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Wood-inhabiting macrofungi in Danish beech-forests – conflicting diversity patterns and their implications in a conservation perspective

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Abstract

Macrofungal diversity was investigated on 281 decaying beech trees distributed across 14 forests in Denmark, based on sporocarp inventories. Two aspects of diversity were considered, i.e., species richness per fallen tree and the incidence of red-listed species occurrence per tree. For both diversity measures the effects of both tree and site variables were tested. In total, 319 fungal species were identified, including 28 red-listed. Decay stage and wood volume were identified as key variables influencing species richness as well as red-listed species incidence. Red-listed species, however, showed a preference for more decayed trees than non red-listed species. Further, red-listed species incidence was found to be significantly higher on broken trees, compared to fallen trees with a distinct root-plate, indicating tree death cause to be important for some red-listed species. The relations between diversity measures and site variables were conflicting. Species richness per tree decreased with increasing maximum tree age and dead wood continuity, possibly a consequence of competitive exclusion of unspecialised opportunistic species in old-grown stands. For red-listed species the opposite trend was evident, and it is concluded that forest history may have fundamental effects on the community structure of wood-inhabiting fungi. Accordingly, simple species richness may be a misleading conservation measure if the aim is to conserve the most threatened aspects of forest biodiversity.
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1. Introduction

Dead wood has been denoted as the most important manageable habitat for biodiversity in forests (e.g. Huston, 1996), supporting a wide diversity of organisms, including birds, mammals, insects, mites, collembolans, nematodes, bryophytes, lichens, fungi, slime moulds and bacteria. Of these, fungi and insects are clearly the most species rich groups (Siitonen, 2001), and as the most important agents of wood decay, fungi can be re-garded as a key group for the understanding and management of biodiversity associated with decaying wood.

Several studies have investigated the relations between fungal diversity and local environmental conditions (e.g. Renvall, 1995; Høiland and Bendiksen, 1996; Lindblad, 1998; Gilbert et al., 2002; Heilmann-Clausen and Christensen, 2003). These studies show that substantial changes occur in the fungal community structure during wood decay, at least judged from the presence of sporocarps, while several other factors, including log size, microclimatic variables, decay history and tree species, have supplementary effects.

Other studies have investigated factors affecting community structure of wood-inhabiting fungi at the

landscape scale. Strid (1975) and Mathiassen (1993) investigated habitat preferences and distribution of wood-inhabiting fungi along climatic gradients in boreal Scandinavia, while Lindblad (2001) studied a similar gradient in Costa Rica. In each case distinct changes in species composition were recorded along the studied gradients. More recently, considerable emphasis has been paid to investigate the importance of forest management as a factor influencing diversity in fungi inhabiting coarse wood debris (cwd). Several studies from boreal forests have reported decreasing species richness with increasing logging (e.g. Bader et al., 1995; Sippola and Renvall, 1999; Sippola et al., 2001; Stokland, 2001; Penttilä et al., 2004), but in most cases it is very difficult to evaluate whether these results reflect more than negative species-area effect, predicting lower species richness with lower substrate abundance (cf., Begon et al., 1990). This is because most studies have investigated species richness on plot basis, implying that bigger and often more varied assortments of cwd have been studied in unmanaged stands compared to managed stands. Even in natural forests cwd amounts have been shown to be a very good predictor of fungal species richness using this approach (Ohlson et al., 1997; Berglund and Jonsson, 2001). The few studies that have attempted to compare diversity of wood-inhabiting fungi in different sites at a directly comparable basis have yielded a less clear picture. Lindblad (1998) and Sippola et al., 2001 found higher species richness on coniferous logs in old-growth stands compared to the situation in nearby managed stands, while Nordén and Paltto (2001), in contrast, found fungal species richness on hazel wood to decrease with increasing stand age and dead wood abundance in hazel-copses. In a fourth case, Høiland and Bendiksen (1996) reported a rather weak gradient, related to logging intensity, to influence fungal community structure of decaying spruce logs across a number of study sites. Similarly, Sippola and Renvall (1999) found cwd logging waste to support different fungal communities of wood-inhabiting fungi compared to natural cwd in coniferous forests.

In the current study we investigate fungal diversity on fallen, decaying beech *Fagus sylvatica* L. trees across 14 forest stands differing in management history, but also with respect to climatic conditions, soil type and geographic location. Two aspects of fungal diversity are considered, viz. species richness per tree and red-listed species incidence per tree. The aim of the study is to investigate: (a) the importance of *site* variables (forest history, soil-type, macro-climate) for the investigated diversity parameters after accounting for *tree* variables (i.e., tree size, decay stage, microclimatic regime) known to have importance for the studied organisms and (b) to test if the occurrence of red-listed species is related to other factors than those affecting species richness in general.

2. Methods

2.1. Study area

The study area is situated close to the north-western distribution limit of European beech (*Fagus sylvatica*) (cf., Larsson, 2001). The climate of the area is mild temperate, with an annual mean temperature ranging from 7.3 to 8.3 °C and an annual mean precipitation of 586–885 mm (Frich et al., 1997). Phytogeographically the area belongs to the nemoral zone (Sjörs, 1965).

Fourteen sites were selected for the study, representing a range of the most common beech forest types in Denmark, and a range of former management histories. All study sites are at present unmanaged, but have been managed to different extend in the past.

2.2. Fungal inventory

A variable number of fallen dead trees were selected at each study site, with the aim of getting a comparable and balanced representation of predefined tree decay classes represented on each site. Within each decay class study trees were selected randomly for each study site. The variable numbers of selected trees at different sites reflect the availability of fallen trees. In some sites not all decay classes were available.

Fungal inventories were conducted on three occasions at all sites, i.e., during late summer, mid-autumn and late autumn/early winter. On each occasion all selected trees, including eventual snag and branches thicker than 10 cm, were carefully inventoried for fungal sporocarps. Sporocarps were identified to taxon in the field or collected for microscopical identification. Within the basidiomycetes all morphological groups, excluding fully resupinate corticoid fungi were included, while non-stromatic pyrenomycetes and inoperculate discomycetes with sporocarps regularly smaller than 10 mm were excluded from the ascomycetes. Seven sites including 71 dead trees were inventoried in 1997 and 1998, while the remaining seven sites, including 210 dead trees, were inventoried in 2000 and 2001, making a grand total of 281 study objects.

2.3. Environmental variables

Environmental variables were recorded at both the tree level and the site level. Tree variables include *tree type* (uprooted, broken at root neck, broken with distinct snag), *dbh* (diameter at breast height), *volume*, *decay stage*, *moss cover*, *soil humidity*, *wind exposure* and *sun exposure*.

Site variables include relative geographical location with zero values defined by the most southerly and westerly located study sites (*east coordinate*, *north coordinate*, *northeast coordinate*, *northwest coordinate*),

climatic characteristics expressed by *Langs index*, *soil type*, *maximum tree age*, historical and present forest cover (*forest cover 1800*, *forest cover 2000*), *fallen trees/ha* and *old cwd ratio*. *Langs index* (annual precipitation/average annual temperature (Lang, 1915)) was calculated for each site based on data from the nearest meteorological stations (Frich et al., 1997; Laursen et al., 1999). Soil type were classified according to GEUS (2002), while forest history variables were based on historical and contemporary maps (Det Kongelige danske Videnskabernes Selskab, 1766–1841; Kort- og Matrikelstyrelsen, 1986–1997), combined with information from Hovedstadsrådet (1986), Møller (1988, 1990, 1997) and Skov- og Naturstyrelsen (1997). *Maximum tree age* gives the known or estimated maximum age of living beech trees at each study sites, based on the above data sources. It gives the minimum age of each site as a beech forest site, but is even a good measure of the logging intensity during the last centuries. *Old cwd ratio* (modified from Stokland, 2001) is an estimate of cwd continuity and was calculated as the ratio between strongly decayed logs (decay stage 4–6) and the total number of logs within each study site, based on own observations. All included environmental variables are listed in Table 1.

2.4. Data analysis

The relationship between environmental variables and fungal diversity per tree were analysed using a four step procedure. First, Kendall rank correlation analysis, one-way ANOVA's and univariate logistic regressions (Zar, 1999; Hosmer and Lemeshow, 2000) were used to evaluate the relations between the selected diversity measures and environmental variables. Secondly, multiple regression analysis was used to identify the complementary set of *tree* variables best able to explain variation in the response variables. In the third step, we included the nominal variable *site* in the model. In case of a distinct effect of this variable a new Kendall rank correlation analysis was carried out between residuals from the *tree* variable based model and the set of *site* variables in order to identify site variables able to account for residual variation in species richness. Finally, in the fourth step, the multiple regression analysis procedure was repeated including both *tree* and *site* variables, guided by the results of step 3. The analyses were run independently for red-listed (following Stoltze and Pihl, 1998) and non red-listed species. For non red-listed species we modelled for species richness per tree using

Table 1
List of recorded tree and site variables, the latter written in italics

Variable	Scale	Range	Median	Source/description
Tree type	Class (nominal)			Three types distinguished (uprooted, broken at root neck, broken with distinct snag)
Volume	m³	0.2–21.1	4.22	Calculated based on diameter measurements of the log, snag and branches >10 cm in diameter at terminal, basal and branching points
Dbh (diameter at breast height)	cm	20–137	78	Measurement (1.3 m above ground)
Decay stage	Class (ordinal)	1–6	3	From undecayed (stage 1) to completely decayed (stage 6)[a]
Moss cover	%	0–100	20	Estimated to the nearest 10% of the log surface
Soil humidity	Class (ordinal)	1–5	2	From dry soils (stage 1) to partly inundated soils (stage 5)[a]
Wind exposure	Class (ordinal)	1–5	3	From open hilltops and edges (stage 1) to sheltered hollows and ravines (stage 5)[a]
Sun exposure	Class (ordinal)	1–5	3	From fully exposed openings (stage 1) to closed, multi-layered forest (stage 5)[a]
East coordinate	km	0–229	164	Based on recent maps[b]
North coordinate	km	0–173	66	Based on recent maps[b]
Northeast coordinate (N-East)	km	8–231	154	Based on recent maps[b]
Northwest coordinate (N-West)	km	0–238	93	Based on recent maps[b]
Langs index	Ratio	73.5–111.9	90.3	Annual precipitation/average annual temperature
Soil type	Class (nominal)			Four types distinguished (sand, sandy till, loamy till and lime stone)
Max tree age	Years	140–350	275	Based on published data[c]
Forest cover 1800 (r. 10 km)	%	1–46	15	Based on historical maps[d]
Forest cover 2000 (r. 10 km)	%	3–45	29	Based on recent maps[b]
Fallen trees/ha (r. 5 km)	Number per ha	1.4–26.5	7.8	Based on personal observations, including only trees with dbh >50 cm.
Old Cwd ratio	%	9–57	38	Number of fallen trees in decay stage 4–6/Total number of fallen dead trees on site

[a] For further details see Heilmann-Clausen and Christensen (2003).
[b] Kort- og Matrikelstyrelsen (1986–1997).
[c] Hovedstadsrådet (1986); Møller (1988, 1990, 1997) and Skov- og Naturstyrelsen (1997).
[d] Det Kongelige danske Videnskabernes Selskab (1766–1841).

a standard linear model (Zar, 1999), while a logistic model structure (Hosmer and Lemeshow, 2000) was chosen for the red-listed species, due the low number of trees hosting more than one red-listed species. The logistic model analyses the incidence (probability of presence) of red-listed species, rather than species richness. Odds ratio's (Hosmer and Lemeshow, 2000) were calculated based on the final logistic model solutions. Odds ratio gives the increase in the estimated incidence when two situations (e.g., two localities) are compared.

A manual forward stepwise variable selection procedure was used in each step of the development of regression models. The response variable, *species richness per tree*, was square root transformed in the regression models in order to make variance constant and residuals normal distributed. Similarly, the variable *volume* was log transformed in the species richness and red listed species incidence models because it was realised that the relations between this variable and the response variables were log-normal rather than linear. All analyses were computed using SAS Version 8.01 (SAS, 1999–2000). The SAS Guided Data Analysis application was used for model control and as a guide for transformation of variables.

3. Results

3.1. General species richness patterns

In total 319 fungal species were identified, including 28 species listed in the Danish red list (Table 2). Of the identified species 31% (98 species) were recorded on one tree only, while only three species were found on more than half of the trees studied. The number of species recorded per tree varied between 1 and 46 with a mean of 16.6. Red-listed species were recorded on 81 trees, of which 19 presented two or three red-listed species.

3.2. Species richness per tree

Species richness per tree was strongly and significantly correlated with several tree variables, especially *decay stage*, *volume*, *soil moisture* and *tree type* as well as several site variables, including *soil type* and *max. tree age* (Table 3). The first regression step showed *volume* to be the tree variable best able to account for variation in species richness, while *decay stage*, *moss cover*, *tree type* and *soil humidity* all appear to have complementary effects (Table 4). As a whole the model based on tree var-

Table 2
Wood-inhabiting red-listed fungal species recorded in the study

Species	Red list status[a]	Number of records	Number of sites	Main host(s) in region[b]
Nemania chestersii	R	24	8	Beech, ash, oak
Pluteus umbrosus	R	12	7	Deciduous spp.
Camarops tubulina	E	11	5	Beech, spruce, silver-fir
Pluteus luctuosus	R	9	4	Deciduous spp.
Mycna picta	R	7	4	Various
Ischnoderma resinosum	V	6	1	Beech
Pluteus hispidulus	R	4	4	Beech
Kavinia himantia	E	3	1	Deciduous and coniferous spp.
Catinella olivacea	R	3	3	Deciduous spp.
Lentaria afflata	R	3	1	Deciduous spp.
Omphalina epichysium	E	2	1	Deciduous and coniferous spp.
Spongipellis delectans	E	2	2	Beech
Aurantioporus alborubescens	V	2	2	Beech
Ceriporiopsis gilvescens	V	2	2	Beech
Entoloma tjallingiorum	R	2	2	Beech, oak
Flammulaster muricatus	E	1	1	Beech
Lentinellus vulpinus	E	1	1	Deciduous spp.
Volvariella caesiotincta	V	1	1	Deciduous and coniferous spp.
Coprinus alopecia	R	1	1	Deciduous spp.
Flammulaster limulatoides	R	1	1	Deciduous spp.
Mycena meliigena	R	1	1	Deciduous spp.
Nemania aenea	R	1	1	Deciduous spp.
Nemania confluens	R	1	1	Beech, oak
Plurotus cornucopiae	R	1	1	Beech, oak, elm
Psathyrella pannuciodes	R	1	1	Deciduous spp.
Porotheleum fimbriatum	R	1	1	Beech
Volvariella bombycina	R	1	1	Beech, oak, maple

[a] According to Stoltze and Pihl (1998): E, Critically threatened; V, Vulnerable; R, Rare.
[b] According to Hansen and Knudsen (1992, 1997, 2000) and Hallingbäck (1994).

Table 3
Summary of univariate relations between fungal diversity measures and environmental variables

Variable	All species		Red-listed species	
	Species richness	Residuals (tree variables model)	Incidence	Residuals (tree variables model)
Dbh	0.42****		ns	
Decay stage	11.45****		24.57***	
Volume	0.55****		5.92*	
Bark cover	0.20****		ns	
Soil contact	−0.13**		ns	
Soil moisture	10.22****		ns	
Sun exposure	4.01**		ns	
Wind exposure	3.60**		ns	
Moss cover	0.30****		ns	
Tree type	11.94****		8.22*	
Soil type	31.80****	5.08**	ns	ns
East coordinate	−0.17****	ns	6.33*	0.12**
North coordinate	0.33****	ns	ns	−0.09*
Northeast coordinate (N-East)	ns	0.09*	ns	0.11**
Northwest coordinate (N-West)	0.33****	ns	−5.46*	−0.11*
Langs index	−0.28****	0.11*	−5.43*	−0.10*
Max tree age	−0.38****	−0.25****	ns	ns
Forest cover 1800 (r. 10 km)	0.15***	−0.14*	ns	ns
Forest cover 2000 (r. 10 km)	0.19****	ns	ns	ns
Fallen trees/ha (r. 5 km)	−0.29****	ns	ns	0.15**
Old cwd ratio	−0.21****	−0.18****	ns	0.10*

Site variables are given in italics. For relations between environmental variables and species richness kendall's τ are given, except for the ordinal variables decay stage, soil moisture, wind exposure, tree type and soil type where F-statistics from one-way ANOVA's are given. The same applies for the relations between site variables and residuals of the tree variables model. For relations between environmental variables and red-listed species incidence G^2-statistics from univariate logistic regressions are given, while relations between site variables and residuals of the tree variables models are indicated by kendall's τ.
ns: non-significant.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.
**** $P < 0.0001$.

Table 4
Summary of multiple regression model ($p < 0.0001$; Adj. $R^2 = 0.66$) for fungal species richness (square root transformed), using only tree variables, with variables sorted according to F-values

Term	DF	Type III sum of squares	F-value	Pr > F
Log (volume)	1	103.4	238.6	<0.0001
Moss cover	1	18.89	42.60	<0.0001
Decay stage	5	13.26	6.12	<0.0001
Tree type	2	3.80	4.38	0.0134
Soil moisture	4	4.268	2.462	0.0456

Adjusted sum of squares (R^2) are given for the full model.

iables accounts for 65% of the variation in species richness according to the adjusted R^2-score. Inclusion of *site* in the model shows this variable to have a highly significant effect ($p < 0.0001$), and comparisons of derived least square means show the predicted species richness per tree to vary significantly between sites (Fig. 1(a)). Correlation scores between residuals of the tree variable based model show the site dependent variation to be highly correlated with forest history variables, especially *max. tree age* and *old cwd ratio* while *soil type*, geographical and climatic variables have less significant ef-

fects (Table 3). In all cases the correlation coefficients are negative, indicating species richness per tree to decrease with dead wood continuity and stand age. The final regression step, including all variables, shows *max. tree age* and *old cwd ratio* to have complementary effects in explaining species richness in combination with *volume*, *decay stage* and *moss cover*, while *tree type* and *soil moisture* are now insignificant. The model explains about 72% of the variation in species richness according to the adjusted R^2-score, and shows species richness per tree to increase with *volume*, and less significantly, with *moss cover* of the individual tree, and to decrease with *maximum tree age* and *old cwd ratio* of the site (Table 5). Parameter estimates of *decay stage* indicate species richness to be highest on trees in decay stage 3 and lowest in decay stage 5.

3.3. Red-listed species incidence

The incidence of red-listed species per tree was found to be significantly correlated with the tree variables *decay stage* and slightly less so with *volume* and *tree type* as well as the site variables *east* and *northwest coordinate* (Table 3). The multiple logistic regression
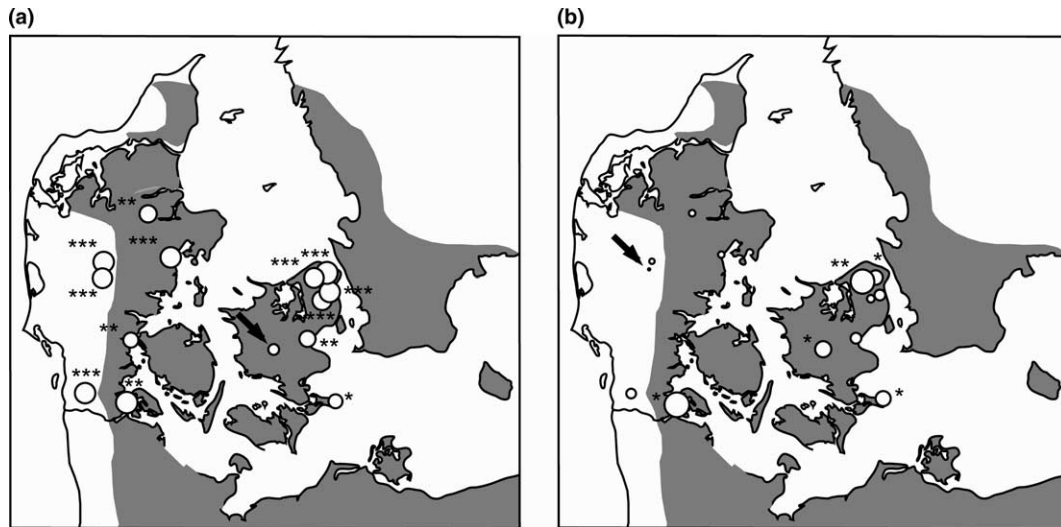
Fig. 1. Predicted species richness per tree (a) and predicted odds ratio for red-listed species (b) for each of the 14 study sites, indicated with variable dot sizes. Odds ratios are calculated with respect to the site (arrowed), which had the lowest incidence for red-listed species of all sites. Sites with significantly higher least square means, in comparison with the sites with the lowest predicted mean/incidence values (arrowed), are indicated as follows: [***]$P < 0.0001$; [**]$P < 0.01$; [*]$P < 0.05$. The shading indicates the mean historical distribution area of beech, generalized from Ødum (1980); Hultén and Fries (1986) and Larsson (2001).

Table 5
Summary of the final multiple regression model ($p < 0.0001$; Adj. $R^2 = 0.72$) for fungal species richness (square root transformed), using both tree and site variables

Variable	Type III SS	*F*-value	Pr > *F*	Variable stage	Parameter estimate (±95% conf. limits)	*t*-value	Pr > *t*
Log (volume)	125.9	351.2	<0.0001		2.0–**2.3**–2.5	18.74	<0.0001
Max tree age	9.05	25.25	<0.0001		−0.002 to **0.004** to −0.006	−5.02	<0.0001
Decay stage[a]	10.91	6.09	<0.0001	1	−0.17–**0.10**–0.37	0.72	0.4709
				2	0.15–**0.39**–0.64	3.17	0.0017
				3	0.28–**0.51**–0.74	4.40	<0.0001
				4	−0.16–**0.08**–0.31	0.63	0.5271
				6	−0.24–**0.12**–0.49	0.66	0.5077
Old cwd ratio	5.447	15.20	0.0001		−0.007 to **−0.014** to −0.021	−3.90	0.0001
Moss cover	3.191	8.91	0.0031		0.001–**0.004**–0.007	2.98	0.0031

Site variables are given in italics. To the left the significance of each variable in the model is indicated by *F*-test statistics, while parameter-estimates and their significances according to *t*-test statistics are given to the right.
[a] Parameter estimates calculated with reference to decay stage 5 (=0).

model for red-listed species incidence including only tree variables (not shown) showed that only *decay stage* and *tree type* had complementary significant effects ($p < 0.05$), while all other tree variables, including *volume*, were insignificant. Inclusion of *site* in this model, showed this variable to have an almost significant effect (*G*-test; $p = 0.09$), and the estimated odds ratio for red-listed species incidence vary considerably, and to some degree significantly between sites (Fig. 1(b)). Correlations between residuals of the tree variable based model and site variable scores shows the incidence of red listed species to relate significantly to *max. tree age*, dead wood abundance (*fallen trees/ha*) and *old cwd ratio*, but also with geographical location (Table 3). The final regression model, including both tree and site variables, shows *Northwest coordi-* *nate* to be the site variable best able to supplement the variables *decay stage* and *tree type* included in tree variable based model. In addition the effect of *volume* is significant (Table 6). Odds ratio scores of the model show the predicted incidence of red-listed species occurrence to increase with volume and to be highest for trees in decay stage 4 and lowest for trees in decay stage 1 (For trees in decay stage 4 odds ratios indicate, with 95% probability, the chance of encountering red-listed species to be between 3.0 and 36.8 times bigger compared to trees in decay stage 1). Similarly, both defined types of broken trees are significantly more likely to host red-listed species compared to uprooted trees. Finally, the odds ratio for a 10 km move in north-westerly direction of 0.97–0.99 corresponds to a decrease of 1–3% in red-listed species incidence.

Table 6
Odds ratios, and significance levels of variable terms in the final logistic model for red-listed species occurrence

Variable	G^2	Pr > G^2	Variable stage	Odds ratio (±95% conf. limits)	Wald χ^2	Pr > χ^2
Decay stage[a]	25.81	<0.0001	2	0.8–**2.7**–9.4	2.37	0.1236
			3	1.9–**6.1**–20.0	9.05	0.0026
			4	3.0–**10.6**–36.8	13.75	0.0002
			5	0.5–**2.0**–7.8	1.05	0.3065
			6	0.6–**3.7**–21.5	2.08	0.1488
N-West[b]	13.50	0.0002	+10 km	0.97–**0.98**–0.99	12.36	0.0004
Tree type[c]	13.27	0.0013	Broken at root neck	1.8–**6.1**–20.7	8.25	0.005
			Broken with distinct snag	1.5–**3.0**–6.0	9.23	0.0024
Log10 (volume)	6.79	0.0092	One step increase in power	1.2–**2.5**–5.0	6.49	0.0109

Site variables are given in italics. To the left the significance of each variable in the model is indicated by G^2-test statistics, while parameter-estimates and their significances according to Wald-test statistics are given to the right.
[a] Odds ratios calculated with reference to decay stage 1 (=1).
[b] Odds ratio calculated for a 10 km move in direction NW.
[c] Odds ratios calculated with reference to uprooted trees (=1).

3.4. Differences between study years

Since the data were obtained from studies conducted in two different periods a nominal variable defining study years were included in the final models. In both cases the effect was insignificant ($p = 0.63$ in the model for species richness; $p = 0.16$ in the model for red-listed species incidence) for which reason we judge it reasonable to treat the two datasets as directly comparable.

4. Discussion

Both species richness per tree and red-listed species incidence showed significant relationships to tree characteristics as well as site differences. The relations between measured tree variables and both diversity parameters were fairly uniform, though differences in the strength and details of some relations differed considerably. For the site variables the situation was different. Thus, most site variables that related positively to species richness showed a negative relation to red-listed species incidence. These results are discussed further below in two sections dealing with tree variables and site variables respectively, while a third section summarises the relevance of the results in a conservation context.

4.1. Importance of tree variables

Decay stage and *volume* appear to be key variables relating significantly to both species richness and red-listed species incidence, which is in agreement with results of earlier, comparable studies (e.g., Bader et al., 1995; Renvall, 1995; Høiland and Bendiksen, 1996; Lindblad, 1998; Kruys et al., 1999; Heilmann-Clausen and Christensen, 2003). The maximal incidence of red-listed species on distinctly decayed trees (decay stage 4), and their low frequency on newly dead trees (decay stage 1) compared to the earlier optima of overall species richness (decay phase 3), points to a general preference among rare wood-inhabiting fungi for distinctly decayed wood, as also noted by Renvall (1995); Kruys et al. (1999) and Sippola and Renvall (1999) from coniferous wood. With respect to *volume* it is notable that this variable was found to be highly important in the model for overall species richness, while the effect in the red-listed species incidence model was weaker. We interpret this as an indication of tree size per se to be of rather limited importance for the occurrence of red-listed species on the studied trees. This is, as discussed in detail elsewhere (Heilmann-Clausen and Christensen, 2004), in contrast with studies from boreal Scandinavia, which persistently have claimed large logs to be crucial for rare wood-inhabiting fungi (Bader et al., 1995; Renvall, 1995; Høiland and Bendiksen, 1996; Bredesen et al., 1997; Kruys et al., 1999; Sippola and Renvall, 1999).

The variable *tree type* showed significant relations to both species richness and red-listed species incidence, but in the final regression models it was only significant in the latter case. Odds ratios show the predicted incidence of red-listed fungi to be highest on broken trees, especially those broken at the root-neck. In an independent previous study (Heilmann-Clausen and Christensen, 2003) we reached a very similar conclusion, and suggested this to reflect the presence of different primary decay agents among tree types. We therefore hypothesised certain heart-rot agents, especially those causing butt rot, to facilitate the subsequent establishment of red-listed species in beech wood, a hypothesis which the present study supports.

Finally, *moss cover* was found to relate positively to diversity, but only for species richness. We find it unlikely that the extent of moss cover is directly responsible for the effect, though a high moss cover may have a stabilising effect on the microclimatic environment, thereby benefiting the production of fungal sporocarps (Chlebicki et al., 1996). Rather, we find it probable that the extent of moss cover reflects

differences in microclimatic conditions influencing both bryophyte and fungal growth, which we have not been able to account for using our roughly estimated micro-climatic variables.

4.2. Patterns and differences at the landscape scale

While the relations between fungal diversity and tree variables were mostly non-controversial, the relations to site variables showed several surprises. Species richness per tree was negatively associated with *maximum tree age* and *old cwd ratio*, a surrogate measure for cwd continuity (cf., Stokland, 2001), when the influence of measured tree variables was accounted for. Thus, species richness per tree was generally lower in sites showing old-growth characteristics, i.e., high tree ages and a balanced representation of wood decay classes. This result is surprising, as several previous studies have suggested the opposite trend (e.g., Bader et al., 1995; Lindblad, 1998; Sippola et al., 2001). However, Nordén and Paltto (2001) found a result very similar to ours in a study from hazel woods in eastern Sweden, and suggested competitive exclusion to be among the explanations for the trend. The same may be the case in the present study. Thus, the decreasing species richness with increasing tree age and dead wood continuity may reflect a loss of weakly competitive non-specialist species to the benefit of highly competitive or narrow niche specialists, as fungal communities mature.

It is important to note that this loss of alpha diversity is not related to a loss of red-listed species: All localities with low red-listed species incidence have high alpha diversity, while the two localities with the lowest alpha diversity have high incidence of red-listed species. Even more importantly, red-listed species incidence showed positive relations to *old cwd ratio* and *fallen trees/ha* when tree variables were accounted for. In the final model for red-listed species incidence these variables were however non-significant, while a clear effect of *northwest coordinate* is evident. We do not find that this result excludes a causal relation between forest history and the occurrence patterns of red-listed fungi. The north-western part of the study area, which show the lowest red-listed species incidence, are at the limit of the natural range of beech in Europe (Fig. 1(b)), and have historically been rather sparse for beech forests (Bradshaw and Holmqvist, 1999; Odgaard and Rasmussen, 2000). Today the forests in this part of Denmark are predominantly plantations of introduced conifers and in this context it is noteworthy that fungal species exclusively associated with beech were recorded less frequently in the north-western sites compared to the south-eastern sites, while ubiquitous species and species with a preference for coniferous wood showed the opposite pattern (Heilmann-Clausen and Christensen unpublished results).

In combination these results indicates beech to lose specific species, including rare associated specialists close to its distribution limit to the benefit of more common ubiquitous species. Lack of regional or local dead wood continuity may very well be an equally or even more important factor for the recorded patterns. Studies from boreal Scandinavia (Siitonen et al., 2001; Stokland, 2001; Stokland and Kauserud, 2004) have indicated that forestry and breaks in dead wood continuity may be critical for red-listed wood-inhabiting fungi, even if amounts of dead wood are restored locally.

4.3. Implications for conservation priorities

In conclusion, the present study shows that landscape history and forestry may have fundamental impact on fungal community structure in decaying wood, a finding which is highly relevant in a conservation context. High species diversity may be maintained or restored locally in forests characterized by low levels of continuity, because dead wood is an attractive substrate for a high number of fungal species with superior dispersal ability (e.g., Hallenberg, 1995). However, in traditionally managed forests conditions suitable for development of heart-rot fungi are rarely present, and as a result, whole species assemblages including red-listed species are sparsely represented. Thus, an uncritical increase of dead wood amounts in managed forests may completely fail to benefit rare fungal species, even though species richness increases. To support populations of red-listed species more careful strategies should be followed. In managed forests, the aim should be to increase the amount of whole old-grown trees left for natural decay. If possible, trees attacked by a diversity of heart-rot agents should be selected for decay, and at least in beech-forests this seems to be possible without a serious increase in the rate of fungal attacks in healthy production trees (Thomsen et al., 2001). Non-intervention forest reserves are a necessary supplement for successful conservation of biodiversity associated with dead wood. Again a careful selection strategy is crucial. The present study shows that there may be considerable differences in red-listed species incidence on comparable substrates between sites. Although these differences were best explained by a major geographical gradient, we suggest that local to regional differences in forest management history are of major importance for the recorded patterns. The relation between forest history and present biodiversity value, however, constitutes a highly complex four-dimensional problem, because continuity in time and space are equally important factors, which may interact in a multitude of ways. Structure-based indicators assessing the natural value of sites (e.g., Lindenmayer et al., 2000) and stand reconstructions (e.g., Groven et al., 2002) may have the potential to guide the selection of sites for reserve networks, but we still

feel that many more studies assessing the relations between forest history, forest structure and biodiversity in relevant target organism groups are needed before such methods are used on a wider scale.

The lack of correlation between species richness per tree and red-listed species incidence also raises a more fundamental question on conservation goals and means. It has repeatedly been found that conservation strategies focussed on simple species richness may be poorly able to protect the most rare and unique species and habitats – and vice versa (e.g., Prendergast et al., 1993; Bonn et al., 2002). In the current case focus on red-listed species is clearly the most relevant, as it is highly probable that the more widespread species will be able to persist very well, even if no conservation efforts are made. However, the focus on red-listed species is not the solution in all cases. Species may be regarded as threatened for many reasons and the qualities of national and regional red-lists differ considerably. Carefully selected indicators of habitat integrity (e.g., Karr et al., 1986; Andreasen et al., 2001) or the use of advanced predictors of habitat quality using whole community data (e.g., Ejrnæs et al., 2002) would be a more favourable approach, as this could focus on communities as functional entities. Some efforts have been made to develop relevant indicator schemes using wood-inhabiting fungi (e.g., Parmasto and Parmasto, 1997; Nitare, 2000; Norstedt et al., 2001; Christensen et al., 2004), and we believe that further testing of such systems will prove their usefulness and relevance in a conservation context.

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