain non-dominant primary decayers, causing heart rot, subsequently allowing the establishment of red-listed species. Accordingly, it is suggested that a high diversity of primary decayers may be a key to the conservation of wood decaying fungi. Microclimatic variables were found to have a limited effect on fruit body diversity on the studied logs; however, the microclimatic regime is discussed as an important factor in relation to management of dead wood for fungal biodiversity.

### Introduction

Coarse woody debris (cwd) is a key element for forest biodiversity, providing habitats and resources for a wide array of organisms (e.g. Harmon et al. 1986; Samuelsson et al. 1994). Managed forests are generally poor in cwd, and are only able to host an impoverished dead wood-associated biodiversity (Bader et al. 1995; Christensen and Emborg 1996; Sittonen 2001). A long history of forest management has, accordingly, led to a considerable decrease for organisms depending on cwd all over Europe (e.g. Berg et al. 1994; Kotiranta et al. 1998; Stoltze and Pihl 1998; Schiegg 2001; Sittonen 2001). In recent years the interest to improve forest biodiversity has, however, increased. New forest reserves have been designed in several European countries (Broekmeyer and Vos 1993; Parviainen 1999), and worldwide there is an increasing awareness that development of sustainable nature-based forestry practices, combining a reasonable economic income with protection of natural biodiversity, is necessary (e.g. Hansen et al. 1991; Lindenmayer 1999).

To achieve optimal results from these initiatives, knowledge of structures and processes facilitating high natural biodiversity is essential (Simberloff 1999), but unfortunately still scarce for many organism groups.

With respect to management of cwd, fungi are essential. They form a very diverse organism group and are, as the primary agents of wood decay, essential for other organisms depending on cwd and for ecosystem functioning. In general, fallen decomposing logs have been considered the most species rich and important type of cwd for wood inhabiting fungi (Rydin et al. 1997; Sippola and Renvall 1999), and several studies have focused on how forest type, management history and substrate abundance influences fungal diversity at site level (e.g. Bader et al. 1995; Høiland and Bendiksen 1996; Penttilä and Kotiranta 1996; Lindblad 1997; Stokland et al. 1997; Sippola and Renvall 1999; Lumley et al. 2000; Nordén and Paltto 2001).

While such studies are valuable for the development of general management guidelines (e.g. number of logs left for natural decay/ha) and for the selection and design of forest reserves, detailed knowledge of factors influencing diversity at log level is necessary for the development of management guidelines at site level (e.g. which types of logs should be selected for natural decay). Several such factors have been highlighted: Bader et al. (1995), Renvall (1995), Høiland and Bendiksen (1996) and Lindblad (1997) found a clear positive relation between log size and the number of fruiting fungal species. Lange (1992), Renvall (1995), Willig and Schlegte (1995) and Høiland and Bendiksen (1996) investigated the changes occurring in fungal community structure during log decay. All found the turnover in species composition to be considerable, with logs in intermediate stages of decay being most rich in fruiting species. Also microclimatic conditions are likely to have a very pronounced effect on species richness at log level (cf. Rayner and Boddy 1988; Boddy 2001), but have only been considered occasionally under field conditions (e.g. Renvall 1995; Lindblad 1997).

Renvall (1995) paid considerable attention to the existence of different decay pathways in conifer logs and claimed primary decay fungi to be crucial for subsequent fungal community development and species diversity. Niemelä et al. (1995) and Holmer et al. (1997) provided further evidence for the existence of decay pathways, and supported the view that certain threatened wood decaying fungi are more or less dependent on specific preceding species. The aim of the present paper is to evaluate relations between environmental factors and fungal species richness on decaying beech logs in a multivariate context. The importance of log size, log age and decay pathways are considered in detail in order to develop guidelines for management of dead wood at site level. A previous paper (Heilmann-Clausen 2001) has presented a general description of the community structure of the studied logs.

## **Material and methods**

### *Site*

The study was conducted in Suserup Skov (19.2 ha, 7–31 m a.s.l. 55°22' N 11°34'

E), a forest reserve situated in eastern Denmark. The reserve has been unmanaged for about 150 years (Fritzbøger and Emborg 1996), and is approaching a dynamic steady state, typical for nemoreal deciduous forests, with storm as the main disturbance agent (Emborg et al. 2000). The forest is rich in cwd of all dimensions and known as an important locality for several organism groups associated with dead wood (Martin 1989; Møller 1997; Heilmann-Clausen and Christensen 2000). Beech (*Fagus sylvatica*) is the dominant tree species in the forest and has been so for about 1000 years (Hannon et al. 2000). Ash (*Fraxinus excelsior*), sessile oak (*Quercus robur*) and wych elm (*Ulmus glabra*) are subdominants (Emborg et al. 1996, 2000). The soils are mostly deeply developed brown mull soils on glacial tills and locally lacustrine sediments (Vejre and Emborg 1996). The pH in the topsoil generally varies between 3.9 and 4.5 (Vejre and Emborg 1996; Møller 1997). The climate is cool-temperate, with an annual mean temperature of 8.1 °C and an annual mean precipitation of 635 mm.

#### *Data collection*

A total of 70 fallen beech logs were randomly selected for the study, but with the tie to be evenly distributed across seven log age classes (1960–1967, 1967–1972, 1972–1978, 1978–1981, 1981–1985, 1985–1990, 1990–1993) determined from aerial photographs and four size classes (diameter at breast height (dbh) 70–89, 90–109, 110–129 and >130 cm). The dissimilarity in the number of years in each age class reflects the availability of the aerial photographs used for dating the logs. Several environmental variables were recorded or estimated for each log (Tables 1–3).

All logs and branches thicker than 10 cm were inventoried on 10 occasions between May 1994 and September 1995. On each occasion sporocarps were identified *in situ* or collected for later identification. However, two of the inventories included only species determinable in the field. Principally, all basidiomycete genera were included in the study, plus ascomycetes, excluding non-stromatic pyrenomycetes. Nomenclature follows Hansen and Knudsen (1992, 1997, 2000).

#### *Data analysis*

The relations between species richness and continuous environmental variables were initially evaluated using Kendall Rank correlation and scatter plots. Non-parametric correlation was preferred, since several variables are on an ordinal scale or were found to have non-normal distributions or unequal variances. Scatter plots were used to search for curvilinear responses. Relations to class variables were investigated using one-way ANOVA, and in the case of statistically significant effects, Tukey's test was applied for pairwise comparisons. In all ANOVAs the response variable was square root transformed to obtain equal variances among groups.

Subsequently, multiple regression was used to investigate the relations between environmental variables and species richness. Polynomial regression was applied in

Table 1. Environmental variables recorded for each log (for further details see Heilmann-Clausen and Christensen 2000).

Variable	Unit	Range	Median	Source/description
Log type	Class			Four types distinguished: uprooted with distinct root plate; broken at root neck; broken 2–7 m above ground level; broken 8–15 m above ground level
Diameter at breast height (dbh)	cm	70–168	110	Measurement (1.3 m above ground)
Log age	Years	2–31	15	Years since tree death, estimated from a sequence of aerial photos
Decay stage	Class	1–5	3	Classified according to Table 2
Bark cover	%	0–100	10	Estimated to the nearest 10% of the log surface
Moss cover	%	0–60	5	Estimated to the nearest 10% of the log surface
Eutypa cover	%	0–70	20	Estimated to the nearest 10% of the log surface
Soil contact	%	10–100	90	Estimated to the nearest 10% of the log surface
Fractures	Number	0–5	2	Counted, considering the number of fractures on the main trunk and branches thicker than 50 cm
Complexity	Number	0–4	1	Counted, considering the number of forks on the main trunk and branches thicker than 50 cm
Soil type	Class	Three types		Generalised from Vejre and Emborg (1996)
Soil humidity	Class	1–5	2	Classified according to Table 3
Wind exposure	Class	1–5	4	Classified according to Table 3
Sun exposure	Class	1–5	4	Classified according to Table 3
Distance to forest edge	M	5–135	70	Measured on stem map to the nearest 5 m
Plant diversity	Number	1–6	2	Counted, considering the presence of 14 vernal plant species <sup>a</sup> within 10 m from the log
Plant cover	%	20–100	90	Estimated to the nearest 10% considering the forest floor within 10 m from the log <sup>b</sup>
Floristic deviance	%	0–80	10	Equivalent to the relative area covered by other plant species than the dominant <i>Anemone nemorosa</i> , within 10 m from the log
Decay rate	Class	–2 to +3	0	Estimated by comparing decay age with decay stage

<sup>a</sup> *Allium ursinum*, *Anemone nemorosa*, *A. ranunculoides*, *A. ranunculoides*, *Arum maculatum*, *Corydalis bulbosa*, *C. intermedia*, *Ranunculus ficaria*, *Gagea spathacea*, *Galium odoratum*, *Lamiasstrum galeobdolon*, *Mercurialis perennis*, *Pulmonaria obscura*, *Santivula europaea* and *Viola riviniana/reichenbachiana*. <sup>b</sup> Further subdivided in eight variables representing *Anemone nemorosa* (Anemone), *A. ranunculoides* (Aneranu), *Corydalis bulbosa* (Corbulb), *Galium odoratum* (Galodor), *Lamiasstrum galeobdolon* (Lamgale), *Mercurialis perennis* (Merpere) and *Viola riviniana/reichenbachiana* (Viola), respectively and a ninth variable (Other species) covering the remaining species mentioned under a.

Table 2. Classification of logs according to decay stage (adapted from Heilmann-Clausen 2001).

Decay stage	Characteristics
Class 1	Wood hard, a knife (with a thin blade) penetrates only a few mm into the wood, bark intact, twigs (diameter <1 cm) intact.
Class 2	Wood rather hard, a knife penetrates <1 cm into the wood, bark starting to break up, twigs $\pm$ lost, branches (diameter 1–4 cm) intact
Class 3	Wood distinctly softened, a knife penetrates ca. 1–4 cm into the wood, except for parts colonized by certain pyrenomycetes (in particular <i>Eutypa spinosa</i> , <i>Kretzschmaria deusta</i> and <i>Xylaria hypoxylon</i> ), bark partly lost, branches $\pm$ lost, original log circumference intact
Class 4	Wood highly decayed, a knife penetrates ca. 5–10 cm into the wood, except for parts colonized by certain pyrenomycetes (see above), bark lost in most places, original log circumference disintegrating
Class 5	Wood very highly decayed, either to a very soft crumbly substance, or being flaky and fragile with numerous remnants of pseudosclerotial plates, these defining the log surface, a knife penetrates in most places more than 10 cm into the wood, original log circumference not or hardly recognizable

cases of detected or suspected curvilinear responses. In all regressions the response variables were square root transformed to make residuals normally distributed.

Indicator Species Analysis (Dufrene and Legendre 1997) was used to investigate whether certain species tended to associate with certain log types or logs supporting a high number of threatened species. Logistic regression analysis was used to investigate whether any species were significantly associated with large diameter logs.

Statistical analyses were run using SAS for windows version 8.00 (SAS Institute 1999). Indicator Species Analyses were run using PC-ORD for windows version 4.10 (McCune and Mefford 1999).

## Results

### *General patterns of species diversity*

In total 277 fungal species were recorded on the investigated logs, of which about 235 appear to be primarily associated with decaying wood (cf. Hallingbäck 1994; Hansen and Knudsen 1992, 1997, 2000). Twenty-three of the recorded species are listed in the national red-data book (Stoltze and Pihl 1998) as ‘critically threatened’, ‘vulnerable’ or ‘rare’ (Table 4).

The number of observed species per log varied between 11 and 76 with a mean of 30.7. The number of observed species listed in the red-data book (in the following referred to as red-listed species) varied between 0 and 5, with a mean of 1.0.

Several of the recorded environmental variables are significantly correlated to the number of species per log (species richness) (Tables 5 and 6). Most evident are the strong positive correlations between species richness and variables related to log size and complexity (*complexity*, *dbh* and *fractures*). Another distinct group of

Table 3. Classification of logs according to soil humidity, wind exposure and sun exposure (adapted from Heilmann-Clausen 2001).

	Soil humidity	Wind exposure	Sun exposure
Class 1	Well-drained forest soils on hill tops	Exposed forest at edges and on hills	Forest edges and open forest on south facing slopes
Class 2	Other high, well-drained forest soils	Open forest, without understorey	Open, sunlit forest
Class 3	Average, well-drained forest soils	Closed forest, with sparse understorey	Closed forest on level areas
Class 4	Low, ± waterlogged soils	Closed forest, with a developed understorey	Closed forest, multilayered, with a dense canopy or on north facing slopes
Class 5	Swamp soils, ± inundated during wintertime	Sheltered places e.g. hollows, protected by a dense understorey	Multilayered forest with a dense canopy and/or on north facing slopes

Table 4. Recorded red-listed species sorted by frequency.

Species	Number of logs	Red-data book status
<i>Ischnoderma resinosum</i>	14	V
<i>Ceriporiopsis gilvescens</i>	9	V
<i>Omphalina epichysium</i>	8	E
<i>Pluteus umbrosus</i>	5	R
<i>Nemania chestersii</i>	4	R
<i>Pluteus inquilinus</i>	4	R
<i>Gloeohyphochnium analogum</i>	3	R
<i>Camarops tubulina</i>	2	E
<i>Cristinia gallica</i>	2	R
<i>Lepiota ochraceofulva</i>	2	V
<i>Coprinus echinosporus</i>	1	R
<i>Entoloma dichroum</i>	1	R
<i>Flammulaster muricatus</i>	1	E
<i>Galerina nana</i>	1	R
<i>Hyphoderma medioburiense</i>	1	R
<i>Lepiota boertmannii</i>	1	E
<i>Melanotus horizontalis</i>	1	R
<i>Micromphale brassicolens</i>	1	V
<i>Protocrea farinacea</i>	1	R
<i>Psathyrella populina</i>	1	E
<i>Tyromyces wynnei</i>	1	R
<i>Xenasma pulverulentum</i>	1	R

Red-data book status refers to Stoltze and Pihl (1998); E: critically threatened, V: vulnerable, R: rare.

correlated variables relates to the vernal plant communities around the logs. The negative correlations with *plant diversity* and *Lamiastrum galeobdolon* cover (*Langale*) and the positive correlation with *Anemone nemorosa* cover (*Anenemo*) indicate that logs situated in rather uniform vernal plant communities, dominated by *Anemone nemorosa*, tend to be most species rich. Finally there is a positive correlation between species richness and *distance to forest edge*, indicating that logs situated far from the forest edge are most species rich. Of the class variables, *decay stage* shows the most significant effect (Table 6). A Tukey test found logs in decay stages 3 and 4 to be significantly more species rich than logs in stages 1 and 5 ( $P < 0.05$ , Figure 1). Also *soil humidity* seems to influence overall species richness, with logs situated in intermediate humidity classes being most species rich. However, none of the five classes were found to be significantly richer than other classes (Tukey's test,  $P > 0.05$ , Figure 2).

The richness of red-listed species seems in general to respond to the same log size variables as does overall species richness, but correlations tend to be weaker (Tables 5 and 6). Significant correlations with floristic variables are absent, but with respect to class variables there is an effect of *log type*, with logs broken at stem base being significantly richer than other types of logs, except those broken 0–7 m above the forest floor (Tukey's test,  $P < 0.05$ , Figure 3). Also *decay stage* has a significant effect, with logs in decay stage 3 being significantly richer in red-listed species than logs in classes 1 and 5 (Tukey's test,  $P < 0.05$ , Figure 4).

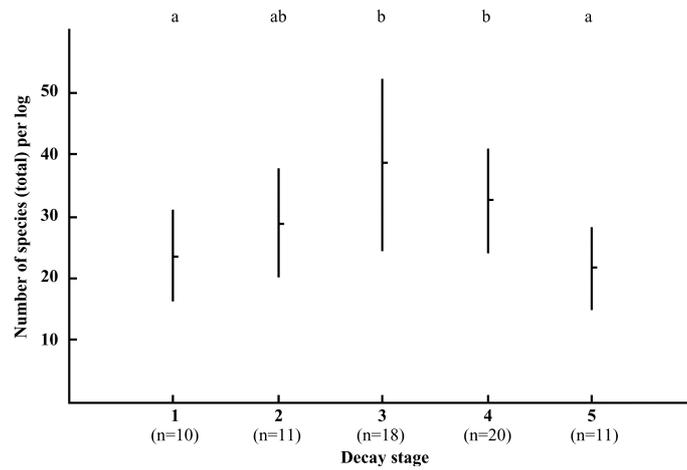


Figure 1. The relation between decay stage and average total species richness,  $\pm$  standard deviation (bars). Different letters distinguish groups with significantly different means ( $P < 0.05$ ) using Tukey's test on the square root transformed data.

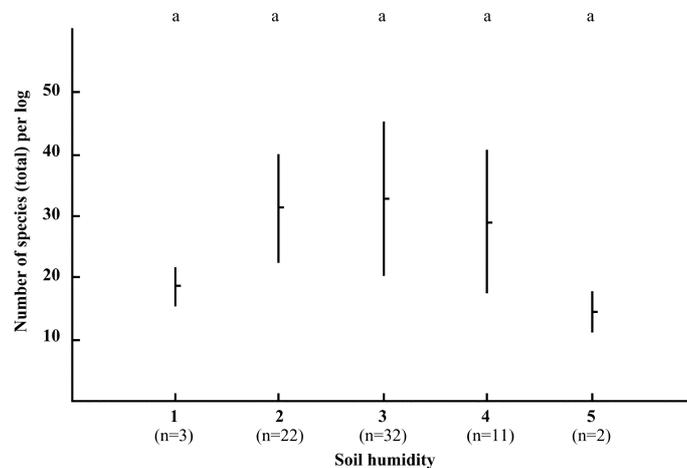


Figure 2. The relation between soil humidity and average total species richness,  $\pm$  standard deviation (bars). No groups have significantly different means ( $P > 0.05$ ) using Tukey's test on the square root transformed data.

Multiple linear regression models were able to explain up to 71% of the variation in species richness and up to 50% of the variation in richness of red-listed species (Table 7). Several competing species richness models were obtained (Table 8), but the overall composition of these differs little. *Complexity* and *log age* (or *decay stage*) are the two most important factors, occurring in all models. In combination the two variables explain 56% of the variation in species richness (Table 7). The presence of variables relating to the vernal vegetation surrounding the logs and to

Table 5. Kendall rank correlations between species richness and environmental variables (Table 1).

Variable	Species richness	Richness of red-listed species
Species richness	1.0000	0.6775****
Complexity	0.5289****	0.3551***
Dbh	0.3584****	0.2844**
Fractures	0.3581****	0.2098*
Anenemo	0.2672**	0.1776
Distance to forest edge	0.2395**	0.1595
Other species	-0.2214*	-0.1035
Lamgale	-0.1966*	-0.1525
Plant diversity	-0.1931*	-0.1347

Only variables significantly correlated with species richness are included. \*\*\*\* $P < 0.0001$ ; \*\*\* $P < 0.001$ ; \*\* $P < 0.01$ ; \* $P < 0.05$ .

Table 6. Summary of one-way ANOVAs for total species richness and richness of red-listed species in response to environmental class variables.

Class variable	DF	Species richness		Richness of red-listed species	
		Pr > F	R <sup>2</sup>	Pr > F	R <sup>2</sup>
Decay stage	4	<0.0001	0.3	0.0016	0.23
Soil type	2	0.2523	0.04	0.1154	0.06
Log type	3	0.0555	0.11	0.0028	0.19
Soil humidity	4	0.0395	0.14	0.669	0.04
Wind exposure	4	0.4397	0.06	0.4796	0.05
Sun exposure	4	0.1881	0.09	0.2259	0.08

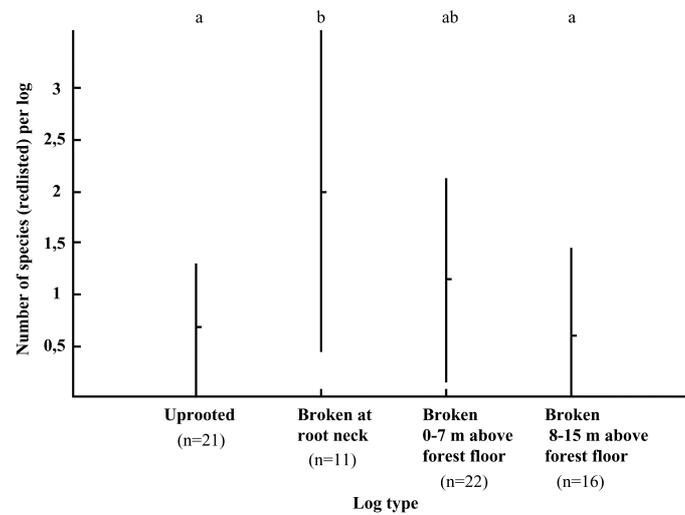


Figure 3. The relation between log type and average richness of red-listed species,  $\pm$  standard deviation (bars). Different letters distinguish groups with significantly different means ( $P < 0.05$ ) using Tukey's test on the square root transformed data.

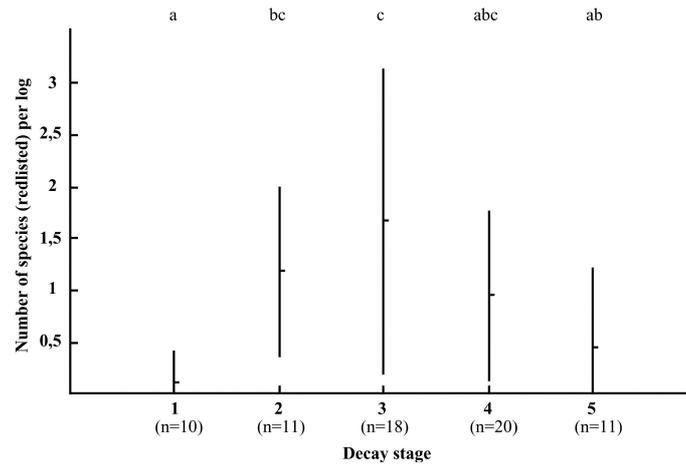


Figure 4. The relation between decay stage and average richness of red-listed species,  $\pm$  standard deviation (bars). Different letters distinguish groups with significantly different means ( $P < 0.05$ ) using Tukey's test on the square root transformed data.

soil conditions is also consistent, while the effect of *distance* to *edge* obviously is accounted for by other variables in the most powerful models. The different models show that complex logs in intermediate stages of decay, with a high degree of soil contact and situated in places with a rather uniform vernal flora dominated by *Anemone nemorosa*, tend to be the most species rich (Figure 5). For richness of red-listed species, no competing models with  $R^2 > 0.45$  were found, except when *log age* was substituted by *decay stage* (not shown). In combination *log age* and *complexity* explain 42% of the variation. Compared with the model for general species richness, the most evident difference, apart from the lower explanatory power, is the substitution of variables relating to flora and soil conditions by *log type* (Table 7, Figure 5), as was also evident from correlation analyses (Table 5) and ANOVAs (Table 6).

#### *Specific associations and indicator values*

A rather limited number of species were found to be associated with certain log types according to indicator values obtained from Indicator Species Analysis (Table 9). Of those showing a preference, the majority (13 species) associate with logs broken at stem base. Only three and two species, respectively, were found to associate with logs broken 8–15 m above ground level or uprooted trees, and no species were found to prefer logs broken 2–7 m above ground level. Of the species associated with logs broken at stem base, *Ganoderma lipsiensis*, *Ischnoderma resinum* and *Xylaria polymorpha* are known or suspected to cause butt-rot, making trees liable to breakage at the stem base.

Several species were associated with logs presenting sporocarps of two or more red-listed species (Table 10) using Indicator Species Analysis. Of these, *Isch-*

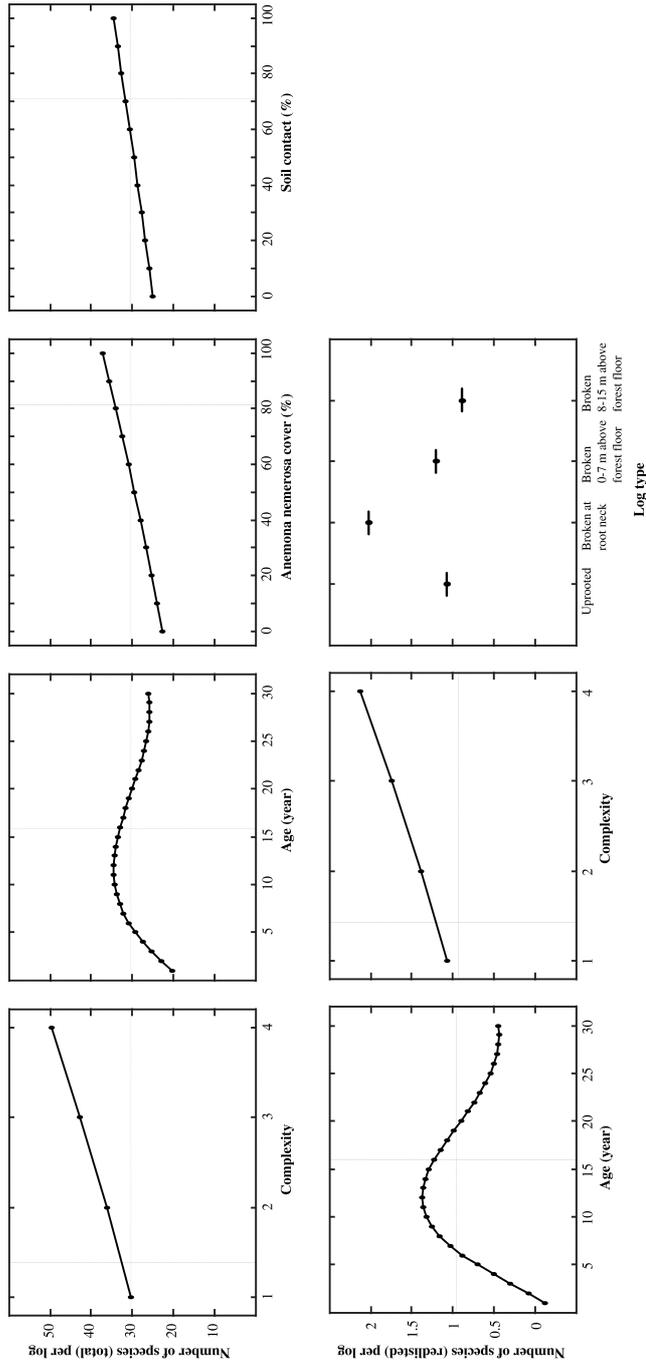


Figure 5. Prediction profiles showing the individual effects of environmental variables in the multiple linear regression models for species richness and richness of red-listed species (Table 7).

Table 7. Multiple regression models for species richness and richness of red-listed species, with variables added in a stepwise manner, according to their ability to increase the predictive power of the models.

Variable	Res. DF	Prob. ( <i>F</i> )	<i>R</i> <sup>2</sup>
Species richness			
Complexity	69	<0.0001	0.40
Log age**3	66	<0.0001	0.56
Anenemo	65	<0.0001	0.68
Soil contact	64	0.0136	0.71
Richness of red-listed species			
Log age**3	66	0.0015	0.34
Complexity	65	0.0059	0.42
Log type	62	0.0184	0.50

Both models are considered in full, highly significant ( $P < 0.0001$ ). \*\*3 denotes that the variable is included in the model as polynomial to the 3rd degree.

Table 8. Competing, highly significant ( $P < 0.0001$ ) models for species richness with  $R^2 > 0.66$ .

Variables in models	<i>F</i>	<i>R</i> <sup>2</sup>
Complexity/Log age**3/Plant diversity/Anenemo	24.26	0.70
Complexity/Log age**3/Plant diversity/Plant cover	24.17	0.70
Complexity/Decay stage/Anenemo/Soil contact	19.87	0.69
Complexity/Log age**3/Plant diversity/Soil contact	23.44	0.68
Complexity/Decay stage/Plant diversity/Anenemo	18.98	0.68
Complexity/Decay stage/Plant diversity/Soil contact	18.78	0.68
Complexity/Log age**3/Plant diversity/Distance to forest edge	23.99	0.67
Complexity/Decay stage/Plant diversity/Soil type	15.79	0.67

The explanatory variables are sorted according to their ability to increase the predictive power of the models.

*Ischnoderma resinosum*, *Polyporus squamosus*, *Ganoderma lipsiensis*, *Xylaria polymorpha* and *Camarops polysperma* are known or suspected heart-rot formers. The strongest indicator, *Ischnoderma resinosum*, is itself red-listed, but it is noteworthy that the species in most cases (78.9% of occupied logs) occurred together with at least one more red-listed species.

In logistic regression analysis only some species showed a preference for large logs (Table 11), and of these only one, *Omphalina epichysium*, is red-listed. The remaining species are generally common saprotrophs and several tend to associate with stumps in managed forests. However, *Camarops polysperma* are likely to cause heart-rot according to own observations.

## Discussion

### *Log size and shape*

The present study confirms that the species diversity of wood-inhabiting fungi

Table 9. Summary of Indicator Species Analysis based on *log* type.

Species	Indicator value		Frequency of occurrence (% of logs with sporocarps)			
	% of perfect indication	<i>P</i>	Uprooted with distinct root plate ( <i>n</i> = 21)	Broken at root neck ( <i>n</i> = 11)	Broken 2–7 m above ground level ( <i>n</i> = 22)	Broken 8–15 m above ground level ( <i>n</i> = 16)
<i>Ganoderma lipsiensis</i> *	37.6	0.0008	24	<b>73</b>	32	13
<i>Peziza micropus</i>	32.9	0.0037	19	<b>73</b>	50	19
<i>Marasmius rotula</i>	31.8	0.0074	14	<b>73</b>	55	25
<i>Lycoperdon pyriforme</i>	30.6	0.0230	43	<b>82</b>	50	44
<i>Botryobasidium aureum</i>	28.1	0.0345	<b>67</b>	36	36	19
<i>Galerina unicolor</i>	27.7	0.0175	38	<b>64</b>	32	13
<i>Xylaria polymorpha</i> *	26.5	0.0199	19	<b>55</b>	14	25
<i>Gloiothele lactescens</i>	25.5	0.0166	29	<b>55</b>	27	6
<i>Psathyrella obtusata</i>	25.5	0.0181	33	<b>55</b>	23	6
<b><i>Omphalina epichysium</i></b>	24.2	0.0046	0	<b>36</b>	18	0
<b><i>Ischnoderma resinosum</i>*</b>	22.9	0.0298	10	<b>45</b>	23	13
<i>Schizophyllum commune</i>	21.2	0.0110	0	0	5	<b>25</b>
<i>Hypoderma praetermissum</i>	20.0	0.0119	<b>24</b>	0	5	0
<i>Peniophora lyci</i>	18.7	0.0123	0	0	0	<b>19</b>
<i>Inonotus nodulosus</i> *	18.3	0.0213	0	0	9	<b>25</b>
<i>Stropharia cyanea</i>	14.5	0.0339	0	<b>18</b>	5	0
<i>Hypochnicium punctulatum</i>	14.5	0.0342	0	<b>18</b>	5	0
<i>Thanatephorus fusisporus</i>	14.5	0.0356	0	<b>18</b>	5	0

Only species with significant indicator values ( $P < 0.05$ ) are included. The *P*-value denotes the proportion of randomised trials resulting in an indicator value equal to or exceeding the observed indicator value, based on 10 000 Monte Carlo permutations. Red-listed species are printed in bold, while an asterisk (\*) denotes primary decayers. Bold values indicate preferred log type.

Table 10. Summary of Indicator Species Analysis based on three log classes defined by the number of red-listed species found on each log (0, 1 or 2 or more).

Species	Indicator value		Frequency of occurrence (% of logs with sporocarps) on logs with various numbers of red-listed species		
	% of perfect indication	<i>P</i>	0 ( <i>n</i> = 30)	1 ( <i>n</i> = 23)	2–5 ( <i>n</i> = 17)
<i>Ischnoderma resinsum</i> *	53.9	0.0001	0	13	<b>65</b>
<i>Peziza micropus</i>	39.1	0.0012	13	43	<b>71</b>
<i>Marasmius alliaceus</i>	38.9	0.0055	40	<b>83</b>	53
<i>Pluteus phlebophorus</i>	38.6	0.0021	13	30	<b>65</b>
<i>Ramaria stricta</i>	36.9	0.0011	10	13	<b>53</b>
<i>Lycoperdon pyriforme</i>	35.6	0.0205	40	48	<b>76</b>
<i>Clitocybe diatreta</i>	34.1	0.0046	17	26	<b>59</b>
<i>Pluteus cervinus</i>	34.1	0.0351	30	65	<b>76</b>
<i>Nemania chestersii</i>	34	0.0007	0	9	<b>41</b>
<i>Physisporinus sanguineus</i>	28.1	0.0132	10	22	<b>47</b>
<i>Mycena pura</i>	27.3	0.0170	17	17	<b>47</b>
<i>Xylaria polymorpha</i> *	27.3	0.0185	17	17	<b>47</b>
<i>Ganoderma lipsiensis</i> *	26.6	0.0451	13	39	<b>53</b>
<i>Camarops polysperma</i> *	25.8	0.0052	0	13	<b>35</b>
<i>Polyporus varius</i>	25.6	0.0143	3	22	<b>41</b>
<i>Lepista flaccida</i>	25.1	0.0232	13	13	<b>41</b>
<i>Hypoxylon rubiginosum</i>	23.9	0.0302	17	13	<b>41</b>
<i>Pluteus chrysophaeus</i>	22.6	0.0259	7	13	<b>35</b>
<i>Subulicystidium longisporum</i>	20.6	0.0465	3	22	<b>35</b>
<i>Omphalina epichysium</i>	20.4	0.0245	0	13	<b>29</b>
<i>Pluteus umbrosus</i>	19.9	0.0149	0	4	<b>24</b>
<i>Ceriporiopsis gilvescens</i>	18.5	0.0486	0	17	<b>29</b>
<i>Polyporus squamosus</i> *	17.6	0.0115	0	0	<b>18</b>
<i>Thanathephorus fusisporus</i>	17.6	0.0133	0	0	<b>18</b>
<i>Cylindrobasidium leave</i>	16.4	0.0451	<b>20</b>	4	0
<i>Mycena speirea</i>	14.2	0.0485	0	4	<b>18</b>
<i>Mutinus caninus</i>	13	0.0455	0	<b>13</b>	0

Only species with significant indicator values ( $P < 0.05$ ) are included. The *P*-value denotes the proportion of randomised trials resulting in an indicator value equal to or exceeding the observed indicator value, based on 10000 Monte Carlo permutations. Red-listed species are printed in bold, while an asterisk (\*) denotes primary decayers. Bold values indicate preferred log category.

increases markedly with log size, as previously reported from other tree species by Renvall (1995), Høiland and Bendiksen (1996), Lindblad (1997) and Allen et al. (2000). This is hardly surprising, as large logs simply provide space for more species. Interestingly, *complexity* is the log size and shape variable which has the strongest effect on total and red-listed species richness. Keeping other variables constant, a log with one or more bole forks will have a larger cumulative log length and a bigger surface area compared to a log without forks. Consequently, log length and/or surface area appear to be more important for fungal diversity than diameter.

Apart from the positive correlation between species richness and log size, Bader et al. (1995), Renvall (1995), Bredesen et al. (1997) and Kruys et al. (1999)

Table 11. Summary of logistic regressions with *dbh* as independent variable.

Species	Parameter estimate (dbh)	<i>P</i> (Wald)	Number of logs with species
<i>Pluteus cervinus</i>	0.0372	0.0070	37
<i>Megacollybia platyphylla</i>	0.0408	0.0071	22
<i>Physisporinus sanguinolentus</i>	0.0462	0.0073	16
<i>Camarops polysperma</i>	0.0641	0.0075	9
<i>Physisporinus vitreus</i>	0.0483	0.0080	14
<i>Marasmius rotula</i>	0.0364	0.0096	27
<i>Lycoperdon pyriforme</i>	0.0342	0.0155	36
<i>Armillaria gallica</i>	0.0333	0.0155	44
<i>Hydropus subalpinus</i>	0.0714	0.0193	5
<i>Mycena haematopus</i>	0.0341	0.0198	50
<i>Coniophora puteana</i>	0.0361	0.0207	17
<i>Omphalina epichysium</i>	0.0478	0.0268	8

Only species with a positive and statistically significant ( $P < 0.05$ ) response are included.

reported several, mostly rare species to be more or less confined to large diameter logs. The present study does not succeed in proving such associations: the correlations between log size and shape variables and red-listed species richness are weaker than the correlations between the same variables and overall species richness (Table 5), and only one red-listed species, *Omphalina epichysium*, shows a significant preference for large logs using logistic regression analysis (Table 11). However, it must be emphasized that the present study only concerns logs with dbh equal to or exceeding 70 cm,  $\pm$  equalling the normal maximum harvest diameter of beech in Denmark. Distinct qualitative effects of log diameter might occur if smaller logs were included, as was the case in the studies mentioned above.

#### Decay stage

Apart from log size and shape variables, *decay stage* and *log age* were found to have the biggest influence on species richness, with logs in intermediate to late stages of decay being most species rich (Figures 1 and 3). This corresponds well with results from previous studies (e.g. Lange 1992; Renvall 1995; Willig and Schlegte 1995; Høiland and Bendiksen 1996; Lindblad 1997; Edmonds and Lebo 1998) involving both coniferous and deciduous logs. The trend probably reflects an increase in the number of available niches during wood decay, as suggested by Renvall (1995). While some parts of a log may decay rapidly, other parts may remain relatively little decayed (cf. Pyle and Brown 1999), allowing the co-occurrence of both early and late stage decay fungi in intermediately decayed logs. In addition, increasing micro- and mesofauna activity will tend to increase the number of niches as decay proceeds.

It is evident from several studies that the turnover in fungal community structure during log decay is considerable, with many species being more or less confined to certain decay stages (e.g. Chapela et al. 1988; Renvall 1995; Høiland and Bendiksen 1996; Heilmann-Clausen 2001). Accordingly, a discontinuous supply of dead wood

may lead to local extinction of demanding species and may, in the long run, have a marked effect on species composition and diversity.

### *Microclimate*

According to several experimental studies, microclimatic regime is crucial for fungal community development in decaying wood (e.g. Rayner and Boddy 1988; Boddy 2001). In the present study, the positive correlation between species richness and *distance to edge* and the response to *soil humidity* (Figure 2) indicate that extreme microclimatic conditions have a negative effect on species richness. However, in the multiple regression model, *soil contact* is the only variable which clearly indicates an effect of microclimate on species richness. Logs with a high degree of soil contact are likely to be buffered against fluctuations in temperature and especially water content compared to logs with little soil contact. For red-listed species no effect of microclimatic variables could be detected.

In a gradient analysis of the same data set, utilising detrended correspondence analysis (DCA), it was concluded that a complex gradient integrating microclimatic stress and decay rate was associated with a pronounced shift in community structure (Heilmann-Clausen 2001). Accordingly it seems that the microclimatic regime has bigger effects on fungal community structure and development than on the overall species richness on the logs studied. However, it is possible that the consistent relation between species richness and variables related to the vernal flora may reflect long-term microclimatic conditions and fluctuations not accounted for by the somewhat imprecise and indirect microclimatic variables. Obviously, *Anemone nemorosa* is very unlikely to have a direct effect on fungal species richness on decaying logs, but a high presence of the species may indicate certain soil properties, microclimatic conditions or a disturbance regime favouring a high number of fruiting fungal species on the logs.

Only few previous studies have attempted to investigate the effects of microclimate on diversity of fungi fruiting on wood. In accord with the present study, Lindblad (1997) found a positive correlation between species richness and the degree of soil contact on decomposing spruce logs in eastern Norway. Likewise, de Vries and Kuyper (1988) found considerable variation in the number of fungi fruiting on wood distributed across several habitat types subject to very different microclimatic regimes in The Netherlands. As these and the present study are solely based on fruitbody inventories, it is unclear whether the reported effects concern the number of species present as mycelia or only the water-requiring production of fruitbodies. At present it seems, however, justified to propose that the effects of microclimate on wood fungal diversity are limited within the normal range of variation at site level. Logs experiencing extreme conditions are likely to be slightly less species rich, but may on the other hand support specialised species adapted to microclimatic stress.

### *Log type*

The effect of *log type* on the richness of red-listed species is very interesting. *Log*

*type* alone explains 19% of the variation in the richness of red-listed species (Table 6) and even in the multiple regression model the variable has a significant effect (Table 7). Of the four defined log types, logs broken at stem base appear to be especially valuable for red-listed species (Figures 4 and 5), and are at the same time the favoured log type for three primary decayers and several succeeding species (Table 9). Renvall (1995) described comparable differences in species composition between different types of conifer logs in Finland, which he explained by the presence of various decay pathways, each initiated by one or more dominant primary decay fungi. Subsequent studies (Niemelä et al. 1995; Holmer et al. 1997) have provided further support for the existence of decay pathways and it seems likely that they are a general feature structuring succession during wood decay. The mechanisms behind decay pathways are not fully understood, but are likely to involve both specific parasitic relationships (cf. Rayner et al. 1987; Zugmaier et al. 1994), selective combative replacement (cf. Holmer et al. 1997) and passive facilitation resulting from species-specific alterations of wood chemistry, moisture contents and structure caused by primary decayers (cf. Boddy et al. 1989; Blanchette et al. 1990).

In the present study *Ganoderma lipsiensis*, *Ischnoderma resinsum* and *Xylaria polymorpha* appear to be key species in decay pathways, supporting a higher than average number of red-listed species (cf. Table 10). All three species cause butt-rot (Rayner and Boddy 1988; personal observations), which explains their occurrence on trees broken at stem base (Table 9), and they do typically cause extensive decay after tree death. Two further heart-rot formers, *Polyporus squamosus* and *Camarops polysperma*, show an association with logs with two or more red-listed species (Table 10), and may be additional key species linked with these decay pathways. Interestingly, all five species discussed above occur with a low to moderate frequency on the studied logs, being far outnumbered by *Eutypa spinosa*, *Fomes fomentarius* and *Kretzschmaria deusta*, which appear to be the dominant primary decayers on beech logs at the study site (cf. Heilmann-Clausen 2001) and evidently in many other Danish localities (M. Christensen and J. Heilmann-Clausen, unpublished data). Further studies are needed to confirm the significance of decay pathways in structuring fungal community development in beech wood and to determine involved key species. At present, the connection between low to moderately frequent primary decayers and high number of red-listed species is remarkable and indicates that at least some of the late stage red-listed species reported in the present study (Table 4) prefer wood decayed by non-dominant, primary decayers. Further, it suggests that a high diversity of primary decayers may be a key to the conservation of rare fungi associated with dead wood. Stands with impoverished communities of primary decayers, e.g. after centuries of management, may on the contrary prove to have a limited potential for short-term conservation of wood decay fungi.

#### *Implications for forestry*

Protection of native biodiversity is increasingly accepted as an important goal in forestry. Some guidelines for the fulfillment of this goal, with respect to wood

decaying fungi, can be given based on the present study. The guidelines, recommended below, are first and foremost applicable with respect to management of beech in Denmark and neighbouring countries, but have most probably also relevance for other tree species and other geographical regions.

- Large logs are generally more species rich than smaller logs, but differences appear to be mostly qualitative within the range of log sizes included in the present study. Accordingly, two smaller logs appear to be just as valuable for fungal biodiversity as one very big one, as long as the log dbh exceeds 70 cm.
- Complex logs with bole forks are more species rich than unforked logs with equal diameter. At the same time forked trees have less commercial value than trees with a straight bole. Accordingly, the selection of trees with bole forks for natural decay is optimal in both economical and ecological terms.
- Logs in intermediate stages of decay are most species rich and support the highest number of red-listed species. As the turnover in species composition is significant during log decay, it is important to secure a continued supply of dead logs and hence a steady representation of logs in intermediate decay stages.
- Intermediate microclimatic conditions seem to give the highest species richness and it should be aimed that a majority of logs left for natural decay are situated in closed forest stands. Logs experiencing extreme conditions, being e.g. partly submerged in swamps or extremely sun-exposed, appear to be a valuable supplement, supporting specialized species, thereby increasing the overall diversity.
- Logs broken at root neck were in the present study found to be especially valuable for red-listed species. The reason for this is not fully understood, but seems to be linked with the presence of certain rather infrequent primary decay fungi. At present it can be recommended to select logs presenting a high diversity of primary decayers for natural decay. If logs are artificially killed in order to improve biodiversity, different methods of killing should be used in order to open up different decay pathways.

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