



# sommerfeltia

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**Bendiksen, E., Økland, R.H., Høiland, K., Eilertsen, O. &  
Bakkestuen, V.**

**Relationships between macrofungi, plants and environ-  
mental factors in boreal coniferous forests in the  
Solhomfjell area, Gjerstad, S Norway**

**2004**



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The macrofungal species composition and its relationships to ecological factors and vegetation were investigated in a boreal coniferous forest area. Macrofungi were recorded in 99 16-m<sup>2</sup> macroplots, each divided into 16 subplots of 1 m<sup>2</sup>. Presence/absence of each species was recorded in every subplot and frequency in 16 subplots was used as abundance measure. Two 1-m<sup>2</sup> plots within each macro plot had previously been analysed with respect to vascular plants, bryophytes and macrolichens. All plots were provided with measurements of 36 environmental variables. Parallel DCA and two-dimensional LNMDS ordinations of macroplots identified the same two coenocline axes. One more coenocline axis identified by DCA was also possible to interpret ecologically. The first fungal coenocline corresponded to the main coenocline for vegetation, comprising the variation from pine to spruce dominated forests; from ridge via slope to valley bottom. This coenocline is interpreted as the response to two independent complex-gradients: (1) a topography-soil depth complex-gradient in the pine forest, and (2) a complex-gradient in soil nutrient status in the spruce forest. While macro-scale topographic variables were relatively more strongly correlated with the vegetational coenocline, soil pH and nitrogen content were more strongly correlated with the fungal coenocline. It is argued that the soil moisture deficiency hypothesis, i.e. that species differ in drought tolerance, proposed as an explanation for variation along the main vegetational coenocline in pine forests, also applies to pine-forest macrofungi. The responses of macrofungi and plants to edaphic conditions in spruce forest were found to differ in one important respect: while plants common on poor soils are normally present also in richer sites, many macrofungal species were absent or rare there. Reasons for this are discussed. The second coenocline (only identified by DCA), only relevant for the spruce forest, reflected the variation from bryophilous fungal species that avoided sites with dense deciduous litter to saprotrophic species living on incompletely decayed *Populus* and *Betula* litter and ectomycorrhizal fungi associated with deciduous trees. The third coenocline strongly correlated with median soil moisture and also related to fine-scale canopy closure was interpreted as due to a fine-scale paludification gradient. The correspondence between ordination results obtained for fungi and plants demonstrates (1) that distributional patterns of macrofungi and plants within forests to a large extent (but not completely) are caused by the same major environmental complex-gradients and (2) that the same field and analytical methods are applicable to both groups of organisms.

Keywords: Boreal coniferous forests, DCA, Environmental factors, Fungi, Gradient, LNMDS, Macromycetes, Mycorrhiza, Norway, Ordination.

*Egil Bendiksen and Vegar Bakkestuen, Norwegian Institute for Nature Research, P.O. Box 736 Sentrum, N-0105 Oslo, Norway; Rune H. Økland, Botanical Museum, Univ. of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway, and Norwegian Institute of Land Inventory, P.O. Box 115, N-1430 Ås, Norway; Klaus Høiland, Department of Biology, Division of Botany and Plant Physiology, University of Oslo, P.O. Box 1045 Blindern, N-0316 Oslo, Norway; and Odd Eilertsen, Norwegian Institute for Nature Research (present address: Norwegian Institute of Land Inventory).*

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## INTRODUCTION

Variation in the macrofunga of coniferous forests is partly known from floristical observations and descriptions in floras, partly from studies relating fungi to predefined vegetation types. Fennoscandian works from coniferous forest vegetation based on recording of fruitbodies include among others Østmoe (1979), Bendiksen (1981), Metsänheimo (1982), Mehus (1986), Brandrud (1987), Hintikka (1988), Såstad (1990), Dahlberg (1991), Gulden et al. (1992), Ohenoja (1993), Blomgren (1994), Väre & Ohtonen (1996), and Dahlberg et al. (1997). These studies have been performed within larger plots with none or few measurements of ecological variables. Except for the studies by Såstad (1990) and Väre & Ohtonen (1996), variation in fungal distribution, presence and abundance has not been related to a wide range of potentially important environmental variables.

Knowledge about the responses of living organisms to ecological gradients under natural conditions is increasingly needed as a background for detecting and understanding biotic effects of man-induced environmental changes. In boreal forests, man induces environmental change by several means. Deposition of long-distance airborne pollutants has been most strongly focused for ectomycorrhizal fungi (e.g. Høiland 1993), while modern forestry practices have been especially emphasized in connection with wood-inhabiting corticiaceous and polyporaceous species (Renvall 1995, Bader et al. 1995, Høiland & Bendiksen 1997, Lindblad 1998).

Multivariate gradient analysis has since long been accepted as a standard tool for summarizing vegetation patterns (e.g., Kent & Ballard 1988, R. Økland 1990). From about 1985 there has been a marked increase in the use of these methods in the macrofungal parallel to vegetation ecology. Nevertheless, the field methodology, including sample procedures, of fungal ecological studies has largely remained unaffected.

In Norway, several reference sites for monitoring of vegetation have been established in the boreal zones during the last decade (T. Økland 1990, 1996, R. Økland & Eilertsen 1993, Eilertsen & Often 1994, T. Økland et al. 2001). The Solhomfjell area in S Norway was among the first sites to be established (in 1988; see R. Økland & Eilertsen 1993, 1996, R. Økland 1995a, 1995b). In this area, vegetation-environment relationships have been studied in 200 permanent plots, 1 m<sup>2</sup> each. These plots are situated in groups of two within each of 100 16-m<sup>2</sup> macro plots, in turn distributed on eight transects intended to cover the main variation in vegetation and local environmental factors in the area. This study of relationships between macrofungi, plants and environmental factors is an extension of the study by R. Økland & Eilertsen (1993), in two respects: (1) it is carried out in the same permanent plots, and (2) previous analyses of vegetation and recordings of environmental variables are related to the observed fungal patterns.

The aims of the study are: (1) to find the main gradients in terricolous macrofungal species composition in an area dominated by oligotrophic boreal coniferous forest vegetation and to relate these gradients to environmental complex-gradients; (2) to compare these gradients in macrofungal species composition with gradients in plant species composition; i.e. to test (i) whether gradients in species composition in each of the two groups of organisms are correlated, (ii) in case, test if their relative importance are similar for the two groups, and (iii) discuss the processes behind the observed patterns; and (3) to explore the suitability of gradient analysis techniques (including multivariate methods such as ordination) for use with macrofungi. This study is also designed to form the basis for monitoring of changes in macrofungal species composition, e.g. resulting from deposition of airborne pollutants or climatic change.



## THE INVESTIGATION AREA

The investigation area, *c.* 2 km<sup>2</sup>, is situated in the Solhomfjell area, Gjerstad, Aust-Agder county, S Norway, 58°58' N, 8°58' E, altitude 350–480 m.a.s.l. (Fig. 1).

## GEOLOGY AND GEOMORPHOLOGY

The bedrock belongs to the central-southern Norwegian Precambrian, consisting mainly of gneisses with intrusions of granites and pegmatite (Ofte Dahl 1980, Sigmond et al. 1984). According to Børset (1979) the area around Svarttjern (the eastern part of the investigation area; Fig. 2) consists of gneissic granites with large pegmatite intrusions, while the Solhomfjell area (the western part of the investigation area) consists of pale granites with numerous pegmatite intrusions and locally a more gneissic structure.

The investigation area is situated in a hilly landscape, with peaks up to 653 m (Solhomfjell), rising from a plateau at 350–400 m, and surrounded by deep valleys at all margins.

Morainic deposits are sparse; the bedrock is covered with morainic deposits in sheltered sites only. Most of the soils have been formed *in situ*. Soils deeper than 50 cm are rarely encountered. Peat

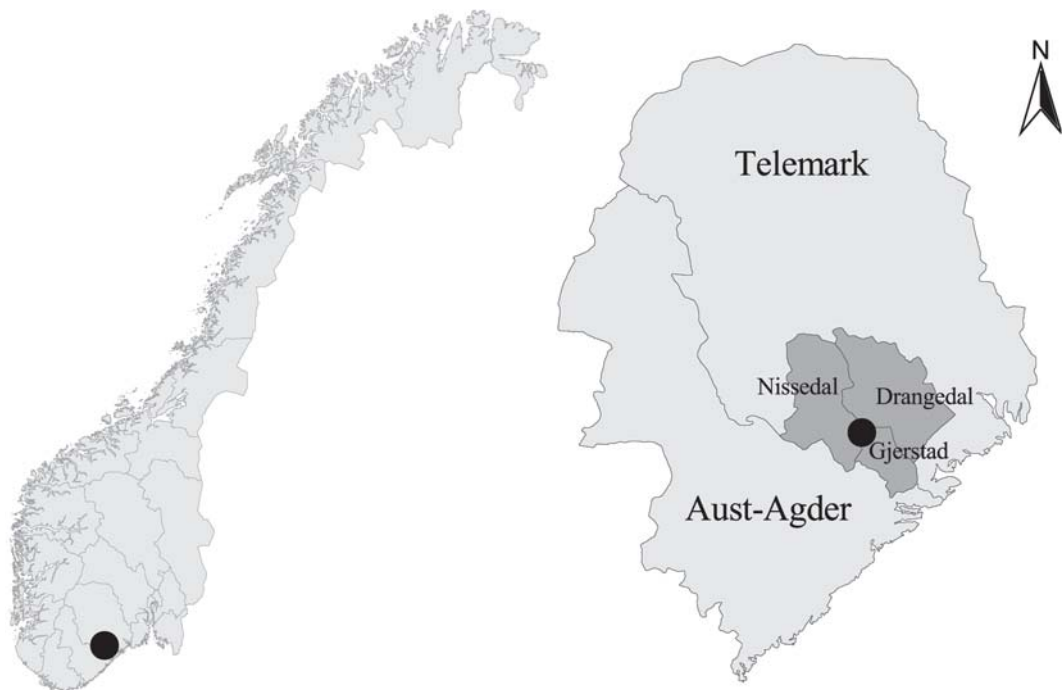


Fig. 1. Maps of Norway (left) and the counties Aust-Agder and Telemark (right) showing the position of the investigation area (dot) close to the border between Gjerstad, Drangedal and Nissedal municipalities. From R. Økland & Eilertsen (1993).

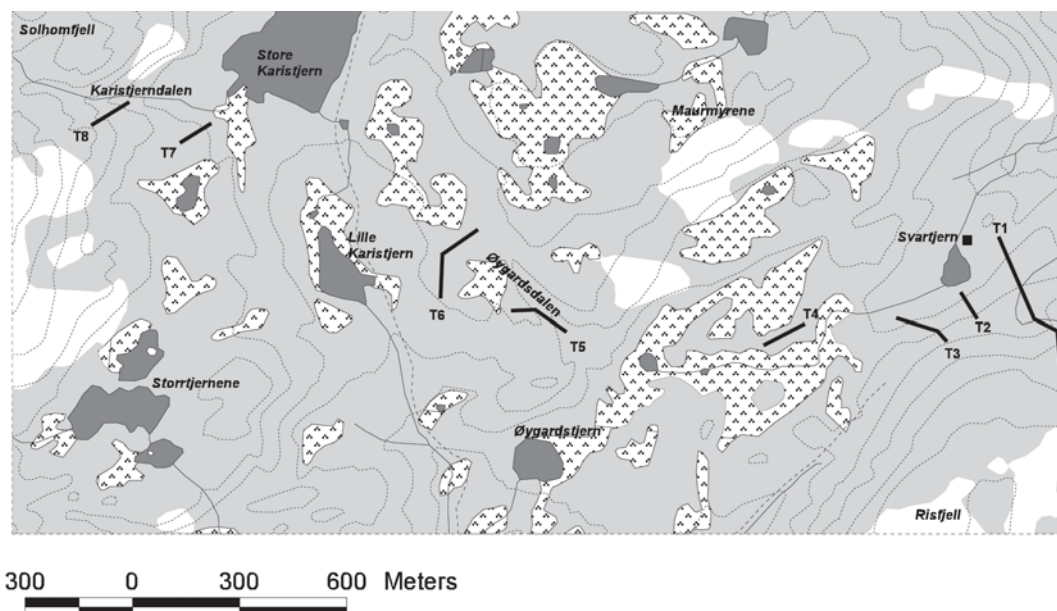


Fig. 2. The investigation area, with transects T1–T8. Contour interval 25 m (reference altitudes: Svartjern 348 m a.s.l.; Store Karistjern 426 m a.s.l.). Altitudes in m. Heavily shaded – lakes and tarns. Dotted – mires. Lightly shaded – forest. From R. Økland & Eilertsen (1993).

covers extensive areas; narrow sloping fens typically split the forest into smaller stands, dominated by Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.).

## CLIMATE

The climate is suboceanic. The estimated annual mean temperature 1961–90 was 4.2 °C [data of Aune (1993) from the nearest meteorological station Tveitsund (20 km WNW of the study area, 252 m.a.s.l.), corrected for altitude according to Laaksonen (1976)]. The mean temperature (1961–90) of the warmest and coldest months (July and February) was 14.4 and –5.5 °C, respectively. Annual mean precipitation (1961–90) at the meteorological station Gjerstad was 1290 mm (Førland 1993); perhaps somewhat higher in the investigation area (R. Økland & Eilertsen 1993).

The main features of climatic *variation* in the study period (1989–91) were as follows (Tab. 1): The 1988/89 winter and the 1989 spring were exceptionally mild: temperature means were above 2.5 °C all months and a permanent snow cover hardly occurred. Temperatures were close to normals for the rest of the year. The growing season was dry (Tab. 1). Another exceptionally mild and rainy winter (203 mm in February; 4× normal) without stable snow cover followed. April and May 1990 were also mild, but rainfall and temperatures deviated slightly from normals for the rest of the year. Except for the dry spring and summer (only 1 mm in May) and the cold June (Tab. 1), 1991 was close to normals.

## FOREST HISTORY AND HUMAN INFLUENCE

The investigation area is protected as a National Nature Reserve (Solhomfjell Forest Reserve), from 1993. The forests in the investigation area have not been commercially exploited [see R. Økland & Eilertsen (1993) for brief summary of conservation history and human activities], and no traces of logging occur. However, the presence of moderate amounts of fallen logs indicates that fallen and standing dead trees have been removed for fuel. Extensive logging has, however, been performed outside the reserve. Trees with fire scars have been observed sporadically but only outside the studied plots. It is likely that the development of vegetation has been continuous for a long time, at least more than one hundred years. Tree ages up to 200 years for Norway spruce and over 350 years for Scots pine have been recorded.

Hafsten (1985) estimated the spruce immigration in the area to have taken place around A.D. 1000).

Annual amounts of acidifying compounds deposited by precipitation (1992 and 1993 averages) were 7.9 kg N·ha<sup>-1</sup>·yr<sup>-1</sup> (4.3 kg NO<sub>3</sub>-N and 3.6 kg NH<sub>4</sub>-N) and 6.4 kg SO<sub>4</sub>-S·ha<sup>-1</sup>·yr<sup>-1</sup>; the annual mean rainwater pH was 4.4 (Tørseth & Røyset 1993, Tørseth & Røstad 1994). The deposition of long distance airborne pollutants is high relative to other parts of Norway (Anonymous 1995).

## PHYTO- AND FUNGAL GEOGRAPHY

The area is situated in the southern (and middle) boreal zone [in the terminology of Ahti et al. (1968); see R. Økland & Eilertsen (1993) and Moen (1998)].

Most of the recorded macrofungal species have a wide distribution in the boreal zones of Norway. Five species are, however, southern: *Mycena inclinata* and *Lactarius quietus*, that are associated with *Quercus* spp; *Laccaria amethystina*, which is markedly southern, common in the nemoral and boreonemoral zones and more accidentally present in the southern boreal zone; and *Lactarius camphoratus* and *Amanita virosa*, typical boreonemoral and southern boreal coniferous forest species that decrease markedly from the southern to the middle boreal zone (E. Bendiksen, pers. obs.). *Amanita virosa* is particularly common in the study area.

Tab. 1. Climate in the study period. Data from the meteorological station Tveitsund (Norske meteorologiske Institutt 1988–92) compared with 1961–90 means (Aune 1993, Fjørland 1993). % – percentage of mean, Δ – difference from mean.

Year	Precipitation				Snow depth		Temperature						
	Year		May–June		May–Sept.		February	Year		May–June		May–Sept.	
	mm	%	mm	%	mm	%	cm	mm	Δ	mm	Δ	mm	Δ
1988	1,329	134	111	74	693	149	53	5.9	0.9	13.4	2.1	13.3	1.0
1989	790	80	44	30	180	39	5	7.1	2.1	11.7	0.5	12.8	0.5
1990	1,157	116	117	79	422	91	4	7.2	2.2	12.5	1.3	12.9	0.6
1991	799	80	90	60	273	59	44	5.9	0.9	9.9	-1.3	12.6	0.3

## MATERIAL AND METHODS

The field work was carried out in the years 1988 (recording of plants and environmental variables 1–33), 1989–1991 (recording of fungi), and 1997 (recording of supplementary environmental variables \*2 and \*3).

### THE SAMPLING DESIGN

Eight transects of different lengths were subjectively selected to cover the variation in boreal forest vegetation, as well as the variation in topography, slope, aspect etc., in the investigation area. Every tenth meter along a transect was a potential site for the lower left corner of a macro plot, 16 m<sup>2</sup>. Macro plot positions were rejected if they included (1) mires, tarns or elements of ecosystems other than forest, (2) more than 50% naked rock, (3) cliffs higher than 1 m, or (4) boulder stones with diameter larger than 1 m. From the accepted positions, macro plots were drawn at random except for the following restrictions: (1) plot number per transect was to be proportional with transect length, and (2) total plot number was to be 100. The study of fungal species composition was performed in the macro plots. Macro plot No. 20 was heavily disturbed by root uplift early in 1989, and excluded from the study.

Each macro plot was divided into 16 macro subplots, of which two (along opposite margins of the macro plot, in fixed positions) were taken as meso plots (1 m<sup>2</sup>). The study of vegetation by R. Økland & Eilertsen (1993) was concentrated to meso plots. Like macro plots, meso plots were rejected and replaced by a neighbouring plot, selected from a fixed priority list, if not meeting a pre-defined set of criteria (see R. Økland & Eilertsen 1993).

All plot corners were permanently marked with subterranean aluminium tubes.

### RECORDING OF MACROFUNGI

The term macrofungi is a practical, not a taxonomical concept. The following groups were included: all agarics and boletes (Agaricales, Russulales and Boletales), terricolous Aphyllorphorales, gasteromycetes, larger heterobasidiomycetes and ascomycetes. With the exception of *Glomus* sp., which was recorded when seen, hypogeous species were not included in this study. Wood-inhabiting species were included only when emerging from soil-buried wood and/or small wood fragments or twigs up to a diameter of 1 cm. For convenience, we will use the term 'fungi' in the meaning 'macrofungi' in this paper.

The recorded species are listed in Appendix 1.

The recorded species are divided into ectomycorrhizal and non-mycorrhizal on basis of information in the literature, e.g. Molina et al. (1992) (an exception of the mycorrhizal group is *Glomus* sp., forming VA mycorrhizae). The *Entoloma* species found in this study are considered as

saprotrophs, except for *E. rhodopolium*, which has been shown to be a mycorrhizal species (Modess 1941; cf. also Agerer & Waller 1993).

Presence/absence of all macrofungi was recorded in each macro subplot on four to five occasions between ultimo July or primo August and primo October (always with two visits in September, the optimal season for fruiting) in each of the three years. Recordings were pooled over visiting occasions to give as a result a data matrix with presence/absence data for fungi in macro subplots in the three-year study period. For practical reasons the vernal and late autumnal aspects were excluded. The production of fruitbodies was considered as close to the average in all three years, but with considerable variation within years. The number of fruitbodies was low in extended drought periods such as in late summer 1990, while September and October were moist to fairly moist in all years.

Frequency in subplots (see T. Økland 1988; R. Økland 1990) was calculated for each of the 235 species of fungi in each of the 99 macro plots. The resulting data set is referred to as the *MAF 99* data set.

The number of fungal species per macro plot is referred to as fungal species density, following Magurran (1988) and Grace (1999).

## RECORDING OF EXPLANATORY VARIABLES

The term explanatory variable is used, in a collective sense, for the three kinds of variables used in interpretation of variation in fungal species composition: (1) vegetational gradients (gradients in composition of the vegetation), (2) environmental variables, and (3) spatial variables. R. Økland & Eilertsen (1993) give a detailed description of the methods used for recording variables of the first two kinds, and also provide thorough analyses of vegetation-environment relationships. Spatial variables are described by R. Økland & Eilertsen (1994).

### *Vegetational gradients*

#### Recording of vegetation

Presence/absence (by cover) of *vegetation*, i.e. humus-dwelling vascular plants (the field layer; including lignified species < 80 cm high), bryophytes and lichens (the bottom layer), was recorded in 1988 in each of 16 0.0625 m<sup>2</sup>-subplots in each of the 200 meso plots. Frequency in the 16 subplots was used as measure of species abundance. The following data sets analyzed by R. Økland & Eilertsen (1993) were used in the present study:

*ME 200* - frequency in subplots data for 171 plant species in 200 meso plots.

*MEV 200* - frequency in subplots data for 65 vascular plants species in 200 meso plots.

*MEB 200* - frequency in subplots data for 106 bryophyte and lichen species in 200 meso plots.

#### Vegetational explanatory variables

R. Økland & Eilertsen (1993) found the main compositional gradients in vegetation by ordination. They applied DCA (Detrended Correspondence Analysis; Hill 1979, Hill & Gauch 1980) and LNMDS (Local Non-Metric Multidimensional Scaling; Kruskal 1964a, 1964b, Minchin 1987) in parallel to the *ME 200* data set. R. Økland & Eilertsen (1993) interpreted the high similarity of the two-

dimensional solutions obtained by the two methods as strong indications that the main gradient structure in the ME 200 data set had been found (cf. R. Økland 1990, 1996), and that two main coenoclines (Whittaker 1967) exist in forest vegetation in the area. These coenoclines were interpreted ecologically by correlating meso plot scores along axes with the measured environmental variables.

As vegetational explanatory variables, to which patterns of variation in fungal species composition was related, we used meso plot positions along axes of three DCA ordinations [performed by the program CANOCO, Version 2.2 (ter Braak 1987a); species with below-median frequency in the data sets were proportionally downweighted (Eilertsen et al. 1990); detrending by segments and otherwise standard options]:

(1) Ordination of the ME 200 data set, axes 1–4 (*DCAG 1*, *DCAG 2*, *DCAG 3*, *DCAG 4*). The ecocline interpretation of the first two axes (R. Økland & Eilertsen 1993, 1994) was: (i) *DCAG 1* was related to topography; running from herb-rich Norway spruce (*Picea abies*) forest on lower slopes and in valleys; via spruce forests on plane to concave slopes, dominated by *Vaccinium myrtillus*; and Scots pine (*Pinus sylvestris*) forests on convex slopes, dominated by ericaceous species; to lichen-rich pine forest on hill tops. Soil nutrient factors are considered important for the differentiation within spruce forest, and soil depth (probably related to risk of extreme drought) within pine forest. (ii) In both forest types, *DCAG 2* mostly affected bryophytes and lichens, and was related to fine-scale paludification and canopy closure. Median soil moisture decreased along the axis from interspaces between trees to below trees. *DCAG 3* and *DCAG 4* were only weakly related to measured environmental variables, and no ecocline interpretation exists for these axes. The set of four DCA ordination axes based upon the ME 200 data set is denoted {D}.

(2) Ordination of the MEV 200 data set, axis 1 (*DCAGV 1*). Axis 1 was the only ecologically interpretable axis in the separate ordination of vascular plants. This axis was strongly correlated with *DCAG 1* (Pearson's  $r = 0.969$ ,  $P \ll 0.0001$ ,  $n = 200$ ; R. Økland & Eilertsen 1993: Tab. 16), and the same ecocline interpretation was therefore valid for both.

(3) Ordination of the MEB 200 data set, axes 1–2 (*DCAGB 1*, *DCAGB 2*). These two axes were strongly correlated with the corresponding axes in the ordination of the entire ME 200 data set (axes 1:  $r = 0.844$ ,  $P \ll 0.0001$ ,  $n = 200$ ; axes 2:  $r = 0.811$ ,  $P \ll 0.0001$ ,  $n = 200$ ; R. Økland & Eilertsen 1993: Tab. 16), and the same ecocline interpretations were therefore valid.

For all axes, the average of the two meso plot scores was used as macro plot score.

### *Environmental variables*

A total of 33 primary and 3 supplementary environmental variables were recorded (Tab. 2). These can be divided into macro-scale variables, meso-scale variables, and meso-scale humus layer variables. Because the basic sampling unit for the vegetation study was 1 m<sup>2</sup>, the influence of trees on the understory was treated among environmental variables; recorded on the macro as well as the meso plot scale.

### Tree measurements

The exact positions of stems and canopy perimeters of all trees (> 2 m high) rooted within a 64 m<sup>2</sup> plot having the 16 m<sup>2</sup> macro plot in the centre, and all other trees with canopies covering the macro plot, were mapped. For each tree, the following measurements were made:

*Diameter at breast height* (1.3 m) was calculated from measurements of stem perimeter in mm.

*Height*, h, from normal stump height to top, in dm.

Tab. 2. Environmental variables; number, abbreviation, unit of measurement, range of scale, frequency distribution, and transformation applied.

No	Abbrev.	Variable	Unit	Range	Distribution	Transformation
01	MA Slo	Slope	E	0–90	uniform	no
02	MA Auf	Aspect unfavourability		0–200	uniform	no
03	MA Ter	Terrain form		0–5	uniform	no
04	MA Une	Surface unevenness		1–4	uniform	no
05	MA S d	Soil depth		1–4	uniform	no
06	MA Bas	Basal area		0–4	uniform	no
07	MA Can	Canopy cover		0–4	uniform	no
*1	MA Bad	Basal area of deciduous trees		0–4	uniform	no
*2	MA Dli	Deciduous litter cover		0–100	uniform	no
*3	MA Bry	Bryophyte cover		0–100	uniform	no
08	ME Slo	Slope	E	0–90	normal–uniform	no
09	ME Auf	Aspect unfavourability		0–200	uniform	no
10	ME Une	Unevenness		0–4	lognormal	ln (1+x)
11	ME Con	Convexity		–4 – +4	normal	no
12	ME Smi	Soil depth, minimum	cm	0–4	lognormal	ln (1+x)
13	ME Sme	Soil depth, median	cm	0–4	lognormal	ln (1+x)
14	ME Sma	Soil depth, maximum	cm	0–4	lognormal	ln (1+x)
15	ME Lit	Litter index		0–4	lognormal	ln (1+x)
16	ME Bas	Basal area		0–4	uniform	no
17	Mois	Soil moisture	vol. %	0–100	normal	no
18	LI	Loss on ignition	%	0–100	bimodal	no
19	pH <sub>H<sub>2</sub>O</sub>	pH, aqueous solution		0–14	normal	no
20	pH <sub>CaCl<sub>2</sub></sub>	pH, measured in CaCl <sub>2</sub>		0–14	normal	no
21	Ca	Exchangeable Ca	ppm/LI	0–4	lognormal	ln (1+x)
22	Mg	Exchangeable Mg	ppm/LI	0–4	lognormal	ln (1+x)
23	Na	Exchangeable Na	ppm/LI	0–4	lognormal	ln (1+x)
24	K	Exchangeable K	ppm/LI	0–4	lognormal	ln (1+x)
25	H	Exchangeable H	ppm/LI	0–4	± lognormal	ln (1+x)
26	N	Total N	weight %/LI	0–100	± lognormal	ln (1+x)
27	P–AL	Total P	ppm/LI	0–4	lognormal	ln (1+x)
28	Al	Exchangeable Al	ppm/LI	0–4	lognormal	ln (1+x)
29	Fe	Exchangeable Fe	ppm/LI	0–4	lognormal	ln (1+x)
30	Mn	Exchangeable Mn	ppm/LI	0–4	lognormal	ln (1+x)
31	Zn	Exchangeable Zn	ppm/LI	0–4	± lognormal	ln (1+x)
32	P	Exchangeable P	ppm/LI	0–4	lognormal	ln (1+x)
33	S	Exchangeable S	ppm/LI	0–4	± lognormal	ln (1+x)

*Height to the crown, h<sub>c</sub>*, the distance from normal stump height to the point on the stem where the lowest green branch whorl (i.e. the lowest green branch whorl which was separated from the rest of the crown by less than two dry branch whorls) emerged.

*Crown area*, a, the area of the crown projection, estimated from a map.

*Crown cover*, b, the projection of living phytomass on the crown area, visually estimated on a percentage scale.

Data for all trees are given in R. Økland & Eilertsen (1993: Appendix 2). Macro plot sketches showing positions of trees as well as special details, are given in R. Økland & Eilertsen (1993: Appendix 3).

#### Macro-scale variables

The following variables were measured to be representative for the macro plots.

(1) *Slope (MA Slo)* was measured by a compass (90° scale).

(2) *Aspect unfavourability (MA Auf)* was recalculated from aspect (measured by a clinometer on a 400° scale) on a linear 0–200 scale, following Dargie (1984), Parker (1988) and Heikkinen (1991): SSW (225°) was considered the most favourable aspect, and given the value 0; NNE (25°) was considered the least favourable aspect and given the value 200. [R. Økland & Eilertsen (1993) refer to this variable partly as Aspect favourability (MA Asf), partly as the Heat index (MA H i). The index does, however, measure aspect unfavourability (or *coldness*), and has therefore been renamed for clarity.]

(3) *Terrain shape (MA Ter)* was scored on a six point scale: 0 – valley bottom or concave terrace, 1 – concave valley side, 2 – plane valley side, 3 – convex valley side, 4 – ridge, 5 – hilltop.

(4) *Surface unevenness (MA Une)* was scored on a four point scale (cf. Rørå et al. 1988): 1 – relatively even (6 terrain roughnesses or less within the 64 m<sup>2</sup> plot enclosing the macro plot; a roughness defined to deviate more than 0.35 m from the surrounding terrain surface), 2 – uneven (7 or more roughnesses), 3 – boulderfield, 4 – coarse, with vertical walls, clefts and cliffs.

(5) *Soil depth (MA S d)* was scored on a four point scale, based on observations of the surface relief within the 64 m<sup>2</sup> plot (cf. Rørå et al. 1988): 1 – < 25 cm (extensive rock outcrops), 2 – 25–50 cm (localized rock outcrops), 3 – 50–100 cm (no rock outcrops, terrain uneven), 4 – > 100 cm (even surface, glaciofluvial material totally concealing unevennesses of the parent material).

(6) *Basal area (MA Bas)* was determined by a relascope (Fitje & Strand 1973). Basal area was measured at breast height from the lower left corner of each meso plot, using relascope factor 1. Values for the two meso plots were averaged to give MA Bas. Basal area is an expression of tree density and thus gives information of the light supply to the understory (also see 16 ME Bas).

(7) *Canopy cover (MA Can)*, c, was calculated as the sum-product of the canopy cover (a) and crown area (b) for all trees covering the macro plot (see R. Økland & Eilertsen 1993). The canopy cover index expresses the relative canopy cover in the macro plot, that also takes trees with overlapping crown projections into account.

Three supplementary variables of potential importance for fungi were recorded in all macro plots (\*2 and \*3 in July 1997):

(\*1) *Basal area of deciduous trees (MA Bad)*, derived from 6 MA Bas by only taking deciduous trees into account.

(\*2) *Deciduous litter cover (MA Dli)*, was recorded as the percentage of ground covered by deciduous litter.

(\*3) *Bryophyte cover (MA Bry)*, was recorded as the percentage of ground covered by bryophytes.

#### Meso-scale variables

The following variables were measured to be representative for the meso plots.

(8) *Slope (ME Slo)* was measured by a compass (see 1).



(9) *Aspect unfavourability (ME Auf)* was calculated from aspect measured by a clinometer (see 2).

(10-11) *Microtopographic indices*. For each meso plot, indices that express terrain shape at the within-plot scale, (10) *Unevenness (Me Une)* and (11) *Convexity (Me Con)*, were calculated from 16 measurements of the relative heights of the soil surface (see R. Økland & Eilertsen (1993) for details).

(12-14) *Soil depth*. Soil depth was measured as the maximum distance a steel rod could be driven into the soil. Measurements were made at eight fixed points 25 cm off the edges of the meso plot; two points along each edge. Three variables were derived: (12) *Soil depth, minimum (ME Smi)*, (13) *Soil depth, median (ME Sme)*, and (14) *Soil depth, maximum (ME Sma)*.

(15) *Litter index (ME Lit)*. The amount of litterfall was estimated from a plot's position relative to all trees covering the plot, and tree characteristics. Trees were considered to be of two kinds: (i) rooted within its crown perimeter ("concentric"); crown then assumed to be conical and gradually tapering, and (ii) rooted outside its crown perimeter ("excentric"); crown assumed to be cylindrical. The amount of litter falling on the plot was considered to be proportional with: (i) crown height ( $h - h_c$ ), (ii) the fraction of the plot lying within the crown perimeter ( $f$ ), (iii) crown cover ( $b$ ), and (iv; only relevant for concentric trees) the position of the proximal end of the plot (the end most close to the centre of the stem) relative to the crown perimeter ( $d_r/d$ , where  $d$  is the length of a line from the stem centre, through the centre of the plot till the crown perimeter, and  $d_r$  is the distance along this line from the proximal end of the plot to the crown perimeter). A relative litter index was calculated as follows:

$$l = \sum_i [(d_r/d_i) \cdot b_i \cdot f_i \cdot (h - h_{ci})] \quad \text{stem rooted within crown perimeter,}$$

$$l = \sum_i [b_i \cdot f_i \cdot (h_i - h_{ci})] \quad \text{stem not rooted within crown perimeter;}$$

sums taken over all trees  $i$  covering the plot. The litter index is considered a measure of canopy cover.

(16) *Basal area (ME Bas)* was determined by a relascope (Fitje & Strand 1973). Basal area was measured at breast height from the lower left corner of each meso plot using relascope factor 1 (also see 6 MA Bas).

#### Meso-scale humus-layer variables

The following variables were measured to be representative for the humus layer (or the upper 5 cm of the humus layer, if thicker).

(17) *Soil Moisture (Mois)*. Samples for determination of soil moisture were collected on 15–16 Oct 1988, after several days without precipitation. These samples probably represented normal (median) moisture conditions (R. Økland & Eilertsen 1993). Two cores, 5 cm high and 98 cm<sup>3</sup> each, were collected just outside the plot (at the lower side of sloping plots). The cores were transferred to plastic bags and kept frozen until analysis. Volumetric soil moisture was determined by weighting the fresh samples, drying the samples at 110 °C until constant weight, and reweighing.

Samples for chemical and physical analysis were taken on 15–16 Sept 1988. Several (5–10) small samples, 50–100 cm<sup>3</sup> each, were collected and mixed. They were kept frozen for several months. Before analysis at Landbrukets Analysesenter, Ås [procedures according to A.R. Selmer-Olsen (pers. comm.)], the samples were dried at 38 °C, ground and sifted with 2 mm mesh width.

Exchangeable cations were determined by adding 50 cm<sup>3</sup> 1 M NH<sub>4</sub>NO<sub>3</sub> solution to 10 g dried soil (cf. Stuanes et al. 1984). The solution was left overnight, filtered, and the sediment washed with 1 M NH<sub>4</sub>NO<sub>3</sub> until the volume of extract amounted to 250 cm<sup>3</sup>. Element concentrations [(21) *Ca*,

(22) *Mg*, (23) *Na*, (24) *K*, (28) *Al*, (29) *Fe*, (30) *Mn*, (31) *Zn*, (32) *P*, and (33) *S*, were determined in the extract by a Jarrell Ash ICAP 1100 instrument.

(18) *Loss on ignition (LI)* was determined by ashing a sample at 550 °C in a muffle furnace.

(19) *pH, aqueous solution ( $pH_{H_2O}$ )*. One part dried sample was mixed with 2.5 parts distilled water and left overnight. pH was measured the next day with an Orion SA 720 meter.

(20) *pH, measured in  $CaCl_2$  ( $pH_{CaCl_2}$ )*. One part dried sample was mixed with 2.5 parts 0.01 M  $CaCl_2$ , otherwise as (19).

(25) *Exchangeable H [ $H_3O^+$ ]*. 50 ml of the extract was titrated with 0.05 M NaOH until pH = 7.0. The volume of NaOH was corrected for the value used with pure extractant, to obtain the exchangeable acidity.

(26) *Total N*. Kjeldahl-N was determined by digestion of the dried sample with  $H_2SO_4$ , and use of a Se catalyst in a Tecator FIA system.

(27) *Total P (P-AL)*. One part dried sample was mixed with 20 parts of a solution 0.1 M with respect to ammoniumlactate and 0.4 M with respect to acetic acid. pH was adjusted to 3.75. P was determined in the extract by Jarrell Ash ICAP 1100.

#### Transformation of environmental variables

Units of measurement for the 36 environmental variables are shown in Tab. 2. All element concentrations (variables 21–33) were converted from ppm (mg/kg dry sample) to fraction of organic content by multiplication with 100/LI, as recommended by T. Økland (1988).

Frequency distributions for the 33 primary environmental variables over the 200 meso plots were inspected (Tab. 2). The transformation  $\ln(1+x)$  was applied to more or less lognormally or lograndomly distributed variables. For meso plot variables, the average of transformed values for the two meso plots was used as macro plot value.

The set of 33 transformed primary environmental variables is denoted {E}.

Values for environmental variables 1–33 are given in R. Økland & Eilertsen (1993: Appendix 4). Values for supplementary variables \*1–\*3 are available from the first author on request.

#### *Spatial variables*

In accordance with R. Økland & Eilertsen (1994), UTM grid co-ordinates (five digits for each co-ordinate, accuracy to nearest m) were used as the primary geographical explanatory variables. Co-ordinates for transect end-points were read from maps 1: 5,000, while relative positions of plots within the same transect were taken from field measurements. To allow for recognition of complex spatial trends, seven derived geographical variables were constructed by including all quadratic and cubic combinations of x and y, as suggested by Legendre (1990) and Borcard et al. (1992). The set of nine spatial explanatory variables is denoted {S}.

## CLASSIFICATION OF VEGETATION AND DIVISION INTO DATA SUBSETS

### *Classification*

Terricolous macrofungi are ecologically dependent on specific green plants, in different ways. Results so far show high concordance between separate classifications of flora and funga (see Arnolds 1992a).

Furthermore, fungal species seem to segregate along the ecological gradients used for classifying forest (also coniferous forests) into types, (e.g. Haas 1932, Krieglsteiner 1977, Østmoen 1979, Bendiksen 1981). We have therefore based this study on the same assumptions of vegetational and ecological continua as described by R. Økland & Bendiksen (1985) and R. Økland & Eilertsen (1993). Furthermore, we have used the gradient terminology of R. Økland & Eilertsen (1993: 25), and their classification of vegetation into site-types as a basis also for this study of fungi.

A direct gradient approach to classification is appropriate in a continuum (R. Økland & Bendiksen 1985, R. Økland 1989, 1990): a multidimensional gradient pattern is then turned into a reticulate, non-hierarchical classification by division of the gradient axes (Tuomikoski 1942, Webb 1954). Each combination of segments (positions) along the gradients is considered as one *site-type*, which is the basic unit of the classification system. A direct gradient approach to classification requires that the main ecoclines (Whittaker 1960) are known. This is the case for few local areas only (see R. Økland & Eilertsen 1993, T. Økland 1996). R. Økland & Eilertsen (1993) used available general knowledge as basis for their direct gradient approach to classification. They assumed that three local ecoclines were the most important: (1) variation along the topographic moisture complex-gradient (from bilberry-dominated spruce forests to lichen-rich pine forests), composed of several single environmental gradients, (2) variation along a complex-gradient in nutrient status, and (3) fine-scale variation in soil moisture (R. Økland & Bendiksen 1985, Bendiksen & Salvesen 1992). These three ecoclines were subsequently divided into site-types intended to be valid for the Solhomfjell area. Later on, R. Økland & Eilertsen (1993) confirmed the existence of these three important ecoclines by ordination of vegetation and subsequent environmental interpretation. As described in detail on p. 00, the main gradient in vegetation (DCAG 1) was related to topography on a broad scale, but with different important complex-gradients in the spruce and the pine forest: (1) a topography-soil depth complex-gradient in the pine forest, suggested by R. Økland & Eilertsen (1993) to be due to the response of plants to soil moisture deficiency, and (2) a complex-gradient in soil nutrient status in the spruce forest. Furthermore, the second ordination axis (DCAG 2) was interpreted as reflecting (3) fine-scale variation in (median) moisture status, as originally supposed. This confirmation of the ecocline structure implies that the site-type classification represents a valid direct gradient approach to classification of vegetation and the environment in the area (see Fig. 3).

In accordance with R. Økland & Eilertsen (1993), the following criteria were used for separation of site-types:

(1) *The topographic moisture gradient* was divided into seven categories, termed *series*. These series intentionally corresponded to the four series distinguished by R. Økland & Bendiksen (1985), considered to be applicable to boreal forest vegetation over S Fennoscandia, and transitions between them: series 1 corresponded to the xeric series of R. Økland & Bendiksen (1985), series 3 to the subxeric series, series 5 to the submesic series, and series 7 to the mesic series. Corresponding types in other classifications of Fennoscandian forest vegetation are given by R. Økland & Eilertsen (1993). Descriptions of vegetation (including vegetation tables) and ecology for each site-type are provided by R. Økland & Eilertsen (1993).

(2) No division of *the complex-gradient in nutrient status* was suggested by R. Økland & Bendiksen (1985), while up to four categories were recognized in the phytosociological classification by Kielland-Lund (1981) and the system of Fremstad (1997). The gradient was divided into four categories: (i) poor forests, negatively characterized, (ii) slightly rich forests, for instance including the 'low fern types', (iii) rich forests, including the poor forms of 'low herb types', and (iv) very rich forests, including the rich forms of 'low herb and tall fern' types.

(3) *The complex-gradient in fine-scale moisture* was divided into two categories; 1 (dry) and 2 (moist).

Every unique combination of positions along the three ecoclines was considered a site-type,

denoted by a three-digit code (see Fig. 3). The first digit indicated the series. In series 5, variation along the nutrient complex-gradient was indicated by a dot followed by a second digit. Variation along this gradient was not found in other series. Variation along the fine-scale moisture gradient was indicated by a hyphen followed by a digit. Examples are 3-2, the moist subxeric site-type; 4-1, the dry subxeric-submesic transitional site-type; and 5.2-2, the moist, slightly rich submesic site-type.

All meso plots were classified to site-type during field work in 1988.

#### *Division into data subsets*

The 99 macro plots were divided into two subsets, Subset A (spruce forest) with 59 plots and Subset B (pine forest) with 40 plots, on the basis of the average position of meso plot scores along the first axis in the ordination of plant species in the ME 200 data set (see p. 00). This corresponds to the division into Subsets A and B in R. Økland & Eilertsen (1993).

## GRADIENT ANALYSIS OF FUNGI

All univariate statistical analyses were made by means of STATGRAPHICS, Version 5.0 (Anonymous 1990).

#### *Ordination*

The nature of gradients in fungal species composition

Applied to a matrix of species abundances recorded in sample plots, ordination methods generally extract the main gradients of co-ordinated variation in species composition, coenoclines in the data (e.g. R. Økland 1990). Coenoclines extracted from data sets with observations of fruitbodies represent real structure gradients in the occurrence of fruitbodies of different fungal species while not necessarily gradients in species (mycelia) composition. Fruitbody coenoclines will be gradients in fungal species composition not only if fruitbody and mycelial distributions of all species along all gradients coincide, but also if species' amplitudes (as sterile mycelia) along major complex gradients extend far beyond the limits for fruitbody production, and there are systematic differences between species in abundance distributions along the gradient, e.g. because of differences in survival of mycelia along the gradient. In the latter case, the gradient length of the fruitbody coenoclines will, however, be much higher than of the corresponding species coenoclines (Eilertsen et al. 1990).

6	5.3				
	5.2-1 5.2-2				
	5.1-1 5.1-2	4-1 4-2	3-1 3-2	2-1 2-2	1-1 1-2

Fig. 3. The classification system adopted in the present study; site-type codes are shown within boxes. The horizontal sequence of types reflects position along the topographic moisture gradient, the vertical sequence reflects position along the complex-gradient in nutrient status. Site-types along the complex-gradient in fine-scale moisture are boxed together; the non-paludified type above, the paludified type below. Shaded boxes indicate site-type combinations not met with in the investigation area. From R. Økland & Eilertsen (1993), redrawn.

During the last decade, new methods for identification of species of below-ground ectomycorrhizal fungal communities have been developed (e.g. Dahlberg 2001, Horton & Bruns 2001). These methods, which comprise morphological descriptions and high-resolution molecular tools for identification of individual mycorrhizae, provide a broader perspective on the nature of gradients in fungal species composition. High abundance in mycorrhizae have been demonstrated for species which never or rarely produce fruitbodies (e.g. Dahlberg & Stenström 1991, Taylor et al. 2000, Horton & Bruns 2001). Furthermore, some typical Agaricales species may be well represented below-ground but rarely occur or lack above-ground in the fruiting period (Mehmann et al. 1995, Gardes & Bruns 1996), but see Laiho (1970) and Agerer (1990). Also the opposite relation occurs; Gardes & Bruns (1996) show that some commonly fruiting species are rare below ground. It has, however, been commented that the strength of correlations between presence above and below ground may be strongly influenced by limitations of methods used for identification of species in the mycorrhiza (Horton & Bruns 2001). As stressed by Dahlberg et al (1997) and Jonsson et al. (1999), below-ground studies are usually based upon sampling of very small areas; thus only a small fraction of all mycorrhizae present within a given area can be analysed. For many taxa, presence below-ground, but absence of fruiting for several years probably occurs because fruiting may require rare combinations of climatical events (cf. Agerer 1985, Ohenoja 1993). Relevant ecological studies on saprotrophs in which abundance above and below ground are compared, are not available. Thus, no methods are currently available that enable complete enumeration of the full fungal species composition within representative areas (like our plots). Until further knowledge has accumulated, gradients identified on the basis of records of fruitbody abundances have to be interpreted with care. With these reservations, we will however for convenience refer to the coenoclines extracted in the present study as gradients in fungal species composition.

#### Ordination methods

Two ordination methods were applied *in parallel* to extract the main gradients in fungal species composition. Ordination axes may be derived (1) by fitting the abundance data to a statistical model or (2) by the geometric process of finding the low-dimensional plot configuration which distorts the floristic similarities between plots as little as possible (cf. R. Økland 1990). Following the recommendation of R. Økland (1990, 1996) the method of each kind now considered the most appropriate was used: DCA (detrended correspondence analysis) and LNMDS (local non-metric multidimensional scaling) (cf. Kenkel & Orłóci 1986, Minchin 1987, Kent & Ballard 1988, R. Økland 1990, T. Økland 1996, Rydgren 1997). Congruent ordinations by the two methods were considered an indication that the main compositional gradients had been successfully recovered.

Plots with fewer than five species are likely to be inappropriately handled by ordination methods due to low representativity (R. Økland 1990). The *MAF 97* data set, derived from *MAF 99* by removal of macro plots 79 and 91 with fewer than 2 species, was therefore used for DCA and LNMDS ordinations. Furthermore, plots Nos 38 and 60 appeared as strong outliers in the DCA ordination of *MAF 97* and were removed as well. The new data set, *MAF 95*, was subjected to new ordinations. Separate DCA ordinations were also performed for two subsets of *MAF 95*; *Subset MAF 58A* with 58 macro plots corresponding to Subset A (spruce forest), and *Subset MAF 37B* with 37 plots corresponding to Subset B (pine forest).

*DCA* (Hill 1979, Hill & Gauch 1980) of frequency in subplots data was performed by means of CANOCO, Version 3.12 (ter Braak 1987b, 1990), using the following options: proportional downweighting of species with frequency in a data set lower than the median frequency (Eilertsen & Pedersen 1989, Eilertsen et al. 1990), detrending-by-segments (as recommended by Knox (1989), R. Økland (1990) and Eilertsen (1991)), and nonlinear rescaling with standard choice of parameters. In

accordance with recommendations by R. Økland (1999), eigenvalues of DCA ordination axes were reported directly as relative measures of the variation in species composition extracted on the axes, rather than as ‘fractions of variation explained’ [obtained by division with the total inertia; the sum of eigenvalues for all axes that could be extracted (cf. Greenacre 1984, Borcard et al. 1992)]. All DCA ordinations were completed before the new, debugged version of Hill’s original algorithm (Oksanen & Minchin 1997) was implemented in the CANOCO package. Essential identity of ordination results as obtained from CANOCO, Version 3.12 and the debugged CANOCO, Version entered in the CANOCO package. We made sure that the ordination results were unaffected by bugs, by comparing the ordination axes, one by one, with axes obtained for the same data sets by the debugged CANOCO, Version 4.0 (ter Braak & Šmilauer 1998). In all cases, Kendall’s nonparametric (rank) correlation coefficients (Kendall 1938)  $|\tau| > 0.98$  were found.

*LNMDs* (Kruskal 1964a, 1964b, Minchin 1987) of frequency in subplots data was performed by the KYST program (Kruskal et al. 1973) as modified and implemented into the DECODA program package, Version 2.01 (Minchin 1986, 1990). The following options were used: dimensionality = 2, dissimilarity measure = percentage dissimilarity (Bray-Curtis, or Czekanowski measure), standardized by division with species maxima (as recommended by Faith et al. 1987), number of random starting configurations = 100–500, maximum number of iterations = 1000, stress reduction ratio for stopping the iteration procedure (stress is a measure of the correspondence between floristic dissimilarities between plots and inter-plot distances in the ordination diagram) = 0.99999. The solution with the lowest stress was used. The number of starting configurations was initially set to 100, but increased to 500 in the LNMDs ordination of the MAF 97 data set to obtain the minimum stress solution from at least two different starting configurations. The LNMDs axes were linearly rescaled in S.D. units by the nonlinear rescaling procedure of the DECORANA and CANOCO programs (cf. Hill 1979, ter Braak 1987a), by use of rescaled hybrid canonical correspondence analysis (rhCCA; cf. ter Braak 1987b, 1987c), with the original LNMDs scores (one axis in turn) as constraining variables (R. Økland 1990, Eilertsen et al. 1990).

#### Comparison of ordinations

Axes of different ordinations were subjected to pair-wise comparison using Kendall’s nonparametric rank coefficient  $\tau$ . Kendall’s  $\tau$  was preferred to Pearson’s  $r$  (cf. Sokal & Rohlf 1995) because it is insensitive to asymmetric frequency distributions and/or inhomogeneous variance distributions. Absolute values of Pearson’s  $r$ , which was used by R. Økland & Eilertsen (1993), are consistently higher than the absolute values of Kendall’s  $\tau$ , and numerical values for the two correlation coefficients are therefore not directly comparable.

#### Interpretation of ordination results

Kendall’s  $\tau$  was calculated between ordination axes and all explanatory variables (36 environmental variables and 7 vegetational variables). Although the main emphasis was put on ordinations of the MAF 95 data set, all ordinations were interpreted in order to enable methodological comparisons.

Relationships between environmental variables and between environmental variables and vegetational variables were thoroughly studied by R. Økland & Eilertsen (1993: 35-44).

#### Variation in species abundance and other properties of the funga along DCA axes

By relating the distribution of a species’ abundance to environmentally interpreted ordination diagrams, valuable information of the species’ autecology can be obtained (cf. T. Økland 1996). Subplot frequencies for all species occurring in more than 5% of the macro plots were plotted onto macro

plot positions in the DCA ordination diagrams for the MAF 95 data set. Furthermore, DCA axes 1–3 were divided into intervals for which mean frequency and mean subplot frequency was calculated for each species. For all species occurring in more than 5% of the macro plots in the MAF 95 data set, *ranges* along DCA axes 1–3 were also found. For species extending beyond axis ends, range was estimated by assuming symmetric distribution along the axis around the species' optimum (as given by the species score).

### *Constrained ordination*

All analyses were based upon the CCA concept (Canonical Correspondance Analysis; ter Braak 1986, 1987a), performed by means of CANOCO, Version 3.12 (ter Braak 1987b, 1990). Frequency in subplots data for fungi in the MAF 95 data set were used, with proportional downweighting of species with frequency lower than the median frequency (Eilertsen et al. 1990).

### Variation explained by single explanatory variables

The variation in species abundances possible to explain by single primary environmental variables was assessed by hybrid CCA, using each explanatory variable in turn as the only constraining variable. Variation is expressed in relative 'inertia units' (IU) as provided by the eigenvalue of the first and only constrained CCA axis. The total inertia of the species-plot matrix was not used for scaling of the explained variation because it is inflated by lack-of-fit-of-data-to-model variation (R. Økland 1999). The hypothesis of non-significant deviation of variation explained by a variable from that explained by a random variable, was tested by the Monte Carlo test in CANOCO (ter Braak 1990), using 199 unrestricted permutations of the constraining variable.

### Variation partitioning

The relative importance of the three sets of explanatory variables (vegetational gradients {V}, environmental variables {E}, and spatial variables {S}) for variation in fungal composition was assessed by variation partitioning (Borcard et al. 1992, R. Økland & Eilertsen 1994, R. Økland 1999), generalized from two to three sets of explanatory variables (see R. Økland in press). With two sets of explanatory variables (termed {T} and {U}, respectively), the variation in a data matrix can be partitioned by the following procedure: Denote the variation explained by {T} and {U} T and U, respectively. T is obtained by CCA after forward selection (here: variables with contribution to variation explained significant at the  $P = 0.01$  level were retained) of variables from the set {T} as the sum of all constrained eigenvalues. U is found by a similar procedure. Eliminating variables that do not contribute significantly to explanation of the variation in species abundances gives more realistic estimates of variation explained (Borcard et al. 1992). Furthermore, the variation explained by {T} not shared with {U},  $T|U$ , is found by partial CCA (Borcard et al. 1992), using the significant variables in {U} as covariables and the significant variables in {T} as constraining variables. The remaining components of the variation may then be calculated as follows (cf. R. Økland & Eilertsen 1994: Fig. 1):

$$T \cap U \text{ (shared variation)} = T - T|U$$

$$U|T \text{ (variation explained by \{U\}, not shared by \{T\})} = U - T \cap U$$

$$T \cup U = TVE \text{ (the total variation explained by the variables; the variation explained by \{T, U\})} = T + U - T \cap U$$

Due to the additivity of variations explained, i.e. that the total variation explained by {T, U}, T∪U, can be found directly in a CCA with all significant variables in {T} and {U} as constraining variables (R. Økland & Eilertsen 1994), the process is easily generalized to three sets of explanatory variables by applying (partial) CCA to different combinations of sets of significant explanatory variables. The Monte Carlo test (in CANOCO; see ter Braak 1990) was used to assess the significance of each variable upon inclusion in the regression model. Only variables significant at the P = 0.01 level were included.

Relative fractions of variation explained were obtained as percentages of the total variation explained by all three sets of variables (R. Økland 1999).

## NOMENCLATURE AND TAXONOMIC NOTES

A list of fungal species with author names is given in Appendix 1. The nomenclature of the orders Agaricales, Russulales and Boletales follows Hansen & Knudsen (1992), with some exceptions and additions: *Armillaria mellea* (Vahl : Fr.) P. Kumm. is used in a collective sense; *Collybia asema* (Fr. : Fr.) P. Kumm. is considered as a species on its own, distinct from *C. butyracea* (Bull. : Fr.) P. Kumm.; species of *Cortinarius* (Pers.) Gray treated by Brandrud et al. (1990-97) follow the latter; *Entoloma rhodopolium* (Fr.) P. Kumm. is used in the sense of Noordeloos (1989); *Galerina borealis* A.H. Sm. & Singer in accordance with Smith & Singer (1964); *Galerina calyptrata* P.D. Orton is included in *G. hypnorum* (Schrank : Fr.) Kühner s. lat.; *Gymnopilus sapineus* (Fr. : Fr.) Maire is used in the sense of Høiland (1990); *Inocybe subcarpta* Kühner & Boursier is used for the better known name *I. boltonii* R. Heim, here also including *I. soluta* Velen. (= *I. brevispora* Huijsman), cf. Vauras (1992); *Leccinum palustre* M. Korhonen follows Korhonen (1995); *Mycena alcalina* (Fr. : Fr.) P. Kumm. coll. is used as a collective name for *M. stipata* Maas Geest. & Schwöbel and *M. silvaenigrae* Maas Geest. & Schwöbel; *Mycena cineroides* Hintikka is considered as a species of its own, distinct from *M. cinerella* P. Karst.; *M. viscosa* Maire is treated as a distinct species; *Psathyrella* aff. *lutensis* refers to an undetermined species in the subsection *Lutenses* Kits van Wav., following Kits van Waveren (1985).

*Camarophyllus* (Fr.) P. Kumm. is considered as part of *Hygrocybe* P. Kumm. as in Boertmann (1995), whereas *Xerocomus* Quéf. is kept as a separate genus.

*Galerina* sp. 1 was identified in the field on its strongly orange colour. It does, however, resemble *G. hypnorum* in microscopic and other macroscopic characters and may well turn out to be only a young stage of that species. The other unidentified collections of Agaricales/Boletales, referred to as 'sp.', have only been represented in the material by single fruitbodies or fruitbodies in bad condition. Most probably, these do not belong to any species recognised in the material.

Aphylophorales s.l., heterobasidiomycetes and gasteromycetes follow Hansen & Knudsen (1997), and ascomycetes follow Hansen & Knudsen (2000).

The nomenclature of vascular plants follows Lid & Lid (1994), and bryophytes follow Frisvoll et al. (1995).



## RESULTS

### CLASSIFICATION

Thirty-seven of the macro plots were inhomogeneous with respect to site-type, even when the paludification (median soil moisture) gradient (21 macro plots were inhomogeneous with respect to this gradient) was not taken into account. The meso plots in these inhomogeneous plots mostly belonged to neighbouring series along the sequence from 6 to 1, in some cases to neighbouring site-types in series 5. The classification of macro and meso plots to site-types is given in Appendix 2. Subplot frequencies for each species in each plot and species frequencies in the MAF 99 data set are given in Appendices 3–4.

### FUNGAL SPECIES DENSITY

Of the totally 235 species found in the 99 macro plots, 122 (52%) were supposed to be mycorrhizal. Tab. 3 shows the fungal species density (average number of species per macro plot in each site-type), totally and separately for mycorrhizal species. Trends were obscured by the low number of macro plots in many site-types, but more reliable figures were obtained by lumping plots near gradient endpoints (bottom rows in Tab. 3). The total number of species increased from c. 6 at the xeric end of the topographic moisture gradient (series 1) via 23 in the poor submesic series, to more than 40 in macro plots influenced by flushing (Tab. 3). Only small differences were found between the submesic site-types along the nutrient gradient. The sparse material gives no indication of differences between non-paludified and paludified plots.

The percentage of mycorrhizal species did not vary in a consistent manner between site-types, except for a distinct increase from the subxeric to the xeric site-type (Tab. 3).

### ORDINATION

#### *Characteristics of, and comparison between, ordinations of fungi*

Characteristics of the ordinations are summarized in Tab. 4.

#### Ordinations of the MAF 97 data set

*DCA.* The gradient length of the first DCA axis was 4.86 S.D. units, while the lengths of the subsequent axes were 3.21, 1.95 and 2.23 S.D. units (Tab. 4). The lowest score along DCA 1 was obtained by macro plot 53 (classified to site-type 6), while plot 60 (one meso plot classified to the xeric and one classified to the xeric-subxeric transitional series) occurred at the opposite end of this axis (Figs

Tab. 3. Mean species density (number of species, total and mycorrhizal, per 16-m<sup>2</sup> macro plot), in each site-type. Data for corresponding non-paludified and paludified types are summarised. Macro plots inhomogeneous with respect to other ecoclines (the topographic moisture and nutrient gradients) are left out. The two bottom rows summarise species numbers for macro plots with two meso plots classified to site-types 1 and/or 2, and macro plots with at least one meso plot classified as slightly flushed (site-type 6), respectively.

Site-type		Number of plots			No. of species	No. of mycorrhizal species	% of mycorrhizal species
		Total	Non-pal.	Pal.			
Code	Name						
1	Xeric	3	2	0	6.3	3.0	47.6
2	Xeric-subxeric transition	2	1	0	12.5	5.5	44.0
3	Subxeric	8	5	1	11.3	3.3	29.2
4	Subxeric-submesic transition	11	6	1	16.4	4.1	25.0
5-1	Poor submesic	22	17	2	23.0	7.3	31.7
5-2	Slightly rich submesic	10	7	3	26.2	10.1	38.5
5-3	Rich submesic	5	5	0	27.4	7.4	27.0
6	Rich slightly flushed	1	–	–	40.0	9.0	22.5
1+2	Widely circumscribed xeric, including xeric-subxeric transition	11	5	0	8.0	3.4	42.5
5+6	Rich, with elements of flush	4	–	–	41.0	12.0	29.3

4–5). The site-types segregated along the axis, making up a sequence from 6, via 5.3 (mainly obtaining scores < 1.0 along this axis), 5.2, 5.1, 4, 3 and 2 to 1. The transition between plots from spruce and pine forest (site-type 4) occurred at *c.* 2.4 S.D. units along this axis. With the exception of plot 60, which occupied an outlying position, the plots made up one continuous cluster, somewhat less dense towards the low-score end of the axis.

Macro plot 38 (representing the slightly rich paludified submesic site-type) occupied an isolated position at the low-score end of DCA 2 (Fig. 4). At the other end of this axis, plots 72 and 73 were found (both representing the poor non-paludified submesic site-type). The spread of plot scores along DCA 2 decreased with increasing DCA-axis 1 score; the two-dimensional point configuration having a characteristic tongue- or trumpet-like shape. The strong concentration of plots near the middle of DCA 2 was reflected in the relative length of the core; small relative to the other axes (Tab. 4).

The end-points with respect to DCA axis 3 were made up by plots 16, 17 and 44 (low-score end), and 21, 95 and 97 (high-score end), respectively. The distribution of plots along DCA 3 was relatively even (Fig. 5), as reflected in the high value for core length (Tab. 4).

*LNMSD*. The gradient lengths of the LNMSD axes were 4.36 and 3.23 S.D. units, respectively. The macro plots near the ends of DCA-axis 1 also occupied end positions along LNMSD 1 (Fig. 6). The plots were evenly distributed along the axis.

Macro plots 78 and 26 (representing xeric and subxeric, partly paludified site-types), obtained low scores along LNMSD 2. High scores were obtained by plots 63, 49 and 93. Macro plots were relatively evenly distributed also along LNMSD 2 (Fig. 6).

*Comparison between DCA and LNMSD ordinations*. Rank-ordered plot positions along the first axes of the two ordinations were virtually identical, as evident from the strong correlation in

Tab. 5. The second LNMDS axis was correlated with DCA 2 (but less strongly), as well as with DCA 4.

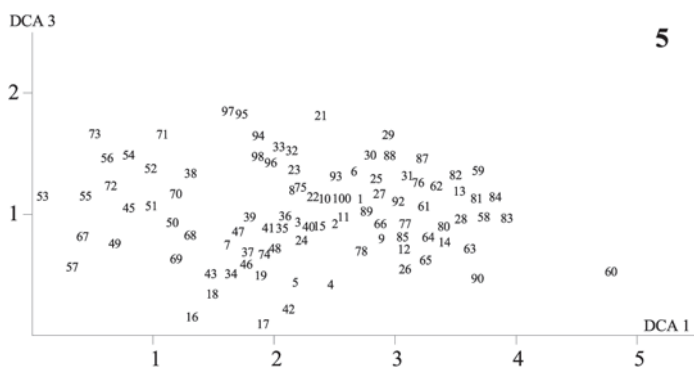
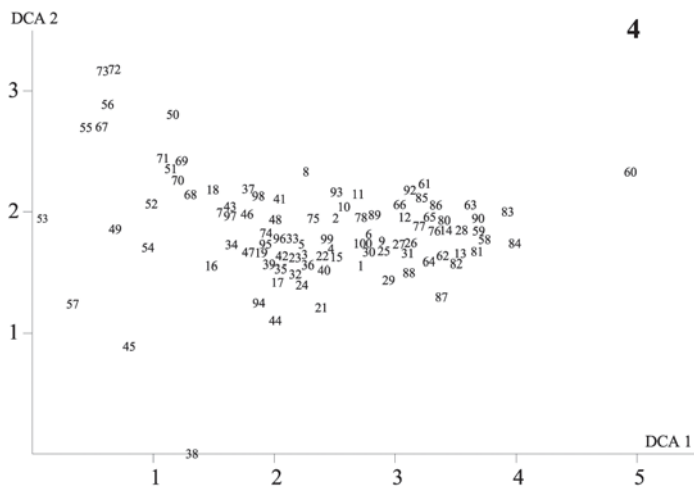
#### Ordinations of the MAF 95 data set

*DCA*. The gradient length of the first DCA axis was 3.81 S.D. units, while the lengths of the subsequent axes were 2.23, 2.24 and 3.15 S.D. units (Tab. 4). DCA 1 had an eigenvalue of 0.471, slightly above

Tab. 4. Summary of ordination results and characteristics of ordination axes. DCA97 and DCA95 – DCA ordinations of the MAF 97 and MAF 95 data sets, respectively; MDS97 and MDS95 – LNMDS ordinations of the same data sets. Total inertia is an expression of the total variation of a data set. For LNMDS, the eigenvalue of first hCCA axis (the hCCA run with the LNMDS scores along one axis as the only constraining variable) is listed. The variation explained relative to a random variable refers to the product  $n \cdot (\text{variation explained})$ , because  $1/n$  is the expected variation explained by a random variable, when the minimum of the number of species and the number of plots is  $n$ . The gradient length is given in S.D. units; of LNMDS axes obtained by hCCA as above. The relative length of core of a gradient is the smallest fraction of the total gradient length that contains at least 90% of the sample plots.

Ordination	Total inertia	Axis	Eigenvalue	Var. expl. relative to random variable	Gradient length	Relative length of core of gradient
DCA97	6.240	1	.484	7.53	4.856	.625
		2	.241	3.74	3.211	.384
		3	.166	2.53	1.946	.631
		4	.137	2.14	2.225	.577
MDS97	6.240	1	.452	7.02	4.356	.675
		2	.269*	4.09	3.232	.611
DCA95	5.186	1	.471	8.63	3.805	.761
		2	.182	3.33	2.232	.609
		3	.151	2.76	2.235	.604
		4	.127	2.33	3.154	.314
MDS95	5.186	1	.442	8.09	3.996	.688
		2	.231*	4.23	3.111	.583
DCA58A	3.866	1	.410	6.15	2.782	.820
		2	.183	2.74	1.973	.741
		3	.145	2.18	2.010	.746
		4	.122	1.83	1.922	.572
DCA37B	3.040	1	.294	3.58	2.819	.585
		2	.216	2.70	2.319	.578
		3	.170	2.07	2.656	.327
		4	.115	1.40	1.956	.612

\* LNMDS axes 1 and 2 are not orthogonal; the cumulative variation explained by the two LNMDS axes are 0.684 in MDS97 and 0.596 in MDS95.



Figs 4–5. DCA ordination of the MAF 97 data set. Axes scaled in S.D. units. Macro plot numbers plotted onto plot positions. Fig. 4. Axes 1 (horizontal) and 2. Fig. 5. Axes 1 (horizontal) and 3.

that of the first DCA axis in the ordination of the MAF 97 data set. The lowest score along DCA 1 was obtained by macro plot 53 (like DCA97 1), while the species-poor plot 84 (one meso plot classified to the xeric and one classified to the xeric-subxeric transitional series) occurred at the opposite end of this axis (Fig. 7). Macro plots classified to site-types 5.3 and 6 mainly obtained scores  $< 1.0$  S.D. units along this axis (Fig. 9). The plots made up one continuous cluster, somewhat less dense towards the low-score end of the axis and with slightly reduced density also at *c.* 2.4 S.D. units along the axis, i.e. at the transition between spruce and pine forest, between Subsets A and B. Only one plot from Subset B obtained a DCA 1 score  $< 2.40$  (No. 93) while only two Subset A plots obtained DCA 1 scores  $> 2.40$  S.D. (Nos 1 and 6).

Several macro plots (16, 17, 44, 45 and 57) obtained low scores along DCA 2, while the high-score end of this axis was occupied by plots 72, 73 and 93 (Fig. 7). Plot scores were relatively evenly distributed along DCA 2, and the range of plot scores along DCA 2 decreased but weakly with increasing DCA-axis 1 score; thus the two-dimensional point configuration in Fig. 7 lacked the tongue-like shape of Fig. 4. No strong concentration of plots occurred near the middle of DCA 2 (cf. the relative length of the core in Tab. 4).

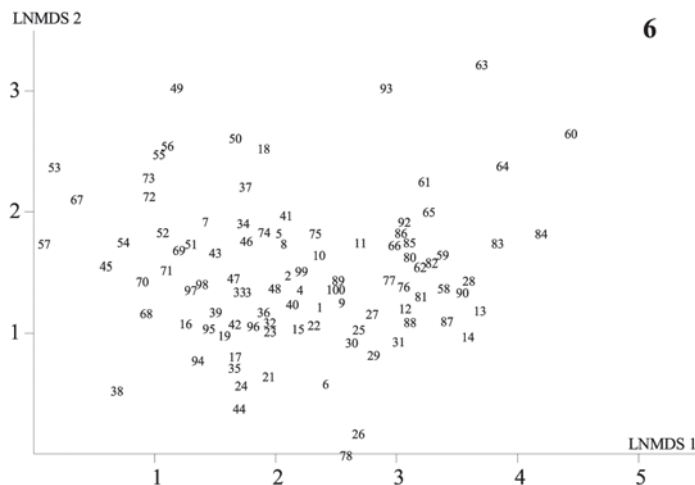


Fig. 6. Two-dimensional LNMDS ordination of the MAF 97 data set, axes 1 (horizontal) and 2. Axes rescaled in S.D. units by means of rhCCA. Macro plot numbers plotted onto plot positions.

The end-points with respect to DCA axis 3 were made up by plots 24 (low-score end) and 41 (high-score end), respectively (Figs 8, 10). The distribution of plots along DCA 3 was relatively even (Fig. 8), as reflected in the high value for core length (Tab. 4).

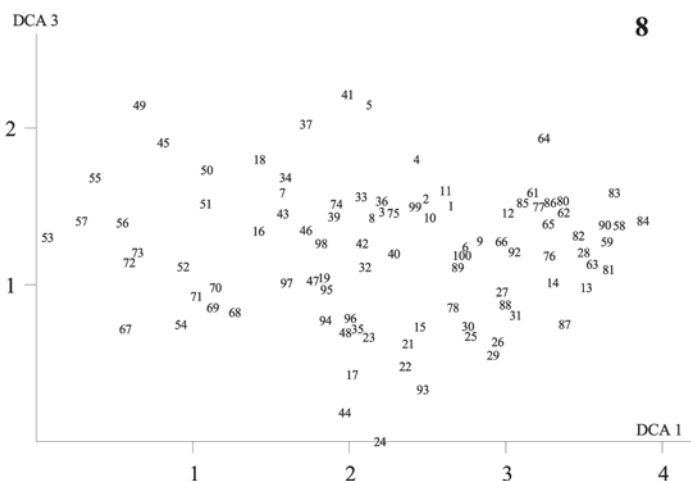
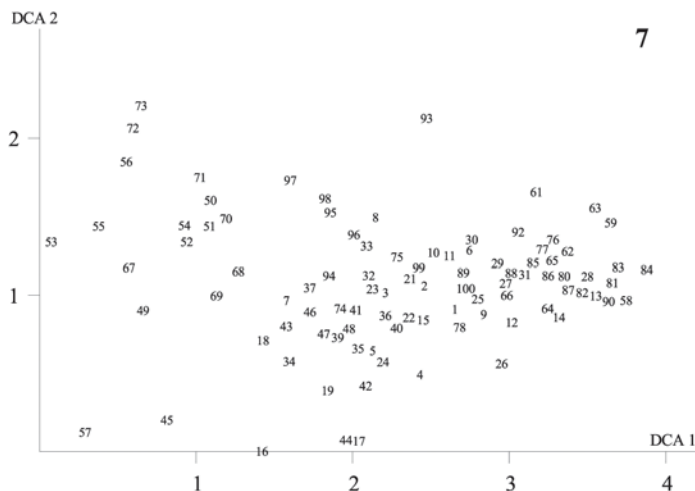
*LNMSD.* The gradient lengths of the LNMSD axes were 4.00 and 3.11 S.D. units, respectively. The macro plots near the ends of DCA-axis 1 also occupied end positions along LNMSD 1 (Fig. 11). The plots were evenly distributed along the axis.

Macro plots 78 and 26 obtained low scores along LNMSD 2, while the highest score was obtained by plot 63. The distribution of plots along LNMSD 2 was relatively even (Fig. 11).

*Comparison between DCA and LNMSD ordinations.* Like the ordinations of the MAF 97 data set, the corresponding first axes in the ordination of the MAF 95 data set were also virtually identical (Tab. 6). The second LNMSD axis was correlated with DCA 3 (but less strongly).

#### Comparison between the ordinations of the MAF 97 and MAF 95 data sets

The first axes of all four ordinations (two data sets, two methods) were virtually identical ( $\tau > 0.85$ , see Tab. 7) and clearly represented the main gradient in fungal species composition in forests in the study area. The second axes of the two LNMSD ordinations were also virtually identical ( $\tau = 0.870$ ). However, the second LNMSD axes showed only moderate correspondence with the second axes of the DCA ordinations ( $\tau < 0.6$ ; Tab. 7), and the same applied to the correspondence between second and subsequent DCA axes in the two ordinations. The second LNMSD axes were significantly correlated with both axes 2 and 4 of the DCA ordination of the MAF 97 data set, while being most strongly correlated with axis 3 of the DCA ordination of the MAF 95 data set (Tabs 5–7). The variation along two of the DCA axes (the second and third) in the ordination of the MAF 97 data set was expressed along DCA 2 in the MAF 95 ordination. Furthermore, DCA 4 of MAF 97 was strongly correlated with DCA 3 of MAF 95, and these axes were also correlated with LNMSD 2. Removal of the outlying plot 38 from the MAF 97 data set thus seemed to stabilize the gradient structure extractable by DCA as some of the variation along the outlier-influenced DCA97 2 was removed while some (the part correlated with LNMSD 2) seemed to be retained by the third DCA95 axis (cf. Tab. 7).



Figs 7–8. DCA ordination of the MAF 95 data set. Axes scaled in S.D. units. Macro plot numbers plotted onto plot positions. Fig. 7. Axes 1 (horizontal) and 2. Fig. 8. Axes 1 (horizontal) and 3.

The ordinations thus lent support to the presence of three gradients in fungal species composition in the area: (1) the main gradient in all ordinations, (2) the gradient expressed by LNMSD 2, DCA97 4 (and partly also DCA97 2) and DCA95 3, and (3) the gradient expressed by DCA95 2 and DCA97 3 (and partly also DCA97 2). Because this gradient structure was most closely reflected by the DCA95 ordination, we focused on this ordination in the subsequent ecological interpretation.

#### DCA ordinations of data subsets

*The MAF 58A subset.* The gradient length of the first axis in the separate ordination of macro plots from the spruce forest was 2.78 S.D. units, corresponding to an eigenvalue of 0.410. The sequence of plots along DCA95 1 was almost perfectly recovered; plot 53 obtained the lowest score and plot 6 the highest (Figs 12, 14). Also the sequences of plots along DCA axes 2-3 resembled the sequences

along corresponding DCA95 axes ( $\tau > 0.6$ ; Tab. 8). The ends of axis 2 were occupied by the same plots as in the ordination of the MAF 95 data set, while plot 21 obtained the lowest and plot 5 the highest score along axis 3 (Figs 13, 15). The fourth axes in the two ordinations were also significantly correlated (Tab. 8). The distribution of plots along the first three axes in this ordination was relatively even; this ordination had the highest values for core length encountered for the three first axes in any ordination (see Tab. 4).

*The MAF 37B subset.* The first axis in the separate ordination of pine-forest plots had a length of 2.82 S.D. units and an eigenvalue of 0.294. It was significantly correlated with the first axis of the DCA95 ordination. Macro-plot 78 (at the transition between the xeric and subxeric series) occupied an isolated position at the low-score end of DCA 1, separated from all other plots by more than 0.6 S.D. units. The xeric plot 63 took a slightly isolated position at the opposite end, where plot 83 (both 63 and 83 close to the xeric-subxeric transition) formed the end of the main point cloud. The bulk of plots obtained DCA 1 scores in the interval 0.6–2.0 (Figs 16, 18). Also DCA axis 2 was influenced by moderate outliers; plot 26 at the low-score end and plots 11 and 61 at the high-score end (Fig. 16). The second DCA37B axis was correlated with the second axis of the DCA95 ordination ( $\tau = 0.384$ ,

Tab. 5. Kendall's rank correlation coefficients  $\tau$  between macro-plot scores in the ordinations of the MAF 97 data set, with significance probabilities (P). Correlations significant at level  $P < 0.0001$  in bold face. n.s. – significance probability less than 0.1.

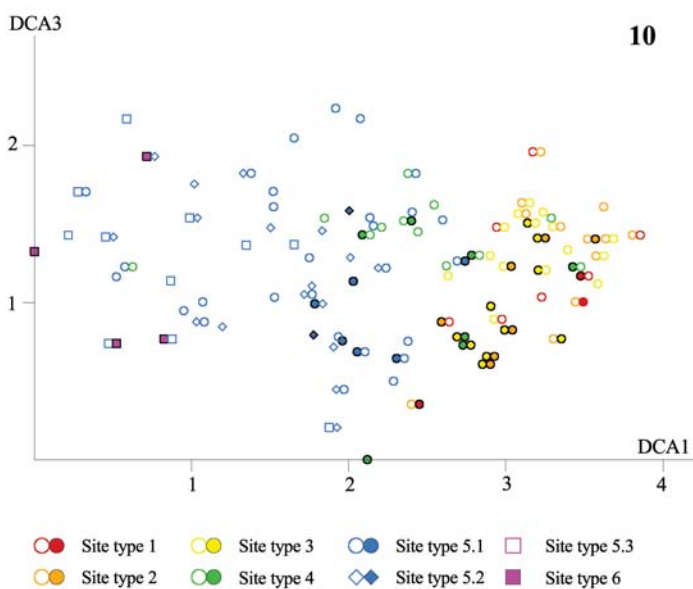
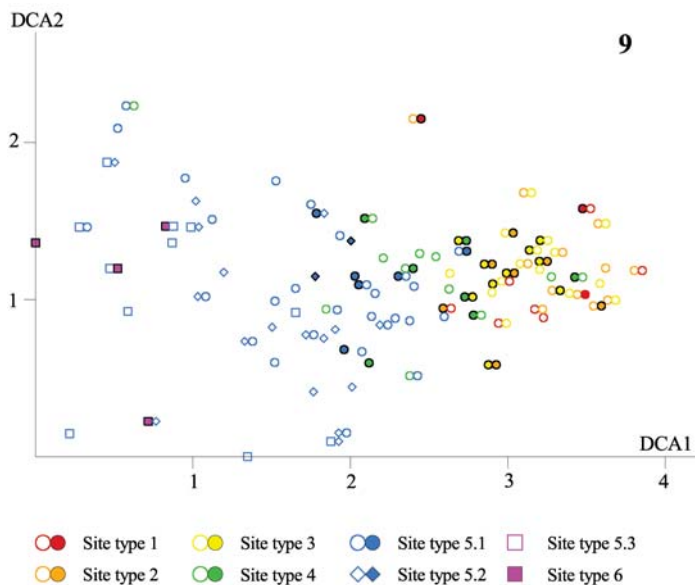
Axis	MDS97 1		MDS97 2	
	$\tau$	P	$\tau$	P
DCA97 1	<b>.8594</b>	<b>.0000</b>	-.1095	n.s.
DCA97 2	-.0389	n.s.	<b>.4841</b>	<b>.0000</b>
DCA97 3	-.0135	n.s.	-.1044	n.s.
DCA97 4	-.0238	n.s.	<b>.2980</b>	<b>.0000</b>

Tab. 6. Kendall's rank correlation coefficients  $\tau$  between macro-plot scores in the ordinations of the MAF 95 data set, with significance probabilities (P). Correlations significant at level  $P < 0.0001$  in bold face. n.s. – significance probability less than 0.1.

Axis	MDS95 1		MDS95 2	
	$\tau$	P	$\tau$	P
DCA95 1	<b>.8634</b>	<b>.0000</b>	-.0269	n.s.
DCA95 2	-.0269	n.s.	.2623	.0002
DCA95 3	.0119	n.s.	<b>.4484</b>	<b>.0000</b>
DCA95 4	-.1884	.0069	-.1792	.0101

Tab. 7. Kendall's rank correlation coefficients  $\tau$  between macro-plot scores in the ordinations of the MAF 95 and MAF 97 data sets, with significance probabilities (P). Correlations significant at level  $P < 0.0001$  in bold face. n.s. – significance probability less than 0.1.

Variable	DCA95 1		DCA95 2		DCA95 3		DCA95 4		MDS95 1		MDS95 2	
	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P
DCA97 1	<b>.9843</b>	<b>.0000</b>	.0233	n.s.	-.0168	n.s.	-.1669	.0166	<b>.8692</b>	<b>.0000</b>	-.0578	n.s.
DCA97 2	-.1418	.0418	<b>.4095</b>	<b>.0000</b>	.1991	.0043	-.1015	n.s.	-.0876	n.s.	<b>.4699</b>	<b>.0000</b>
DCA97 3	.0262	n.s.	<b>.5344</b>	<b>.0000</b>	-.2000	.0041	.1897	.0065	.0123	n.s.	-.0762	n.s.
DCA97 4	-.0477	n.s.	-.0636	n.s.	<b>.6524</b>	<b>.0000</b>	-.1387	.0466	-.0123	n.s.	<b>.3158</b>	<b>.0000</b>
MDS97 1	<b>.8534</b>	<b>.0000</b>	.0356	n.s.	.0237	n.s.	-.1949	.0052	<b>.9775</b>	<b>.0000</b>	.0222	n.s.
MDS97 2	-.1507	.0305	.2540	.0003	<b>.4517</b>	<b>.0000</b>	-.1893	.0066	-.0795	n.s.	<b>.8704</b>	<b>.0000</b>



Figs 9–10. DCA ordination of the MAF 95 data set. Axes scaled in S.D. units. Site-type classification of macro plots plotted onto plot positions. Fig. 9. Axes 1 (horizontal) and 2. Fig. 10. Axes 1 (horizontal) and 3. Colour symbols for each actual site-type are shown. Open and filled circle/square represent the non-paludified and the paludified types, respectively. Inhomogeneous plots with respect to paludification are shown by a composite symbol.

$P = 0.0009$ ), but even more strongly with DCA95 3 ( $\tau = 0.508$ ,  $P < 0.0001$ ) and DCA95 4 ( $\tau = 0.526$ ,  $P < 0.0001$ ; cf. Tab. 8). The second axis of the pine forest ordination of fungi thus contained elements of the variation expressed along three of the axes of the total data set. The third DCA axis separated



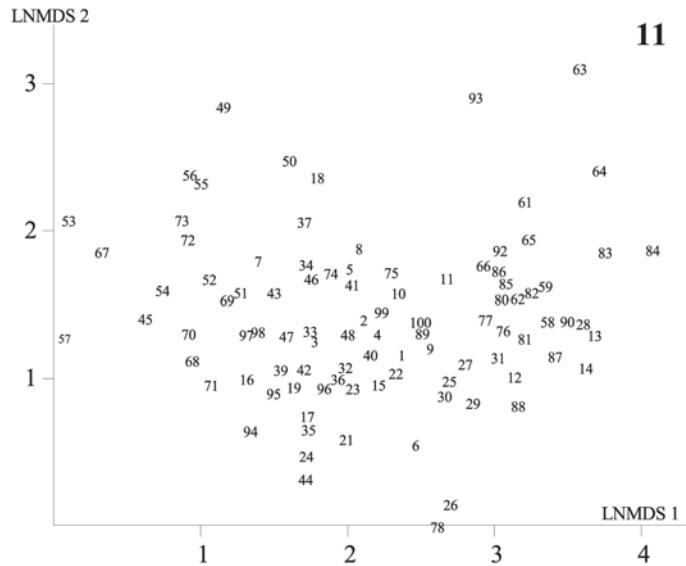


Fig. 11. Two-dimensional LNMDS ordination of the MAF 95 data set, axes 1 (horizontal) and 2. Axes rescaled in S.D. units by means of rhCCA. Macro plot numbers plotted onto plot positions.

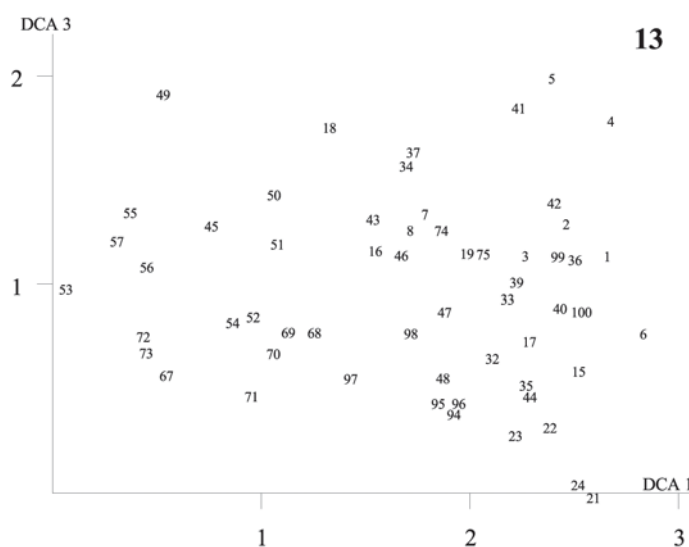
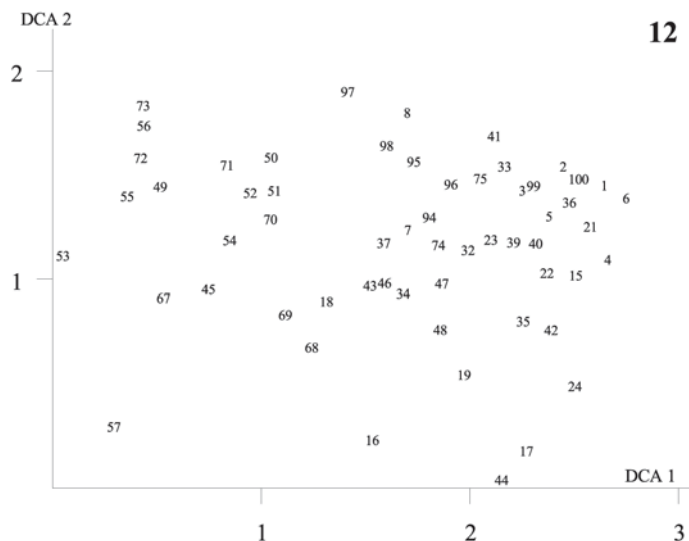
plots 93 (score 1.1 S.D. units higher than any other plot) and 84 (score  $> 0.6$  units lower than all other plots), while the bulk of plots occurred between 0.65 and 1.55 S.D. units along this axis (Figs 17, 19). This axis was strongly correlated with DCA95 1.

Separate DCA ordinations of data subsets indicated that the gradient structure of fungi in the study area was the result of strong, partly coincident and partly different, gradients in species composition in the spruce and pine forests. The main gradient in fungal composition in the area consisted of the main gradients in either forest type. The secondmost important gradient in the material, DCA95 2, was mainly present in the spruce forest, while the thirdmost important gradient, DCA95 3, occurred as the secondmost important coenocline in the pine forest and the thirdmost important coenocline in the spruce forest.

### *Relationship between fungal ordinations and vegetational variables*

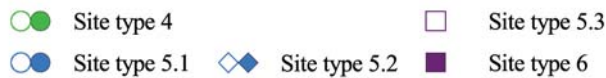
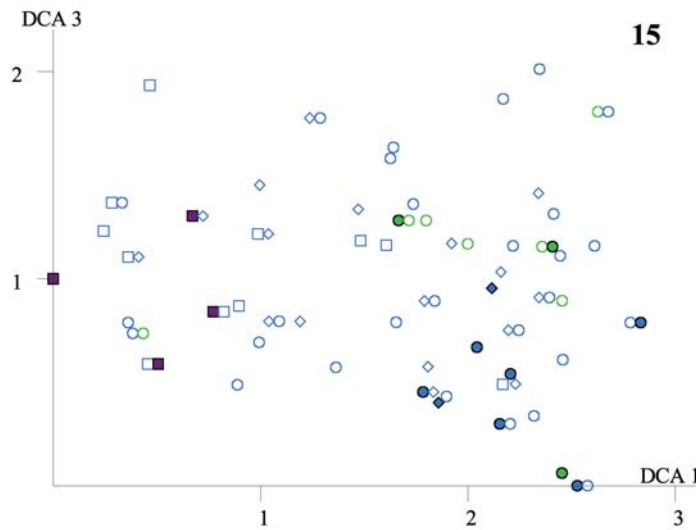
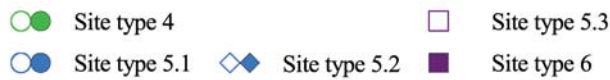
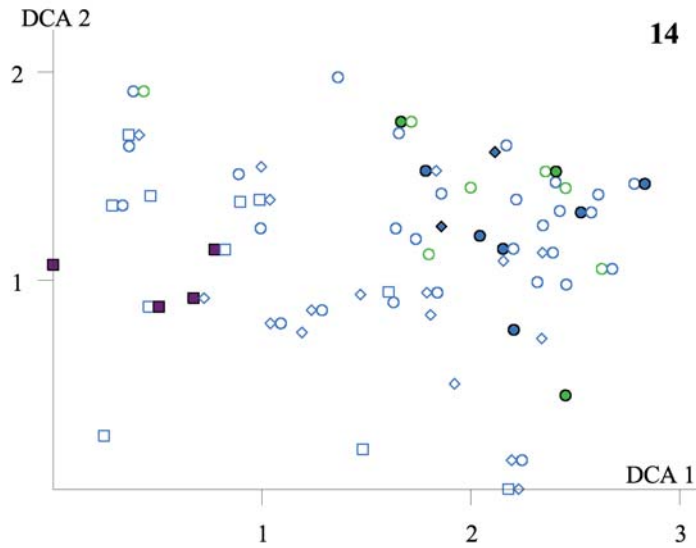
#### Ordinations of the MAF 95 data set

Macro-plot positions along the first axes of the DCA and LNMDS ordinations of the MAF 95 data set were strongly correlated ( $\tau = 0.7$ ) with averaged meso-plot positions along the first axes of all vegetational ordinations (of the total species composition, and separate ordinations made for the field and bottom layers, see Tab. 9). The correspondence between plot positions along DCA95 1 and positions along corresponding vegetational ordination axes was strong in the spruce forest (Subset A), less strong and significant at the  $P < 0.05$  level only for the bottom-layer gradient in the pine forest (Subset B; see Tab. 10). Thus the main gradients in species composition of fungi, vascular plants and cryptogams (bryophytes and lichens) were parallel in the spruce forest, but only partly so in the pine forest.

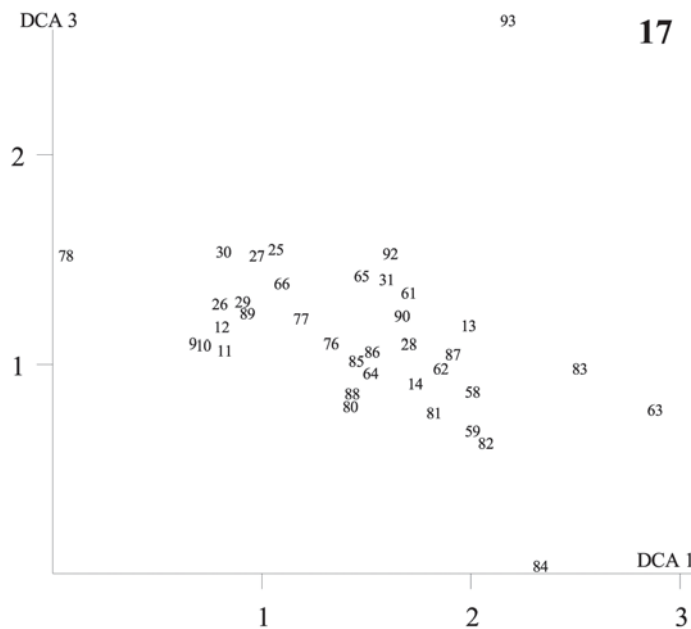
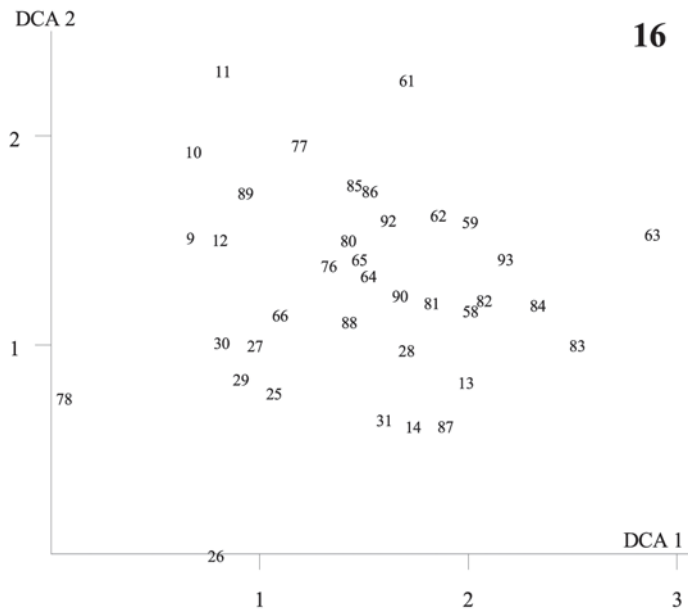


Figs 12–13. DCA ordination of the MAF 58A data set. Axes scaled in S.D. units. Macro plot numbers plotted onto plot positions. Fig. 12. Axes 1 (horizontal) and 2. Fig. 13. Axes 1 (horizontal) and 3.

The second axes in the DCA ordination of the MAF 95 data set was significantly correlated only with the fourth DCA axis in the vegetational ordination ( $\tau = 0.370$ ,  $P < 0.0001$ ; Tab. 9), while the third fungal ordination axis (DCA95 3) and the second LNMDS axis were significantly correlated with the second vegetational DCA ordination axis ( $\tau > 0.3$ ,  $P < 0.0001$ ), both in the ordination of all species and in the separate ordination of species in the bottom layer (DCAG 2 and DCAGB 2, cf. Tab. 9). Thus the secondmost important gradient for the bottom layer (and the vegetation as a whole) corresponded to the thirdmost important gradient in the composition of fungi, while the secondmost important gradient in fungal species composition (at least as indicated by DCA) seemed to have a counterpart in the fourthmost important gradient in vegetation.



Figs 14–15. DCA ordination of the MAF 58A data set. Axes scaled in S.D. units. Site-type classification of macro plots plotted onto plot positions. Fig. 14. Axes 1 (horizontal) and 2. Fig. 15. Axes 1 (horizontal) and 3. Colour symbols for each actual site-type are shown. Open and filled circle/square represent the non-paludified and the paludified types, respectively. Inhomogeneous plots with respect to paludification are shown by a composite symbol.



Figs 16–17. DCA ordination of the MAF 37B data set. Axes scaled in S.D. units. Macro plot numbers plotted onto plot positions. Fig. 16. Axes 1 (horizontal) and 2. Fig. 17. Axes 1 (horizontal) and 3.

#### DCA ordinations of data subsets

The first axis in the DCA ordination of the spruce-forest subset (MAF 58A) was significantly correlated with the first axis of vegetational ordinations (all species groups; see Tab. 11). The second MAF 58A

Tab. 8. Kendall's rank correlation coefficients  $\tau$  between macro-plot scores in the DCA ordination of the MAF 95 data set and DCA ordinations of the MAF 58A and MAF 37B subsets, with significance probabilities (P). Correlations significant at level  $P < 0.0001$  in bold face. n.s. – significance probability less than 0.1.

Axis	DCA95 1		DCA95 2		DCA95 3		DCA95 4	
	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P
DCA58A 1	<b>.8572</b>	<b>.0000</b>	-.2772	.0021	-.0780	n.s.	-.0920	n.s.
DCA58A 2	.0538	n.s.	<b>.6185</b>	<b>.0000</b>	.1954	.0303	.2530	.0050
DCA58A 3	-.0986	n.s.	-.1646	.0681	<b>.7374</b>	<b>.0000</b>	-.2070	.0218
DCA58A 4	.0284	n.s.	-.1005	n.s.	-.1736	.0542	<b>.3861</b>	<b>.0000</b>
DCA37B 1	<b>.6396</b>	<b>.0000</b>	.1592	n.s.	.0751	n.s.	.0931	n.s.
DCA37B 2	-.0631	n.s.	.3814	.0009	<b>.5075</b>	<b>.0000</b>	<b>.5255</b>	<b>.0000</b>
DCA37B 3	<b>.4865</b>	<b>.0000</b>	-.0601	n.s.	.2883	.0120	-.1441	n.s.
DCA37B 4	.0721	n.s.	-.2042	.0753	.2462	.0320	-.2102	.0671

axis was also relatively strongly correlated with the first vegetational axis, while the third MAF 58A axis was correlated with DCAG 2, DCAGB 2 and DCAG 3, but at lower significance levels ( $\tau < 0.3$ ;  $P < 0.02$ , cf. Tab. 11).

The first three axes of the DCA ordination of the pine forest subset (MAF 37B) was correlated with the corresponding axes of ordinations of vegetation (all  $\tau > 0.3$ ,  $P < 0.01$ ; Tab. 11). Correlations were much stronger with ordinations of the bottom layer than with the ordination of vascular plants (see Tab. 11).

### *Interpretation of ordinations by means of environmental variables*

#### Ordinations of the MAF 95 data set

The same 13 environmental variables were strongly correlated ( $P < 0.0001$ ) with the first axis in the DCA and LNMDS ordinations of the MAF 95 data set (Tab. 12). The highest correlation,  $\tau = -0.601$ , was obtained between DCA 1 and  $\text{pH}_{\text{CaCl}_2}$ . Five variables had  $\tau$  values  $> 0.45$  with this axis in both ordinations: macro plot soil depth, pH (2 variables) and Total N (negatively correlated) and total macro-plot terrain shape (positively correlated with DCA 1; indicating transition from valley bottom to convex ridge). Other variables strongly correlated with this axis were slope, deciduous litter cover and basal area, notably of deciduous trees (decreasing along the axis), and loss on ignition (increasing). Except for basal area, macro-plot variables were in most cases more strongly correlated with plot scores than the corresponding meso plot variables (see Tab. 12).

Variables related to topography (such as terrain shape and soil depth) and tree cover were only moderately strongly correlated with this axis in the subsets (cf. Tab. 13), indicating that these variables reflected broad-scale differences between spruce and pine forests. Slope was strongly correlated with DCA 1 only in the pine forest; loss on ignition, soil pH, N and Ca in the spruce forest only.

No variable was strongly correlated with DCA 2 (Tab. 12). Correlations significant at the  $P < 0.01$  level were observed for Mn ( $\tau = -0.237$ ,  $P = 0.0007$ ), bryophyte cover ( $\tau = -0.231$ ,  $P = 0.0012$ ), loss on ignition ( $\tau = 0.226$ ,  $P = 0.0012$ ) and K ( $\tau = -0.224$ ,  $P = 0.0013$ ). Five more variables were

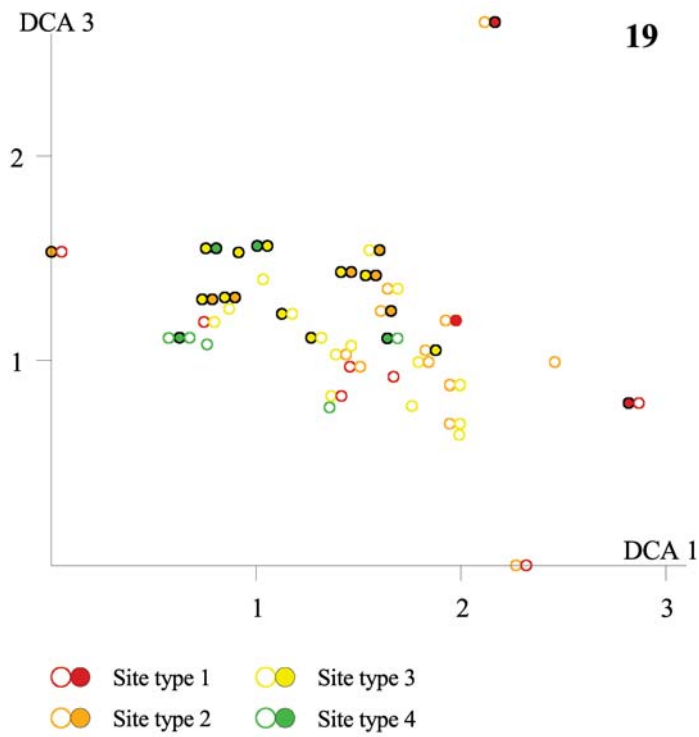
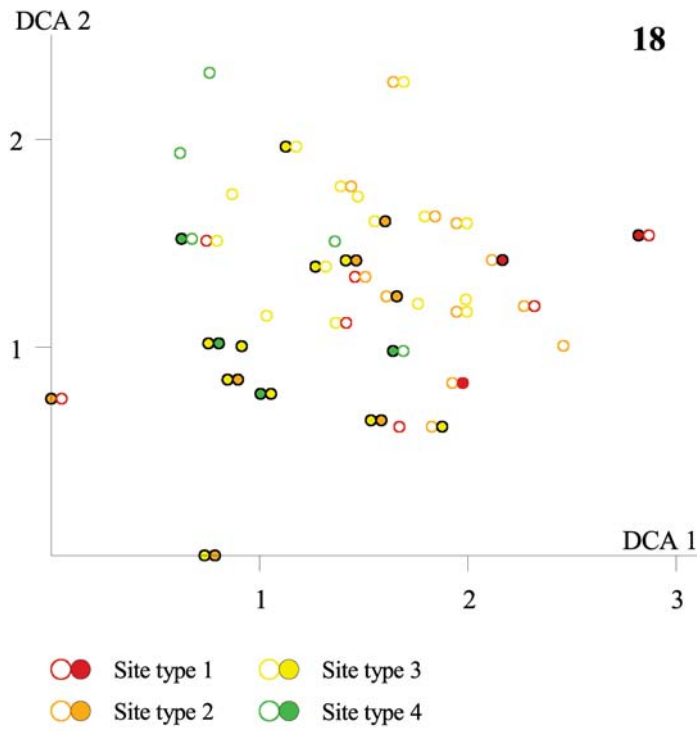
Tab. 9. Kendall's rank correlation coefficients  $\tau$  between macro-plot scores in the ordinations of the MAF 95 data set and averaged meso plot scores in DCA ordinations of green plants, with significance probabilities (P). Correlations significant at level  $P < 0.0001$  in bold face. n.s. – significance probability less than 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2. Ordinations of green plants: DCAG – DCA ordination of the full species composition; DCAGV – DCA ordination of vascular plants; DCAGB – DCA ordination of bryophytes and macrolichens (the bottom layer).

Variable	DCA95 1		DCA95 2		DCA95 3		DCA95 4		MDS95 1		MDS95 2	
	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P
DCAG 1	<b>.6981</b>	<b>.0000</b>	.1166	.0945	-.0155	n.s.	-.1177	.0914	<b>.7134</b>	<b>.0000</b>	.0202	n.s.
DCAG 2	-.0528	n.s.	.0912	n.s.	<b>.3181</b>	<b>.0000</b>	-.1318	.0591	-.0492	n.s.	<b>.3350</b>	<b>.0000</b>
DCAG 3	-.0871	n.s.	-.1547	.0267	-.0772	n.s.	-.0067	n.s.	-.0602	n.s.	-.0546	n.s.
DCAG 4	.0787	n.s.	<b>.3695</b>	<b>.0000</b>	.0454	n.s.	-.1026	n.s.	.0729	n.s.	.2822	.0001
DCAGV 1	<b>.6823</b>	<b>.0000</b>	.1524	.0288	-.0294	n.s.	-.1347	.0533	<b>.6854</b>	<b>.0000</b>	.0300	n.s.
DCAGB 1	<b>.6983</b>	<b>.0000</b>	.0821	n.s.	-.0096	n.s.	-.1424	.0412	<b>.7207</b>	<b>.0000</b>	.0161	n.s.
DCAGB 2	-.1201	.0859	-.0155	n.s.	<b>.2999</b>	<b>.0000</b>	-.1264	.0707	-.1178	.0920	.2431	.0005

Tab. 10. Kendall's rank correlation coefficients  $\tau$  between macro-plot scores along the first axis in the DCA ordination of the MAF 95 data set and the first axes in three ordinations of vegetation, with significance probabilities (P), calculated for the whole data set and separately for subsets MAF 58A and MAF 37B. Correlations significant at level  $P < 0.0001$  in bold face. n.s. – significance probability less than 0.1. Explanatory variables derived from ordinations of green plants: DCAG – DCA ordination of the full species composition; DCAGV – DCA ordination of vascular plants; DCAGB – DCA ordination of bryophytes and macrolichens (the bottom layer).

Data set	MAF 95		MAF 58A		MAF 37B	
	$\tau$	P	$\tau$	P	$\tau$	P
DCAG 1	<b>.6981</b>	<b>.0000</b>	<b>.5150</b>	<b>.0000</b>	.2239	.0513
DCAGV 1	<b>.6823</b>	<b>.0000</b>	<b>.5309</b>	<b>.0000</b>	.0782	n.s.
DCAGB 1	<b>.6983</b>	<b>.0000</b>	<b>.4876</b>	<b>.0000</b>	.3012	.0089

Figs 18–19. DCA ordination of the MAF 37B data set. Axes scaled in S.D. units. Site-type classification of macro plots plotted onto plot positions. Fig. 18. Axes 1 (horizontal) and 2. Fig. 19. Axes 1 (horizontal) and 3. Colour symbols for each actual site-type are shown. Open and filled circle/square represent the non-paludified and the paludified types, respectively. Inhomogeneous plots with respect to paludification are shown by a composite symbol.



correlated with DCA 2 at the  $P < 0.05$  level, among them deciduous litter cover ( $\tau = 0.151$ ,  $P = 0.037$ ).

DCA 3 was strongly correlated with one variable, soil moisture, which decreased along the axes ( $\tau = -0.465$ , cf. Tab. 12). LNMDS 2 was also strongly correlated with soil moisture ( $\tau = -0.328$ ), but even more strongly with bryophyte cover ( $\tau = -0.431$ , cf. Tab. 12) which was moderately strongly correlated with DCA 3 ( $\tau = -0.234$ ,  $P = 0.0011$ ). Variables related to canopy closure, at the macro-(MA Can) as well as the meso-plot (ME Lit) scales were positively correlated with these axes, most strongly with DCA 3 (Tab. 12). Only four variables; soil moisture, pH, deciduous litter cover and slope, had  $\tau > 0.2$  ( $P = 0.005$ ) with DCA 4.

#### DCA ordination of the spruce-forest subset MAF 58A

The variables strongly correlated with the first axis of fungal species composition in the spruce forest subset were the same that were strongly correlated with DCA95 1 (in this subset): pH, total-N and Ca (all negatively correlated; Tab. 14). Loss on ignition (positively) and bryophyte cover (negatively) were correlated with the second DCA axis at the  $P < 0.001$  level. Less strong correlations ( $\tau > 0.2$ ) were noted for deciduous litter cover (positively), Mg and N (both negatively). Soil moisture was strongly negatively correlated with the third DCA axis ( $P < 0.0001$ , Tab. 14). Other variables correlated with DCA58 3 and with  $\tau > 0.25$  were the tree indices (positively correlated;  $0.27 \leq \tau \leq 0.30$ ,  $P < 0.003$ ), exchangeable acidity (H; negatively) and Ca and Mn (positively).

#### DCA ordination of the pine-forest subset MAF 37B

Slope was most strongly correlated with the first axis in the ordination of fungi from pine forest ( $\tau = -0.363$ ,  $P = 0.002$ ). Terrain shape was also correlated with this axis (transition from valley side to convex ridge). Several soil variables, such as Mn, K, S, Na and loss on ignition, and bryophyte cover, were negatively correlated with position along this axis at  $P < 0.05$  (Tab. 14). Soil moisture was strongly negatively correlated with DCA 2 ( $\tau = -0.542$ ,  $P < 0.0001$ ). Soil depth (four variables) and tree indices (most strongly at the macro plot scale) were positively correlated with this axis ( $\tau > 0.25$ ), while pH, N, Al and Mn were negatively correlated with DCA 2 at the  $P < 0.05$  level. DCA 3 was negatively correlated with pH and slope, and positively correlated with tree variables (Tab. 14).

#### *Variation in species abundances in the DCA ordination of the MAF 95 data set*

Characteristics of species responses to the first three DCA axes are summarized in Tab. 15. Differences between mycorrhizal species and saprotrophs with respect to range along these axes are summarized in Figs 20–22. Mycorrhizal fungi generally have much narrower amplitude along the main gradient than was observed for saprotrophs (Fig. 20). More than 50% of the mycorrhizal species had amplitudes  $< 2$  S.D. units, while only 10% of the saprotrophs had such narrow amplitudes. Amplitude  $> 6$  S.D. units was found for no mycorrhizal species but 14% of the saprotrophs. Both groups tended to have wider amplitudes along DCA-axes 2 and 3. For DCA 2, amplitudes were generally wider for the mycorrhizal species (Fig. 21), while for DCA 3 only small differences were found between the two groups (Fig. 22).

Species optima along the first three ordination axes are shown in Figs 23–24 (mycorrhizal species), and Figs 25–26 (saprotrophs). The variation in frequency in subplots for species along the first three ordination axes (species present in above 5% of the plots are shown as Figs 27–188. A wealth of information about the autecology of the species may be deduced from these tables and figures. Here only some points of general interest will be focused.



Tab. 11. Kendall's rank correlation coefficients  $\tau$  between macro-plot scores in the ordinations of the MAF 95 data subsets (MAF 58A and MAF 37B) and averaged meso-plot scores in DCA ordinations of green plants, with significance probabilities (P). Correlations significant at level  $P < 0.0001$  in bold face. n.s. – significance probability less than 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2. Ordinations of green plants: DCAG – DCA ordination of the full species composition; DCAGV – DCA ordination of vascular plants; DCAGB – DCA ordination of bryophytes and macrolichens (the bottom layer).

Variable	DCA58 1		DCA58 2		DCA58 3		DCA58 4		DCA37 1		DCA37 2		DCA37 3		DCA37 4	
	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P
<b>DCAG 1</b>	.4253	.0000	<b>.2993</b>	<b>.0009</b>	<b>-.0691</b>	n.s.	<b>.1151</b>	n.s.	<b>.3501</b>	<b>.0023</b>	<b>-.1518</b>	n.s.	<b>.1247</b>	n.s.	<b>-.1698</b>	n.s.
DCAG 2	-.1619	.0732	.1959	.0302	.2104	.0199	-.0673	n.s.	.0918	n.s.	.3175	.0058	.3175	.0058	-.2603	.0236
DCAG 3	.0982	n.s.	-.1722	.0567	.2716	.0027	-.2292	.0112	-.0541	n.s.	-.1534	n.s.	-.3820	.0009	-.2075	.0710
DCAG 4	-.3433	.0001	.2193	.0154	-.1221	n.s.	.0930	n.s.	.1402	n.s.	.1944	.0914	-.0347	n.s.	-.1613	n.s.
<b>DCAGV 1</b>	.4268	.0000	<b>-.2984</b>	<b>.0009</b>	<b>-.0648</b>	n.s.	<b>.1156</b>	n.s.	<b>.1865</b>	n.s.	<b>-.0692</b>	n.s.	<b>-.0541</b>	n.s.	<b>-.0241</b>	n.s.
<b>DCAGB 1</b>	.4294	.0000	<b>.2017</b>	<b>.0255</b>	<b>-.0527</b>	n.s.	<b>.0890</b>	n.s.	<b>.3916</b>	<b>.0007</b>	<b>-.1687</b>	n.s.	<b>.1657</b>	n.s.	<b>.2048</b>	<b>.0752</b>
DCAGB 2	-.0358	n.s.	.1659	.0670	.2582	.0043	-.0030	n.s.	.0045	n.s.	.3898	.0007	.2814	.0144	.2062	.0731

Tab. 12. Kendall's rank correlation coefficients  $\tau$  between macro-plot scores in the ordinations of the MAF 95 data set and the 36 environmental variables, with significance probabilities (P). Correlations significant at level  $P < 0.0001$  in bold face. n.s. – significance probability less than 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Variable	DCA95 1		DCA95 2		DCA95 3		DCA95 4		MDS95 1		MDS95 2	
	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P
01 MA Slo	-.3567	.0000	-.1158	n.s.	-.0633	n.s.	.1733	.0141	-.3635	.0000	-.1930	.0062
02 MA Auf	-.0614	n.s.	.0355	n.s.	-.0776	n.s.	.0709	n.s.	-.0578	n.s.	-.1125	n.s.
03 MA Ter	.5586	.0000	.0986	n.s.	-.0099	n.s.	-.1252	n.s.	.5965	.0000	.0976	n.s.
04 MA Une	-.3261	.0001	-.1317	n.s.	.1349	.0949	.0929	.0148	-.3030	.0002	-.0447	n.s.
05 MA S d	-.5613	.0000	.0282	n.s.	.0537	n.s.	.0517	n.s.	-.5910	.0000	.0274	n.s.
06 MA Bas	-.2494	.0005	-.0953	n.s.	.1599	.0267	-.1436	.0466	-.2335	.0012	.1214	.0923
07 MA Can	-.2775	.0001	.0032	n.s.	.2541	.0003	-.1274	.0692	-.2541	.0003	.2250	.0013
*1 MA Bad	-.4128	.0000	.0732	n.s.	-.0373	n.s.	.1145	n.s.	-.3898	.0000	.0503	n.s.
*2 MA Dli	-.3822	.0000	.1512	.0368	-.0952	n.s.	-.2024	.0052	-.3864	.0000	-.0485	n.s.
*3 MA Bry	.0608	n.s.	-.2314	.0012	-.2339	.0011	-.0470	n.s.	-.0046	n.s.	-.4309	.0000
08 ME Slo	-.3335	.0000	-.0632	n.s.	-.1113	n.s.	.2017	.0041	-.3394	.0000	-.1838	.0088
09 ME Auf	-.0865	n.s.	-.0300	n.s.	-.0725	n.s.	.1002	n.s.	-.0829	n.s.	-.1218	.0845
10 ME Une	-.1358	.0514	-.0177	n.s.	.0067	n.s.	.0659	n.s.	-.1667	.0168	-.1279	.0664
11 ME Con	-.0925	n.s.	-.0387	n.s.	-.0434	n.s.	.1069	n.s.	-.0763	n.s.	-.0023	n.s.
12 ME Smi	.0027	n.s.	.1114	n.s.	-.0378	n.s.	-.0509	n.s.	-.0252	n.s.	.0619	n.s.
13 ME Sme	-.1420	.0418	.1131	n.s.	.0828	n.s.	-.1331	.0566	-.1739	.0127	.0974	n.s.
14 ME Sma	-.2642	.0002	.0708	n.s.	.0885	n.s.	-.0854	n.s.	-.2817	.0001	.0897	n.s.
15 ME Lit	-.2579	.0002	.0244	n.s.	.2426	.0005	-.0481	n.s.	-.2304	.0010	.1891	.0070
16 ME Bas	-.3316	.0000	-.1035	n.s.	.1554	.0273	-.0600	n.s.	-.3157	.0000	.1157	n.s.
17 Mois	-.0587	n.s.	-.0666	n.s.	-.4654	.0000	.2781	.0001	-.0807	n.s.	-.3280	.0000
18 LI	.3829	.0000	.2259	.0012	.0446	n.s.	-.1244	.0744	.3681	.0000	.0175	n.s.
19 pH <sub>H<sub>2</sub>O</sub>	-.5010	.0000	-.0349	n.s.	-.1235	.0877	.2208	.0023	-.4603	.0000	-.0271	n.s.
20 pH <sub>CaCl<sub>2</sub></sub>	-.6008	.0000	-.0311	n.s.	-.0216	n.s.	.1901	.0082	-.5637	.0000	.0214	n.s.
21 Ca	-.3684	.0000	-.1259	.0708	.1256	.0713	-.0078	n.s.	-.3223	.0000	.1702	.0145
22 Mg	-.2470	.0004	-.1420	.0415	.0813	n.s.	-.0540	n.s.	-.2358	.0007	.0766	n.s.
23 Na	-.0992	n.s.	-.0004	n.s.	-.1158	.0965	.0773	n.s.	-.0835	n.s.	-.0327	n.s.
24 K	-.2551	.0003	-.2244	.0013	.1073	n.s.	.0347	n.s.	-.2573	.0002	-.0488	n.s.
25 H	.3062	.0000	.0869	n.s.	-.2004	.0040	.0249	n.s.	.2887	.0000	-.1622	.0199
26 N	-.5153	.0000	-.0788	n.s.	-.1333	.0558	.1915	.0060	-.4602	.0000	.0188	n.s.
27 P-AL	-.2663	.0001	-.0251	n.s.	-.0347	n.s.	-.0101	n.s.	-.2479	.0004	.0063	n.s.
28 Al	.0903	n.s.	-.1129	n.s.	-.1476	.0341	.1781	.0106	.0791	n.s.	-.2141	.0021
29 Fe	.2004	.0040	-.0681	n.s.	-.1297	.0627	.0159	n.s.	.1758	.0116	-.1935	.0055
30 Mn	-.2569	.0002	-.2370	.0007	.1109	n.s.	.0822	n.s.	-.2385	.0006	.0004	n.s.
31 Zn	-.0311	n.s.	-.1523	.0288	.0625	n.s.	-.0065	n.s.	-.0271	n.s.	-.0336	n.s.
32 P	.0293	n.s.	-.1514	.0297	.0495	n.s.	-.0697	n.s.	.0289	n.s.	-.0914	n.s.
33 S	-.1082	n.s.	-.1429	.0402	.0455	n.s.	.0500	n.s.	-.1050	n.s.	-.0623	n.s.

### Ectomycorrhizal fungi

*Cortinari* *obtus* (Figs 47, 48) was the only very common mycorrhizal species, spanning nearly the whole first axis, and being observed in more than twice as many plots as the secondmost common species. It occurred in most site-types, had a distinct abundance maximum in site-type 5.1 near the middle of the axis, and was absent from the plots with the lowermost DCA 1 scores. These plots mostly had a dense field layer and/or high litterfall, while *C. obtus* seemed to find its optimum in sites with a dense bryophyte carpet.

A few less frequent species also had very wide amplitudes. *Amanita fulva* (Figs 27, 28, also see Tab. 15) occurred accidentally from site-type 5.2 till the driest plots in series 1, and was one of very few species that fruited during the extremely dry period in August 1990. *Cortinarius scaurus* (Figs 51, 52, Tab. 15) spanned the range from site-types 5.3 to 2.

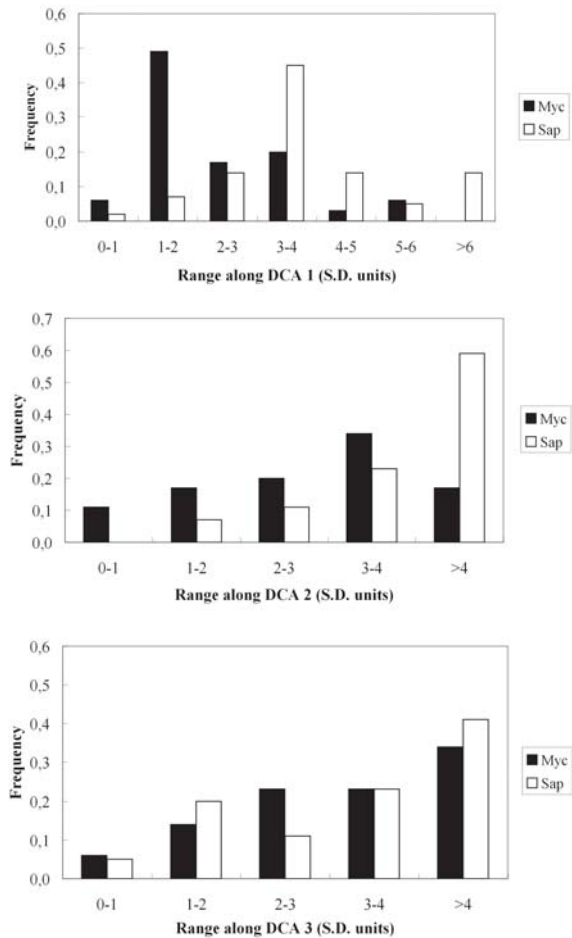
Several species (many of them with low frequency) were restricted to the low-score end of DCA-axis 1, and to site-types associated with higher nutrient concentrations (5.2, 5.3, and 6). The most frequent among these species were *Hygrophorus pustulatus* (Figs 63, 64) and *Entoloma rhodopolium* (Figs 55, 56), both restricted to DCA 1 < 2.0 S.D. units. *E. rhodopolium* occurred in (fine-scale) paludified sites characterized by low DCA 3 scores, and reached its highest frequency in plot 38 which acted as an outlier in the ordination of the MAF 97 data set and hence was not included in the MAF 95 set.

Many species typical of the 'bilberry-dominated spruce forest' showed concentrations to the middle parts of DCA 1 and site-type 5.1. Examples are *Cortinarius flexipes* (Figs 45, 46), which occurred in 22 of 23 plots classified to series 5 and had a distinct optimum in site-type 5.1; *Amanita virosa* (Figs 29, 30), *Cantharellus tubaeformis* (Figs 31, 32), *Cortinarius albovariegatus* (Figs 33, 34), *C. armeniacus* (Fig. 37, 38), *C. brunneus* (Figs 41, 42), and *Russula emetica* (Figs 89, 90), the latter one almost exclusively confined to series 5, but with a wide amplitude from 5.1 to 5.3.

Wider amplitudes towards higher DCA 1 scores (the pine forest) were observed for *Cortinarius bififormis* (Figs 39, 40; DCA 1 > c. 0.7 S.D.), *Cortinarius stillatitius* (Figs 53, 54; DCA 1 > c. 1.5 S.D.), and *Russula vinosa* (Figs 97, 98, 1.9 < DCA 1 < 3.2 S.D.).

Obligate or preferential pine forest species had their main occurrence in plots with high DCA 1 scores. An example is *Lactarius rufus* (Figs 69, 70), with only accidental occurrences in spruce-forest plots. The quantitatively most important species with optimum at high DCA 1 scores were *Suillus variegatus* (Figs 99, 100) with a narrow amplitude (2.9 < DCA 1 < 4.5 S.D.; cf. Tab. 15), and *Russula decolorans* (Figs 87, 88) and *R. paludosa* (Figs 91, 92) with a wider amplitudes.

Most of the species mentioned above had wide amplitudes along ordination axes 2 and 3. A limited number of species showed variation in abundance along the second axis. Of these, especially *Leccinum versipelle* (Fig. 77), *Leccinum* sp. (Fig. 79) and *Russula puellaris* (Fig. 93) showed



Figs 20–22. Frequency distributions for estimated range along DCAF 95 ordination axes, for ectomycorrhizal and saprotrophic species. Fig. 20. DCA axis 1. Fig. 21. DCA axis 2. Fig. 22. DCA axis 3.

Tab. 13. Kendall's rank correlation coefficients  $\tau$  between macro-plot scores along the first axis in the DCA ordination of the MAF 95 data set and 36 environmental variables, with significance probabilities (P). Correlation coefficients are calculated for the whole data set and for subsets MAF 58A and MAF 37B. Correlations significant at level  $P < 0.0001$  in bold face. n.s. – significance probability less than 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Data set	MAF 95		MAF 58A		MAF 37B	
	$\tau$	P	$\tau$	P	$\tau$	P
<b>01 MA Slo</b>	-.3567	.0000	<b>.0289</b>	<b>n.s.</b>	<b>-.2958</b>	<b>.0114</b>
02 MA Auf	-.0614	n.s.	-.0462	n.s.	-.1580	n.s.
<b>03 MA Ter</b>	.5586	.0000	<b>.1019</b>	<b>n.s.</b>	<b>.2750</b>	<b>.0379</b>
04 MA Un	-.3261	.0001	-.1497	n.s.	-.0301	n.s.
<b>05 MA S d</b>	-.5613	.0000	<b>-.2233</b>	<b>.0340</b>	<b>-.1762</b>	<b>n.s.</b>
06 MA Bas	-.2494	.0005	-.1249	n.s.	.1147	n.s.
07 MA Can	-.2775	.0001	-.1873	.0387	.1548	n.s.
<b>*1 MA BaD</b>	-.4128	.0000	<b>-.2550</b>	<b>.0064</b>	<b>-.0684</b>	<b>n.s.</b>
<b>*2 MA Dli</b>	-.3822	.0000	<b>-.2212</b>	<b>.0171</b>	<b>-.1733</b>	<b>n.s.</b>
*3 MA Bry	.0608	n.s.	.3666	.0001	-.1577	n.s.
<b>08 ME Slo</b>	-.3335	.0000	<b>-.0843</b>	<b>n.s.</b>	<b>-.2701</b>	<b>.0197</b>
09 ME Auf	-.0865	n.s.	.0873	n.s.	-.1760	n.s.
10 ME Une	-.1358	.0514	.0000	n.s.	-.0270	n.s.
11 ME Con	-.0925	n.s.	-.0838	n.s.	-.1494	n.s.
12 ME Smi	.0027	n.s.	-.0134	n.s.	-.0075	n.s.
13 ME Sm	-.1420	.0418	-.0709	n.s.	.0376	n.s.
14 ME Sm	-.2642	.0002	-.1343	n.s.	.1566	n.s.
15 ME Lit	-.2579	.0002	-.1511	.0947	.1510	n.s.
<b>16 ME Bas</b>	-.3316	.0000	<b>-.0974</b>	<b>n.s.</b>	<b>.1085</b>	<b>n.s.</b>
17 Mois	-.0587	n.s.	-.0472	n.s.	-.0616	n.s.
<b>18 LI</b>	.3829	.0000	<b>.3311</b>	<b>.0002</b>	<b>-.1187</b>	<b>n.s.</b>
<b>19 pH<sub>H<sub>2</sub>O</sub></b>	-.5010	.0000	-.4831	.0000	<b>-.2419</b>	<b>.0451</b>
<b>20 pH<sub>CaCl<sub>2</sub></sub></b>	-.6008	.0000	-.5355	.0000	<b>-.2883</b>	<b>.0174</b>
<b>21 Ca</b>	-.3684	.0000	-.3769	.0000	<b>-.0961</b>	<b>n.s.</b>
22 Mg	-.2470	.0004	-.2305	.0106	-.1231	n.s.
23 Na	-.0992	n.s.	-.2111	.0192	-.1982	.0843
24 K	-.2551	.0003	-.0127	n.s.	-.1862	n.s.
<b>25 H</b>	.3062	.0000	<b>.2220</b>	<b>.0138</b>	<b>.0841</b>	<b>n.s.</b>
<b>26 N</b>	-.5153	.0000	-.4967	.0000	<b>-.0601</b>	<b>n.s.</b>
27 P-AL	-.2663	.0001	-.1688	.0613	-.2432	.0341
28 Al	.0903	n.s.	.1918	.0335	-.0360	n.s.
29 Fe	.2004	.0040	.3176	.0004	-.0781	n.s.
30 Mn	-.2569	.0002	-.0502	n.s.	-.1892	.0994
31 Zn	-.0311	n.s.	.1325	n.s.	-.0120	n.s.
32 P	.0293	n.s.	.2874	.0014	-.0360	n.s.
33 S	-.1082	n.s.	.0357	n.s.	-.1622	n.s.

Tab. 14. Kendall's rank correlation coefficients  $\tau$  between macro-plot scores in the ordinations of the MAF 95 data subsets (MAF 58A and MAF 37B) and the 36 environmental variables, with significance probabilities (P). Correlations significant at level  $P < 0.0001$  in bold face. n.s. – significance probability less than 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Variable	DCA58 1		DCA58 2		DCA58 3		DCA58 4		DCA37 1		DCA37 2		DCA37 3		DCA37 4	
	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P
01 MA Slo	.0191	n.s.	-.0301	n.s.	.0031	n.s.	-.0412	n.s.	-.3633	.0019	-.1518	n.s.	-.2100	.0723	-.0812	n.s.
02 MA Auf	-.0669	n.s.	.0109	n.s.	-.0304	n.s.	.0122	n.s.	-.1008	n.s.	.0316	n.s.	-.2002	.0819	-.0376	n.s.
03 MA Ter	.0826	n.s.	.0409	n.s.	.1421	n.s.	-.0975	n.s.	.2950	.0260	-.0080	n.s.	.1435	n.s.	.0598	n.s.
04 MA S d	-.1153	n.s.	-.0120	n.s.	.2230	.0303	.0075	n.s.	-.1504	n.s.	.0602	n.s.	-.0962	n.s.	.1444	n.s.
05 MA S d	-.2638	.0123	.0307	n.s.	-.0696	n.s.	-.0518	n.s.	-.2046	n.s.	.3750	.0065	.1136	n.s.	.0170	n.s.
06 MA Bas	-.0873	n.s.	-.1538	.0985	.2856	.0022	-.1237	n.s.	.0828	n.s.	.2707	.0243	.3313	.0058	-.1561	n.s.
07 MA Can	-.1934	.0328	-.0231	n.s.	.2712	.0028	-.1034	n.s.	.0850	n.s.	.2974	.0103	.2944	.0111	-.1032	n.s.
*1 MA BalD	-.2841	.0024	.0664	n.s.	.0563	n.s.	.0715	n.s.	.0760	n.s.	.1216	n.s.	-.0190	n.s.	-.1292	n.s.
*2 MA Dli	-.2861	.0020	.2124	.0220	-.2399	.0097	-.1587	.0870	-.1896	n.s.	-.1961	n.s.	.2484	.0424	-.0098	n.s.
*3 MA Bry	.4340	.0000	-.2457	.0080	-.2369	.0105	-.0686	n.s.	-.2845	.0156	-.1144	n.s.	.0990	n.s.	.2010	.0876
08 ME Slo	-.0623	n.s.	-.0208	n.s.	-.0464	n.s.	-.0257	n.s.	-.2549	.0278	-.1912	.0989	-.2823	.0148	.1051	n.s.
09 ME Auf	.0467	n.s.	.0283	n.s.	-.0418	n.s.	-.0283	n.s.	-.1821	n.s.	-.0425	n.s.	-.1821	n.s.	.0880	n.s.
10 ME Une	-.0315	n.s.	-.0327	n.s.	-.0036	n.s.	-.0303	n.s.	-.0931	n.s.	.1111	n.s.	-.0420	n.s.	.0841	n.s.
11 ME Con	-.0826	n.s.	.0656	n.s.	-.0328	n.s.	-.0790	n.s.	-.1253	n.s.	-.1374	n.s.	-.0589	n.s.	.1585	n.s.
12 ME Smi	-.0645	n.s.	.0997	n.s.	-.1946	.0318	.2226	.0140	-.2376	n.s.	.2724	.0179	.1008	n.s.	-.0436	n.s.
13 ME Sme	-.1121	n.s.	.1376	n.s.	-.0709	n.s.	-.0055	n.s.	-.0977	n.s.	.3171	.0058	.1007	n.s.	-.0105	n.s.
14 ME Sma	-.1622	.0722	.0718	n.s.	-.0533	n.s.	-.0278	n.s.	.0211	n.s.	.2982	.0096	.1536	n.s.	.0181	n.s.
15 ME Lit	-.1644	.0690	.0297	n.s.	.2725	.0026	-.1110	n.s.	.0870	n.s.	.2456	.0345	.1968	.0903	-.0015	n.s.
16 ME Bas	-.0680	n.s.	-.1158	n.s.	.2997	.0010	-.0741	n.s.	.1391	n.s.	.2032	.0812	.2583	.0267	-.1513	n.s.
17 Mois	.0097	n.s.	-.1865	.0388	-.4214	.0000	.0920	n.s.	.0646	n.s.	-.5424	.0000	-.2299	.0454	-.0406	n.s.
18 LI	.2318	.0102	.3142	.0005	-.1047	n.s.	.1265	n.s.	-.2329	.0426	.1818	n.s.	-.0947	n.s.	-.0015	n.s.
19 pH <sub>H2O</sub>	-.4451	.0000	-.1171	n.s.	.0057	n.s.	.0298	n.s.	-.1842	n.s.	-.3444	.0043	-.3220	.0077	-.1682	n.s.
20 pH <sub>CaCl2</sub>	-.5106	.0000	-.0772	n.s.	.1096	n.s.	-.0224	n.s.	-.2206	.0688	-.2689	.0265	-.2303	.0575	-.1176	n.s.
21 Ca	-.3600	.0001	-.1881	.0370	.2644	.0034	-.1869	.0382	-.1562	n.s.	-.1021	n.s.	-.0571	n.s.	.0390	n.s.
22 Mg	-.2039	.0238	-.2184	.0155	.1397	n.s.	-.1373	n.s.	-.2012	.0797	-.0090	n.s.	-.0480	n.s.	.0480	n.s.
23 Na	-.2039	.0238	-.1095	n.s.	-.0127	n.s.	.0272	n.s.	-.2643	.0213	-.2042	.0753	-.2012	.0797	-.0691	n.s.
24 K	.0381	n.s.	-.1531	.0897	.2414	.0074	-.0139	n.s.	-.2763	.0161	-.0841	n.s.	-.1231	n.s.	-.0450	n.s.
25 H	-.2172	.0160	.0841	n.s.	-.3345	.0002	.1748	.0525	.1862	n.s.	-.1081	n.s.	-.0631	n.s.	-.1832	n.s.
26 N	-.4580	.0000	-.2063	.0222	-.0466	n.s.	-.1204	n.s.	.0901	n.s.	-.3243	.0047	-.1171	n.s.	.0691	n.s.
27 P-AL	-.1785	.0478	-.0817	n.s.	.0079	n.s.	-.2329	.0098	-.1892	.0994	.0330	n.s.	.1081	n.s.	-.0541	n.s.
28 Al	.2063	.0222	-.0623	n.s.	-.1567	.0823	.1446	n.s.	-.0360	n.s.	-.2462	.0320	-.0931	n.s.	.0270	n.s.
29 Fe	.3418	.0002	-.0284	n.s.	-.1034	n.s.	-.0321	n.s.	-.0060	n.s.	-.0480	n.s.	-.0751	n.s.	.0631	n.s.
30 Mn	-.0430	n.s.	-.1349	n.s.	.3055	.0007	-.1797	.0463	-.3393	.0031	-.2553	.0262	-.0661	n.s.	.0781	n.s.
31 Zn	.1155	n.s.	-.0514	n.s.	.0986	n.s.	-.1567	.0823	-.1802	n.s.	-.0300	n.s.	.1291	n.s.	.2553	.0262
32 P	.2753	.0023	-.0272	n.s.	.0744	n.s.	-.1397	n.s.	-.2162	.0597	-.0120	n.s.	.2012	.0797	.1532	n.s.
33 S	.0236	n.s.	-.0563	n.s.	.1373	n.s.	-.0841	n.s.	-.2643	.0213	-.0961	n.s.	-.0270	n.s.	.1652	n.s.



Tab. 16. Characteristics of saprotrophic species in the MAF 95 data set: range and species score (estimate for optimum; in bold face) with respect to the first three DCA axes; total frequency, and frequency (given as exponent) in each interval along each axis.

Species	Range and score with respect to DCA axis			Tot.	DCA 1			DCA 2			DCA 3												
	DCA 1	DCA 2	DCA 3		-0.6	-1.1	-1.7	-2.1	-2.5	-2.9	-3.3	>3.3	-0.6	-0.95	-1.25	-1.6	>1.6	-0.7	-1.1	-1.45	-1.8	>1.8	
<i>Baeospora myosura</i>	<-0.63→	<-0.00→	(0.32)-0.7(-1.8)	15 <sup>2</sup>	38 <sup>3</sup>	25 <sup>3</sup>	22 <sup>1</sup>	5 <sup>1</sup>	31 <sup>2</sup>	. . .	6 <sup>1</sup>	9 <sup>1</sup>	27 <sup>2</sup>	10 <sup>3</sup>	15 <sup>3</sup>	10 <sup>3</sup>	22 <sup>2</sup>	. . .	21 <sup>1</sup>	14 <sup>2</sup>	16 <sup>1</sup>	13 <sup>1</sup>	
<i>Calocera viscosa</i>	0.5-1.32-2.9	<-1.50→	0.7-1.20-1.6	19 <sup>1</sup>	13 <sup>2</sup>	44 <sup>1</sup>	32 <sup>1</sup>	23 <sup>1</sup>	18 <sup>2</sup>	. . .	. . .	. . .	27 <sup>2</sup>	19 <sup>2</sup>	9 <sup>1</sup>	24 <sup>1</sup>	33 <sup>1</sup>	33 <sup>2</sup>	25 <sup>1</sup>	10 <sup>2</sup>	24 <sup>1</sup>	. . .	
<i>Clavariadelphus junceus</i>	-0.56(-1.1(-1.5))	<-2.28→	0.7-1.20-1.6	18 <sup>1</sup>	100 <sup>10</sup>	100 <sup>6</sup>	11 <sup>1</sup>	. . .	. . .	. . .	. . .	. . .	18 <sup>6</sup>	5 <sup>1</sup>	6 <sup>1</sup>	29 <sup>1</sup>	67 <sup>1</sup>	25 <sup>1</sup>	21 <sup>10</sup>	12 <sup>5</sup>	25 <sup>5</sup>	. . .	
<i>Collybia arrata</i>	0.5-2.41	<-2.24→	0.7-0.78→	16 <sup>1</sup>	13 <sup>1</sup>	13 <sup>1</sup>	44 <sup>2</sup>	16 <sup>2</sup>	. . .	9 <sup>1</sup>	19 <sup>2</sup>	18 <sup>2</sup>	9 <sup>1</sup>	10 <sup>2</sup>	3 <sup>1</sup>	19 <sup>2</sup>	33 <sup>1</sup>	11 <sup>1</sup>	8 <sup>1</sup>	7 <sup>1</sup>	. . .	13 <sup>1</sup>	
<i>Collybia dryophila</i>	0.5-0.76-0.9(-1.7)	(0.48-30.6→)	(0.56-30.7→)	6 <sup>1</sup>	25 <sup>1</sup>	13 <sup>2</sup>	. . .	9 <sup>1</sup>	6 <sup>1</sup>	. . .	. . .	. . .	9 <sup>1</sup>	10 <sup>2</sup>	3 <sup>1</sup>	5 <sup>1</sup>	11 <sup>1</sup>	11 <sup>1</sup>	8 <sup>1</sup>	7 <sup>1</sup>	. . .	13 <sup>1</sup>	
<i>Collybia tuberosa</i>	0.5-3.08→	<-1.86→	<-0.80→	64 <sup>1</sup>	63 <sup>2</sup>	25 <sup>3</sup>	89 <sup>7</sup>	79 <sup>3</sup>	62 <sup>3</sup>	63 <sup>3</sup>	82 <sup>2</sup>	45 <sup>2</sup>	82 <sup>2</sup>	82 <sup>3</sup>	43 <sup>3</sup>	78 <sup>1</sup>	56 <sup>6</sup>	67 <sup>2</sup>	72 <sup>3</sup>	56 <sup>3</sup>	63 <sup>3</sup>	. . .	
<i>Cystoderma jansoni</i>	1.0-2.68→	-0.12(-1.6)	-0.16→	38 <sup>1</sup>	. . .	25 <sup>3</sup>	33 <sup>3</sup>	54 <sup>3</sup>	25 <sup>3</sup>	25 <sup>3</sup>	24 <sup>1</sup>	11 <sup>1</sup>	73 <sup>3</sup>	43 <sup>3</sup>	39 <sup>2</sup>	24 <sup>1</sup>	11 <sup>1</sup>	67 <sup>2</sup>	42 <sup>2</sup>	41 <sup>2</sup>	24 <sup>2</sup>	25 <sup>2</sup>	
<i>Enzotoma centratum</i>	1.1-2.86→	-0.26(-1.5)	-0.05-1.5	16 <sup>1</sup>	. . .	13 <sup>1</sup>	22 <sup>1</sup>	32 <sup>1</sup>	18 <sup>1</sup>	19 <sup>1</sup>	9 <sup>1</sup>	18 <sup>1</sup>	19 <sup>1</sup>	18 <sup>1</sup>	19 <sup>1</sup>	14 <sup>1</sup>	. . .	33 <sup>1</sup>	17 <sup>1</sup>	17 <sup>1</sup>	12 <sup>1</sup>	. . .	
<i>Galerina atkinsoniana</i>	<-2.64→	<-0.38→	<-0.74→	71 <sup>2</sup>	13 <sup>1</sup>	63 <sup>2</sup>	67 <sup>2</sup>	89 <sup>3</sup>	92 <sup>3</sup>	100 <sup>2</sup>	75 <sup>2</sup>	27 <sup>2</sup>	82 <sup>3</sup>	86 <sup>3</sup>	67 <sup>2</sup>	44 <sup>1</sup>	100 <sup>2</sup>	100 <sup>2</sup>	83 <sup>3</sup>	48 <sup>3</sup>	76 <sup>3</sup>	63 <sup>3</sup>	
<i>Galerina atkinsoniana</i>	<-2.64→	<-0.38→	<-0.74→	84 <sup>1</sup>	50 <sup>1</sup>	100 <sup>3</sup>	89 <sup>4</sup>	95 <sup>2</sup>	92 <sup>1</sup>	91 <sup>1</sup>	75 <sup>3</sup>	73 <sup>3</sup>	100 <sup>6</sup>	81 <sup>6</sup>	88 <sup>3</sup>	71 <sup>4</sup>	89 <sup>3</sup>	100 <sup>7</sup>	96 <sup>6</sup>	79 <sup>8</sup>	80 <sup>4</sup>	63 <sup>4</sup>	
<i>Galerina hypnorum</i>	<-2.62→	<-0.38→	<-0.74→	6 <sup>1</sup>	63 <sup>1</sup>	13 <sup>1</sup>	. . .	. . .	. . .	. . .	. . .	. . .	. . .	3 <sup>1</sup>	10 <sup>2</sup>	33 <sup>1</sup>	. . .	. . .	8 <sup>1</sup>	10 <sup>1</sup>	4 <sup>1</sup>	. . .	
<i>Galerina marginata</i>	-0.88(-1.0)	1.2-2.73	0.7-1.27-1.7	6 <sup>1</sup>	13 <sup>1</sup>	. . .	11 <sup>1</sup>	47 <sup>1</sup>	46 <sup>1</sup>	36 <sup>1</sup>	6 <sup>1</sup>	. . .	64 <sup>3</sup>	24 <sup>3</sup>	21 <sup>1</sup>	14 <sup>1</sup>	. . .	44 <sup>3</sup>	33 <sup>3</sup>	24 <sup>3</sup>	8 <sup>1</sup>	13 <sup>1</sup>	
<i>Galerina mniophila</i>	(0.5)-1.3-2.22-2.9	-0.48(-1.5)	-0.35(->)	23 <sup>1</sup>	. . .	. . .	11 <sup>1</sup>	37 <sup>2</sup>	46 <sup>3</sup>	45 <sup>3</sup>	6 <sup>1</sup>	36 <sup>1</sup>	45 <sup>2</sup>	29 <sup>2</sup>	30 <sup>2</sup>	14 <sup>2</sup>	. . .	56 <sup>3</sup>	29 <sup>2</sup>	21 <sup>2</sup>	16 <sup>2</sup>	25 <sup>1</sup>	
<i>Galerina</i> sp.1	(1.2)-1.8-3.45	<-0.02-1.4	<-0.25(->)	25 <sup>1</sup>	. . .	. . .	33 <sup>1</sup>	16 <sup>2</sup>	. . .	9 <sup>1</sup>	6 <sup>1</sup>	. . .	36 <sup>2</sup>	10 <sup>2</sup>	3 <sup>1</sup>	5 <sup>2</sup>	. . .	11 <sup>1</sup>	17 <sup>2</sup>	7 <sup>2</sup>	4 <sup>1</sup>	. . .	
<i>Galerina</i> sp.2	1.2-1.74-1.9(-3.2)	-0.59(-0.9(-1.2))	<-0.30-1.4(-1.7)	8 <sup>1</sup>	. . .	. . .	13 <sup>1</sup>	22 <sup>1</sup>	11 <sup>1</sup>	8 <sup>1</sup>	27 <sup>1</sup>	6 <sup>1</sup>	18 <sup>1</sup>	. . .	5 <sup>1</sup>	18 <sup>1</sup>	19 <sup>1</sup>	11 <sup>1</sup>	. . .	2 <sup>1</sup>	14 <sup>1</sup>	8 <sup>1</sup>	13 <sup>1</sup>
<i>Gymnopilus sapiens</i>	1.1-3.20→	0.8-1.6(-2.1)	0.8-0.96→	13 <sup>1</sup>	. . .	. . .	5 <sup>1</sup>	8 <sup>1</sup>	27 <sup>1</sup>	13 <sup>1</sup>	18 <sup>1</sup>	. . .	. . .	5 <sup>1</sup>	6 <sup>1</sup>	29 <sup>1</sup>	. . .	. . .	8 <sup>1</sup>	17 <sup>1</sup>	8 <sup>1</sup>	. . .	
<i>Heyderia abietis</i>	(1.8)-2.4-3.94	0.9-1.5(-2.00)	(0.85)-30.9-1.5	9 <sup>1</sup>	. . .	. . .	50 <sup>1</sup>	38 <sup>1</sup>	78 <sup>1</sup>	89 <sup>3</sup>	92 <sup>3</sup>	100 <sup>1</sup>	100 <sup>1</sup>	100 <sup>1</sup>	100 <sup>1</sup>	100 <sup>1</sup>	64 <sup>1</sup>	100 <sup>1</sup>	88 <sup>1</sup>	90 <sup>1</sup>	88 <sup>1</sup>	75 <sup>1</sup>	
<i>Marasmius androsaceus</i>	<-3.81	<-1.16→	<-1.78→	88 <sup>1</sup>	50 <sup>2</sup>	33 <sup>2</sup>	26 <sup>2</sup>	15 <sup>1</sup>	. . .	. . .	. . .	. . .	64 <sup>1</sup>	100 <sup>1</sup>	88 <sup>1</sup>	90 <sup>1</sup>	56 <sup>1</sup>	89 <sup>1</sup>	79 <sup>1</sup>	90 <sup>1</sup>	88 <sup>1</sup>	75 <sup>1</sup>	
<i>Marasmius epiphyllus</i>	-0.02(-2.4)	0.7-3.27	0.7-2.42	22 <sup>3</sup>	88 <sup>6</sup>	50 <sup>3</sup>	33 <sup>2</sup>	26 <sup>2</sup>	15 <sup>1</sup>	. . .	. . .	. . .	14 <sup>2</sup>	9 <sup>1</sup>	38 <sup>2</sup>	78 <sup>6</sup>	. . .	17 <sup>2</sup>	24 <sup>2</sup>	24 <sup>2</sup>	50 <sup>2</sup>	. . .	
<i>Micromphale perforans</i>	<-1.49-2.6	<-0.01-1.8	<-2.92	38 <sup>1</sup>	50 <sup>2</sup>	38 <sup>2</sup>	67 <sup>4</sup>	74 <sup>3</sup>	62 <sup>5</sup>	9 <sup>1</sup>	. . .	. . .	55 <sup>5</sup>	57 <sup>4</sup>	27 <sup>4</sup>	29 <sup>2</sup>	33 <sup>2</sup>	22 <sup>3</sup>	38 <sup>2</sup>	24 <sup>2</sup>	48 <sup>5</sup>	75 <sup>5</sup>	
<i>Mycena alcalina</i> coll.	-0.07(-1.1(-2.6))	1.2-2.41	-0.20(-1.5)	7 <sup>1</sup>	38 <sup>2</sup>	25 <sup>2</sup>	. . .	. . .	8 <sup>1</sup>	9 <sup>1</sup>	. . .	. . .	18 <sup>1</sup>	. . .	6 <sup>1</sup>	19 <sup>2</sup>	11 <sup>1</sup>	. . .	13 <sup>1</sup>	10 <sup>1</sup>	4 <sup>1</sup>	. . .	
<i>Mycena amica</i>	-0.18(-1.3)	-0.42(-1.5)	-0.49(-1.4)	5 <sup>1</sup>	25 <sup>3</sup>	13 <sup>2</sup>	22 <sup>1</sup>	. . .	. . .	. . .	. . .	. . .	. . .	6 <sup>1</sup>	5 <sup>2</sup>	. . .	. . .	. . .	13 <sup>1</sup>	7 <sup>1</sup>	. . .	. . .	
<i>Mycena cinerella</i>	0.5-1.08-2.9	<-2.25→	0.7-1.10-1.9	16 <sup>1</sup>	25 <sup>1</sup>	25 <sup>1</sup>	11 <sup>1</sup>	32 <sup>3</sup>	15 <sup>3</sup>	9 <sup>1</sup>	6 <sup>1</sup>	. . .	9 <sup>1</sup>	10 <sup>1</sup>	15 <sup>3</sup>	19 <sup>3</sup>	33 <sup>1</sup>	11 <sup>1</sup>	29 <sup>1</sup>	10 <sup>2</sup>	12 <sup>2</sup>	13 <sup>1</sup>	
<i>Mycena cineroides</i>	<-0.91-3.2	<-0.86→	<-1.76→	52 <sup>1</sup>	63 <sup>1</sup>	100 <sup>4</sup>	78 <sup>4</sup>	74 <sup>2</sup>	62 <sup>2</sup>	27 <sup>1</sup>	25 <sup>1</sup>	. . .	73 <sup>5</sup>	52 <sup>4</sup>	39 <sup>4</sup>	52 <sup>3</sup>	67 <sup>6</sup>	22 <sup>2</sup>	63 <sup>4</sup>	59 <sup>4</sup>	44 <sup>4</sup>	50 <sup>4</sup>	
<i>Mycena epipterygia</i>	<-0.43-2.1(-2.6)	-0.36(->)	<-0.25(->)	14 <sup>1</sup>	50 <sup>1</sup>	63 <sup>1</sup>	16 <sup>1</sup>	. . .	9 <sup>1</sup>	. . .	. . .	. . .	18 <sup>1</sup>	14 <sup>1</sup>	6 <sup>1</sup>	19 <sup>2</sup>	22 <sup>1</sup>	11 <sup>1</sup>	13 <sup>1</sup>	17 <sup>2</sup>	8 <sup>1</sup>	25 <sup>1</sup>	
<i>Mycena filipes</i>	<-0.11-1.9	-0.50(-1.4)	-0.18(-1.5)	9 <sup>1</sup>	38 <sup>1</sup>	13 <sup>1</sup>	22 <sup>1</sup>	16 <sup>1</sup>	. . .	. . .	. . .	. . .	27 <sup>1</sup>	10 <sup>1</sup>	6 <sup>1</sup>	10 <sup>1</sup>	. . .	11 <sup>1</sup>	8 <sup>1</sup>	14 <sup>1</sup>	8 <sup>1</sup>	. . .	
<i>Mycena flavoalba</i>	<-0.78-2.6	<-1.90→	<-2.00→	33 <sup>1</sup>	75 <sup>3</sup>	63 <sup>2</sup>	78 <sup>2</sup>	37 <sup>2</sup>	38 <sup>1</sup>	9 <sup>1</sup>	. . .	. . .	36 <sup>1</sup>	29 <sup>2</sup>	24 <sup>3</sup>	38 <sup>2</sup>	56 <sup>1</sup>	11 <sup>1</sup>	25 <sup>1</sup>	34 <sup>4</sup>	44 <sup>3</sup>	38 <sup>2</sup>	
<i>Mycena galericulata</i>	<-0.66-2.3(-2.6)	<-1.35→	<-0.06→	20 <sup>1</sup>	50 <sup>3</sup>	38 <sup>2</sup>	33 <sup>2</sup>	32 <sup>1</sup>	8 <sup>1</sup>	. . .	18 <sup>1</sup>	. . .	27 <sup>1</sup>	24 <sup>1</sup>	15 <sup>2</sup>	24 <sup>1</sup>	11 <sup>1</sup>	22 <sup>1</sup>	38 <sup>1</sup>	14 <sup>2</sup>	8 <sup>2</sup>	25 <sup>1</sup>	
<i>Mycena galopus</i>	<-2.10→	<-0.72→	<-0.22→	71 <sup>1</sup>	50 <sup>3</sup>	75 <sup>4</sup>	89 <sup>1</sup>	100 <sup>2</sup>	92 <sup>6</sup>	82 <sup>3</sup>	44 <sup>3</sup>	18 <sup>1</sup>	91 <sup>5</sup>	76 <sup>6</sup>	64 <sup>4</sup>	71 <sup>4</sup>	56 <sup>6</sup>	89 <sup>7</sup>	83 <sup>6</sup>	62 <sup>4</sup>	60 <sup>3</sup>	75 <sup>5</sup>	
<i>Mycena longiseta</i>	<-0.79-2.7	<-2.82	<-0.08-1.6	23 <sup>2</sup>	38 <sup>2</sup>	50 <sup>3</sup>	44 <sup>2</sup>	26 <sup>2</sup>	38 <sup>1</sup>	9 <sup>1</sup>	. . .	. . .	27 <sup>1</sup>	5 <sup>1</sup>	18 <sup>2</sup>	38 <sup>3</sup>	44 <sup>4</sup>	22 <sup>1</sup>	38 <sup>2</sup>	21 <sup>2</sup>	20 <sup>1</sup>	. . .	
<i>Mycena metata</i>	<-0.75-3.4	<-0.20→	<-2.01→	58 <sup>1</sup>	100 <sup>8</sup>	88 <sup>6</sup>	89 <sup>7</sup>	79 <sup>3</sup>	62 <sup>3</sup>	36 <sup>2</sup>	25 <sup>1</sup>	9 <sup>1</sup>	91 <sup>5</sup>	62 <sup>4</sup>	42 <sup>4</sup>	57 <sup>4</sup>	67 <sup>4</sup>	56 <sup>4</sup>	54 <sup>5</sup>	59 <sup>6</sup>	56 <sup>5</sup>	75 <sup>5</sup>	
<i>Mycena pura</i>	-0.16(-1.7)	<-1.61→	(0.14)-0.7(-1.4)	7 <sup>1</sup>	38 <sup>2</sup>	25 <sup>2</sup>	22 <sup>1</sup>	. . .	. . .	. . .	. . .	. . .	9 <sup>1</sup>	5 <sup>1</sup>	6 <sup>1</sup>	5 <sup>1</sup>	22 <sup>2</sup>	. . .	8 <sup>1</sup>	17 <sup>1</sup>	. . .	. . .	
<i>Mycena rosea</i>	<-2.42→	<-2.01→	0.8-2.04→	80 <sup>1</sup>	50 <sup>1</sup>	100 <sup>6</sup>	78 <sup>4</sup>	84 <sup>1</sup>	100 <sup>1</sup>	91 <sup>1</sup>	88 <sup>1</sup>	36 <sup>2</sup>	73 <sup>4</sup>	76 <sup>6</sup>	76 <sup>6</sup>	90 <sup>8</sup>	89 <sup>8</sup>	78 <sup>8</sup>	83 <sup>3</sup>	79 <sup>6</sup>	92 <sup>6</sup>	38 <sup>3</sup>	
<i>Mycena rosella</i>	<-0.81-2.6	-0.25(-1.5)	<-2.49→	14 <sup>1</sup>	13 <sup>1</sup>	38 <sup>2</sup>	22 <sup>1</sup>	21 <sup>1</sup>	9 <sup>1</sup>	. . .	. . .	. . .	27 <sup>1</sup>	14 <sup>1</sup>	6 <sup>1</sup>	24 <sup>1</sup>	. . .	. . .	13 <sup>1</sup>	10 <sup>1</sup>	16 <sup>1</sup>	38 <sup>1</sup>	
<i>Mycena rubromarginata</i>	0.6-1.82-3.4	<-1.15-1.6	<-2.49→	26 <sup>1</sup>	13 <sup>1</sup>	50 <sup>3</sup>	33 <sup>3</sup>	37 <sup>3</sup>	38 <sup>2</sup>	18 <sup>2</sup>	13 <sup>1</sup>	9 <sup>1</sup>	36 <sup>1</sup>	38 <sup>1</sup>	24 <sup>2</sup>	19 <sup>1</sup>	11 <sup>3</sup>	11 <sup>2</sup>	21 <sup>1</sup>	21 <sup>2</sup>	28 <sup>2</sup>	75 <sup>1</sup>	
<i>Mycena sanguinolenta</i>	0.5-1.22-2.4(-3.4)	<-2.28→	(0.0)-30.8-2.39	24 <sup>1</sup>	25 <sup>3</sup>	38 <sup>3</sup>	88 <sup>3</sup>	78 <sup>2</sup>	79 <sup>2</sup>	69 <sup>2</sup>	64 <sup>2</sup>	50 <sup>1</sup>	9 <sup>1</sup>	18 <sup>2</sup>	29 <sup>2</sup>	24 <sup>2</sup>	14 <sup>2</sup>	44 <sup>4</sup>	33 <sup>2</sup>	29 <sup>2</sup>	16 <sup>2</sup>	25 <sup>1</sup>	
<i>Mycena stylobates</i>	<-1.56-3.6(-?)	<-0.57→	<-2.70	62 <sup>1</sup>	63 <sup>1</sup>	88 <sup>1</sup>	78 <sup>2</sup>	79 <sup>2</sup>	69 <sup>2</sup>	64 <sup>2</sup>	50 <sup>1</sup>	9 <sup>1</sup>	64 <sup>6</sup>	76 <sup>4</sup>	48 <sup>3</sup>	71 <sup>4</sup>	56 <sup>6</sup>	33 <sup>4</sup>	42 <sup>4</sup>	55 <sup>2</sup>	92 <sup>5</sup>	88 <sup>1</sup>	
<i>Mycena stylobates</i>	0.6-0.98-2.3	0.6-1.34-1.8	0.7-2.09→	8 <sup>1</sup>	13 <sup>1</sup>	13 <sup>1</sup>	22 <sup>1</sup>	16 <sup>1</sup>	8 <sup>1</sup>	. . .	. . .	. . .	9 <sup>1</sup>	14 <sup>1</sup>	3 <sup>1</sup>	10 <sup>1</sup>	11 <sup>1</sup>	. . .	17 <sup>1</sup>	12 <sup>1</sup>	13<		

concentrations to plots with high DCA 2 scores and *Lactarius theiogalus* (Fig. 71) and to a lesser degree *Cortinarius albovariegatus* (Fig. 33) to low-score plots. Most typical pine-forest species were absent from plots with high DCA 2 scores. Species with decreasing abundance along the third axis were, among others, *Cortinarius flexipes* (Fig. 46), *Hygrophorus olivaceoalbus* (Fig. 62), and *Russula betularum* (Fig. 86), while the abundances of *Russula rhodophoda* (Fig. 96) and *Russula vinosa* (Fig. 98) increased along this axis.

### Saprotrophs

Several saprotrophic species were very common, spanning most of the first DCA axis (see Tab. 16): *Galerina atkinsoniana* (Figs 119, 120), *G. hypnorum* (Figs 121, 122), *Marasmius androsaceus* (Figs 135, 136), *Mycena galopus* (Figs 157, 158), *M. rorida* (Figs 165, 166), and *M. septentrionalis* (Figs 173, 174). *Marasmius androsaceus* had its optimum displaced towards the pine-forest end of DCA 1 because of high occurrence in *Calluna*-dominated vegetation. The other species had quantitative optima near the middle of the axis. Other species with wide amplitude but somewhat lower frequencies include *Cystoderma jasonis* and *Mycena sanguinolenta*.

Species restricted to special substrates had wide amplitudes with respect to DCA 1 [e.g. *Calocera viscosa* (Figs 103, 104) and *Mycena rubromarginata* (Figs 169, 170) which were found on small pieces of wood, and *Collybia tuberosa* (Figs 111, 112) which grew on dead agaric fruitbodies] if their preferred substrate was present in all forest types. An alternative case is represented by *Strobilurus esculentus* (Figs 181, 182), which was restricted to spruce cones. This species was very common at low DCA 1 scores while stopped abruptly at 2.6 S.D. units along DCA 1 and was thus restricted to plots classified to series 4-6.

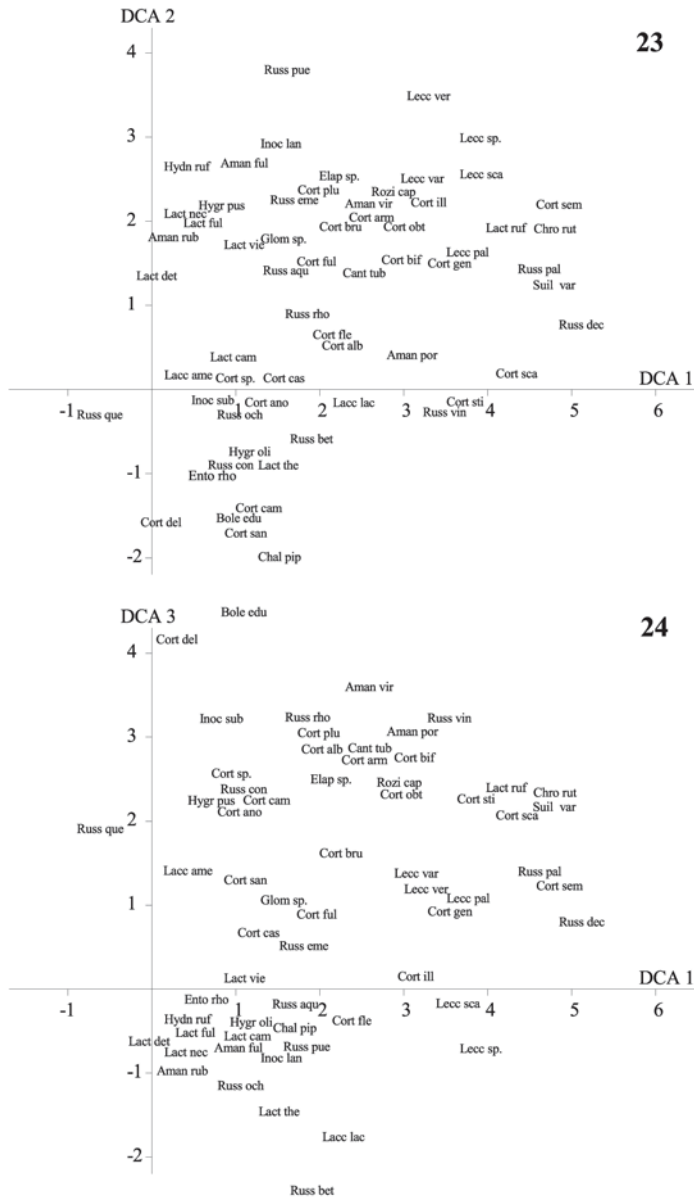
Very common species with wide amplitudes but with a limit towards high DCA 1 scores, were *Mycena metata* which was restricted to plots with DCA 1 < 3.4 S.D. units (Figs 161, 162), *M. cineroides* (DCA 1 < 3.2 S.D., cf. Figs 147, 148), and *M. rosella* (Figs 167, 168; DCA 1 < 2.6 S.D.). These *Mycena* species fruited in rainy periods late in the autumn. Similar distributions along DCA 1 but with lower frequencies were observed for *M. flavoalba* (Figs 153, 154) and *M. longiseta* (Figs 159, 160).

Several species were largely restricted to plots with low DCA 1 scores (series 5 and 6). Examples are *Mycena pura* (Figs 163, 164, DCA < 1.7 S.D. units) and *M. vulgaris* (Figs 179, 180, DCA 1 < 2.0 S.D.), the wood-inhabiting species *Galerina marginata* (Figs 123, 124, DCA 1 < 1.0 S.D.), and the litter-decomposing species *Clavariadelphus junceus* (Figs 105, 106, DCA 1 < 1.1(-1.5) S.D.) and *Marasmius epiphyllus* (Figs 137, 138, DCA 1 < 2.4 S.D. units). Few saprotrophs had narrow or intermediately narrow amplitudes along DCA 1 and optimum in site type 5.1. Exceptions were *Micromphale perforans* (Figs 139, 140, DCA 1 < 2.6 S.D.), which grew on spruce needles, and *Galerina mniophila* (Figs 125, 126,  $r = (0.5-1.3-2.9)$ ).

Only a few infrequent species were restricted to plots with high DCA 1 scores. Of these, especially *Collybia putilla* and *Mycena clavicularis* seemed to have distinct optima in dry pine forests.

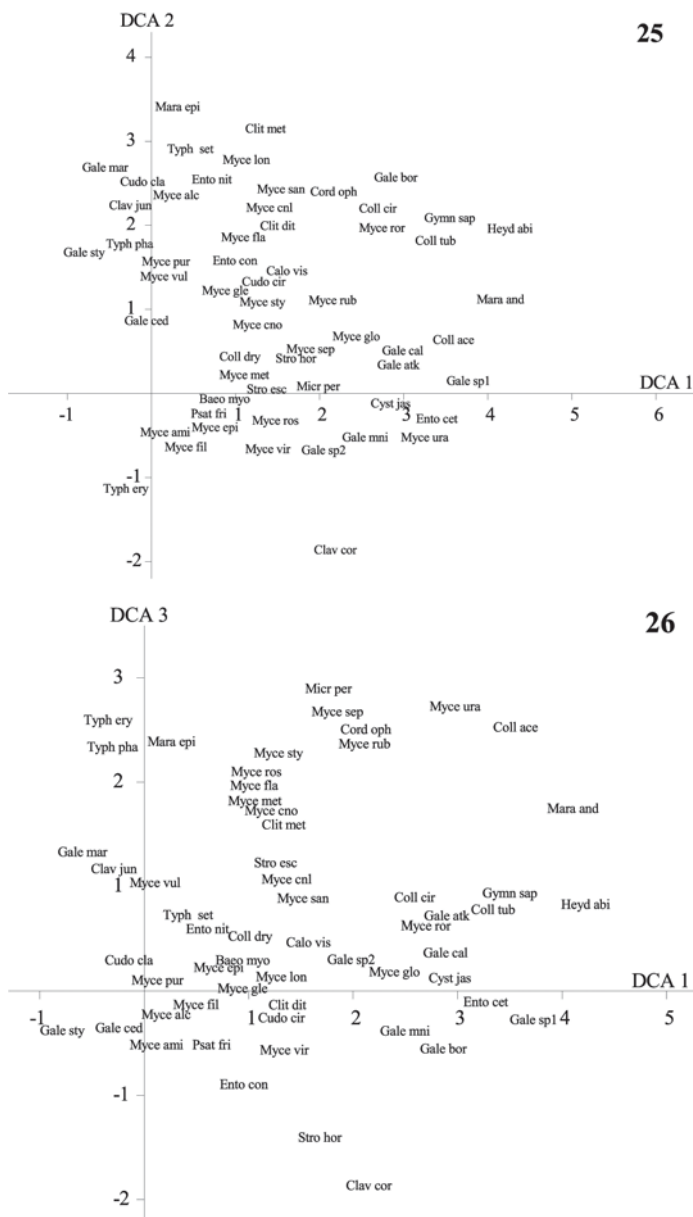
Two of the three *Typhula* species, *T. phacorrhiza* (Figs 185, 186) and the very common and highly abundant *T. setipes* (Figs 187, 188), had restricted distributions along DCA 1 as well as DCA 2. These species were concentrated to plots with high DCA 2 scores while DCA 1 scores were low (< 2.3 S.D. and < 1.1 S.D., respectively). A similar pattern was shared by *Clavariadelphus junceus* (Figs 105, 106) and *Marasmius epiphyllus* (Figs 137, 138), which increased markedly along DCA 2 and occurred in plots with DCA 1 scores below 1.1 (-1.5) and 2.4, respectively. Restriction to low DCA 1 and high DCA 2 scores were observed for *Galerina marginata* (Figs 123, 124), a wood-inhabitant with low frequency in our material. The third *Typhula* species, *T. erythropus* (Figs 183, 184), resembled its congeners with respect to amplitude along DCA 1, but had a different distribution along DCA-axis 2.





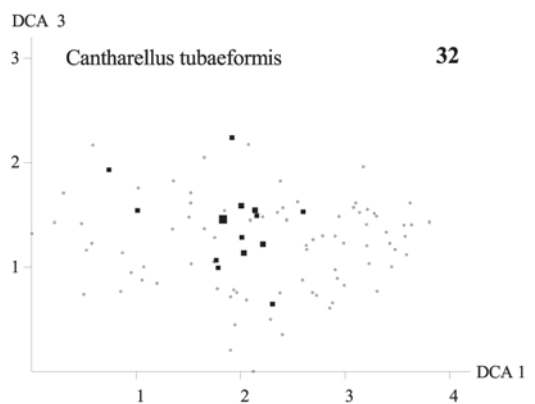
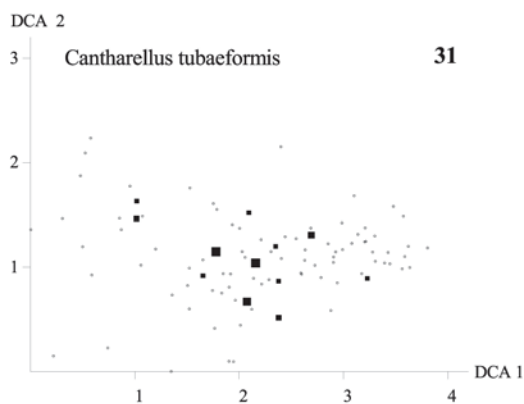
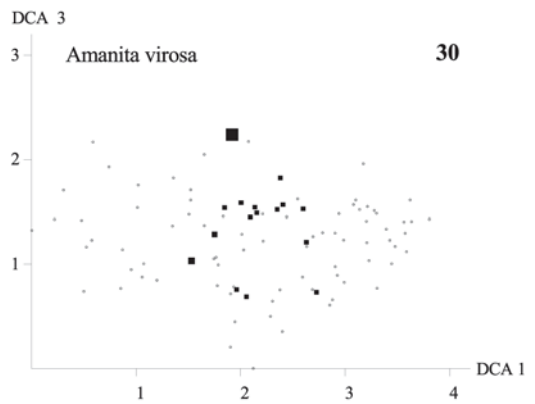
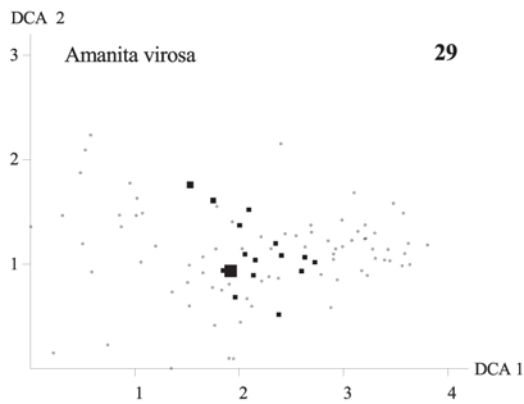
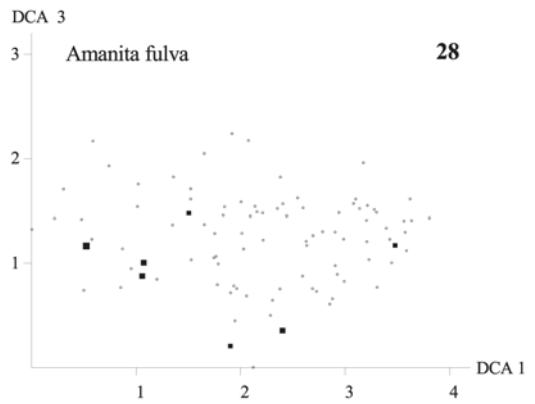
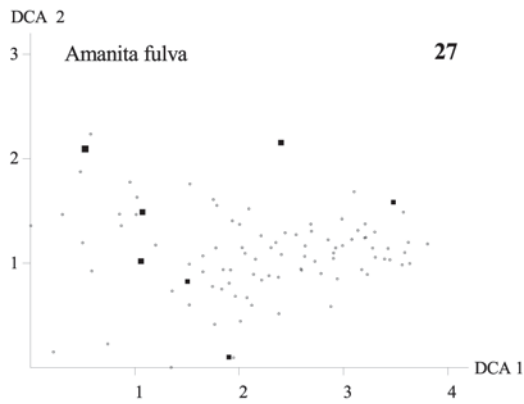
Figs 23–24. DCA ordination of the MAF 95 data set; species optima for ectomycorrhizal species along axes scaled in S.D. units. Fig. 23. Axes 1 (horizontal) and 2. Fig. 24. Axes 1 (horizontal) and 3. Species names are abbreviated in accordance with Appendix 1. Species present in only one or two macro plots are excluded.

A group of species with decreasing abundances along DCA 2 was represented by *Cystoderma jasonis* (Fig. 113), *Galerina* sp.1 (Fig. 127), *G.* sp.2 (Fig. 125), *G. mniophila* (Fig. 125), and *Mycena rubromarginata* (Fig. 169). All of these species were also scarce or lacking at very low DCA 1 scores.

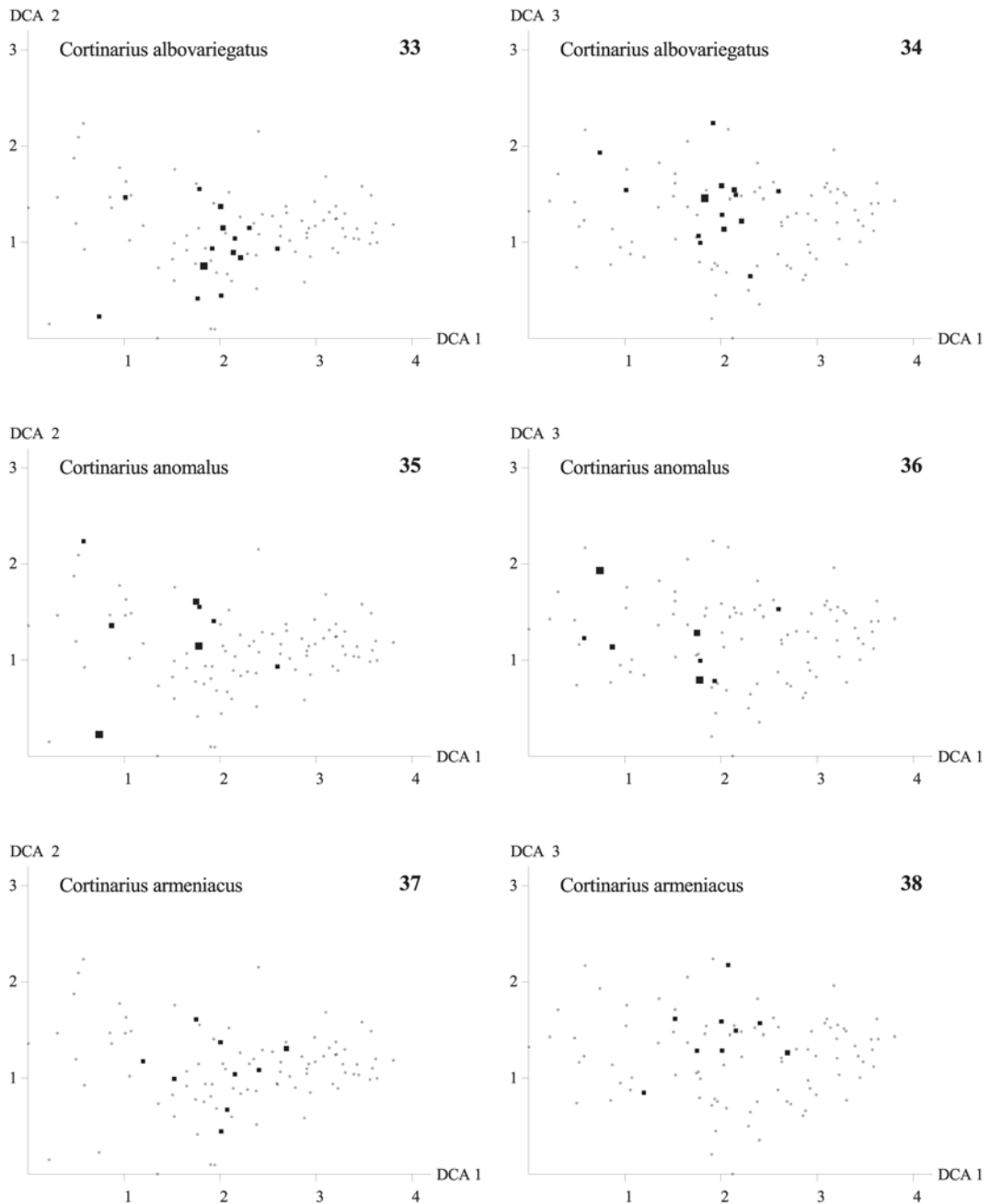


Figs 25–26. DCA ordination of the MAF 95 data set; species optima for saprotrophic species along axes scaled in S.D. units. Fig. 25. Axes 1 (horizontal) and 2. Fig. 26. Axes 1 (horizontal) and 3. Species names are abbreviated in accordance with Appendix 1. Species present in only one or two macro plots are excluded.

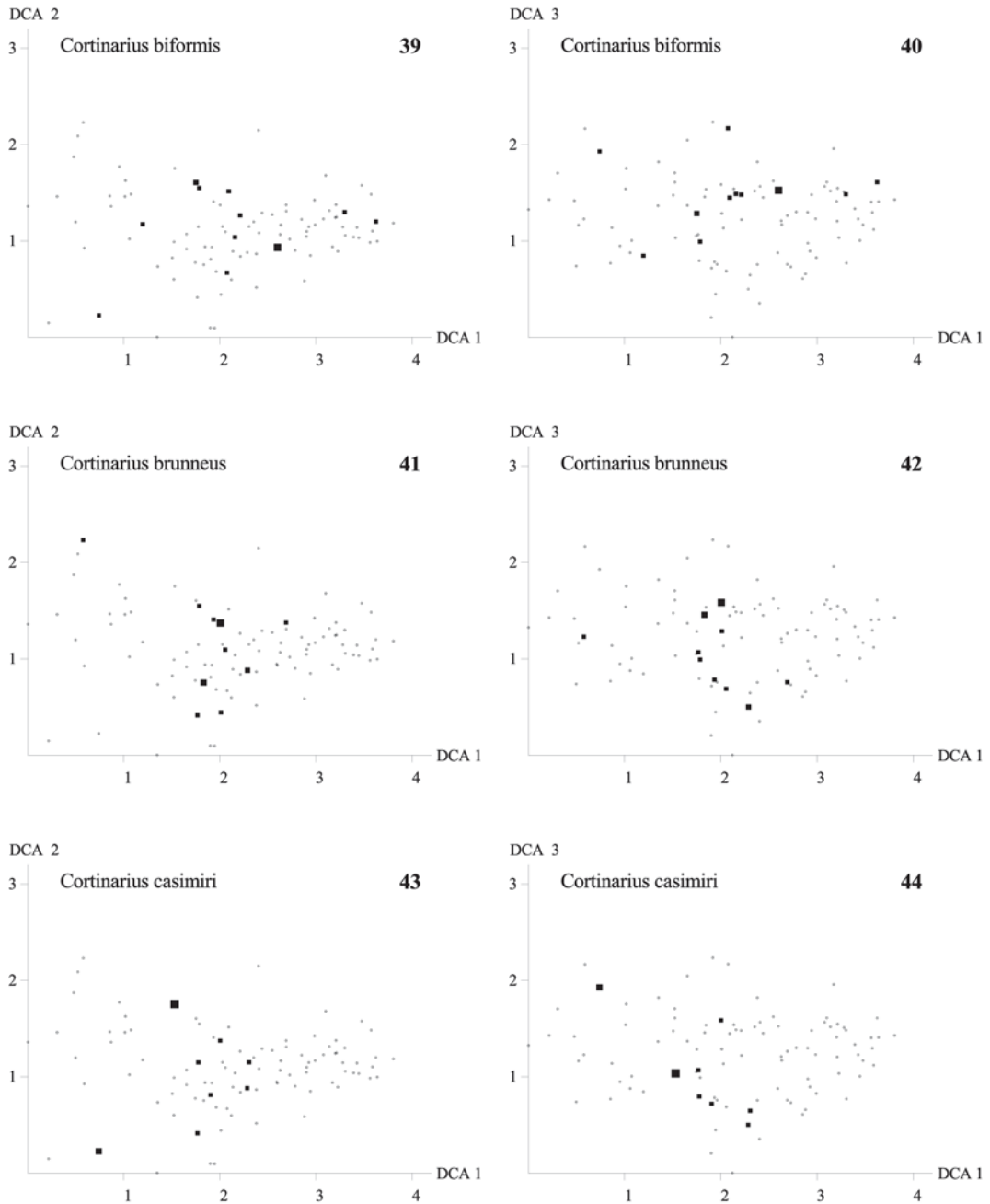
Examples of species that decreased along the third axis are *Entoloma cetratum* (Fig. 116), *Mycena galopus* (Fig. 158) and *G. mniophila* (Fig. 126), while *Marasmius epiphyllus* (Fig. 138), *Micromphale perforans* (Fig. 140), *Mycena septentrionalis* (Fig. 174), *Typhula erythropus* (Fig. 184), and *T. phaecorrhiza* (Fig. 186) increased along that axis.



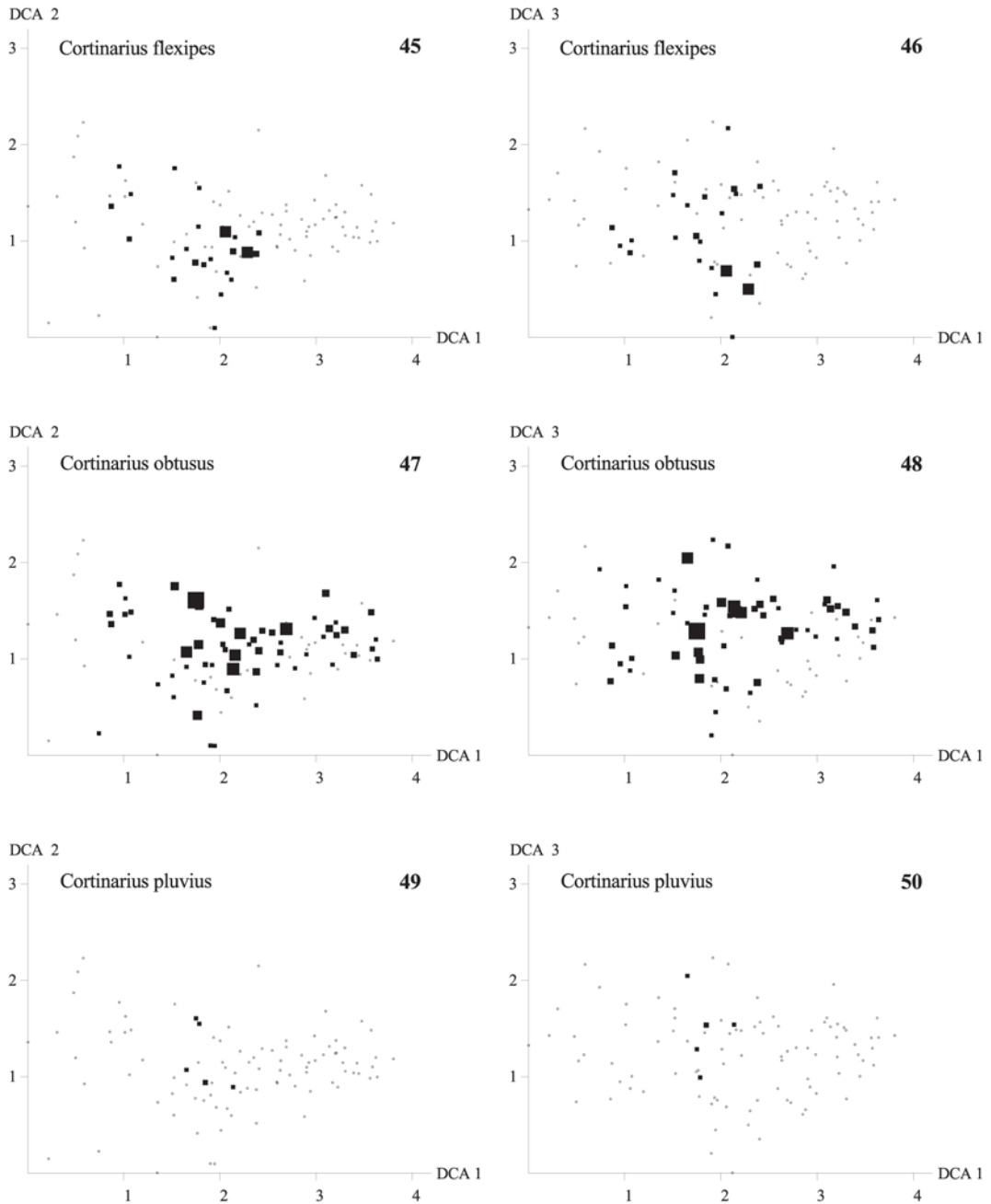
Figs 27–32. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 27–28. *Amanita fulva*, Figs 29–30. *Amanita virosa*, Figs 31–32. *Cantharellus tubaeformis*.



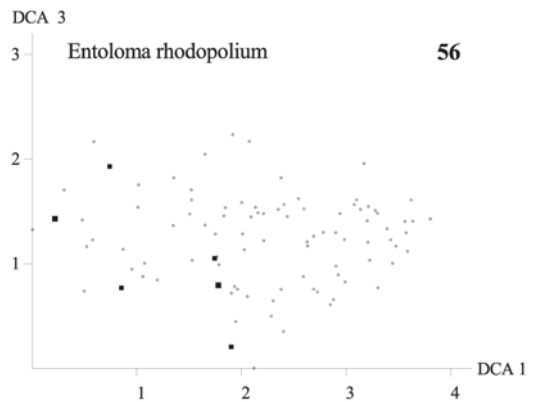
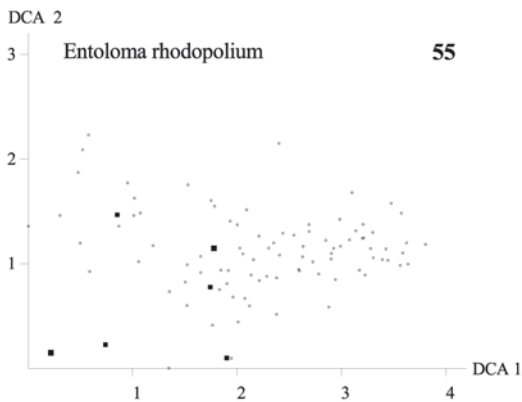
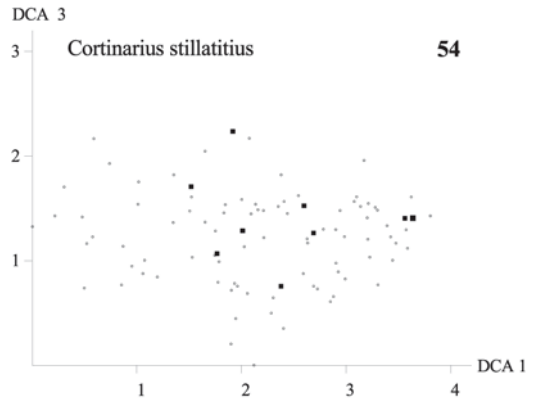
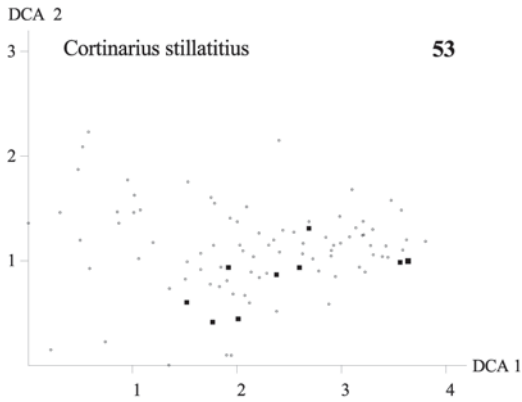
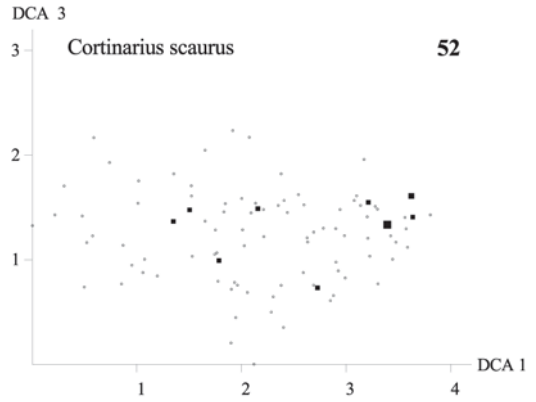
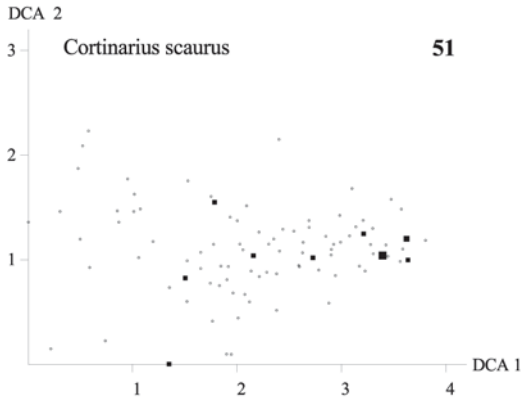
Figs 33–38. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 33–34. *Cortinarius albovariegatus*, Figs 35–36. *Cortinarius anomalus*, Figs 37–38. *Cortinarius armeniacus*.



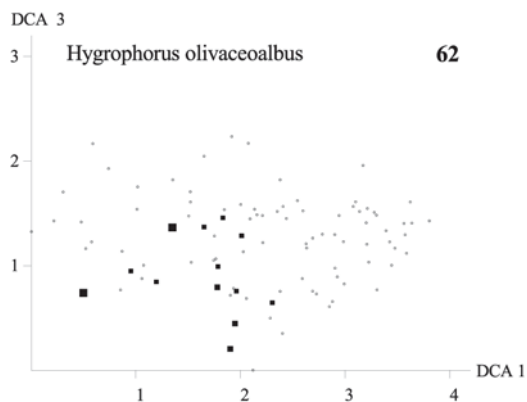
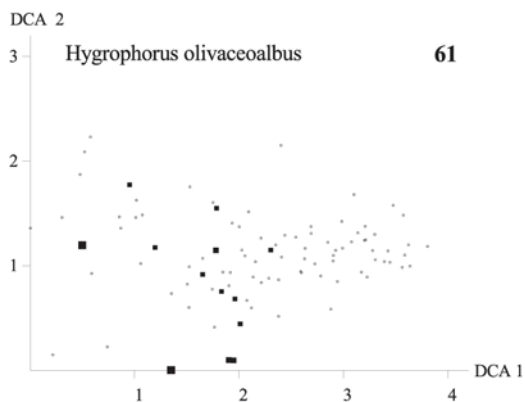
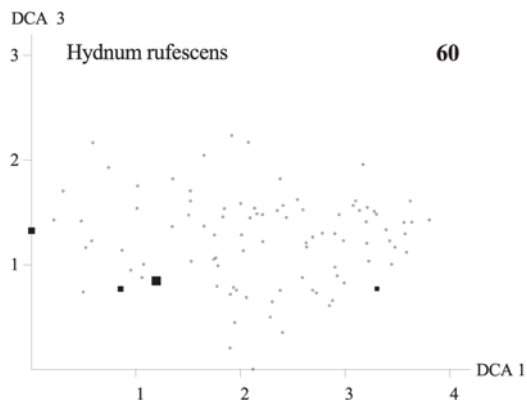
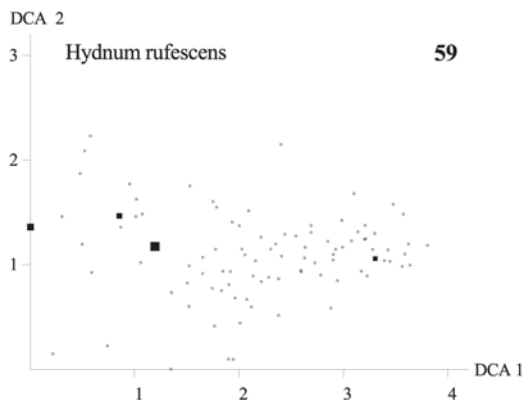
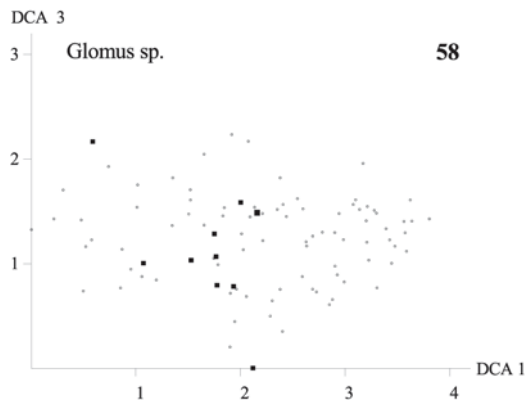
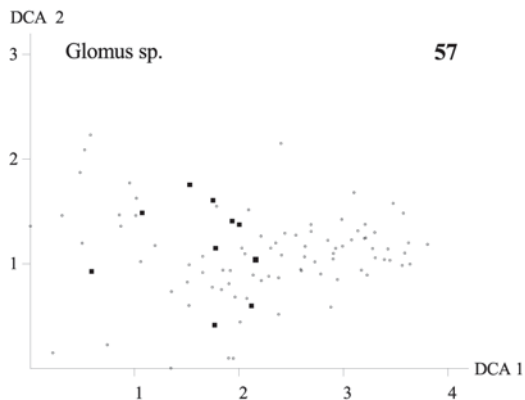
Figs 39–44. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 39–40. *Cortinarius biformis*, Figs 41–42. *Cortinarius brunneus*, Figs 43–44. *Cortinarius casimiri*.



Figs 45–50. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 45–46. *Cortinarius flexipes*, Figs 47–48. *Cortinarius obtusus*, Figs 49–50. *Cortinarius pluvius*.

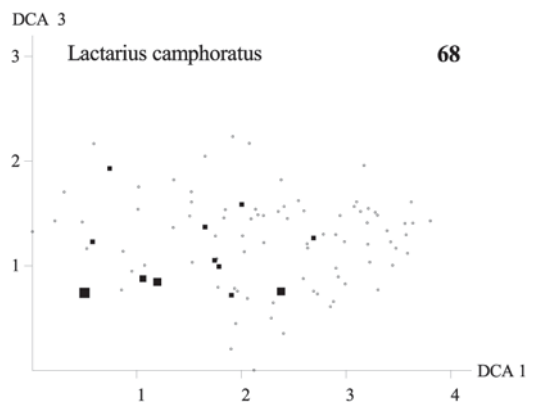
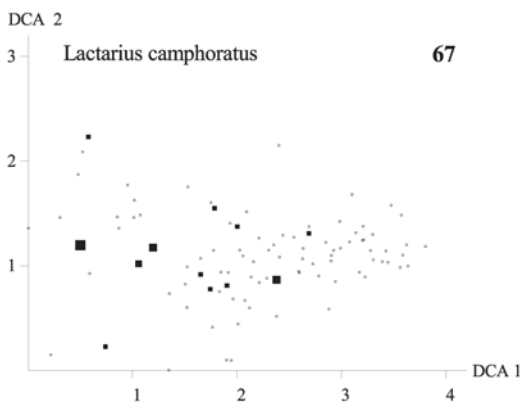
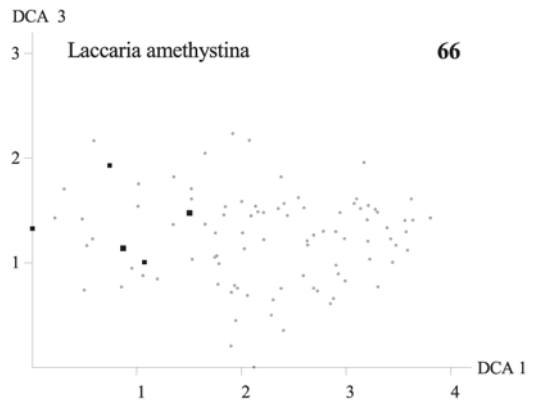
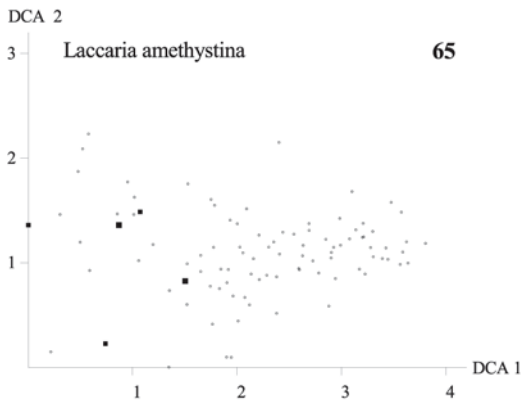
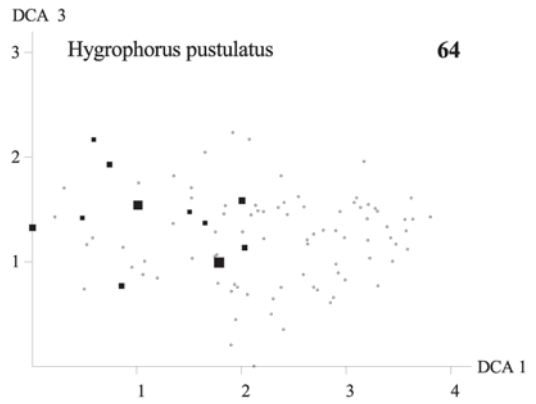
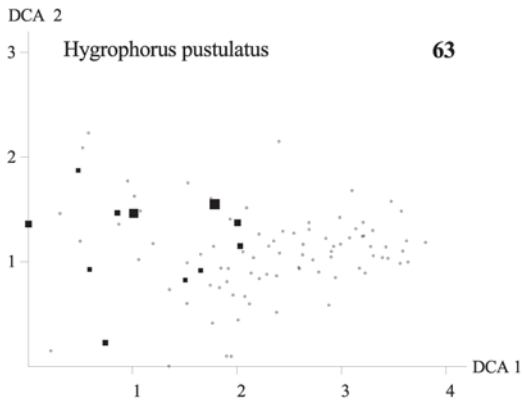


Figs 51–56. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 51–52. *Cortinarius scaurus*, Figs 53–54. *Cortinarius stillatitius*, Figs 55–56. *Entoloma rhodopolium*.

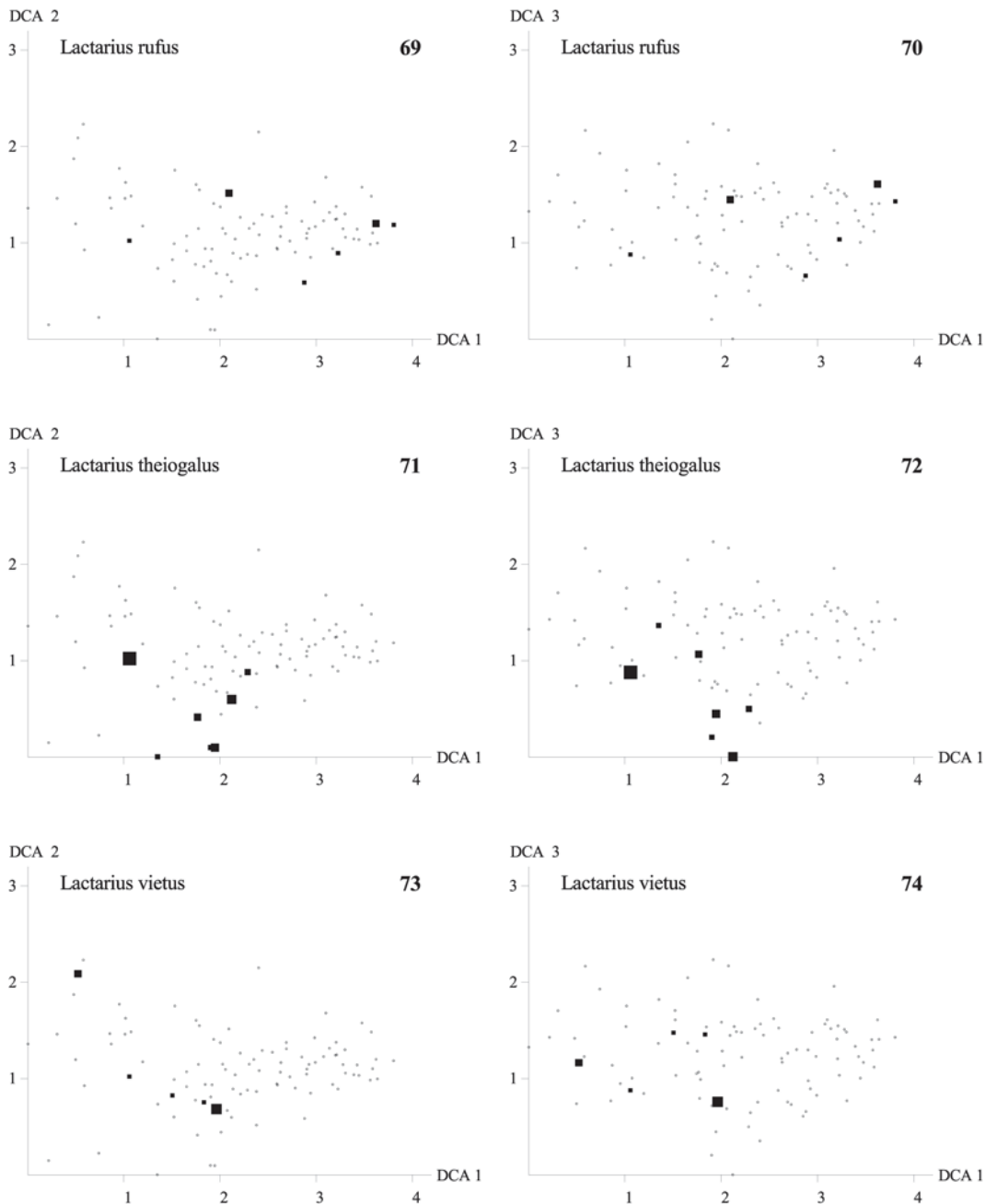


Figs 57–62. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 57–58. *Glomus* sp., Figs 59–60. *Hydnum rufescens*, Figs 61–62. *Hygrophorus olivaceoalbus*.

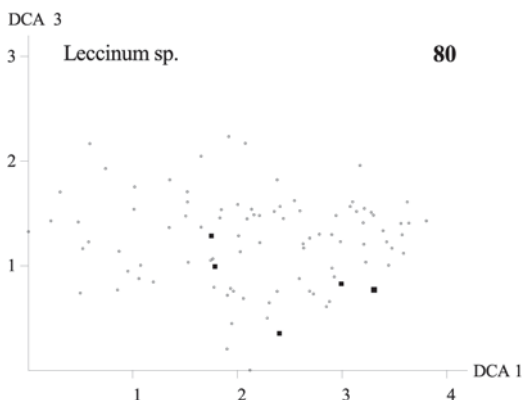
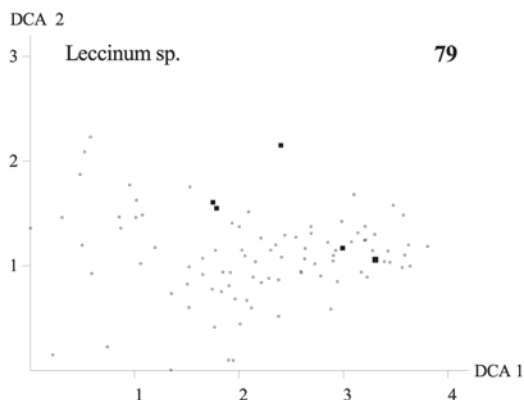
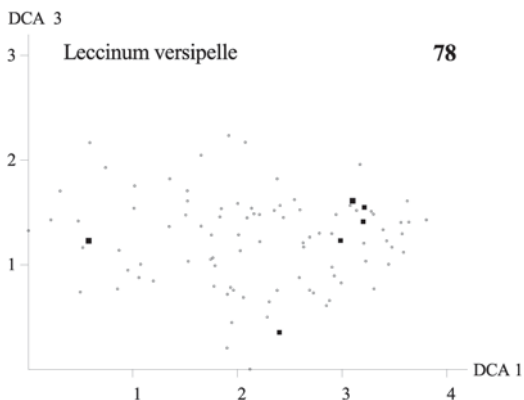
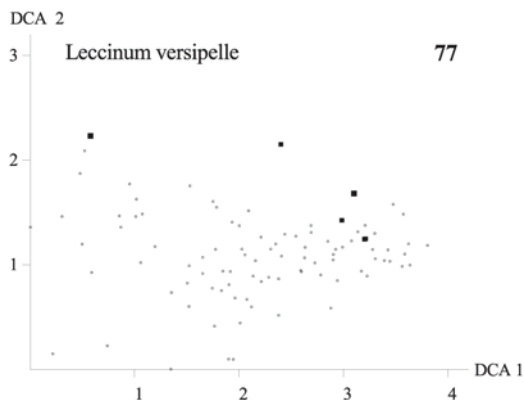
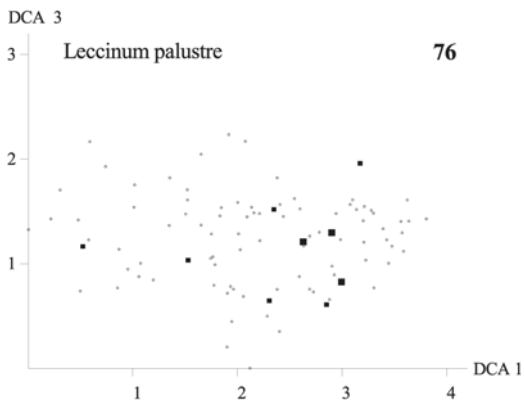
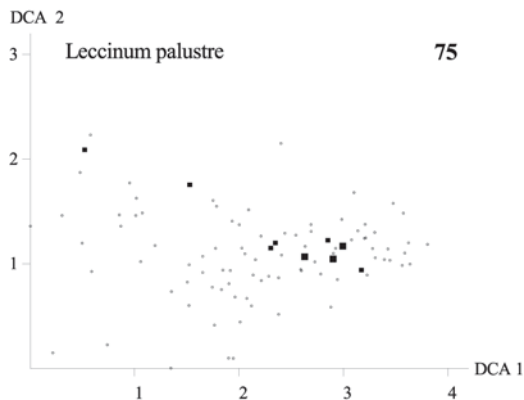




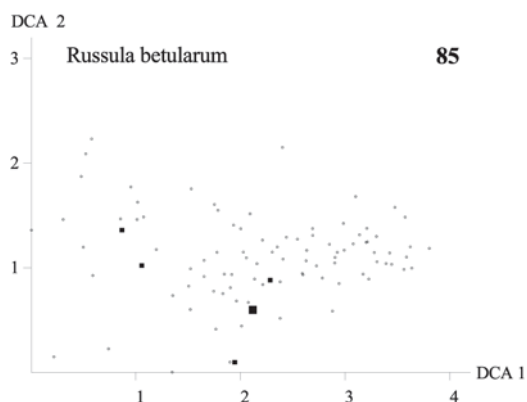
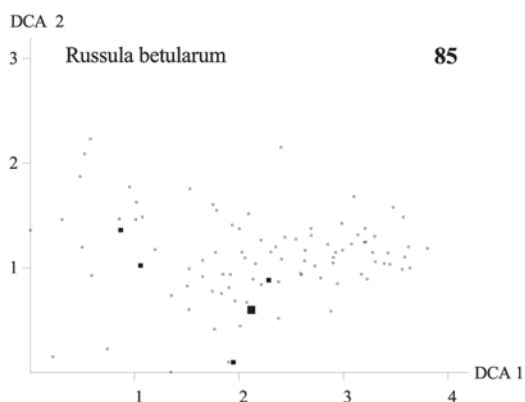
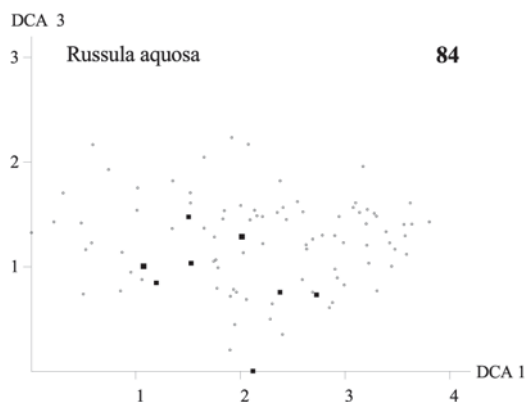
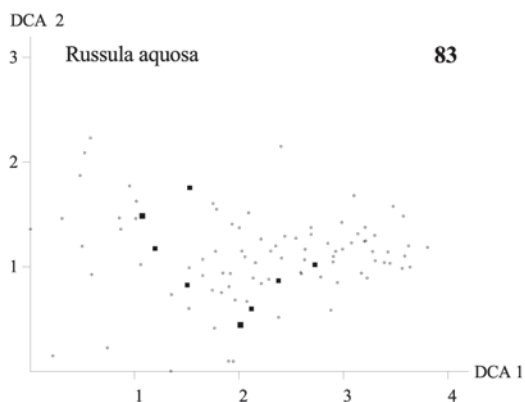
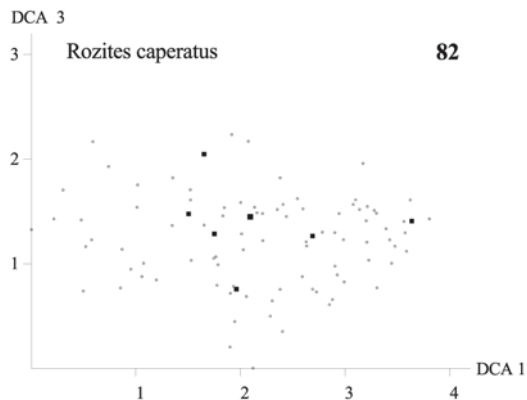
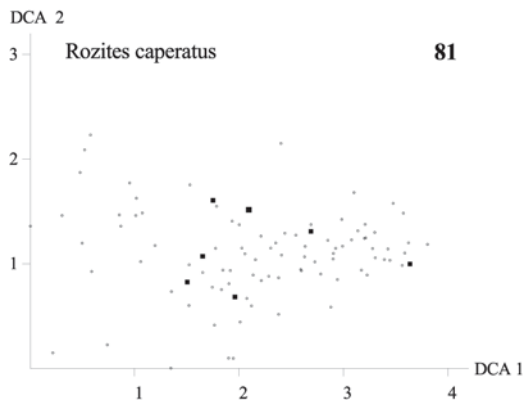
Figs 63–68. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 63–64. *Hygrophorus pustulatus*, Figs 65–66. *Laccaria amethystina*, Figs 67–68. *Lactarius camphoratus*.



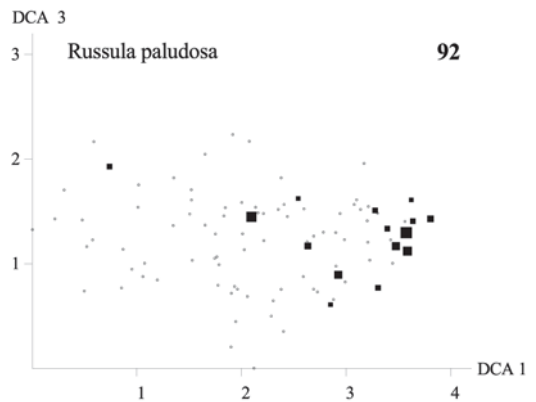
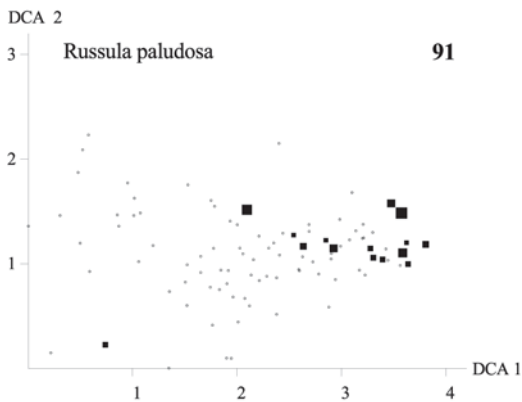
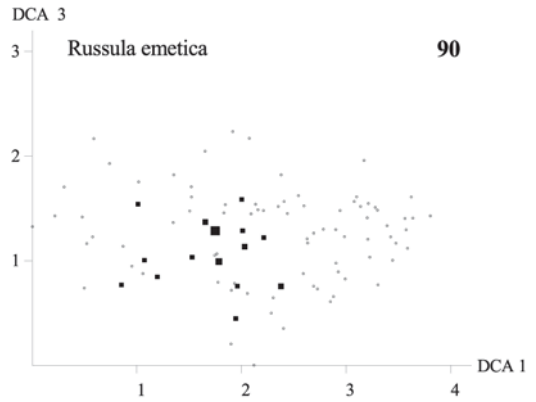
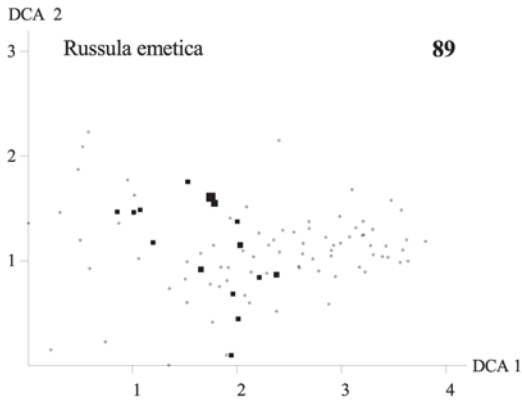
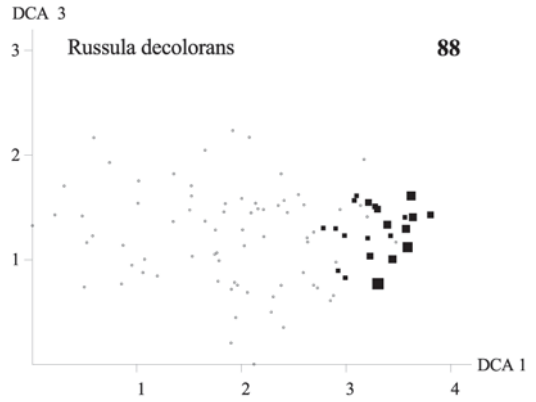
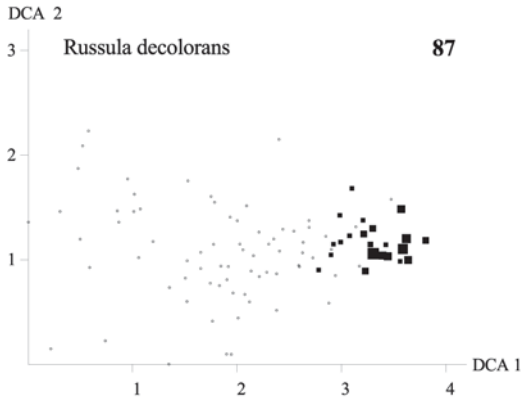
Figs 69–74. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 69–70. *Lactarius rufus*, Figs 71–72. *Lactarius theiogalus*, Figs 73–74. *Lactarius vietus*.



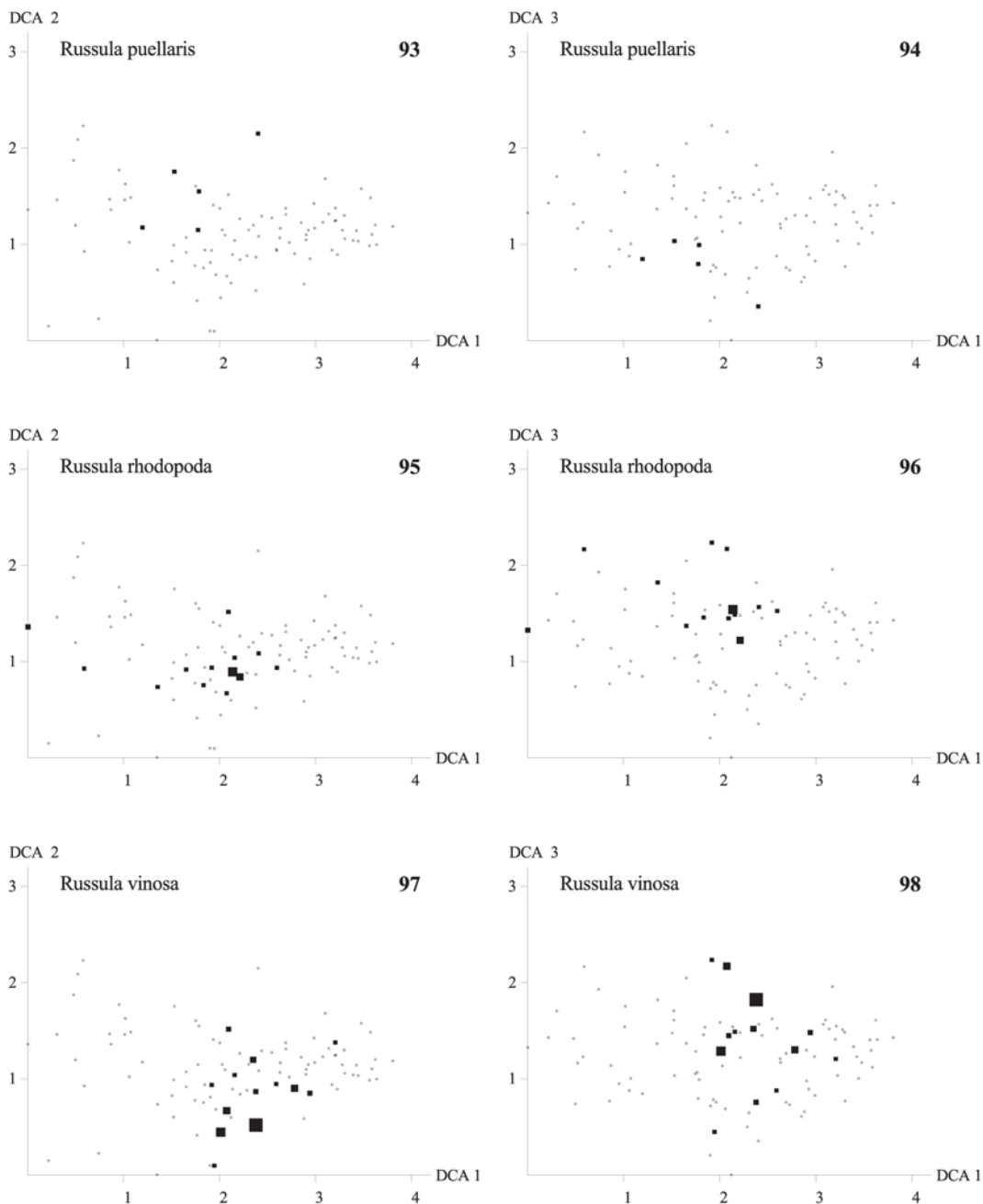
Figs 75–80. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 75–76. *Leccinum palustre*, Figs 77–78. *Leccinum versipelle*, Figs 79–80. *Leccinum sp.*.



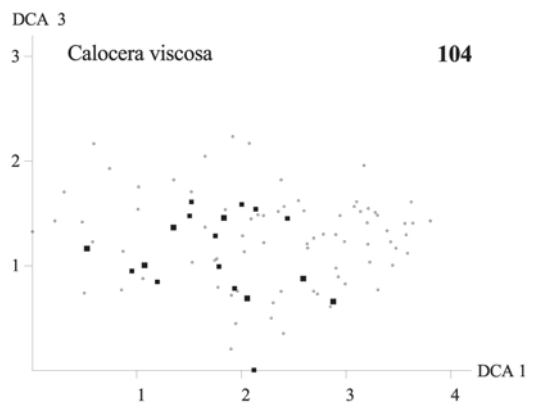
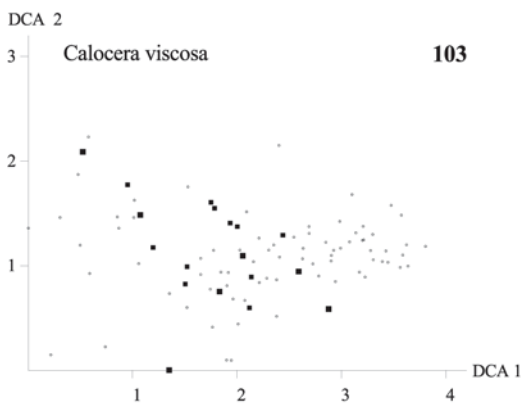
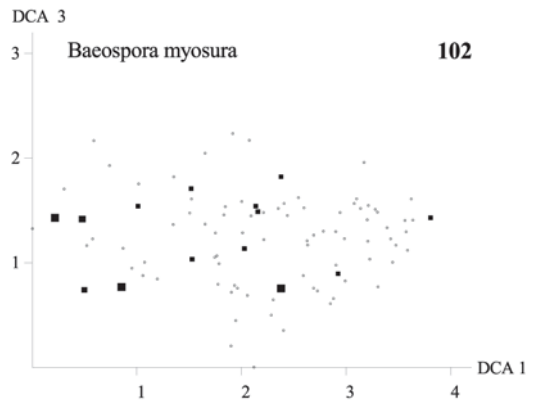
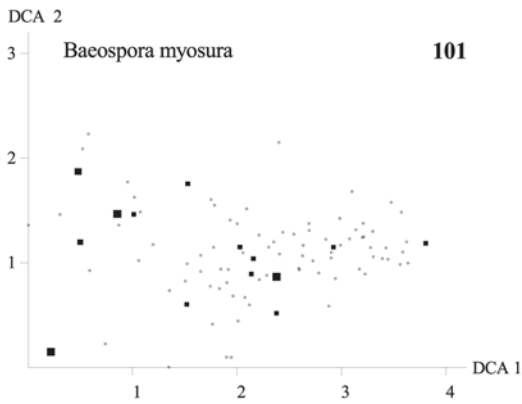
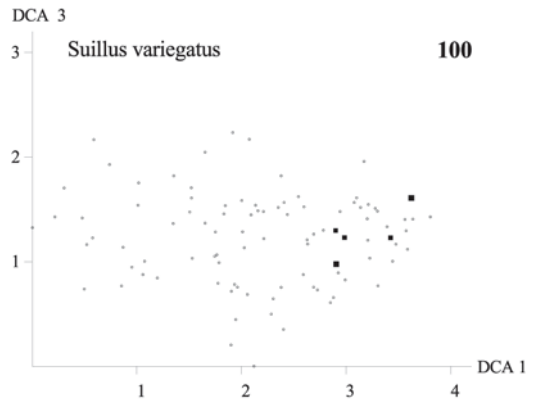
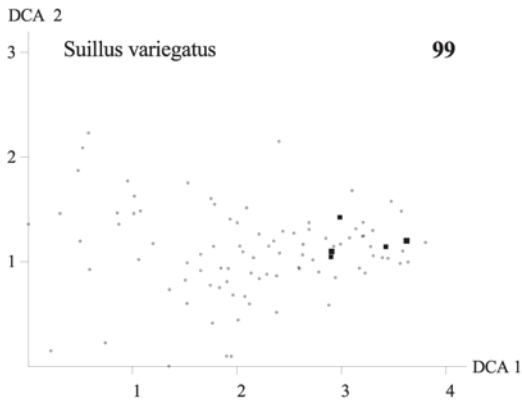
Figs 81–86. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 81–82. *Rozites caperatus*, Figs 83–84. *Russula aquosa*, Figs 85–86. *Russula betularum*.



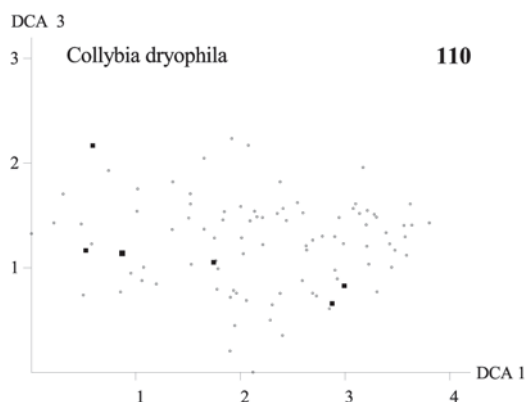
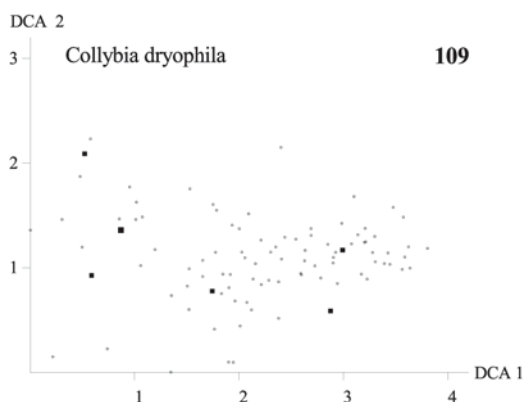
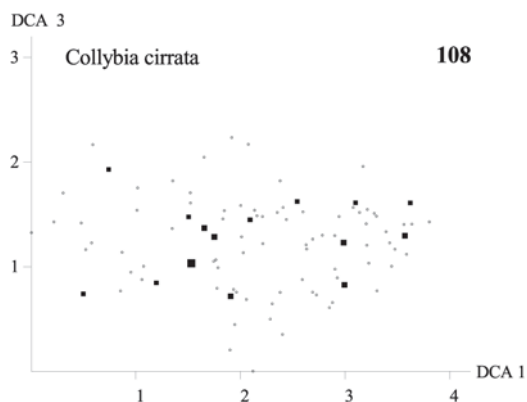
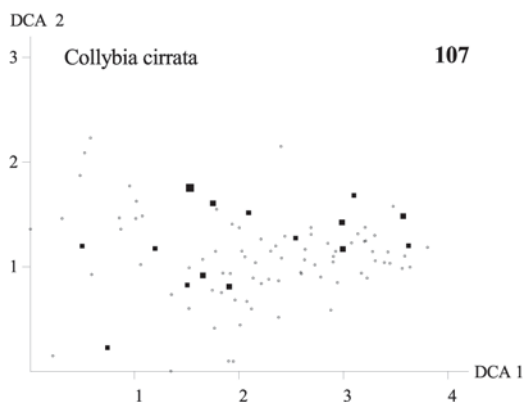
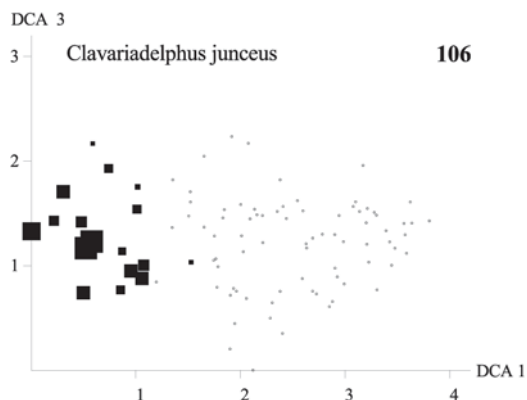
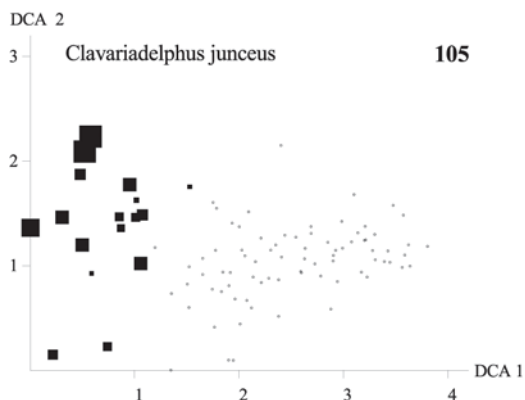
Figs 87–92. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 87–88. *Russula decolorans*, Figs 89–90. *Russula emetica*, Figs 91–92. *Russula paludosa*.



Figs 93–98. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 93–94. *Russula puellaris*, Figs 95–96. *Russula rhodopoda*, Figs 97–98. *Russula vinosa*.

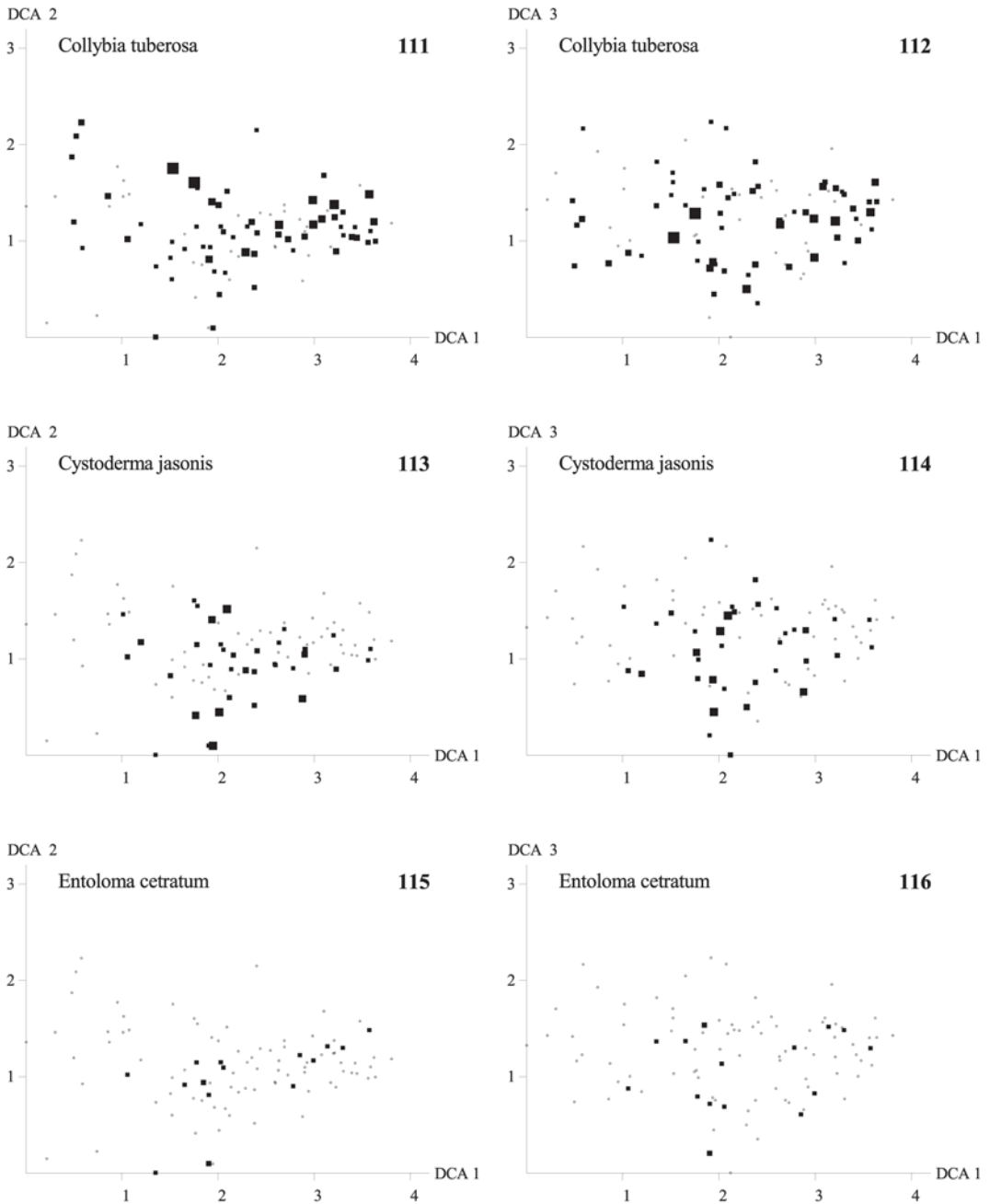


Figs 99–104. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 99–100. *Suillus variegatus*, Figs 101–102. *Baeospora myosura*, Figs 103–104. *Calocera viscosa*.

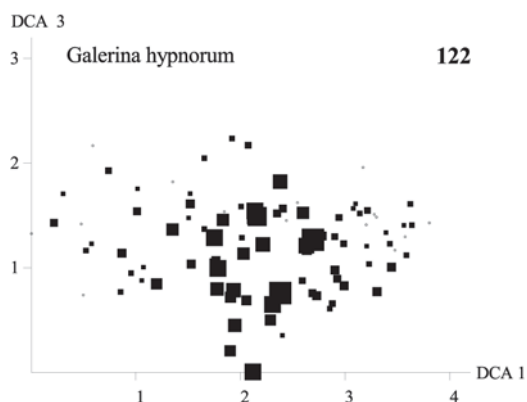
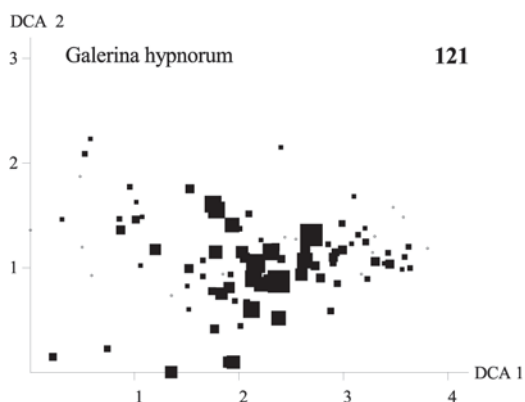
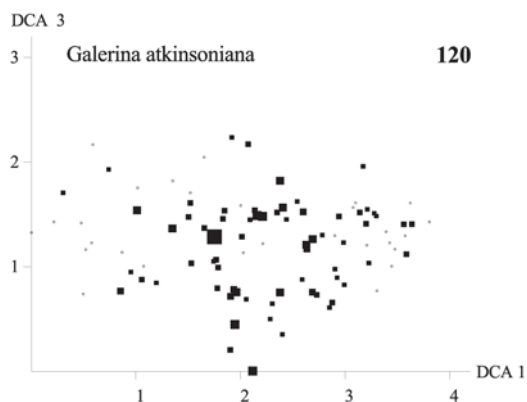
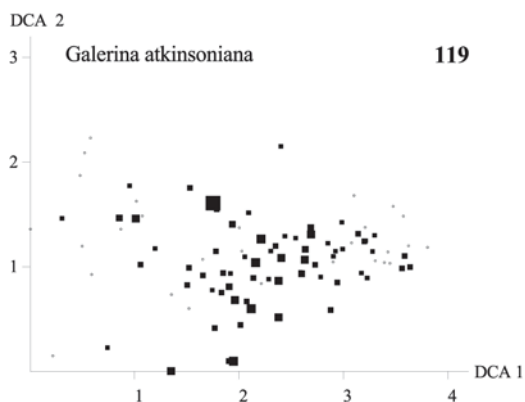
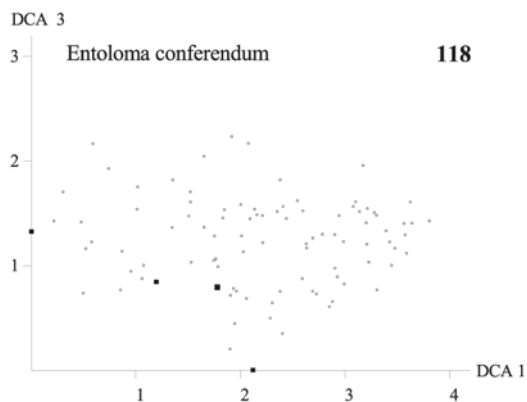
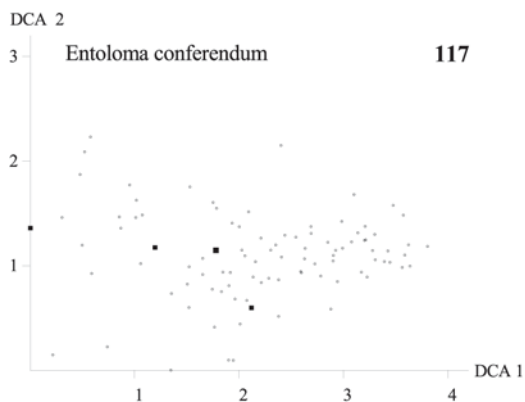


Figs 105–110. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 105–106. *Clavariadelphus junceus*, Figs 107–108. *Collybia cirrata*, Figs 109–110. *Collybia dryophila*.

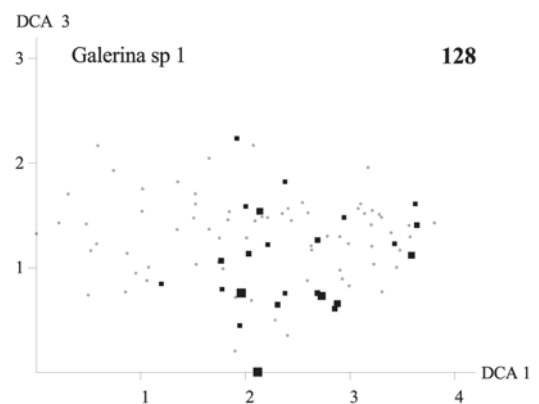
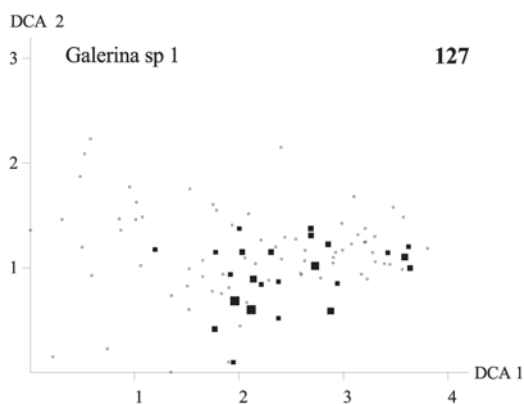
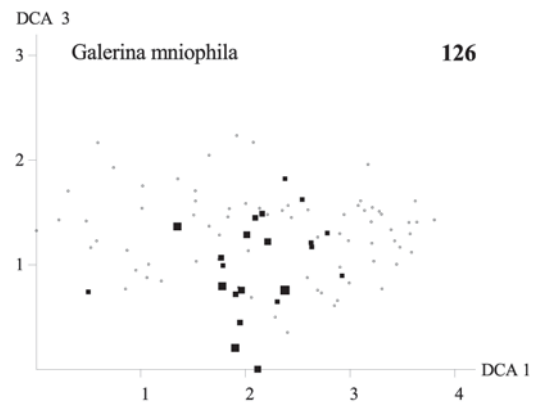
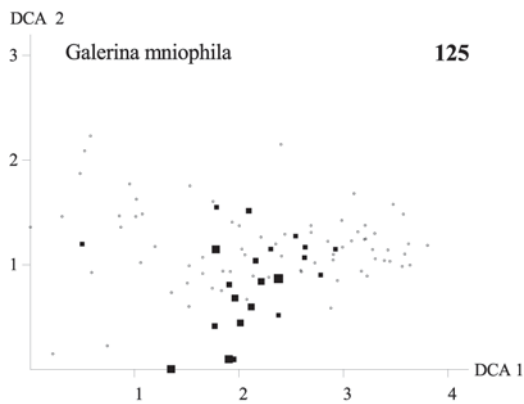
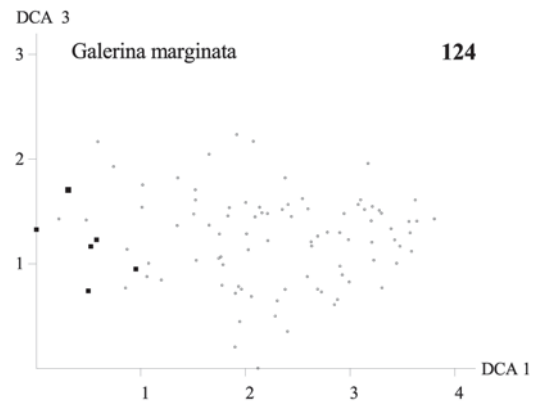
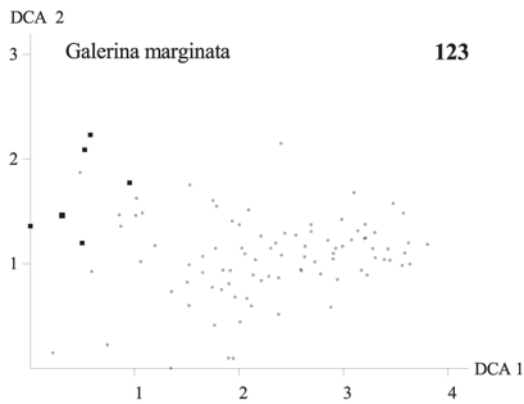




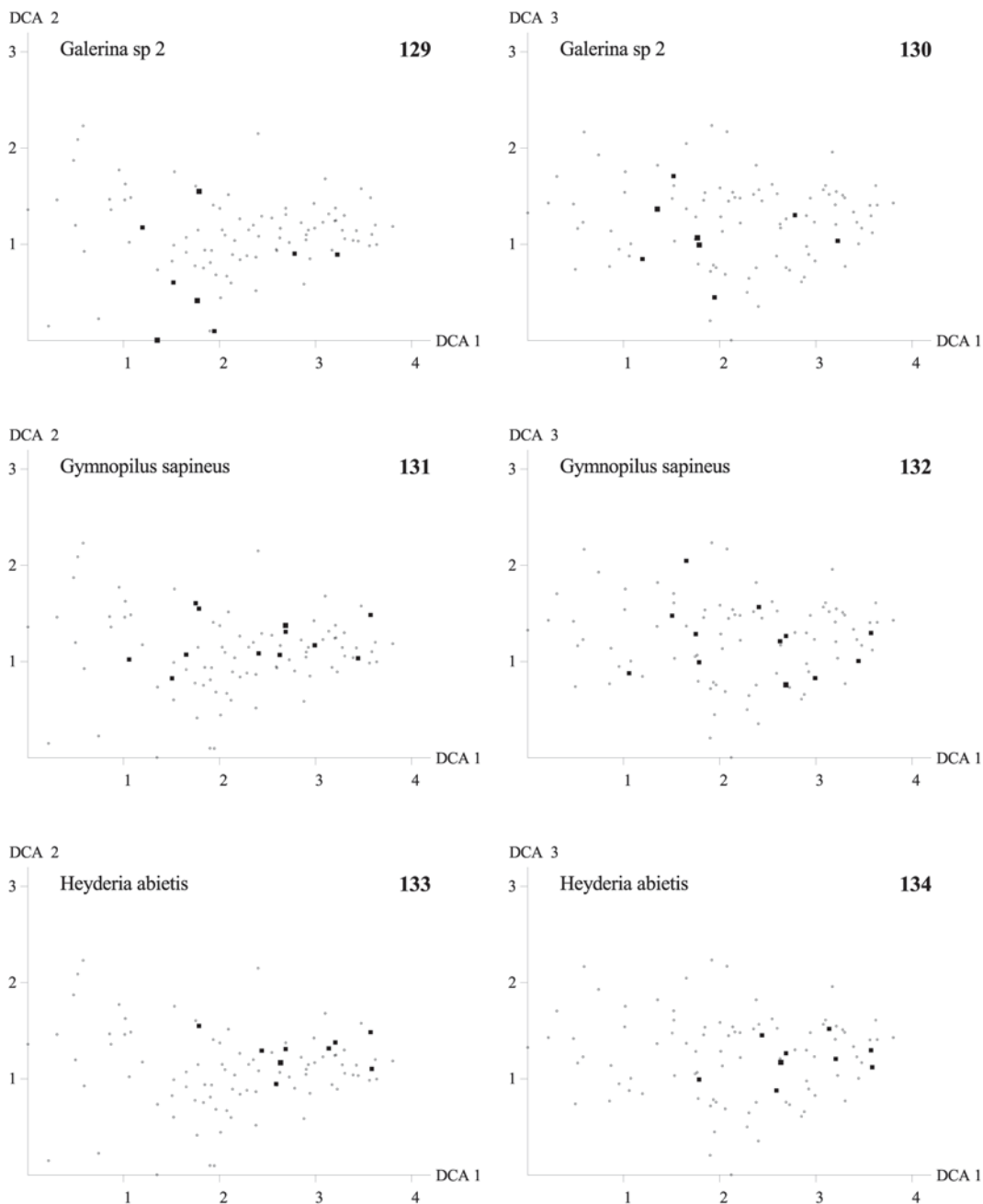
Figs 111–116. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 111–112. *Collybia tuberosa*, Figs 113–114. *Cystoderma jasonis*, Figs 115–116. *Entoloma cetratum*.



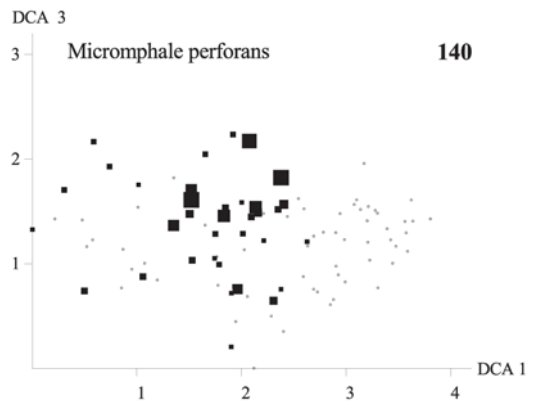
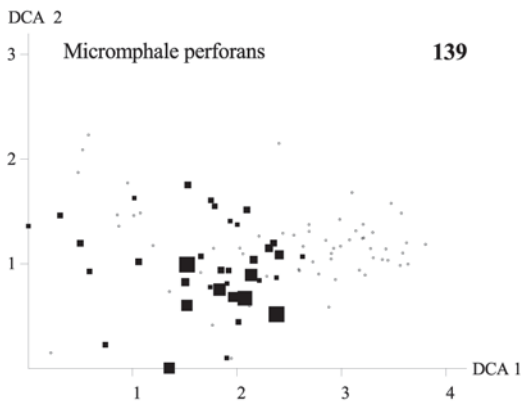
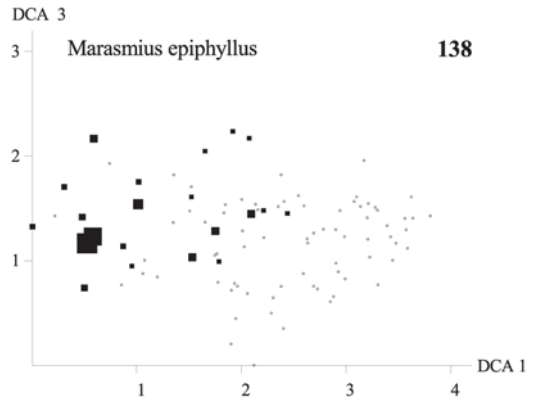
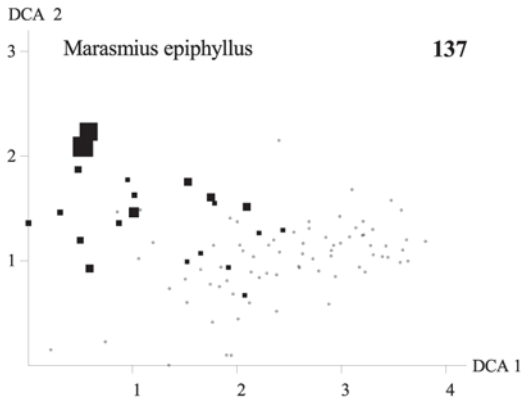
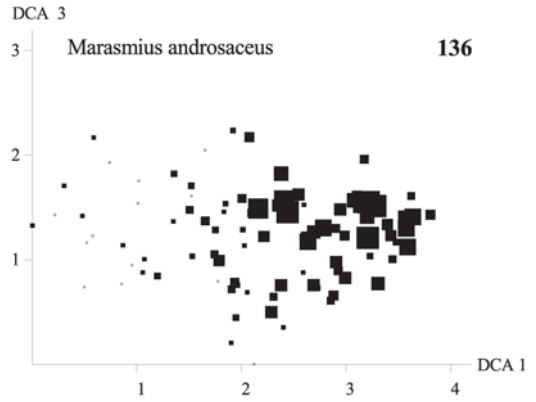
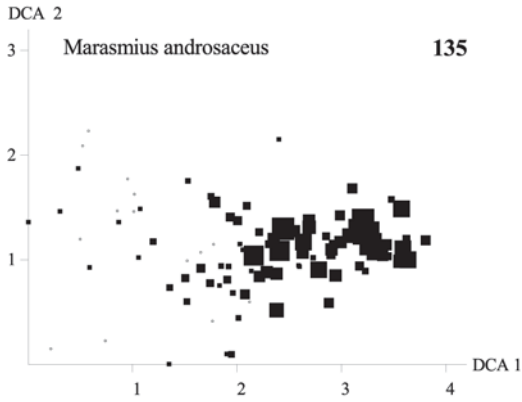
Figs 117–122. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 117–118. *Entoloma conferendum*, Figs 119–120. *Galerina atkinsoniana*, Figs 121–122. *Galerina hypnorum*.



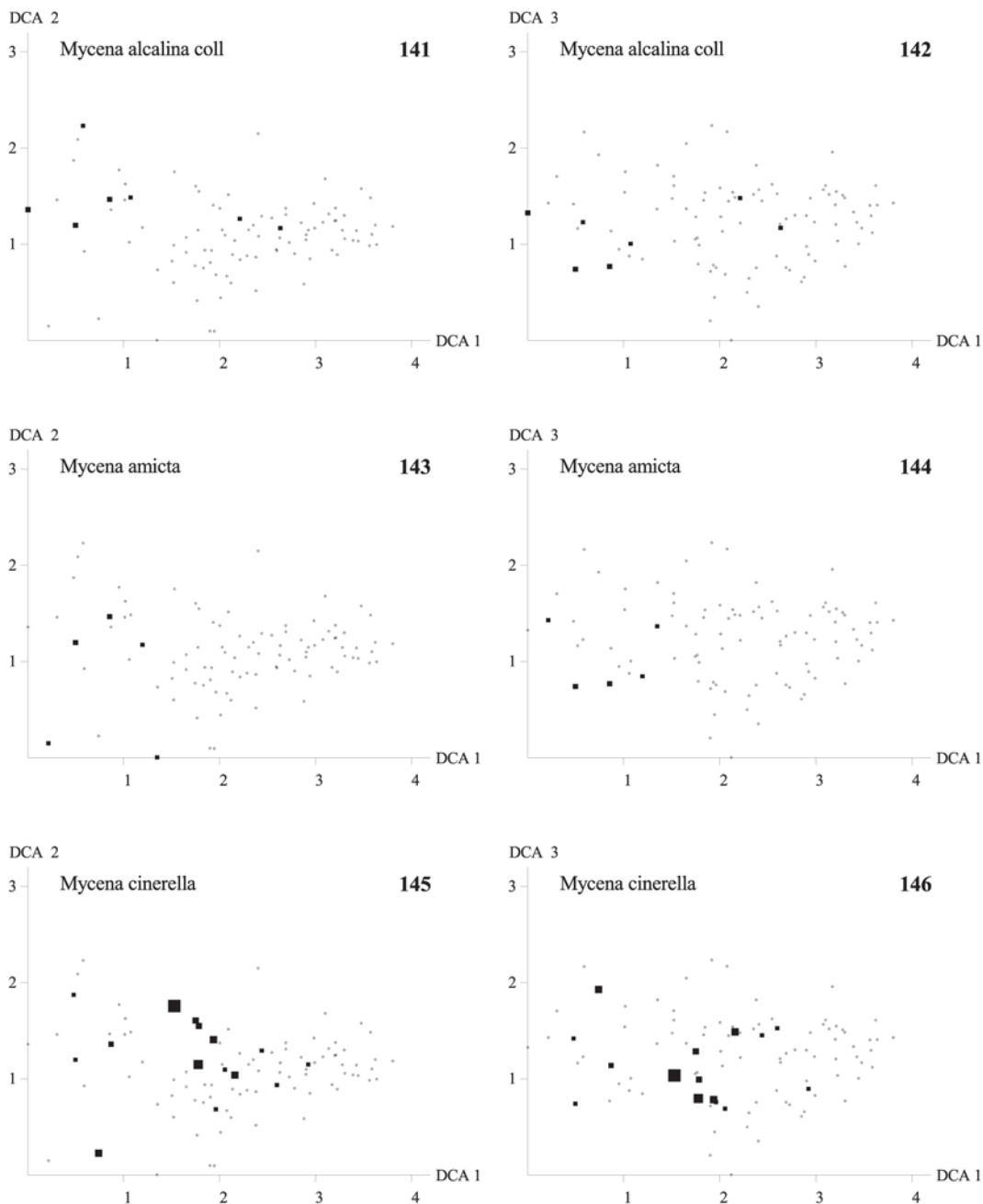
Figs 123–128. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 123–124. *Galerina marginata*, Figs 125–126. *Galerina mniophila*, Figs 127–128. *Galerina* sp 1.



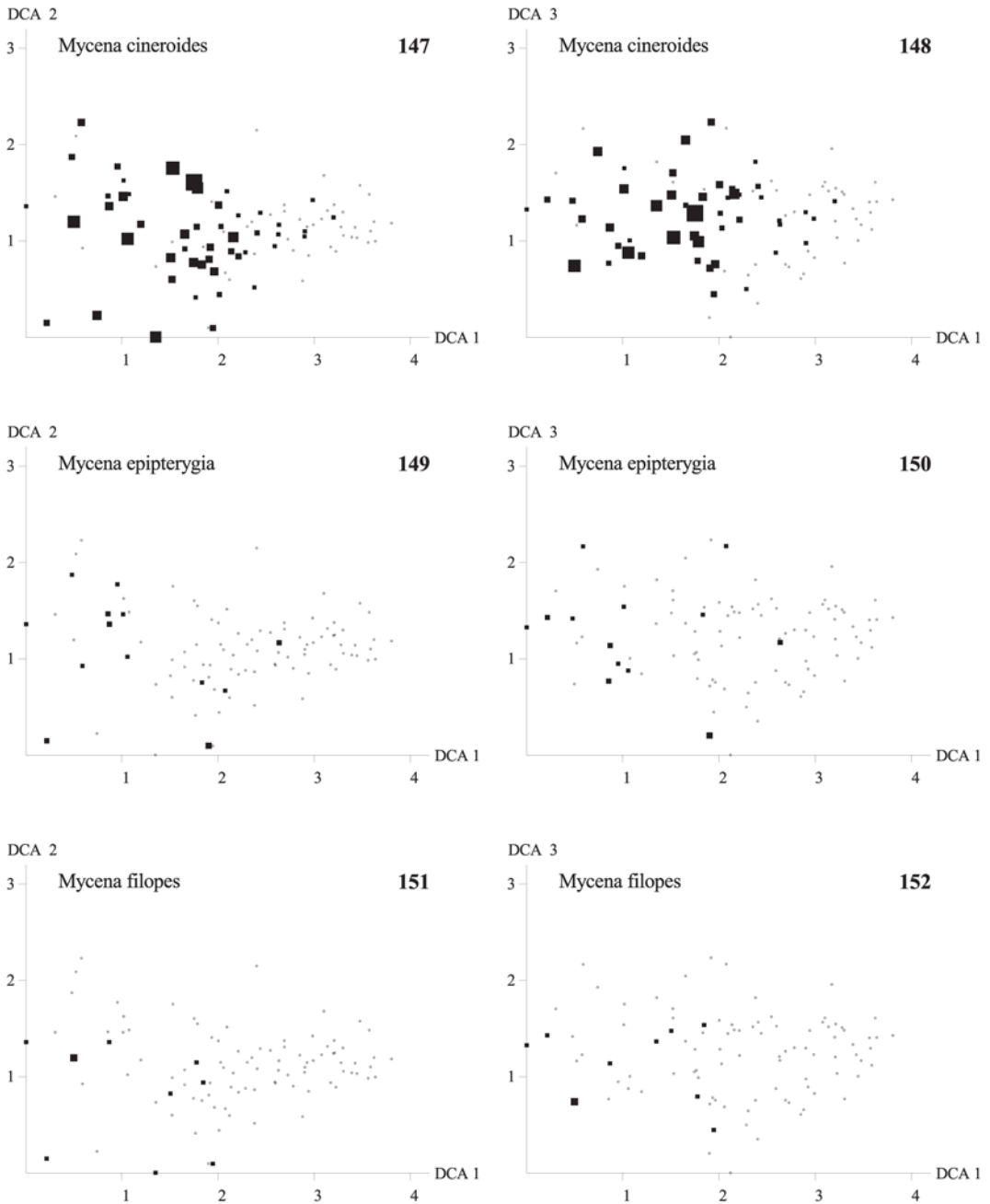
Figs 129–134. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 129–130. *Galerina sp 2*, Figs 131–132. *Gymnopilus sapineus*, Figs 133–134. *Heyderia abietis*.



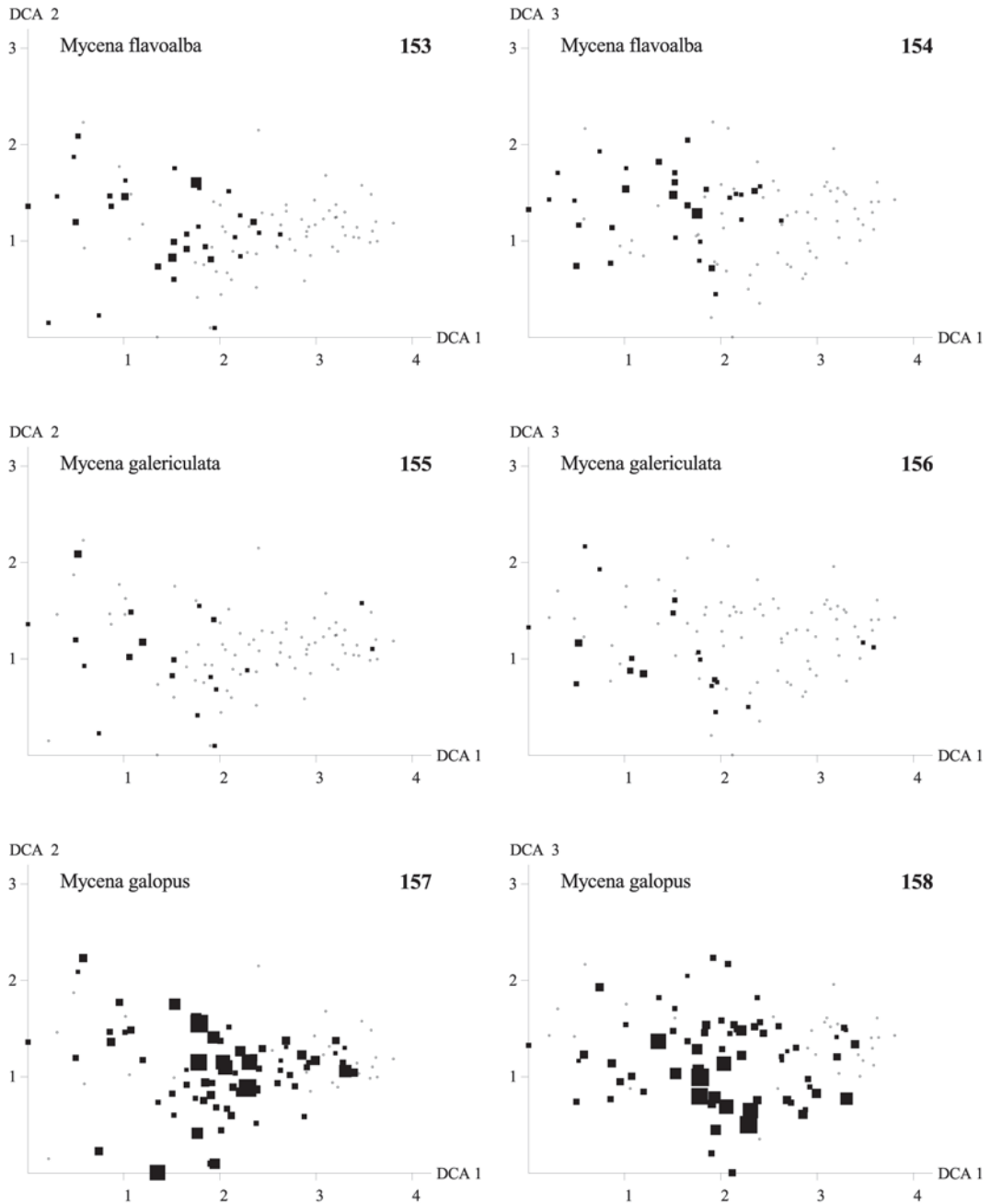
Figs 135–140. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 135–136. *Marasmius androsaceus*, Figs 137–138. *Marasmius epiphyllus*, Figs 139–140. *Micromphale perforans*.



Figs 141–146. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 141–142. *Mycena alcalina coll.*, Figs 143–144. *Mycena amicta*, Figs 145–146. *Mycena cinerella*.

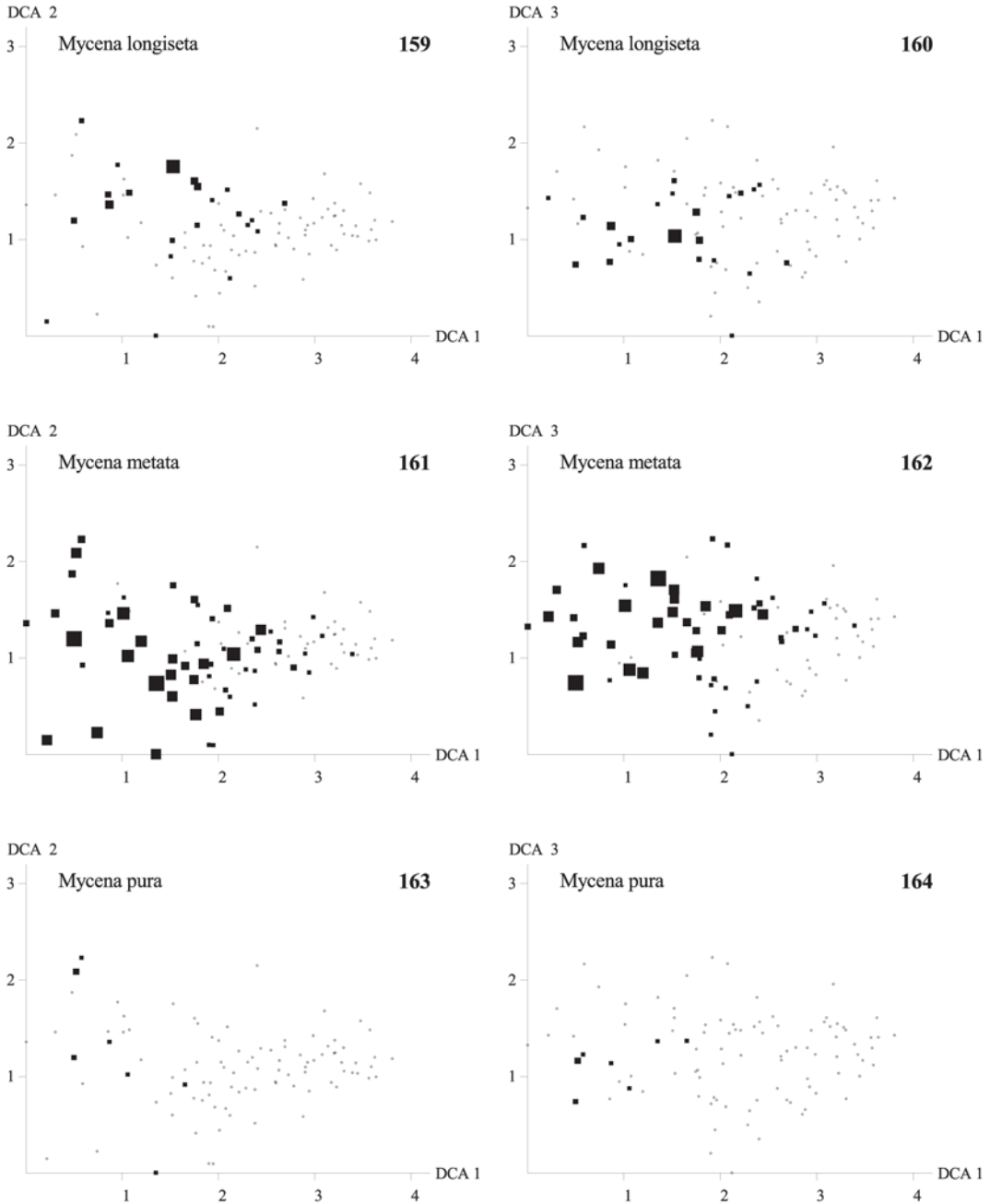


Figs 147–152. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 147–148. *Mycena cineroides*, Figs 149–150. *Mycena epipterygia*, Figs 151–152. *Mycena filopes*.

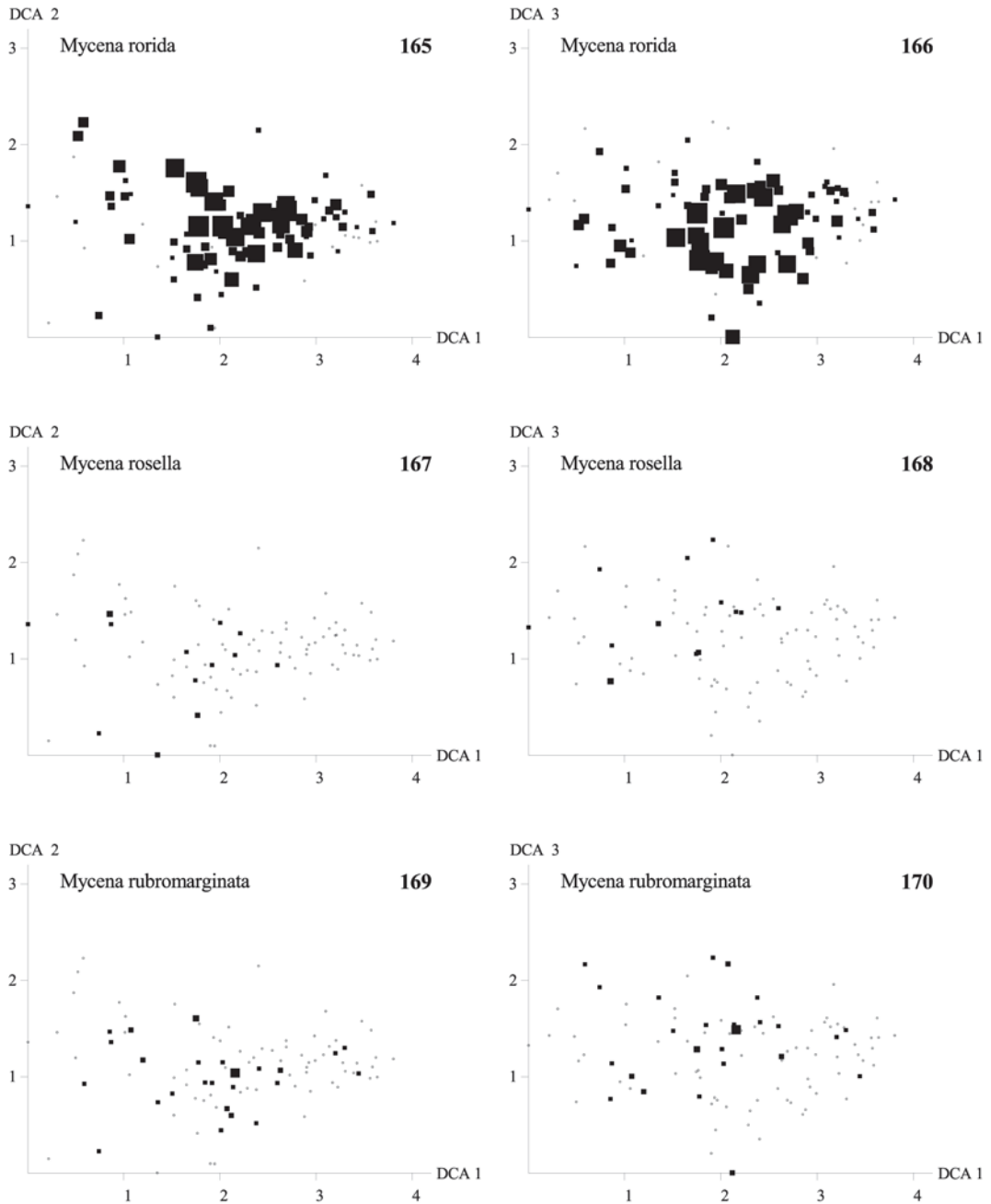


Figs 153–158. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 153–154. *Mycena flavoalba*, Figs 155–156. *Mycena galericulata*, Figs 157–158. *Mycena galopus*.

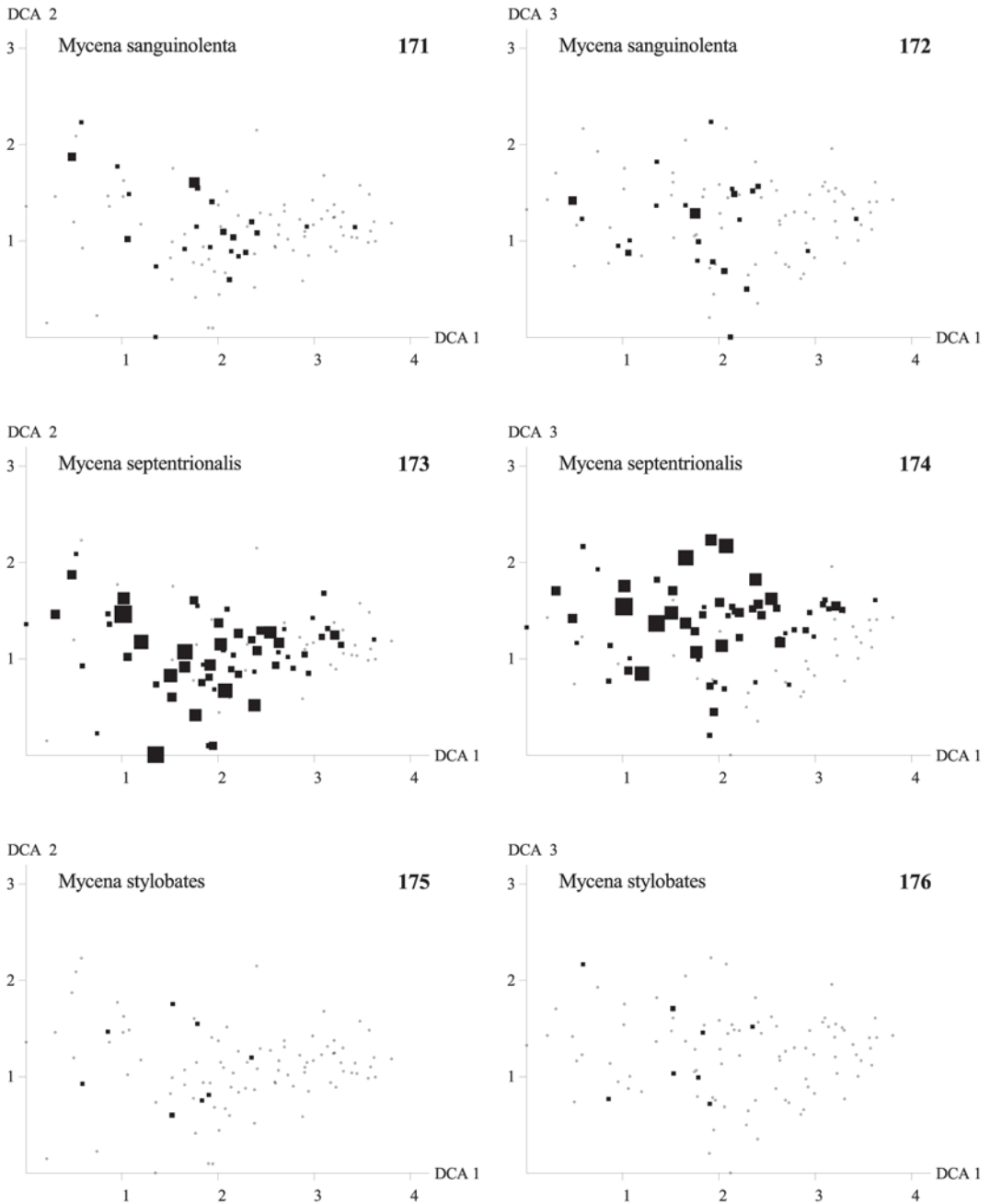




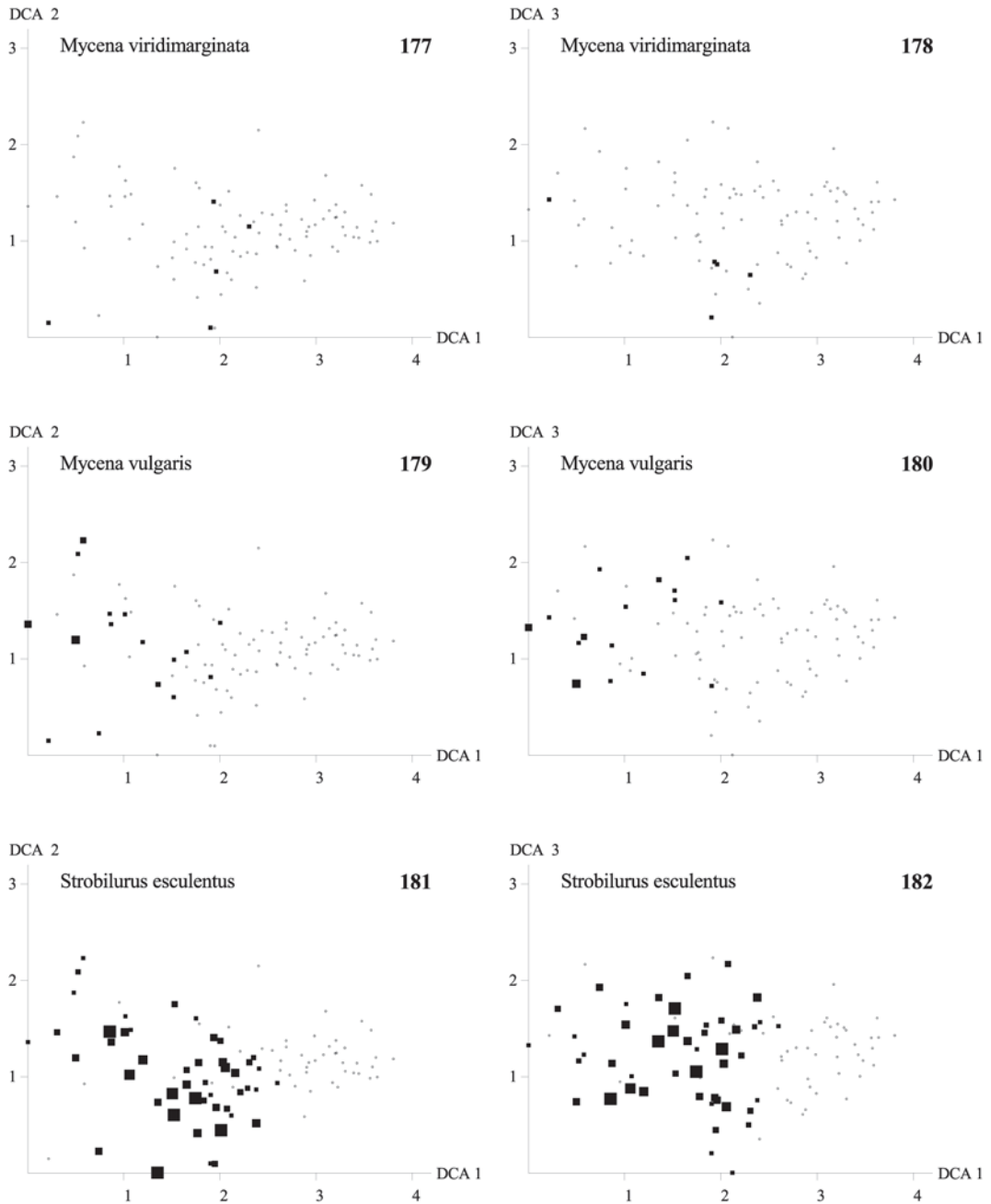
Figs 159–164. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 159–160. *Mycena longisetata*, Figs 161–162. *Mycena metata*, Figs 163–164. *Mycena pura*.



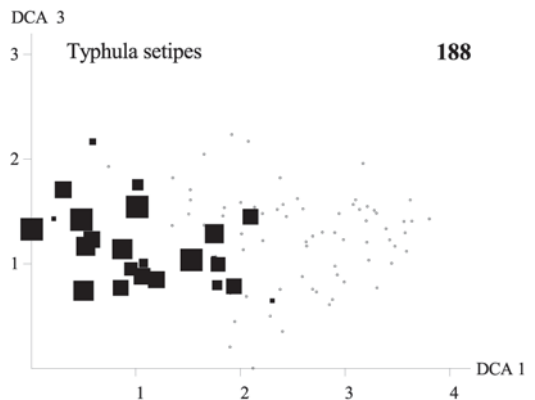
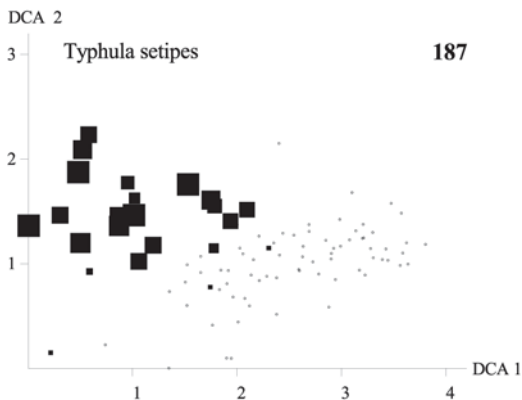
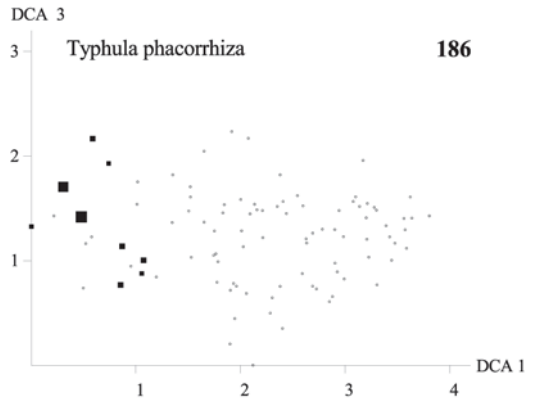
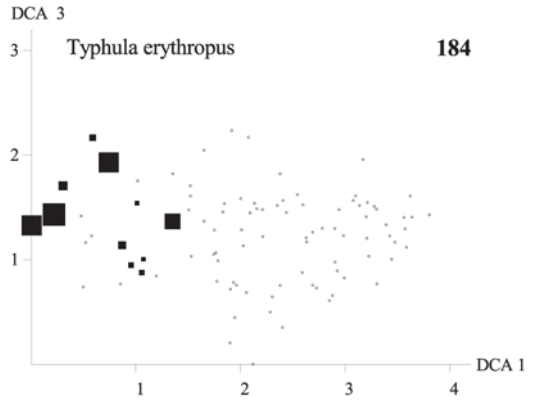
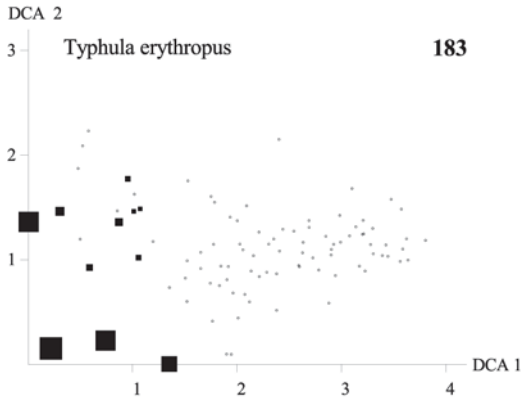
Figs 165–170. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 165–166. *Mycena rorida*, Figs 167–168. *Mycena rosella*, Figs 169–170. *Mycena rubromarginata*.



Figs 171–176. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 171–172. *Mycena sanguinolenta*, Figs 173–174. *Mycena septentrionalis*, Figs 175–176. *Mycena stylobates*.



Figs 177–182. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 177–178. *Mycena viridimarginata*, Figs 179–180. *Mycena vulgaris*, Figs 181–182. *Strobilurus esculentus*.



Figs 183–188. DCA ordination of the MAF 95 data set, axes 1 and 2 (left) and 1 and 3 (right). Frequency in subplots for actual species in macro plots plotted onto the macro plot positions. Scaling of axes in S.D. units. Small circle – absent. Square – present; area of square proportional to frequency in subplots. Figs 183–184. *Typhula erythropus*, Figs 185–186. *Typhula phacorrhiza*, Figs 187–188. *Typhula setipes*.

## CONSTRAINED ORDINATION

*Variation explained by single explanatory variables*

Tab. 17 shows that the variation in fungal species abundances in the MAF 95 data set explained by the main vegetational gradient [DCAG 1; 0.38 IU (inertia units)] was not much lower than the variation explained by the main gradient in fungal species composition (0.47 IU; cf. Tab. 4). Relatively high amounts of variation were also explained by the second and fourth vegetational gradients (Tab. 17).

The largest amounts of variation explained by single primary environmental variables were noted for  $\text{pH}_{\text{CaCl}_2}$  (0.32 IU), N (0.30 IU), loss on ignition and terrain shape (0.23 IU), and soil depth at macro scale (0.22 IU). Soil moisture explained an amount of variation in fungal species abundances amounting to 0.12 IU only. Spatial variables explained 0.11 IU or less, i.e. below  $2.5 \times$  the variation expected to be explained by a random variable (which is  $n^{-1}$ ; where  $n$  is the number of plots; see Tab. 4).

Tab. 17. Variation (VE) in the MAF 95 data set explained by each explanatory variable (in inertia units, IU), as determined by hCCA using the variable in question as the only constraining variable. Significance (P) of each variable determined by a Monte Carlo permutation test; 199 permutations. Explanatory variable sets: E – environmental variables; S – spatial variables; D – DCA ordination axes based on vascular plants, bryophytes and macrolichens.

Set	Variable	VE	P	Set	Variable	VE	P
D	01 DCAG 1	0.38	.005	S	06 $xy^2$	0.11	.005
E	20 $\text{pH}_{\text{CaCl}_2}$	0.32	.005	E	16 ME Rel	0.11	.005
E	26 N	0.30	.005	S	02 y	0.11	.005
E	19 $\text{pH}_{\text{H}_2\text{O}}$	0.27	.005	S	08 xy	0.11	.005
E	18 LI	0.23	.005	S	07 $x^2$	0.11	.005
E	3 MA Ter	0.23	.005	E	32 P	0.11	.005
E	5 MA SD	0.22	.005	S	09 $y^2$	0.11	.005
E	25 H	0.20	.005	E	28 Al	0.10	.005
E	21 Ca	0.18	.005	S	04 $y^3$	0.10	.005
E	30 Mn	0.16	.005	E	14 ME Sma	0.10	.010
D	02 DCAG 2	0.14	.005	D	03 DCAG 3	0.10	.005
E	01 MA Slo	0.14	.005	S	01 x	0.10	.010
D	04 DCAG 4	0.13	.005	E	23 Na	0.10	.005
E	22 Mg	0.13	.005	E	04 MA Une	0.09	.020
E	08 ME Slo	0.13	.005	E	06 MA Rel	0.09	.010
E	27 P	0.12	.005	E	13 ME Sme	0.09	.015
E	07 MA Lig	0.12	.005	E	12 ME Smi	0.09	.005
E	15 ME Lit	0.12	.005	E	33 S	0.08	.020
E	17 Mois	0.12	.005	E	09 ME Auf	0.08	.020
S	05 $x^2y$	0.11	.005	E	10 ME Une	0.08	.040
E	24 K	0.11	.005	E	02 MA Auf	0.07	.040
S	03 $x^3$	0.11	.005	E	31 Zn	0.07	n.s.
E	29 Fe	0.11	.005	E	11 ME Con	0.04	n.s.

Tab. 18. Partitioning the variation in the MAF 95 data set onto three sets of explanatory variables; {E} – the set of 33 environmental variables; {S} – the set of 9 spatial variables, and {V} – the set of 4 vegetational variables (DCA axes based on the ME 200 data set including vascular plants, bryophytes and macrolichens). Notation (explained by reference to data sets {E} and {S}):  $E \cup S$  – total variation explained by {E} and {S};  $E \cap S$  – variation shared between {E} and {S};  $E|S$  – variation explained by E, not shared with S. Variation explained (VE) is given in inertia units (IU), and as percentage of the total variation explained by all three sets of variables, TVE (in this case,  $E \cup S \cup V = 1.791$  IU, which amounts to 34.54 % of the total inertia). TVE is the sum of seven components of explained variation, as shown by boldface letters. The number of variables in each set retained by forward selection (P # 0.01) is given in brackets.

Data set	VE	VE, % of TVE	Component	VE	VE, % of TVE
E (8)	1.061	59.2	<b><math>E (S \cup V)</math></b>	0.573	32.0
			<b><math>(E \cap S) V</math></b>	0.047	2.6
			<b><math>(E \cap V) S</math></b>	0.201	11.2
			<b><math>E \cap S \cap V</math></b>	0.240	13.4
S (7)	0.742	41.4	<b><math>S (E \cup V)</math></b>	0.431	24.1
			<b><math>(E \cap S) V</math></b>	0.047	2.6
			<b><math>(S \cap V) E</math></b>	0.023	1.3
			<b><math>E \cap S \cap V</math></b>	0.0463	13.4
V (4)	0.740	41.3	<b><math>V (E \cup S)</math></b>	0.0532	15.4
			<b><math>(E \cap V) S</math></b>	0.0388	11.2
			<b><math>(S \cap V) E</math></b>	0.0044	1.3
			<b><math>E \cap S \cap V</math></b>	0.0463	13.4
<b><math>E \cup S</math></b>	1.515				
<b><math>E \cup V</math></b>	1.360				
<b><math>S \cup V</math></b>	1.218				
<b><math>E \cup S \cup V</math></b>	1.791				

#### Variation partitioning

The fraction of the total variation in fungal species composition in the MAF 95 data set (total inertia) explained by significant primary explanatory variables was 34.5% (= TVE; Tab. 18). The eight significant environmental variables {E} explained 59.2% of TVE while the seven significant spatial variables {S} and the four significant vegetational variables {V} explained 41.4 and 41.3% of TVE, respectively. Variation unique to one set of variables made the largest contributions to TVE (32.0, 24.1 and 15.4% of TVE for {E}, {S}, and {V}, respectively), followed by the variation shared among all three variable groups (13.4%) and the non-spatial variation shared between environmental and vegetational variables (11.2%; Tab. 18). The contributions by the remaining two (out of seven) variation components, shared between {S} and only one other set, were negligible.

While only 37% of the variation explained by {V} was not shared with other data sets, 55–58% of the variation explained by environmental and spatial variables was uniquely explained by these sets. As much as 60% of the variation explained by vegetational variables was shared with the environmental variable set {E}.

## DISCUSSION

### ENVIRONMENTAL INTERPRETATION OF GRADIENTS IN FUNGAL SPECIES COMPOSITION

#### *The main gradient and its relation to broad-scale topography and soil nutrient content*

##### Relationships with environmental variables in spruce and pine forests

The results of fungal ordinations point to the existence of one major gradient in species composition that closely corresponds to the main gradient in vegetation identified by R. Økland & Eilertsen (1993). The main fungal and vegetational gradients are correlated with the same environmental variables [compare Tab. 12 with R. Økland & Eilertsen (1993): Tab. 11] although macro-scale terrain variables are relatively more strongly correlated with the vegetational gradient while soil pH and nitrogen content are more strongly correlated with the fungal gradient [even after differences in absolute values between Pearson's  $r$  (used by R. Økland & Eilertsen 1993) and Kendall's  $\tau$  have been taken into account]. Thus the conclusion of R. Økland & Eilertsen (1993) that the variation from pine to spruce dominated forests depends *primarily* on a macro-scale topographic (ridge-slope-valley) gradient appears to hold true also for fungi.

R. Økland & Eilertsen (1993) suggest, from the different patterns of correlations between ordination scores and environmental variables within spruce and pine forests, that different complex-gradients are responsible for the differentiation of vegetation within these two main forest types; that a nutrient complex-gradient is most important in spruce forest, while topography and soil depth are the most important factors in pine forest. Correlations between environmental variables and fungal ordination axes, calculated separately for spruce and pine forests, resemble those of vegetational coenoclines. However, the significant correlation of this coenocline with pH also in the pine forest (while correlations with soil depth are less strong) open for the possibility that the main gradient in fungal species composition is related to a complex-gradient in soil nutrients in both forest types. On the other hand, the strong relationship of the main gradient with terrain variables may well indicate that factors related to topography contribute *independently* to explain variation along the main gradient in the pine forest. Variation in spruce and pine forests will therefore be discussed separately.

##### Spruce forest: the complex-gradient in nutrient status

Except for some differences in the variables' rank order (variables ranked by correlation with ordination score), correlation patterns for fungi and plants in spruce forest (Subset A) are closely similar, with  $\text{pH}_{\text{CaCl}_2}$  and nitrogen concentration as the variables most strongly (negatively) correlated with the main gradient for both groups and calcium concentrations (negatively) and loss on ignition (positively) as other important correlated variables. As for vegetation (R. Økland & Eilertsen 1993, 1994), variation along the main fungal coenocline in the spruce forest is mainly related to the nutrient status of the humus layer. Factors controlling the nutrient status of the humus layer are discussed by R. Økland & Eilertsen (1993).

*Soil pH* is the most frequently focused single factor affecting the composition of the funga. For instance, Bohus (1984) arranged fungi from deciduous forests in a system of pH-classes. The restricted pH-amplitudes of many species and the high compositional turnover from acid to basic coniferous



forest soils are stressed in several mycological studies (e.g. Haas 1932, Šmarda 1973, Krieglsteiner 1977, Østmoie 1979, Bendiksen 1980, 1981, Metsänheimo 1982, Salo 1993). Differences between species in physiological optima along pH gradients are also demonstrated in pure cultures (Melin 1924, Modess 1941, Norkrans 1950, Theodorou & Bowen 1969, Hung & Trappe 1983). Furthermore, high importance of soil acidity to macrofungi is demonstrated by the decrease in number of mycorrhizal root-tips in soils subjected to experimental acidification (Reich et al. 1985, 1986, Blaschke 1986, Dighton et al. 1986, Göbl 1986, Dighton & Skeffington 1987, Entry et al. 1987, Keane & Manning 1987, Dighton 1988). However, Høiland & Jenssen (1994) and Agerer et al. (1998) showed in experiments with acidified irrigation of coniferous forests that acid rain does not necessarily adversely affect the number of fruitbodies of all ectomycorrhizal fungi; for some species the abundance increased in response to acidification.

Although saprotrophic fungal species on average occupy broader intervals along the main coenocline than mycorrhizal species (see p. 38), both groups differentiate along the main gradient. Culture studies demonstrate that the litter-decomposing ability of saprotrophs is pH-dependent and differs among species. For instance, Hintikka (1960) demonstrate poor ability of some coniferous forest species of *Mycena* with ecological pH optima of 4–5 to decompose substrates with pH > 6.0. Other *Mycena* species first grew very slowly, while growth rates increased later on due to the species' ability to acidify their immediate surroundings. Hintikka's observations suggest that saprotrophic species respond to a nutrient gradient because of pH-dependent, interspecific differences in decomposing ability. Competition between decomposers, a probable result for species with ecological ranges that are considerably narrower than physiological tolerances, further increase the compositional turnover along a coenocline. If, however, the range spanned by fruitbodies is narrower than the species' total range, the observed  $\beta$ -diversity exceeds the  $\beta$ -diversity of the fungal *species*.

Even if pH is more strongly correlated with the main fungal gradient than any other measured variable, it cannot be concluded that pH is the *cause* of the differentiation along the gradient. Other variables, alone or in combination, may be important as well.

*Soil nitrogen.* High importance of nitrogen concentrations in the humus layer, secondmost strongly correlated with the main fungal coenocline in our study, accords with results of many studies, especially of mycorrhizal fungi. Reduction of species number, fruitbody production and/or number of mycorrhiza types are normal effects of experimental fertilization and nitrogen addition (see, among others, Menge & Grand 1978, Ritter & Tölle 1978, Wästerlund 1982, Shubin 1988, Ohenoja 1989, Rühling & Tyler 1991, Termorshuizen & Ket 1991, Arnebrant & Söderström 1992, Termorshuizen 1993, Brandrud 1995, Wiklund et al. 1995, Brandrud & Timmermann 1998, Peter et al. 2001).

Abundance decrease or extinction, as observed over parts of Europe for several mycorrhizal species in the 20th century (see Fellner 1993, Høiland 1993), are often attributed to high atmospheric loads of nitrogen (Arnolds 1988, 1991, Termorshuizen & Schaffers 1987, 1991, Taylor et al. 2000).

Macrofungal species may differ in their response to nitrogen fertilisation because they differ in ability to utilise chemically different nitrogen sources (cf. Ohenoja 1989): not only nitrate and ammonium, but also organic nitrogen which can be utilised by several mycorrhizal species (cf. Lundeberg 1970) in the forms of soluble amino acids, peptides and soluble proteins (Abuzinadah & Read 1986a, 1988). Organic nitrogen may be made accessible to vascular plants by mycorrhiza (Abuzinadah et al. 1986, Abuzinadah & Read 1986b, 1989a, 1989b), but direct uptake of amino acids has also been demonstrated for vascular plants (Chapin et al. 1993, Kielland 1994, Raab et al. 1996, Nordin et al. 2001). When nitrogen may be utilized in many (most?) chemical forms, concentrations of specific forms of nitrogen such as ammonium ions are ecologically inadequate as measures of nitrogen supply (Abuzinadah et al. 1986). This may explain why total nitrogen is strongly correlated with vegetational gradients in forests, as demonstrated for instance by R. Økland & Eilertsen (1993) and T. Økland (1996), and with the main fungal gradient in this study.

Tyler (1985, 1989a, 1989b) demonstrates that abundances of most species of macrofungi in South Swedish deciduous forests (quantified as fruitbody numbers in large plots) may be modelled as a response to edaphic factors, notably base saturation and organic matter content of the humus layer. Hansen (1988a, 1988b) adds soil nitrogen content, which is positively related to base saturation and negatively related to organic matter content, and point to soil pH as important on mor sites and nitrogen mineralisation rate and leaf litter quality on mull sites. The similarity with factors correlated with the main fungal coenocline in the Solhomfjell area is striking, even though the areas differ in climate, the range of variation in important environmental factors and vegetation. This indicates that a main gradient associated with soil nutrient status may be important for fungi in most boreal (and nemoral?) forests. The results of Hansen (1988a, 1988b) may also be interpreted as an indication that concentrations of some heavy metals not measured by us, such as cadmium, influence fungal species abundances under normal field conditions, and hence gradients in fungal species composition.

Loss on ignition, a factor significantly correlated with the main fungal gradient, and other important factors as pH and nitrogen (cf. Økland & Eilertsen 1993, Fig. 5), may also represent independent, ecologically important properties of the humus. Mor and mull soils differ strongly in many physical properties (Green et al. 1993), and Tyler (1989a) points out that, apart from the inorganic soil chemical differences, differences in the organo-chemical properties of the litter and humus may be of importance for the species composition of macrofungi (cf. Romell 1935).

Calcium concentrations are also correlated with plot positions along the main coenocline, in accordance with the results of liming experiments in which negative effects similar to those resulting from nitrogen fertilization are often observed (cf. Kuyper 1989). One example is provided by Eilertsen et al. (1997a), who observe reduced abundance of the saprotrophs *Galerina atkinsoniana* and *Mycena sanguinolenta* in coniferous forests close to the Solhomfjell area after addition of dolomite lime in small concentrations (cf. Eilertsen et al. 1997b). Kuyper (1989) suggests that soil calcium concentrations affect fungi via effects on nitrogen mineralisation and nitrification. This parallels the hypothesis forwarded for natural forest soils, that Ca is the primary environmental variable limiting nitrogen mineralisation rates in humus (Hesselman 1926, Dahl et al. 1967) which has not, however, general validity (T. Økland 1996). The correlation of calcium concentrations with position along the main gradient may thus indicate correlations of both with a third, causal factor. However, a primary role of Ca (and/or Mg) is supported by the experimental liming study of Jonsson et al. (1999). Comparing controls with plots added dolomite in low and high quantities, Jonsson et al. (1999) found that the number of root tips per metre root length was significantly lower in the control than in both of the dolomite treatments. This result was taken as an indication that the calcium concentrations as such was more important for the development of fine roots than the resulting pH, since the mean pH in the control and low dolomite plots was 4.1 and 4.0, respectively, whereas the mean pH in the high dolomite plots was 5.5.

Soil phosphorus concentrations are not correlated with the main fungal gradient even though phosphorus is physiologically important to macrofungi; the phosphorus content of mycorrhizal and saprotrophic fungi average 5.7 and 11.1 per cent of their dry weight, respectively (Miller & Laursen 1978). Similar results were found for plants in the same plots by R. Økland & Eilertsen (1993). Results of experimental studies in which phosphorus is supplied are not unambiguous: while phosphorus is considered the growth-limiting element for *Mycena galopus* (Frankland et al. 1978), increase as well as decrease depending on species and site conditions is reported by Kuyper (1989).

The closely parallel responses of fungi and plants to edaphic conditions has one important exception: plants, even those common on poor soil (site-type 5.1) are normally present also in richer sites (R. Økland & Eilertsen 1993) while many fungal species are absent or very rare there (see Figs 27-188). R. Økland & Eilertsen (1993) interpret the presence of vascular plants typical of poor sites

also in richer sites as an indication of low importance of competition among established vascular plants along the gradient. These differences between organisms open for different mechanisms as important for species' responses to the nutrient gradient in the two groups, e.g. in one of the following ways (or a combination): (1) The competition among macrofungal species (between the mycelia of different fungal species (cf. Lindahl et al. 2002) as well as with plants, for water and soil nutrients) is more intense than between plants. The mechanisms behind the patterns of distribution of macrofungal species will, however, remain obscure until all species present in a plot as mycelium can be confidently recorded, considering both time and space. (2) Absence of many fungal species from the richer part of the gradient due to physiological reasons; by avoidance of soils with high pH or high concentrations of nitrogen and/or other elements. (3) Responses to other environmental variables such as bryophyte cover, or other variables.

#### Pine forest: relative importance of factors related to topography and nutrients

While pH and concentrations of soil nutrients such as nitrogen, alone or in combination, appear to be responsible for the distribution of fungal species along the main gradient in spruce forest, environmental interpretation of the main gradient in pine forest is more difficult due to several, less strong correlations: with pH, AL-extractable phosphorus concentrations, terrain shape and slope (see Tab. 13), and with vascular plant coenoclines (cf. Tab. 10). Along the main vegetational gradient in pine forest, pH does not show systematic variation, nitrogen concentrations *increase*, terrain shape varies from convex slopes to ridge tops and soil depth decreases significantly (R. Økland & Eilertsen 1993). At least three explanations of the main fungal coenocline (from poor spruce forest to pine forest) may accord with these patterns: (1) that the nutrient complex-gradient extends into pine forest, (2) that topographic factors are decisive, e.g. via a gradient in soil moisture deficiency, as hypothesized for the corresponding plant coenocline by R. Økland & Eilertsen (1993), and (3) that other causes are in operation.

Data comparable to ours, viz. on the variation in fungal occurrence and abundance from bilberry-dominated spruce forest to lichen-dominated pine forest, are not available. Furthermore, the small range of variation in nutrient conditions in our material reduces the relevance of results from fertilisation studies. A natural starting point for further discussions is therefore the applicability of the soil moisture deficiency hypothesis to macrofungi.

The soil moisture deficiency hypothesis implies that, in rain-free periods, a drought front more rapidly penetrates the humus layer towards lichen-rich pine forests, partly due to more shallow soils, partly for topographic reasons, resulting in longer duration of low moisture availability. Topographic position, soil depth, median particle size and the decomposition rate are often mentioned as important factors varying along this gradient (R. Økland & Eilertsen 1993). Soil moisture deficiency probably affects cryptogams and vascular plants via different mechanisms. While the main vegetational coenocline (DCAG 1) is strongly correlated with soil depth [the most strongly correlated topographic variable, cf. R. Økland & Eilertsen (1993): Tab. 11] in the Solhomfjell area mainly because the main bottom-layer coenocline is strongly correlated with soil depth (R. Økland & Eilertsen 1993: Tab. 17), the vascular plant coenocline is not more strongly correlated with topographic factors than the fungal gradient. R. Økland & Eilertsen (1993) hypothesise that the variation in species composition in the bottom layer is indirectly related to soil moisture deficiency, via the decreasing cover of (and shelter from direct insolation by) the uppermost layers. This interpretation rests upon the assumption that ectohydric and poikilohydric organisms (such as most bryophytes and lichens) have poor capacity for uptake of water directly from the soil and is supported by physiological evidence such as the intolerance of dominant forest bryophytes to direct sun (e.g. Busby et al. 1978; see discussion by R. Økland & Eilertsen 1993). Recent studies do, however, indicate a much stronger dependence of

bryophytes on the soil than previously assumed, both for supply of water and for dissolved nutrients (T. Økland et al. 1999; also see Lewis Smith 1978, Brown & Bates 1990, van Tooren et al. 1990). Most likely, there is a close relationship between cumulative distribution curves for topsoil moisture (duration of soil moisture levels above a given level) and the length of the period a cryptogamic species is hydrated and thus actively photosynthesising; which is considered to be the most important single factor for the growth of forest bryophytes (R. Økland 1997).

The results of this study lead us to hypothesize that the soil moisture deficiency hypothesis may apply also to fungi. Like vascular plant roots, including mycorrhizal roots (cf. Kivenheimo 1947), fungal mycelia have highest density in the humus or upper mineral soil layers, for some species even concentrated to the uppermost litter sublayer (cf. Shantz & Piemeisel 1917, Mikola & Laiho 1962, Mikola et al. 1966, Pirozynski 1968, Harvey et al. 1976, Newell 1984). This suggests that soil-dwelling fungi are subjected to the same constraints on moisture supply from the soil as bryophytes and lichens. The mobility of fungal mycelia may, however, be comparable to that of vascular plant roots, much higher than that of bryophytes and lichens (R. Økland 1995c, 1995e, Dix & Webster 1995). Duddridge et al. (1980) found, by use of tritiated water, that mycorrhizal rhizomorphs have the ability to absorb water and facilitate its transport over long ecological distances and that mycorrhizal species differ in capacity to produce rhizomorphs. Correspondingly, Boddy (1999) infer that the extensive rhizomorphs (including cords) of many saprotrophs are likely to be important for transport of water (and nutrients). Some physiological evidence with relevance for applicability of the soil moisture deficiency hypothesis to fungi exists, for some ecological groups. The minimum water potentials required for growth under controlled conditions vary considerably between the nine leaf-litter decomposing fungi reviewed by Dix (1984), and between the nine wood- and litter-decay species studied by Koske & Tessier (1986). Variation among species in growth rates under low water potentials is also demonstrated for wood-inhabiting fungi in the experiments by Boddy (1983) and Griffith & Boddy (1991); some species growing on twigs are found to survive dry periods with soil moisture levels far below the normal limit for growth (cf. Loman 1965). Laboratory experiments on different ectomycorrhizal fungal species demonstrate interspecific differences in the ability of mycelia to grow in substrates with low water potentials (Uhlig 1972, Mexal & Reid 1973, Theodorou 1978, Coleman & Bledsoe 1989). In the North American study by Coleman & Bledsoe (1989) pine forest species as *Suillus luteus* and *S. granulatus* are shown to have high growth rates by low water potentials, as is the case also for *Boletus edulis*, which was found accidentally in dry pine forest in the present study. On the other hand, the low tolerance of *Hebeloma crustuliniforme*, a species typical for moister forest types, for dry soils is, however, shared by *Lactarius rufus*, known as a typical dry pine-forest species. The possibility that genetic population properties different from those occurring in North Europe are encountered in that study does, however, limit its value for direct comparisons. The American authors do not find any correlation between their results and the aridity of the collection sites, measured crudely as annual precipitation. They do, however, find that the most drought-resistant species also have maximum growth rates under higher water-deficiency stress than less resistant species. Furthermore, Uhlig (1972) finds for six tested ectomycorrhizal species a good ability to survive at much lower water potentials than needed for growth. Several studies in different kinds of dry forests demonstrate that *Cenococcum geophilum* has a high share of the total mycorrhiza (Worsley & Hacskaylo 1959, Meyer 1964, Vogt et al. 1981, Dahlberg et al. 1997). The hyphae of this species are highly specialized to dry conditions (e.g. Pigott 1982). Moser (1964, 1993) recognises one group of species with large fruitbodies, morphologically adapted to dry sites such as pine forests. This group is exemplified by some *Russula* and *Lactarius* species which have slow development of primordia and fruitbodies with low transpiration rate, among others because of small surface area compared to the volume. The existence of such adaptations may indicate that the soil moisture deficiency hypothesis also applies to fungi.

Our results may indicate that similar differences exist between species of soil- and litter-dwelling saprotrophs and mycorrhizal fungi in coniferous forests, with respect to ability for growth and survival. Observations in the study area during the dry period in August 1990 suggest adaptation to fruiting of several mycorrhizal species in pine forest under dry conditions. Most of the very few fruitbodies observed during this period were observed in dry pine-forest plots. This was especially the case for species with large fruitbodies, such as *Russula paludosa* and *R. decolorans*, which obviously have high demands on water supply for development. Another species commonly observed as fruiting was *Amanita fulva*, which may be adapted to dry conditions by its rather broad and dense gills that may assist in keeping air humidity high in the spore-producing region (cf. Moser 1964). Furthermore, the volva may protect against water loss in young stages.

Most saprotrophic fungal species show declining abundance towards the dry end of the gradient (see Figs 101–188 and Tab. 16), their limits, based upon fruitbodies, are, however, not very sharp. This is exemplified by bryophilous species such as *Galerina hypnorum*, *G. atkinsoniana*, *Mycena galopus* and *M. septentrionalis*; for which the presence of their preferred substrate seems to be more important than the risk of drought. A plausible explanation is the higher potential of most saprotrophs compared with most mycorrhizal species to initiate fruitbody formation by rapid swelling of primordia after rain because of the smaller fruitbodies of the former. Furthermore, species with small fruitbodies may more efficiently utilize small paludified patches. A noticeable adaptation to drought endurance is seen in *Marasmius androsaceus*, a ubiquitous species with particularly high abundance in dry pine forests, which possesses drought-resistant rhizomorphs and fruitbodies with high ability to revive when rain follows drought. For instance, *M. androsaceus* is the only abundant saprotroph in dense *Calluna*-dominated vegetation. Only two of the recorded saprotrophs seem to be more or less confined to dry pine forest: *Collybia putilla*, that grows among pine needles and is observed once in series 1, and *Mycena clavicularis*, for which three of four recordings are made in pine forest.

For mycorrhizal fungi, the picture is somewhat more complicated. The dependence or preference of many species for either spruce or pine as their mycorrhizal partner contributes strongly to the main fungal coenocline. Such species have more or less sharp limits for fruitbody production that coincide with the border between pine and spruce forests. Possible influences by environmental factors such as soil moisture conditions can in these cases not easily be separated from the mycorrhizal factor. Furthermore, the uncertainty remains that fruitbody production does not necessarily occur throughout a species' whole range of occurrence as mycelium. For several fungal species that produce fruitbodies exclusively in association with one specific host, Molina & Trappe (1982) demonstrate ability to form well-developed ectomycorrhizae with one or more other hosts in culture. This opens for the possibility that typical spruce-forest species (especially those with known ability to form associations also with pine), are present as sterile mycorrhizal partners of pine in drier site-types. Observations of each of the typical species of submesic sites (series 5), *Boletus edulis*, *Hydnum rufescens*, and *Cantharellus tubaeformis*, once in pine forest support the hypothesis that species have wider tolerances towards the dry pine forest as mycelia than indicated by the occurrence of fruitbodies. Incidental fruiting in drier sites is likely to be favoured by suitable combinations of climatic factors.

Many species typically associated with spruce may associate with pine in locally favourable, e.g. moister, sites (e.g. Metsänheimo 1982, Väre et al. 1996) This is true for most *Cortinari* species recorded in this study (E. Bendiksen, pers. obs.), which are present in the poor bilberry-dominated spruce forest (site-type 5.1) and in some regions also in more or less suberic pine forest sites (corresponding to series 4 and 3), cf. Høiland (1986), Sâstad (1990), and Sâstad & Jenssen (1993). Their failure to follow the mycorrhizal host to the dry end of its range strongly indicates restriction by soil moisture deficiency.

Many pine-associated species are not restricted to well-drained soils, as they also occur in bog pine forest (cf. Kalamees 1979). Some typical pine mycorrhizal species have also been observed in

forests totally devoid of pines, e.g. *Russula paludosa* and *R. decolorans* [sparse in bilberry-dominated spruce forest (site-type 5.1); E. Bendiksen, pers. obs. in SE Norway], and *Lactarius rufus* [having a wide ecological amplitude that includes pure *Picea* and *Betula* forests (E. Bendiksen, pers. obs.), but with distinct preference for pine forests where it may be highly abundant]. These species seem to have preferences for *Pinus* as mycorrhizal host. Competitive interactions may contribute to their low abundance in spruce forest. Some species, e.g. *Chroogomphus rutilus*, *Cortinarius mucosus*, and *Suillus variegatus*, are obligate or almost obligate pine mycorrhizal species. Other species restricted to the pine forest in this material, but also growing in *Picea*-forest (without *Pinus*) elsewhere, are *Cortinarius lux-nymphae*, *C. semisanguineus*, and *C. mucifluus* (cf. Bendiksen 1981, Høiland 1984, Bendiksen et al. 1993).

Species density (number per plot) decreases for saprotrophs and mycorrhizal species (cf. Tab. 3) [like for vascular plants (cf. R. Økland & Eilertsen 1993, 1996)] towards the dry end of the gradient, indicating that the ecological demands of most fungi are decreasingly well satisfied from poor bilberry-dominated spruce forest to dry pine forests.

R. Økland & Eilertsen (1993) observe relatively sharp limits for many vascular plants along the main coenocline towards the pine forest, and note that these limits contribute considerably to high compositional turnover along the coenocline.

The stronger overlap between site-types in the ordinations of fungi than in ordinations of plants, and the lower compositional turnover along the main fungal gradient (lower gradient length), are likely to be caused by the generally more ubiquitous nature of fungi: contrary to spruce forest vascular plants and mosses like *Maianthemum bifolium*, *Trientalis europaea*, *Hylocomiastrum umbratum* and *Rhytidiadelphus loreus* many fungal species with optima in poor bilberry-dominated spruce forest (site-type 5.1) also occur in the driest pine forests (series 1 and 2).

The significant correlation in pine forest between plot position along the gradient and pH (and AL-extractable phosphorus concentrations) indicates that soil acidity and/or soil nutrient availability may be a third factor contributing to the coenocline, in addition to soil moisture deficiency and the shift from spruce to pine as mycorrhizal host. However, while high importance of soil nutrient factors for the observed shifts in species composition in the pine forest is hardly supported by external evidence, numerous counter-arguments exist: (1) The incidental occurrence of fruitbodies of species with a distinct optimum in spruce forests in pine forest as well, lending support to soil moisture deficiency as an important factor for regulation of fruiting. (2) Restriction of species with well-defined limits towards poorer sites to spruce forest (e.g. *Hygrophorus pustulatus* and *Entoloma rhodopolium*; neither of which are observed in plots classified to the poor submesic site-type, 5.1) while no such examples are known from the pine forest. (3) The paradox that pine-forest plots along comparable first axes in ordinations of fungi and plants are so similar (see Tab. 10) if due to completely different causes. (4) The correlation of the gradient with pH may result from correlations of both with slope and terrain shape. In that case, soil moisture deficiency may be the decisive factor while correlations with pH (and nutrient concentrations) are without causal ecological significance.

One reason why spruce and pine forest subsets overlap along the first fungal ordination axes while a moderate discontinuity is observed in ordinations of vegetation may be that soil moisture deficiency influences plants and fungi in different ways. Thus the fungal ordination does not provide evidence for existence of a point along the gradient like that claimed by R. Økland & Eilertsen (1993) for plants [near the transition between spruce and pine forest in series 4, cf. R. Økland & Eilertsen (1993): Fig. 137], where duration (probability) of soil moisture below a critical level takes over for soil nutrient status as the important complex-gradient. One possibility is that fungi have higher demands for moisture than plants, thus being influenced by soil moisture deficiency even in spruce forest, perhaps along the entire main fungal coenocline. However, this interpretation is not supported by correlations between topographical variables and the main gradient in the spruce forest.

We conclude that increasing soil moisture deficiency is likely to restrict the occurrence and fruiting of several species of fungi towards dry pine forests, and that the main gradient in fungal species composition is accentuated by the preference of mycorrhizal species for either spruce or pine as their main mycorrhizal symbiont.

*Spruce forests: a gradient in cover by deciduous litter and bryophytes?*

A second fungal coenocline, relevant for spruce forest only, is expressed along the second axis in the ordination of the F95 data set, the third axis in ordination of the F97 data set, and the second axis in a separate ordination of spruce-forest plots. This coenocline is correlated with the fourth axis for vegetation, which R. Økland & Eilertsen (1993) found not to be ecologically interpretable. No ecological variable is correlated with this coenocline at the  $P < 0.0001$  level and, with the exception of bryophyte cover, all variables correlated with this coenocline at the  $P < 0.025$  level are more strongly correlated with the main coenocline. We hypothesize that this coenocline is due to variation along a complex-gradient in spruce forest from high bryophyte cover and low cover of deciduous litter (notably *Betula* and *Populus*) to low bryophyte cover and high litter cover. Support for this interpretation comes from: (1) The positive correlation with deciduous litter cover ( $\tau = 0.1512$ ,  $P = 0.0368$ ) and the negative correlation with bryophyte cover ( $\tau = -0.2314$ ,  $P = 0.0012$ ). (2) The optima of fungal species associated with deciduous trees at high DCA 2 scores (cf. Fig. 23, 25), viz. the mycorrhizal *Cortinarius armillatus*, *C. raphanoides*, *Lactarius glyciosmus*, *Lactarius vietus*, *Leccinum* spp., and *Tricholoma fulvum*, and the leaf-decaying saprotrophs *Clavariadelphus junceus*, and *Collybia confluens*, *Marasmius epiphyllus*, *Typhula setipes*, and *T. phacorrhiza* (of which several are, however, poorly represented in our material). (3) The optima of bryophilous species that avoid sites with dense litter at low DCA 2 scores, viz. *Cortinarius albovariegatus*, *Cystoderma jasonis*, *Galerina* sp.1, and *G. mniophila* (for the strong decrease in abundance of *Lactarius theiogalus* along this axis, see p. 00). (4) The negative characterization of plots with high score along this axis by lack of bryophilous fungi. (5) The almost complete absence of deciduous trees in pine forests, explaining the lack of variation along this coenocline there. Both *Populus tremula* (cf. Johansson 1996) and *Betula* spp. have wide amplitudes with respect to climatic and local environmental factors, but prefer moist, fertile sites.

*Betula* and *Populus* provide suitable substrates for fungi, by formation of ectomycorrhizae and by shedding leaves which form a persistent, compact mat. Incompletely decayed *Betula* and *Populus* litter, soaked with water for longer periods, is an important substrate for saprotrophs that fruit in late autumn. Most *Typhula* species have high abundance in plots with high DCA 2 scores and are particularly abundant on this kind of substrate (*T. erythropus* differs by having a low optimum along this axis, probably because of high abundance in the species-rich plots Nos 45 and 57, which occupy outlier positions along this axis). *Quercus* leaves share the properties of *Betula* and *Populus*, but oak is too sparse in the area to be of quantitative importance. Litter produced by the common *Sorbus aucuparia* decay rapidly and hence lacks the qualities of *Betula* and *Populus*.

Few large (or several smaller) deciduous trees may be sufficient to impact moss cover negatively, because shoots of most bryophyte species are unable to survive recurrent burial under large deciduous leaves (R. Økland 1995d, 2000). The negative impact on bryophyte cover increases with increasing leaf size and with increasing decomposition time (cf. Kujala 1926, Tamm 1953, During & Verschuren 1988, R. Økland 1995c); *Populus* litter is thus more detrimental to bryophytes than *Betula* litter (R. Økland, pers. obs.). Large spruce trees negatively impact the moss cover below the crown because of high litterfall, reduced amounts of throughfall precipitation compared to below deciduous trees (cf. Lukkala 1942, Päivänen 1966, Mahendrapa & Kingston 1982) and lowered incident light.

Loss on ignition is positively correlated with position along the coenocline, most likely because litterfall and the thickness of the organic topsoil layer increases along the gradient. A probable reason for the lack of correlation between this coenocline and tree variables is the wind-mediated dispersal of leaves over a large area around each tree, in ways not adequately reflected in indices neither at the 1-m<sup>2</sup> nor at the 16-m<sup>2</sup> scales. The relatively weak relationship between deciduous litter cover and this coenocline indicates that ample litter supply may be one among several factors which make up a complex-gradient. Large deciduous trees occur in, or close to, plots in transects 5 and 8 with high DCA-2 score. These plots differ with respect to aspect, altitude and other local conditions. Presence of large deciduous trees in spruce forest largely reflects forest history and successional state (cf. Hytteborn et al. 1991).

Most saprotrophic species have wider ranges than mycorrhizal species along this coenocline (cf. Fig. 21); perhaps because the number of specialists for dense leaf mats is low (see above), perhaps because sites of this kind occur patchily on scales considerably finer than the plot site of 16 m<sup>2</sup>. Specific niches related to factors that vary on scales finer than the plot size are likely to be undetected by multivariate analyses, because within-plot variation is treated as noise (Gauch 1982a, 1982b, Wiens 1989). Patterns of mycorrhizal species may be more adequately represented because they are more broad-scaled, and because they are likely to be accentuated by the restricted distributions of several mycorrhizal host tree species along the gradient.

#### *Pine and spruce forests: the fine-scale paludification gradient*

A third fungal coenocline occurs in all ordinations and all subsets – as the third axis in DCA ordinations of F95 and the spruce forest subset F58A, and the second axis in DCA ordinations of F97, the pine forest subset F37B and both LNMDS ordinations. This fungal coenocline is strongly correlated with the second axis in the ordination of vegetation, interpreted by R. Økland & Eilertsen (1993) as ‘the response to a complex-gradient consisting of more or less parallel gradients in soil moisture, fine-scale canopy closure (under trees – between trees gradient), soil depth and exchangeable amounts of Al and Fe’. R. Økland & Eilertsen (1993) interpret this vegetational gradient as a fine-scale gradient because it is reflected primarily in the composition of the bottom layer. Furthermore, they stress the difference between this fine-scale paludification gradient which reflects variation in the normal, or median, soil moisture conditions and the soil moisture deficiency gradient (reflecting variation in the danger and duration of extreme drought, see p. 81). R. Økland & Eilertsen (1993) discuss how fine-scale paludifications of different kinds are related to ecological conditions.

This fungal coenocline is most strongly correlated with the corresponding axis in the ordination of cryptogams, perhaps indicating that fungi (fruitbody production) responds to paludification in the same way as bryophytes and lichens, and on the same scale. Strong support for interpretation of this fungal coenocline (like corresponding plant coenoclines) as the response to fine-scale paludification comes from the correlations with soil moisture (which decreases along the gradient). Furthermore, the coenocline is moderately correlated with several tree indices and also weakly correlated with the concentration of extractable aluminium, which decrease along the gradient. In pine forest, plot scores are also moderately strongly correlated with soil depth (increasing) and pH and nitrogen concentrations (decreasing along the gradient). The shift of this coenocline from the second to the third axis in the ordinations suggests that its importance is comparable to the coenocline related to deciduous litter and bryophyte cover.

In the separate ordination of the pine forest subset MAF37B, the second axis, which is most strongly correlated with soil moisture (cf. Tab. 14), is strongly correlated both with the second and third (and fourth) axes in the ordination of MAF95 (cf. Tab. 8). This indicates that in pine forest one



fungal coenocline is the response to a complex gradient made up by deciduous litter and bryophyte cover and variation in fine-scale paludification, running from moist moss-covered (often with *Sphagnum*) to dry litter-covered ground.

Fungi are well known to respond to the fine-scale paludification gradient, e.g. by the frequent reference in mycoecological studies and floras to 'association with *Sphagnum*'. Both mycorrhizal fungi (e.g., *C. flexipes*, *Hygrophorus olivaceoalbus*) and saprotrophs (e.g., *Mycena galopus*) that seem to find their optima in *Sphagnum*-dominated patches have low scores along the ordination axes representing this coenocline. The great water-holding capacity of *Sphagnum* is probably the most important single factor, although saprotrophs may also respond to *Sphagnum* as a substrate. It is not yet known if the different species' mycelia segregate along this gradient or if this coenocline merely reflects specific requirements for fruiting.

Mycorrhizal and saprotrophic species have comparable ranges along this coenocline (Fig. 22). A majority of species in both of the major groups have wide ranges along this coenocline, indicating that species of moist sites are able to grow drier sites as well, while the number of specialist species is low. Conversely, many species typical of the dry end of this coenocline, e.g. *Mycena septentrionalis* which is able to grow in needle beds under dense spruce canopies, may thrive in locally moist sites. Species with special adaptations to paludified sites first appear in sites with a permanently high subsoil water table, such as swamps and mires (see Arnolds 1992b).

Aluminium concentrations are invariably less strongly correlated with the fungal coenocline than with the corresponding plant coenocline, even after differences in absolute values between correlation coefficients are taken into account. Aluminium concentration explains a low fraction of variation in species abundances in tests by single-variable CCA (cf. Tab. 17), indicating that its correlation with the coenocline results because both are correlated with median soil moisture. R. Økland & Eilertsen (1993) ascribe the positive correlations between a vegetation coenocline and Al and Fe concentrations and (median) soil moisture to accumulation of these elements higher in the soil profile in sites where leakage is counteracted by high water supply rates, high content of median soil moisture, and upward capillary movement of water in *Sphagnum* stands.

As discussed for the corresponding vegetational coenocline by R. Økland & Eilertsen (1993), the correlation of this coenocline with (spruce) canopy closure and tree influence indices may indicate a causal relationship. Spruce (and pine) canopies efficiently intercept precipitation, and dense spruce needle litter has low water retention capacity (cf. R. Økland & Eilertsen 1993, T. Økland 1996). Both of these factors will tend to increase the range of soil moisture variation. Needle beds are particularly well developed under vigorous spruce trees with low height to the crown. Many saprotrophs that are able to decompose spruce needles are equally common in moss-rich plots as in needle beds, but some (e.g. *Micromphale perforans* and *M. septentrionalis*) that increase in abundance with increasing plot score along this axis appear to profit from large amounts of substrate available for decomposition. *Mycena septentrionalis* is for many needle-bed dominated plots represented in almost every subplot. Several saprotrophs that grow on deciduous litter, e.g. *Marasmius epiphyllus*, *Typhula erythropus* and *T. phaeocorrhiza*, increase in abundance towards the dry end of this gradient. The high correlation of the second axis in the LNMDS ordination of F95 and significant correlations of the second and third axes in the corresponding DCA ordination with bryophyte cover reflects this element of variation in common between the second and third fungal coenoclines, from bryophyte-rich, paludified sites poor in litter to litter-rich, drier sites. Species with peak abundance in needle-bed sites may benefit from lower intensity of competition – with vascular plants, bryophytes and lichens which suffer from adverse moisture conditions, litterfall and strong shade, and other fungi which are negatively affected by the dryness of the substrate. These species normally produce fruitbodies late in the autumn when moisture conditions are more favourable also in litter-bed sites (high amounts of precipitation, low temperatures and low evaporation rates). An important exception to late fruiting is *Marasmius*

*androsaceus* with its specialized rhizomorphs, which gives this species access to different substrates over a wide area (Lehmann & Hudson 1977, Holmer & Stenlid 1991). Despite of its great ability to grow in dry places this ubiquitous species does not show any clear trend along the third axis (Tab. 16).

#### FACTORS DETERMINING VARIATION IN FUNGAL ABUNDANCE

The fraction of variation in fungal species abundances in 16-m<sup>2</sup> plots which could be explained by significant environmental variables, 20.5%, is considerably lower than reported by R. Økland & Eilertsen (1994) for plants in 1-m<sup>2</sup> plots (36.5% for vascular plants, 25.1% for cryptogams). R. Økland & Eilertsen (1994) find that the fraction of variation explained by environmental variables at the 0.0625-m<sup>2</sup> plot scale is considerably lower than at the 1-m<sup>2</sup> scale, and attribute this difference to the change of dominant process from environmental control at the broader scale to control by interspecific interaction, clonal processes and random events at the finer scale. The fine-scaled patterns of variation in factors like soil moisture and deciduous litter cover indicate that the difference between fungi and plants in variation explained is likely to be due to a combination of two factors: (1) high amount of within-plot variation in important environmental factors at the 16-m<sup>2</sup> plot scale, and (2) high importance also of factors not included among the measured variables for fruiting of fungi, such as climate, litter quality and quantity, and mycorrhizal partner. However, the inappropriateness of total inertia as a measure of the total variation in species composition (R. Økland 1999), even for data sets that are collected in comparable ways, precludes firm conclusions to be drawn from these figures.

The fraction of the total explained variation in fungal abundance explained by spatial variables is comparable with that reported for plants by R. Økland & Eilertsen (1994). A relatively large fraction of spatial variation, 61%, is not shared with environmental variables. Strictly spatial variation may be due to (1) causes that are stochastic functions of geographic distance, such as clonal growth, aggregated dispersal and mortality, and common (fine-scale disturbance) history, and (2) variation along geographically structured, not measured environmental variables (Borcard et al. 1992, Legendre 1993, R. Økland & Eilertsen 1993). All of these processes are highly important for fungi. For instance, several fungal species have aggregated distribution patterns, e.g. *Lactarius theiogalus* and *Russula puellaris*. The abundance of the former decrease strongly along the second DCA axis in the ordination of the F95 data set, even if *Lactarius theiogalus* seems unaffected by the factors considered important for variation along this coenocline. Localised dispersal patterns may explain why five of the seven plots in which it occurs in our material are from the middle part of transect 1. Similarly, four of the six occurrences of *Russula puellaris* are from southwest of Lake Karistjern; three in adjacent submesic plots from transect 8 and the fourth in the nearest plot in the neighbouring transect 7, in dry pine forest (a most unusual habitat for this species in Scandinavia; E. Bendiksen, pers. obs.). Dispersal, both of spores which fall at higher density and also may have a higher chance of successful establishment close to an earlier established fruiting mycelium (cf. Kallio 1970, Nordén & Larsson 2000), and of mycelia, will contribute to strictly spatial variation in abundance. Both kinds of dispersal are likely to operate on scales where variation is reflected as spatial variation in our data set. Dahlberg & Stenlid (1990) and Dahlberg (1997) demonstrate clonal diameters up to 30 and 27 m, respectively, for *Suillus bovinus* and *S. variegatus*, by somatic incompatibility pairings of isolates, and find mycelial spread to be more important than spore dispersal in areas with low disturbance.

Positions of plots in which we have studied fungi along the four plant ordination axes (vegetational coenoclines) explained the same amount of variation in fungal species abundance as

spatial variables. Forty percent of this variation was strictly due to these vegetational variables, indicating that the species composition of plants is a good predictor of fungal species composition, in part explaining variation in fungal species composition other than the variation explained by environmental variables. Most likely this is because plants (notably bryophytes) often respond to the same, complex sets of environmental conditions as fungi. A consequence of this result is that forest typifications based upon plants are likely to have relevance for fungi as well (cf. Pirk 1948, Barkman 1987).

#### COMMENTS ON FIELD METHODOLOGY AND INTEGRATED APPROACHES TO MACROFUNGI AND PLANTS

The results obtained by the approach adopted in this study, notably the use of a systematic sampling design as basis for multivariate analyses of patterns, show that this is a powerful approach for elucidating the ecology of fungi. The evaluations of sampling designs by R. Økland & Eilertsen (1993), and of ordination methods by R. Økland & Eilertsen (1993) and T. Økland (1996), both indicating a slight preference for DCA over LNMDS, are also supported by this study.

Since a general discussion of problems related to methodology in studies of macrofungal occurrence patterns will be provided in another study (E. Bendiksen, in prep.), among others with reference to the present study, we will restrict ourselves here to one methodological problem: the choice of plot size. Viewed in the light of our results, the 16-m<sup>2</sup> plot appears as an acceptable compromise; good arguments exist for smaller as well as larger plots. The 16-m<sup>2</sup> plot is too large to represent variation along fine-scaled gradients such as the deciduous litter and paludification/median soil moisture gradients – c. 50% of the 16-m<sup>2</sup> plots are inhomogeneous with respect to site-type. However, the nested plot design used in the present study also opens for autecological and other studies based upon 1584 1-m<sup>2</sup> plots (cf. Austin 1981, R. Økland & Eilertsen 1993). A plot size of 1 m<sup>2</sup> may be particularly well suited for saprotrophs, sometimes associated with very local substrates, while the occurrence of mycorrhizal fungi is mostly determined by factors operating on a broader scale (cf. placement of trees).

#### GENERAL CONCLUSIONS

The closely corresponding results obtained by use of parallel DCA and LNMDS ordinations of fungal abundance data, and the parallel between fungal and vegetational coenoclines, demonstrate (1) that distributional patterns of terricolous macrofungi and plants within forests to a large extent are caused by the same major environmental complex-gradients and (2) that the same field and analytical methods are applicable to both groups of organisms.

Just like the corresponding study of plants in the same plots has provided a valuable basis for studying vegetation dynamics over short time-spans (R. Økland 1995d, R. Økland & Eilertsen 1996, T. Økland et al. 2001), this study should provide a good starting-point for studies of changes in the funga with time; natural and due to man-induced environmental change. The high species richness of the macrofunga, also at oligotrophic sites, and that fact that this funga represents two major and

several minor ecological life-form types, make macrofungi important as indicators of environmental change. Furthermore, an integrated study where many groups of organisms are studied in the same permanent plots opens for new insights of many kinds.

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## APPENDICES

Appendix 1. Full list of species recorded in the investigation area, sorted in (supposed) mycorrhizal and non-mycorrhizal species, respectively. Abbreviations are shown for species occurring in = 5% of the macro plots, for which optima along DCA ordination axes are shown in Figs. 23-26.

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Abbr.	Species
	<i>Albatrellus ovinus</i> (Schaeff. : Fr.) Kotl. & Pouzar
Aman ful	<i>Amanita fulva</i> (Schaeff.) Pers.
	<i>Amanita muscaria</i> (L. : Fr.) Hook.
Aman por	<i>Amanita porphyria</i> (Alb. & Schwein. : Fr.) Mlady
	<i>Amanita regalis</i> (Fr.) Michael
Aman rub	<i>Amanita rubescens</i> (Pers. : Fr.) Gray
Aman vir	<i>Amanita virosa</i> (Fr.) Bertillon
	<i>Bankera fuligineoalba</i> (J.C. Schmidt : Fr.) Pouzar
Bole edu	<i>Boletus edulis</i> Bull. : Fr.
	<i>Cantharellus cibarius</i> Fr.
Cant tub	<i>Cantharellus tubaeformis</i> (Bull. : Fr.) Fr.
Chal pip	<i>Chalciporus piperatus</i> (Bull. : Fr.) Bat.
Chro rut	<i>Chroogomphus rutilus</i> (Schaeff. : Fr.) O.K. Miller
Cort alb	<i>Cortinarius albovariegatus</i> (Velen.) Melot
	<i>Cortinarius angelesianus</i> A.H. Sm.
Cort ano	<i>Cortinarius anomalus</i> (Fr. : Fr.) Fr.
Cort arm	<i>Cortinarius armeniacus</i> (Schaeff. : Fr.) Fr.
	<i>Cortinarius armillatus</i> (Fr. : Fr.) Fr.
	<i>Cortinarius badiovinaceus</i> M.M. Moser
	<i>Cortinarius balteatus</i> (Fr.) Fr.
Cort bif	<i>Cortinarius bififormis</i> Fr.
Cort bru	<i>Cortinarius brunneus</i> (Pers. : Fr.) Fr.
Cort cam	<i>Cortinarius camphoratus</i> Fr.
Cort cas	<i>Cortinarius casimiri</i> (Velen.) Huijsman
	<i>Cortinarius collinitus</i> (Sow. : Fr.) Gray
	<i>Cortinarius croceus</i> (Schaeff.) Gray
	<i>Cortinarius decipiens</i> (Pers. : Fr.) Fr.
Cort del	<i>Cortinarius delibutus</i> Fr.
	<i>Cortinarius evernius</i> (Fr. : Fr.) Fr.
	<i>Cortinarius fervidus</i> P.D. Orton
Cort fle	<i>Cortinarius flexipes</i> (Pers.: Fr.) Fr.
Cort ful	<i>Cortinarius fulvescens</i> Fr.
Cort gen	<i>Cortinarius gentilis</i> (Fr.) Fr.
Cort ill	<i>Cortinarius illuminus</i> Fr.
	<i>Cortinarius limonius</i> (Fr. : Fr.) Fr.
	<i>Cortinarius lux-nymphae</i> Melot
	<i>Cortinarius mucifluus</i> Fr.

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## Appendix 1 (cont.)

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		<i>Cortinarius mucosus</i> (Bull.) Kickx
Cort	obt	<i>Cortinarius obtusus</i> (Fr. : Fr.) Fr.
Cort	plu	<i>Cortinarius pluvius</i> (Fr. : Fr.) Fr.
		<i>Cortinarius purpurascens</i> Fr.
		<i>Cortinarius</i> cf. <i>quarciticus</i> H. Lindstr.
		<i>Cortinarius raphanoides</i> (Pers. : Fr.) Fr.
		<i>Cortinarius rubellus</i> Cooke
Cort	san	<i>Cortinarius sanguineus</i> (Wulfen in Jacq. : Fr.) Fr.
		<i>Cortinarius saturninus</i> (Fr.) Fr.
Cort	sca	<i>Cortinarius scaurus</i> (Fr. : Fr.) Fr.
Cort	sem	<i>Cortinarius semisanguineus</i> (Fr. : Fr.) Fr.
Cort	sti	<i>Cortinarius stillatitius</i> Fr.
		<i>Cortinarius subtortus</i> (Pers. : Fr.) Fr.
		<i>Cortinarius tortuosus</i> (Fr. : Fr.) Fr.
		<i>Cortinarius traganus</i> (Fr. : Fr.) Fr.
		<i>Cortinarius turmalis</i> Fr.
		<i>Cortinarius varius</i> (Schaeff. : Fr.) Fr.
		<i>Cortinarius violaceus</i> (L. : Fr.) Gray
Cort	sp.	<i>Cortinarius</i> sp.
Elap	sp.	<i>Elaphomyces</i> sp.
Ento	rho	<i>Entoloma rhodopolium</i> (Fr.) P. Kumm.
Glom	sp	<i>Glomus</i> sp.
		<i>Hebeloma remyi</i> Bruchet ex Quadraccia
Hydn	ruf	<i>Hydnum rufescens</i> Schaeff. : Fr.
		<i>Hygrophorus camarophyllus</i> (Alb. & Schwein. : Fr.) Dumèè, Grandjean & Maire
Hygr	oli	<i>Hygrophorus olivaceoalbus</i> (Fr. : Fr.) Fr.
Hygr	pus	<i>Hygrophorus pustulatus</i> (Pers. : Fr.) Fr.
		<i>Hygrophorus tephroleucus</i> (Fr.) Fr.
		<i>Inocybe cincinnata</i> (Fr.) Quél.
		<i>Inocybe geophylla</i> (Sow. : Fr.) P. Kumm.
Inoc	lan	<i>Inocybe lanuginosa</i> (Bull. : Fr.) P. Kumm.
		<i>Inocybe mixtilis</i> Britzelm.
		<i>Inocybe napipes</i> J.E. Lange
		<i>Inocybe nitidiuscula</i> (Britzelm.) Sacc.
Inoc	rel	<i>Inocybe relicina</i> (Fr.) Quél.
Inoc	sub	<i>Inocybe subcarpta</i> Kühner & Boursier
Lacc	ame	<i>Laccaria amethystina</i> Cooke
Lacc	lacc	<i>Laccaria laccata</i> (Scop. : Fr.) Berk. & Broome
Lact	cam	<i>Lactarius camphoratus</i> (Bull. : Fr.) Fr.
Lact	det	<i>Lactarius deterrimus</i> Gröger
Lact	ful	<i>Lactarius fuliginosus</i> (Fr. : Fr.) Fr.
		<i>Lactarius glyciosmus</i> (Fr. : Fr.) Fr.
		<i>Lactarius mammosus</i> (Fr. ex Weinm.) Fr.
		<i>Lactarius mitissimus</i> (Fr.) Fr.
Lact	nec	<i>Lactarius necator</i> (Bull. : Fr.) P. Karst.
		<i>Lactarius quietus</i> (Fr. : Fr.) Fr.

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## Appendix 1 (cont.)

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Lact	ruf	Lactarius rufus (Scop. : Fr.) Fr. Lactarius sphagneti (Fr.) Neuhoff
Lact	the	Lactarius theiogalus (Bull. : Fr.) Gray ss. Neuhoff Lactarius trivialis (Fr. : Fr.) Fr.
Lact	vie	Lactarius vietus (Fr.) Fr. Leccinum aurantiacum (Bull.) Gray Leccinum niveum (Fr.) Rauschert
Lecc	pal	Leccinum palustre M. Korhonen
Lecc	sca	Leccinum scabrum (Bull. : Fr.) Gray
Lecc	var	Leccinum variicolor Watling
Lecc	ver	Leccinum versipelle (Fr.) Snell
Lecc	sp.	Leccinum sp. Paxillus involutus (Batsch : Fr.) Fr.
Rozi	cap	Rozites caperatus (Pers. : Fr.) P. Karst. Russula adusta Fr.
Russ	aqu	Russula aquosa Leclair Russula atrorubens Quéf.
Russ	bet	Russula betularum Hora
Russ	con	Russula consobrina (Fr. : Fr.) Fr.
Russ	dec	Russula decolorans (Fr.) Fr. Russula elaeodes (Bres.) Bon
Russ	eme	Russula emetica (Schaeff. : Fr.) Pers. Russula fragilis (Pers. : Fr.) Fr. Russula laricina Velen. Russula lutea (Huds. : Fr.) Gray
Russ	och	Russula ochroleuca Pers.
Russ	pal	Russula paludosa Britzelm.
Russ	pue	Russula puellaris Fr.
Russ	que	Russula queletii Fr.
Russ	rho	Russula rhodopoda Zwára Russula vesca Fr.
Russ	vin	Russula vinosa Lindbl. Russula xerampelina (Schaeff.) Fr.
Suil	var	Suillus variegatus (Schwein. : Fr.) Kuntze Thelephora palmata Scop. : Fr. Tricholoma fulvum (DC. : Fr.) Sacc. Tricholoma saponaceum (Fr. : Fr.) P. Kumm. Tylopilus felleus (Bull. : Fr.) P. Karst. Xerocomus subtomentosus (L. : Fr.) Quéf. Agrocybe erebia (Fr. : Fr.) Kühn. Armillaria mellea (Vahl : Fr.) P. Kumm. coll.
Baeo	myo	Baeospora myosura (Fr. : Fr.) Singer
Calo	vis	Calocera viscosa (Pers. : Fr.) Fr.
Clav	junc	Clavariadelphus junceus (Alb. & Schwein. : Fr.) Corner
Clav	cor	Clavulina coralloides (L. : Fr.) J. Schröt. Clitocybe candicans (Pers. : Fr.) P. Kumm.

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## Appendix 1 (cont.)

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		<i>Clitocybe diatreta</i> (Fr. : Fr.) P. Kumm.
Clit	dit	<i>Clitocybe ditopus</i> (Fr. : Fr.) Gill.
Clit	met	<i>Clitocybe metachroa</i> (Fr.) P. Kumm.
Coll	ace	<i>Collybia acervata</i> (Fr.) P. Kumm.
		<i>Collybia asema</i> (Fr. : Fr.) P. Kumm.
Coll	cir	<i>Collybia cirrata</i> (Pers.) P. Kumm.
		<i>Collybia confluens</i> (Pers. : Fr.) P. Kumm.
		<i>Collybia cookei</i> (Bres.) J.D. Arnold
Coll	dry	<i>Collybia dryophila</i> (Bull. : Fr.) P. Kumm.
		<i>Collybia putilla</i> (Fr. : Fr.) Sing.
Coll	tub	<i>Collybia tuberosa</i> (Bull. : Fr.) P. Kumm.
		<i>Conocybe striipes</i> (Cooke) S. Lundell
		<i>Conocybe sulcatipes</i> (Peck) Kühner
Cord	oph	<i>Cordyceps ophioglossoides</i> (Ehrh. ex Pers. : Fr.) Fr.
Cudo	cir	<i>Cudonia circinans</i> (Pers. : Fr.) Fr.
		<i>Cudonia confusa</i> Bres.
Cudo	cla	<i>Cudoniella clavus</i> (Alb. & Schwein. : Fr.) Dennis
		<i>Cystoderma carcharias</i> (Pers.) Konrad & Maubl.
		<i>Cystoderma fallax</i> A.H. Sm. & Singer
Cyst	jas	<i>Cystoderma jasonis</i> (Cooke & Masee) Harmaja
Ento	cetr	<i>Entoloma cetratum</i> (Fr. : Fr.) M.M. Moser
Ento	con	<i>Entoloma conferendum</i> (Britzelm.) Noordel.
		<i>Entoloma juncinum</i> (Kühner & Romagn.) Noordel.
Ento	nit	<i>Entoloma nitidum</i> (Quél.) Quél.
		<i>Entoloma rhodocylix</i> (Lasch : Fr.) M.M. Moser
		<i>Entoloma turbidum</i> (Fr.) Quél.
		<i>Fayodia gracilipes</i> (Britzelm.) Bresinsky & Stangl
		<i>Flammulina subincarnatus</i> (Joss. & Kühner) Watling
		<i>Galerina allospora</i> A.H. Sm. & Singer
Gale	atk	<i>Galerina atkinsoniana</i> A.H. Sm.
Gale	bad	<i>Galerina badipes</i> (Fr.) Kühner
Gale	bor	<i>Galerina borealis</i> A.H. Sm. & Singer
Gale	hyp	<i>Galerina hypnorum</i> (Schränk : Fr.) Kühner ss. lat.
Gale	mar	<i>Galerina marginata</i> (Batsch) Kühner
Gale	mni	<i>Galerina mniophila</i> (Lasch) Kühner
		<i>Galerina pumila</i> (Pers. : Fr.) Singer
Gale	sty	<i>Galerina stylifera</i> (Atk.) A.H. Sm. & Singer
		<i>Galerina triscopa</i> (Fr.) Kühner
		<i>Galerina unicolor</i> (Vahl : Fr.) Singer
Gale	sp1	<i>Galerina</i> sp.1
Gale	sp2	<i>Galerina</i> sp.2
Gymn	sap	<i>Gymnopilus sapineus</i> (Fr. : Fr.) Maire
		<i>Hemimycena delectabilis</i> (Peck) Singer
Heyd	abi	<i>Heyderia abietis</i> (Fr.) Link
		<i>Hygrocybe virginea</i> (Wulfen. : Fr.) P.D. Orton & Watling var. <i>fuscescens</i> (Bres.) Arnolds

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## Appendix 1 (cont.)

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		<i>Hygrophoropsis aurantiaca</i> (Wulfen. : Fr.) J. Schröt.
		<i>Hypholoma capnoides</i> (Fr.) P. Kumm.
		<i>Hypholoma marginatum</i> (Pers. : Fr.) J. Schröt.
		<i>Hypholoma polytrichii</i> (Fr. : Fr.) Singer
		<i>Lycoperdon nigrescens</i> (Pers. : Pers.) Pers.
		<i>Lyophyllum rancidum</i> (Fr.) Singer
		<i>Lyophyllum semitale</i> (Fr.) Kühner
Mara	and	<i>Marasmius androsaceus</i> (L. : Fr.) Fr.
		<i>Marasmius bulliardii</i> Quéf. f. <i>acicola</i> (S. Lundell) Noordel.
Mara	epi	<i>Marasmius epiphyllus</i> (Pers. : Fr.) Fr.
Micr	per	<i>Micromphale perforans</i> (Hoffm. : Fr.) Gray
Myce	alc	<i>Mycena alcalina</i> (Fr. : Fr.) P. Kumm. coll.
Myce	ami	<i>Mycena amicta</i> (Fr.) Quéf.
		<i>Mycena aurantiomarginata</i> (Fr.) Quéf.
Myce	cnl	<i>Mycena cinerella</i> P. Karst.
Myce	cno	<i>Mycena cineroides</i> Hintikka
		<i>Mycena clavicularis</i> (Fr.) Gill.
Myce	epi	<i>Mycena epipterygia</i> (Scop. : Fr.) Gray
Myce	fil	<i>Mycena filopes</i> (Bull. : Fr.) P. Kumm.
Myce	fla	<i>Mycena flavoalba</i> (Fr.) Quéf.
		<i>Mycena floridula</i> (Fr.) P. Karst.
Myce	gle	<i>Mycena galericulata</i> (Scop. : Fr.) Gray
Myce	glo	<i>Mycena galopus</i> (Pers. : Fr.) P. Kumm.
		<i>Mycena haematopus</i> (Pers. : Fr.) P. Kumm.
		<i>Mycena inclinata</i> (Fr.) Quéf.
Myce	lon	<i>Mycena longiseta</i> Höhn.
		<i>Mycena maculata</i> P. Karst.
		<i>Mycena megaspora</i> Kauffman
Myce	met	<i>Mycena metata</i> (Fr.) P. Kumm.
		<i>Mycena oregonensis</i> A.H. Sm.
Myce	pur	<i>Mycena pura</i> (Pers. : Fr.) P. Kumm.
Myce	ror	<i>Mycena rorida</i> (Fr. : Fr.) Quéf.
Myce	ros	<i>Mycena rosella</i> (Fr.) P. Kumm.
Myce	rub	<i>Mycena rubromarginata</i> (Fr. : Fr.) P. Kumm.
Myce	san	<i>Mycena sanguinolenta</i> (Alb. & Schwein. : Fr.) P. Kumm.
Myce	sep	<i>Mycena septentrionalis</i> Maas Geest.
		<i>Mycena speirea</i> (Fr. : Fr.) Gill.
Myce	sty	<i>Mycena stylobates</i> (Pers. : Fr.) P. Kumm.
Myce	ura	<i>Mycena urania</i> (Fr. : Fr.) Quéf.
Myce	vir	<i>Mycena viridimarginata</i> P. Karst.
		<i>Mycena viscosa</i> Maire
Myce	vul	<i>Mycena vulgaris</i> (Pers. : Fr.) P. Kumm.
		<i>Mycocalia</i> sp.
		<i>Omphalina oniscus</i> (Fr. : Fr.) Quéf.
		<i>Pholiota lubrica</i> (Pers. : Fr.) Singer
		<i>Pholiota mixta</i> (Fr.) Singer

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## Appendix 1 (cont.)

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		<i>Pholiota scamba</i> (Fr. : Fr.) M.M. Moser
Psat	fri	<i>Psathyrella friesii</i> Kits van Wav.
		<i>Psathyrella</i> aff. <i>lutensis</i> (Romagn.) Bon
		<i>Psilocybe inquilina</i> (Fr. : Fr.) Bres.
Stor	esc	<i>Strobilurus esculentus</i> (Wulfen. : Fr.) Singer
Stor	hor	<i>Stropharia hornemannii</i> (Fr. : Fr.) S. Lundell
		<i>Tubaria confragosa</i> (Fr.) Kühner
		<i>Tubaria conspersa</i> (Pers. : Fr.) Fayod
Typh	ery	<i>Typhula erythropus</i> (Pers. : Fr.) Fr.
Typh	pha	<i>Typhula phacorrhiza</i> (Reichard : Fr.) Fr.
Typh	set	<i>Typhula setipes</i> (Grev.) Berthier
		<i>Xeromphalina campanella</i> (Batsch : Fr.) Kühner & Maire
		<i>Xeromphalina cornui</i> (Quél.) J. Favre
		<i>Xylaria filiformis</i> (Alb. & Schwein. : Fr.) Fr.

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Appendix 2. Classification of macro plots to site-type: position along the topographic moisture and nutrient status gradients. Position of two meso plots along the fine-scale moisture gradient (1 – dry; 2 ! moist) indicated as exponents (all 5.3 and 6 plots are dry). Macro sample plots inhomogeneous with respect to the former two gradients are listed below the table, with site-type classification of its two meso plots in brackets.

Site-type	n	Plots
1	3	14 <sup>11</sup> , 63 <sup>21</sup> , 79 <sup>11</sup>
2	3	83 <sup>11</sup> , 85 <sup>11</sup> , 90 <sup>12</sup>
3	9	27 <sup>22</sup> , 65 <sup>22</sup> , 66 <sup>11</sup> , 76 <sup>21</sup> , 77 <sup>21</sup> , 81 <sup>11</sup> , 82 <sup>11</sup> , 86 <sup>11</sup> , 89 <sup>11</sup>
4	11	8 <sup>21</sup> , 9 <sup>21</sup> , 10 <sup>11</sup> , 11 <sup>11</sup> , 24 <sup>22</sup> , 28 <sup>21</sup> , 74 <sup>11</sup> , 75 <sup>11</sup> , 80 <sup>11</sup> , 99 <sup>12</sup> , 100 <sup>11</sup>
5.1	22	1 <sup>11</sup> , 2 <sup>11</sup> , 3 <sup>11</sup> , 5 <sup>11</sup> , 6 <sup>12</sup> , 7 <sup>11</sup> , 15 <sup>11</sup> , 21 <sup>21</sup> , 22 <sup>11</sup> , 23 <sup>21</sup> , 32 <sup>22</sup> , 34 <sup>11</sup> , 35 <sup>22</sup> , 36 <sup>11</sup> , 37 <sup>11</sup> , 41 <sup>11</sup> , 70 <sup>11</sup> , 71 <sup>11</sup> , 72 <sup>11</sup> , 96 <sup>11</sup> , 97 <sup>11</sup> , 98 <sup>11</sup>
5.2	10	19 <sup>11</sup> , 33 <sup>22</sup> , 38 <sup>22</sup> , 39 <sup>11</sup> , 42 <sup>11</sup> , 43 <sup>11</sup> , 48 <sup>11</sup> , 50 <sup>11</sup> , 68 <sup>11</sup> , 94 <sup>22</sup>
5.3	5	16, 46, 49, 52, 57
6	1	53

#### Inhomogeneous plots:

4 (4–1, 5.1–1), 12 (1–1, 3–1), 13 (2–1, 1–2), 17 (5.2–1, 5.1–1), 18 (5.2–1, 5.1–1), 25 (4–2, 3–2), 26 (3–2, 2–2), 29 (3–2, 2–2), 30 (3–2, 4–2), 31 (3–2, 2–2), 40 (5.2–1, 5.1–1), 44 (5.3, 5.2–1), 45 (6, 5.2–1), 47 (5.2–1, 5.1–1), 51 (5.3, 5.2–1), 54 (6, 5.3), 55 (5.3, 5.1–1), 56 (5.3, 5.2–1), 58 (2–1, 3–1), 59 (2–1, 3–1), 60 (2–2, 1–1), 61 (2–1, 3–1), 62 (3–1, 2–1), 64 (1–1, 2–1), 67 (6, 5.3), 69 (5.2–1, 5.1–1), 73 (5.1–1, 4–1), 78 (2–2, 1–1), 84 (2–1, 1–1), 87 (2–1, 3–2), 88 (3–1, 1–1), 91 (3–1, 1–1), 92 (3–1, 2–2), 93 (2–1, 1–2), 95 (5.1–2, 5.2–1)





Appendix 3 (continued).

Sample plot	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Albatrellus ovinus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Amanita fulva	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Amanita muscaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Amanita porphyria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Amanita regalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amanita rubescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amanita virosa	0	0	0	0	0	0	1	0	1	1	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0
Bankera fulgineoalba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Boletus edulis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Cantharellus cibarius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cantharellus tubaeformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Chalciporus piperatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Chroogomphus rutilus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius albobariegatus	0	0	0	0	0	2	2	0	0	2	0	0	4	2	1	1	0	0	1	0	0	0	0	0	0
Cortinarius angelesianus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius anomalus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0
Cortinarius armeniacus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Cortinarius armillatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius badiovinaceus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius balteatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cortinarius biformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cortinarius brunneus	0	0	0	1	0	0	4	0	0	0	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0
Cortinarius camphoratus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3	0	1	0	0	0
Cortinarius casimiri	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1	0	0	0
Cortinarius collinitus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius croceus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius decipiens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius delibutus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	4	0	0	0	0	0	0
Cortinarius evernius	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius fervidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Cortinarius flexipes	0	0	0	0	0	0	2	0	3	0	2	0	0	1	1	0	0	1	3	1	0	0	0	0	0
Cortinarius fulvescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius gentilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius illuminus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius limonius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius lux-nymphae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius mucifluus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius mucosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius obtusus	0	0	0	0	0	2	6	1	0	9	8	2	1	0	1	0	1	1	1	1	0	0	0	0	1
Cortinarius pluvius	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius purpurascens	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius cf. quarcticus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius raphanoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius rubellus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius sanguineus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius saturninus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius scaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Cortinarius semisanguineus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius stillatitius	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Cortinarius subtortus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius tortuosus	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius traganus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius turmalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius varius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius violaceus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Elaphomyces sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entoloma rhodopolium	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0	1	1	0	1	0	0	0	0	0
Glomus sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hebeloma remyi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydnum rufescens	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hygrophorus camarophyllus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hygrophorus olivaceoalbus	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	2	0	1	0	0	0	0	0	0
Hygrophorus pustulatus	0	0	0	0	0	2	3	0	0	0	2	0	0	0	0	1	0	2	1	0	0	0	1	0	0
Hygrophorus tephroleucus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inocybe cincinnata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inocybe geophylla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Inocybe lanuginosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inocybe mixtilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Inocybe napipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0
Inocybe nitidiuscula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0
Inocybe relicina	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Inocybe subcarpa	0	0	0</																						



Appendix 3 (continued).

Sample plot	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Albatrellus ovinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amanita fulva	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
Amanita muscaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amanita porphyria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amanita regalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amanita rubescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amanita virosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	1
Bankera fulgineoalba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Boletus edulis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cantharellus cibarius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cantharellus tubaeformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	1	0
Chalciporus piperatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chroogomphus rutilus	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Cortinarius albobariegatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Cortinarius angelesianus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius anomalus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1	1	1	0	3	0	0
Cortinarius armeniacus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Cortinarius armillatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Cortinarius badiovinaceus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius balteatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius biformis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0
Cortinarius brunneus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Cortinarius camphoratus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius casimiri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	5	0	0	0	0
Cortinarius collinitus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius croceus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius decipiens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius delibutus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius evernius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius fervidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius flexipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Cortinarius fulvescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius gentilis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius illuminis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Cortinarius limonius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius lux-nymphae	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius mucifluus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius mucosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius obtusus	1	4	0	0	0	2	3	1	0	1	3	0	0	1	0	0	1	0	6	5	2	5	13	3	3
Cortinarius pluvius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
Cortinarius purpurascens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Cortinarius cf. quarcticus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius raphanoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius rubellus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Cortinarius sanguineus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius saturninus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius scaurus	0	0	0	0	0	4	2	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cortinarius semisanguineus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Cortinarius stillatitius	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Cortinarius subtortus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0
Cortinarius tortuosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius traganus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius turmalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius varius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius violaceus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cortinarius sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Elaphomyces sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entoloma rhodopolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Glomus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0
Hebeloma remyi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Hydnum rufescens	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hygrophorus camarophyllus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hygrophorus olivaceoalbus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0
Hygrophorus pustulatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0
Hygrophorus tephroleucus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inocybe cincinnata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inocybe geophylla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inocybe lanuginosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Inocybe mixtilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inocybe napipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inocybe nitidiuscula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inocybe relicina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Inocybe subcarpa	0	0																							













Appendix 4 (continued).

Sample plot	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	
Agrocybe erobia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Armillaria mellea coll.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Baeospora myosura	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Calocera viscosa	2	0	0	0	0	0	0	1	0	0	1	0	0	2	0	0	0	1	0	0	0	0	0	0	0	
Clavariadelphus junceus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	2	
Clavulina coraloides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	1	0	0	0	0	
Clitocybe candicans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
Clitocybe diatreta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
Clitocybe ditopus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
Clitocybe metachroa	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Collybia acervata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Collybia asema	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Collybia cirrata	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	1	2	0	2	0	0	0	
Collybia confluens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Collybia cookii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Collybia dryophila	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	
Collybia putilla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Collybia tuberosa	0	0	1	0	0	5	1	3	1	1	0	0	0	0	0	1	2	1	0	0	1	0	4	1	0	
Conocybe stripes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Conocybe sulcatipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Cordyceps ophioglossoides	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Cudonia circinans	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Cudonia confusa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
Cudoniella clavus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Cystoderma carcharias	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
Cystoderma fallax	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Cystoderma jasonis	4	2	0	0	0	1	0	0	0	1	0	0	0	0	1	5	2	1	0	0	0	0	0	0	0	
Entoloma cetratum	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	2	0	1	0	1	0	1	0	0	
Entoloma conferendum	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	
Entoloma juncinum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Entoloma nitidum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	
Entoloma rhodocylix	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Entoloma turbidum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Fayodia gracilipes	0	0	0	0	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Flammulaster subincarnatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Galerina allospora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Galerina atkinsoniana	2	1	0	1	3	1	0	0	0	4	2	0	0	2	0	1	2	2	1	2	1	2	1	3	0	0
Galerina badipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
Galerina borealis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Galerina hypnorum	3	5	2	2	4	5	8	2	1	12	12	2	0	8	10	2	2	1	7	3	2	4	7	0	1	
Galerina marginata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Galerina mniophila	0	0	0	0	0	0	0	0	3	0	0	0	0	0	3	0	3	0	4	0	0	0	2	0	0	
Galerina pumila	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Galerina stylifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Galerina triscopa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Galerina unicolor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Galerina sp.1	3	0	1	2	2	0	2	1	0	5	3	0	0	0	1	1	0	0	0	0	0	0	0	0	0	
Galerina sp.2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Gymnopilus sapineus	0	0	0	0	2	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	
Hemimyccena delectabilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Heyderia abietis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Hygrocybe virginea var. fuscescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Hygrophoropsis aurantiaca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Hypholoma capnoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Hypholoma marginatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Hypholoma polytrichii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Lycoperdon nigrescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
Lyophyllum rancidum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
Lyophyllum semitale	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Marasmius androsaceus	6	8	7	4	8	8	1	5	3	2	1	0	1	1	7	2	2	4	1	0	5	4	4	1	0	
Marasmius bulliardii f. acicola	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	3	0	
Marasmius epiphyllus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	4	2	0	
Micromphale perforans	0	0	0	0	0	0	1	7	6	8	2	4	8	1	2	2	4	1	2	0	1	1	2	1	0	
Mycena alcalina coll.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Mycena amicta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Mycena aurantiomarginata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	
Mycena cinerella	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	
Mycena cineroides	0	1	0	0	0	0	2	4	5	3	6	0	5	3	4	2	6	0	6	2	6	4	0	1	0	
Mycena clavicularis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Mycena epipterygia	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3	0	0	0	0	1	0	0	
Mycena filopes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
Mycena flavoalba	0	0	0	0	0	0	0	2	0	0	2	0	0	1	0	0	5	0	1	3	0	3	0	1	0	
Mycena floridula	0	0																								

## Appendix 4 (continued).

Sample plot	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
<i>Agrocybe erebia</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Armillaria mellea</i> coll.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Baeospora myosura</i>	1	0	0	4	0	3	4	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
<i>Calocera viscosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	1	2	0	0	0
<i>Clavariadelphus junceus</i>	5	4	13	5	9	7	6	0	0	0	0	0	0	0	0	9	0	9	7	9	16	16	0	0	0
<i>Clavulina coralloides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Clitocybe candicans</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Clitocybe diatreta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Clitocybe ditopus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Clitocybe metachroa</i>	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Collybia acervata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2
<i>Collybia asema</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Collybia cirrata</i>	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
<i>Collybia confluens</i>	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Collybia cookei</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Collybia dryophila</i>	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Collybia putilla</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Collybia tuberosa</i>	0	0	0	3	0	2	0	2	5	1	2	2	0	0	0	3	2	1	3	0	0	2	3	1	0
<i>Conocybe stripes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Conocybe sulcatipes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
<i>Cordyceps ophioglossoides</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cudonia circinans</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cudonia confusa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cudoniella clavus</i>	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Cystoderma carcharias</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Cystoderma fallax</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cystoderma jasonis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	3	2	0	0	0	0	0	0	0
<i>Entoloma cetratum</i>	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	2	0	0
<i>Entoloma conferendum</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Entoloma juncinum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Entoloma nitidum</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Entoloma rhodocylix</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Entoloma turbidum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Fayodia gracilipes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Flammulaster subincarnatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0
<i>Galerina allospora</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0
<i>Galerina atkinsoniana</i>	4	0	0	3	1	0	0	2	0	0	1	0	1	2	0	0	1	2	0	1	0	0	2	5	0
<i>Galerina badipes</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Galerina borealis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Galerina hypnorum</i>	4	5	0	2	1	0	4	2	0	0	1	0	0	0	0	3	0	7	1	1	2	2	1	0	1
<i>Galerina marginata</i>	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0
<i>Galerina mniophila</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Galerina pumila</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Galerina stylifera</i>	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
<i>Galerina triscopa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Galerina unicolor</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Galerina</i> sp.1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Galerina</i> sp.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Gymnopilus sapineus</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Hemimycena delectabilis</i>	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Heyderia abietis</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hygrocybe virginea</i> var. <i>fuscescens</i>	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hygrophoropsis aurantiaca</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Hypoloma capnoides</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hypoloma marginatum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hypoloma polytrichii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lycoperdon nigrescens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lyophyllum rancidum</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lyophyllum semitale</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Marasmius androsaceus</i>	0	1	1	0	1	1	0	12	12	3	6	9	3	5	10	5	0	3	1	1	0	0	0	2	4
<i>Marasmius bulliardii</i> f. <i>acicola</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Marasmius epiphyllus</i>	6	2	2	0	2	3	0	0	0	0	0	0	0	0	0	3	0	0	0	1	15	13	0	1	
<i>Micromphale perforans</i>	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	3	0	3	0	0	0	0	3	0	0
<i>Mycena alcalina</i> coll.	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	1	0	1	0
<i>Mycena amicta</i>	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0
<i>Mycena aurantiomarginata</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mycena cinerella</i>	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Mycena cineroides</i>	6	5	1	2	0	3	3	0	0	0	0	0	1	1	9	4	9	1	3	0	4	0	1	0	1
<i>Mycena clavicularis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Mycena epipterygia</i>	1	2	1	2	0	1	2	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
<i>Mycena filipes</i>	0	1	1	0	0	0	1	0	0	0	0														

Appendix 4 (continued).

Sample plot	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Agrocybe erebia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Armillaria mellea coll.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Baeospora myosura	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
Calocera viscosa	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0
Clavariadelphus junceus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Clavulina coralloides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Clitocybe candicans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Clitocybe diatreta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Clitocybe ditopus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Clitocybe metachroa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0
Collybia acervata	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Collybia asema	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Collybia cirrata	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	4	2	0	0	0
Collybia confluens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Collybia cookii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Collybia dryophila	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Collybia putilla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Collybia tuberosa	6	0	0	0	1	1	3	4	0	4	3	1	0	5	2	0	5	1	1	1	4	8	8	3	3
Conocybe stripes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Conocybe sulcatipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cordyceps ophioglossoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cudonia circinans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cudonia confusa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cudoniella clavus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Cystoderma carcharias	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cystoderma fallax	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cystoderma jasonis	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	2	1	4	0	1	0	0	0
Entoloma cetratum	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Entoloma conferendum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Entoloma juncinum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entoloma nitidum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entoloma rhodocylix	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Entoloma turbidum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fayodia gracilipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Flammulaster subincarnatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galerina allospora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galerina atkinsoniana	0	2	1	0	1	2	0	0	0	1	0	1	3	2	0	1	1	2	2	3	2	10	2	4	4
Galerina badipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galerina borealis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Galerina hypnorum	1	2	3	0	0	2	1	2	0	1	3	5	4	6	1	2	3	1	9	12	10	5	12	4	11
Galerina marginata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galerina mniophila	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	4	1	0	0	0	0	0	1
Galerina pumila	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galerina stylifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galerina triscopa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galerina unicolor	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galerina sp.1	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Galerina sp.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Gymnopilus sapineus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1
Hemimycena delectabilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heyderia abietis	1	1	1	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0
Hygrocybe virginea var. fuscescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hygrophoropsis aurantiaca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hypholoma capnoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hypholoma marginatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Hypholoma polytrichii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lycoperdon nigrescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lyophyllum randidum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lyophyllum semitale	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Marasmius androsaceus	16	11	1	0	16	12	7	4	6	10	16	9	5	12	9	7	6	1	0	7	5	2	3	8	8
Marasmius bulliardii f. acicola	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Marasmius epiphyllus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	4	4	0	0	0	0
Micromphale perforans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	3	2	3	1	1	1
Mycena alcalina coll.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Mycena amicta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mycena aurantiomarginata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mycena cinerella	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	6	3	4	9	3	0	0	0
Mycena cineroides	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	3	8	0	10	13	0	1	1	1
Mycena clavicularis	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mycena epipterygia	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Mycena filopes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mycena flavoalba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	7	3	1	1
Mycena floridula	0</																								





## Appendix 4 (continued).

Sample plot	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
<i>Mycena galericulata</i>	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	2	4	3	2	0	4	0	0	0
<i>Mycena galopus</i>	2	5	2	3	0	0	0	0	0	0	0	1	0	0	1	0	3	3	0	4	4	1	5	5	7
<i>Mycena haematopus</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mycena inclinata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
<i>Mycena longiseta</i>	0	5	0	3	0	0	1	0	0	0	0	0	0	0	0	0	3	0	0	3	1	0	2	0	2
<i>Mycena maculata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mycena megaspora</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mycena metata</i>	9	5	3	1	5	4	7	0	0	0	0	0	0	0	0	1	12	8	9	10	0	7	4	7	0
<i>Mycena oregonensis</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mycena pura</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	3	1	0	0
<i>Mycena rorida</i>	5	4	1	6	0	0	0	4	0	2	2	0	0	2	2	1	0	7	11	9	7	7	5	4	0
<i>Mycena rosella</i>	0	1	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Mycena rubromarginata</i>	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	2	0	2	0	0	0	1	0
<i>Mycena sanguinolenta</i>	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	3	1	1	0	1	0	0	0
<i>Mycena septentrionalis</i>	14	2	1	2	6	6	0	0	0	2	0	0	0	0	0	3	0	11	5	1	0	1	0	1	6
<i>Mycena spirea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Mycena stylobates</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mycena urania</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mycena viridimarginata</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mycena viscosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Mycena vulgaris</i>	1	1	4	1	0	0	1	0	0	0	0	0	0	0	0	5	1	0	0	0	1	3	0	0	0
<i>Mycocalia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Omphalina oniscus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pholiota lubrica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0
<i>Pholiota mixta</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pholiota scamba</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
<i>Psathyrella Lutenses</i> coll.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Psathyrella friesii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0
<i>Psilocybe inquilina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0
<i>Strobilurus esculentus</i>	5	4	1	9	3	1	0	0	0	0	0	0	0	0	0	4	6	7	1	0	2	1	2	0	0
<i>Stropharia hornemannii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
<i>Tubaria confragosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tubaria conspersa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
<i>Typhula erythropus</i>	1	4	15	0	5	0	16	0	0	0	0	0	0	0	0	0	0	2	1	2	0	0	0	0	0
<i>Typhula phacorrhiza</i>	0	2	1	2	6	7	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0
<i>Typhula setipes</i>	16	15	16	11	12	16	1	0	0	0	0	0	0	0	0	15	12	12	5	9	14	12	0	0	0
<i>Xeromphalina campanella</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Xeromphalina cornui</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Xylaria filiformis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0



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