

**A mycogeographical study of
Norwegian macrofungi based on
GLM analyses of herbarium data**

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Cand. scient. thesis



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ACKNOWLEDGEMENTS

Understanding is always a journey, not a destination, but to open up for new journeys, projects also have to be brought to an end. I know myself to be more focused on the journey and it's learning process, than on the formally correct finished product. This is probably even more evident to the people who have viewed this process from a distance. Being aware of this, I have gladly accepted the critique and help of friends and supervisors. I sincerely appreciate your efforts in helping me conclude this project, but even more, I appreciate the part you have played in this mycogeographical journey.

The story started in 2001, at the office of Gro Gulden, who with her enthusiasm of macrofungi in general and mycogeography specifically, led me into a qualitatively different way of looking at fungi. Thank you Gro! Ironically, Gro retired before I managed to conclude my Cand. Scient. thesis, but, luckily, there is no change in her enthusiasm for the subject. The end of the story was initiated by my other formal supervisor, Håvard Kausrud, who suggested including Vegar Bakkestuen and his GIS based methods and Rune Økland with his ordination methods, as parameters in the journey, leading me yet again onto a different way of looking at fungi – significantly different.

Rune has repeatedly accused me of good timing. I tend to think that lack of timing and good luck is probably closer to the truth. I was, however, very lucky to have good supervisors. Also, as I spent so much time working and traveling during my work on this thesis, new possibilities for data analyses appeared. Finally, I was lucky enough to get started before the ineptly named “Quality reform”, which would not have allowed for neither the prolonged maturation, the development of the thesis, nor the supervision I have experienced.

With so many supervisors involved, the journey has at times developed in several directions, simultaneously, creating some frustration at times, but hopefully ending as a successful fusion. Insight into the perspectives, preferred methods and working habits of the four of my supervisors ultimately being an added advantage for me. I have surely enjoyed the process and learned a lot. – Thank you Gro, Håvard, Rune and Vegar!

The most important protagonists are, however the fungi and nature in general. Being an atheist, it's hard to address my gratitude for nature, but a special thanks goes to Vegar for making available all the environmental variables of Norway, to Oddvar Pedersen for helping me getting 10.000 distribution coordinates correctly sorted and formatted, and to Torgeir A Ruden at USIT, for programming in R and putting up the communication line enabling me to do the analyses. I am in great debts to ‘Kartleggingsprosjektet’; the enthusiasts who run it, and to all those of you who have contributed in collecting the specimens now resting for eternity at the Mycological herbaria. Thank you all! I also appreciate the access given to me to the data in the University herbaria in Bergen, Oslo, Trondheim and Tromsø.

Thanks to good friends for valuable support, help and advise in various phases of the journey; to my “old” friends Tormod V. Berkey and Thomas F. Hansen from when I first started studying biology (back in 1986), to Runar Ile, Anders Bryn and Anette Edvardsen.

Thanks to all other inhabitants at the Botanical museum in Oslo, to Inger Nordal and the mycological musketeers Klaus Høyland, Leif Ryvarden and Trond Schumacher at the Biological institute at the University in Oslo. Hopefully this is not the end station of my mycological – and botanical – journey, and I look forward to enjoying your company also in the future.

Finally, a special thanks to my dear wife Aslaug Watten, for her enthusiasm and tolerance of my long lasting relationship with mushrooms. I love you!

The content of this thesis is of course my responsibility alone, but much of the credit for what's worth reading should go to my official and unofficial supervisors. Their contributions can hardly be overestimated.

The focus on deadlines – in plural – has always seemed absurd to me. There is only one deadline, and until then the journey continues.

But the mushroom has landed!

The Botanical museum, University of Oslo Oslo, 2007
Anders K Wollan

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ONLINE MATERIAL

Online material at Bioportal, Institute of biology, UiO:

http://www.bioportal.uio.no/onlinemat/online_material.php

Online material 1. Script *F*-values

Online material 2. Script regression analysis

Online material 3. Output *F*-values

Online material 4. Output regression analysis

ABSTRACT

This study focuses on the mycogeography of 83 selected macrofungi in Norway. The fungi's distribution patterns were related to a dataset of 81 environmental variables through GLM in order to reveal which factors that accounts for the species distributions. The GLM models for the 83 species were generally dominated by variables in the categories 'Temperature', 'Energy', 'Humidity' and 'Topography', plus the variable *Geology richness*, confirming established knowledge about which environmental variables that govern the distribution of fungi. Some species distribution patterns could be rather precisely modelled by the environmental variables through the GLM analyses – in some species up to 60% of the variation was accounted for in models. Highest proportions of the variation were explained in species with restricted distributions. A PCA analysis of the *F*-values from the GLM analyses supported that temperature conditions were the most important structuring factors. These results suggest that global warming could have large impacts on the Norwegian funga. Furthermore, the analyses indicated that species within predefined mycogeographic elements to some extent are governed by the same environmental variables, but there were also great overlaps between various elements. This study represents a first exploration of how digitized fungal herbarium data can be analyzed alongside with other types of data using powerful statistical methods, but exemplifies though, that digitized herbarium data represent a valuable resource for research within the fields of ecology, conservation biology and biogeography.

INTRODUCTION

The study of macrofungi distribution and patterns across the globe is only starting to accelerate. This is probably mainly due to practical difficulties involved with the study of macrofungi. Fruit bodies of macrofungi are much more ephemeral compared to plants and thus more difficult to collect, the technique for conserving macrofungi is more complicated and was developed at a much later stage than the conservation (pressing) of plants, and the taxonomy is in general poorly developed in many groups. Any conclusions concerning causes for observed distributions depend entirely on the assumption that our accumulated knowledge of the species and their distribution represents reality. This is by no means to be taken for granted, and several critical questions have to be asked: How well do we know the funga? Are the specimens correctly identified? How well do we know the distribution of the different species? What do distribution maps of fungi tell us? How well does the distribution of the fruit bodies represent the distribution of the mycelium? Redhead (1989) states, that accumulation of accurate data is a common problem, and Mueller, Bills and Foster (2004) blamed the lack of generalized protocols for sampling fungal diversity and for documenting changes in fungal diversity and distribution over time for the sorry state of the kingdom.

Older publications on mycogeography based on macrofungi are few (Raitviir 1964). However, there have been some studies accomplished more recently. In a few studies global or continental distribution patterns have been investigated, e.g. in the works by Demoulin (1973), Watling (2001), Wu and Mueller (1997), Tullos (2005), Baroni et al. (1997) and Redhead (1989). Lange (1974) grouped fungi into various distribution types in Europe, finding distribution limits largely corresponding to temperature, and often comparable to northern limits for well known plant species such as oak (*Quercus robur* L.) beech (*Fagus sylvatica* L.) and vine (*Vitis vinifera* L.). In Norway, Eckblad (1981) suggested 13 mycogeographical elements. Since then, Gulden et al. (1996) and Brandrud et al. (2001) have discussed and developed Eckblads mycogeographical elements. Previous efforts to explain distribution patterns of macrofungi by analysing ecological variables have been few. Bendiksen et al. (2004) studied relationships between macrofungi, plants and environmental factors in a boreal coniferous forest in South-Norway, and demonstrated that distributional patterns of macrofungi and plants to a large extent are caused by the same major environmental complex-gradients, such as temperature and humidity. Ohenoja's (1993) work on the effect of weather conditions on macrofungi at forest sites in Finland showed that the funga associated with various forest types responds differently to the same climatic variables, and that various functional groups of fungi (mycorrhizal, saprotrophic and xylophilous) react differently to specific temperature- and precipitation conditions.

New powerful statistical techniques and GIS tools have made it possible to relate the geographical distribution of species to their present environment. The development of models predicting species' potential spatial distributions is a growing field in ecological research in general, with specific models developed for the respective disciplines biogeography, conservation biology, species and habitat management, climate change etc. (reviewed by Guisan and Zimmermann (2000)). With binary data (i.e. presence/absence) GLM with binomial distribution and logistic link are commonly used, but relying on the assumption that the data are independently and identically distributed – if not, the model estimates might be biased and have lessened predictive ability. The vast majority of data available today consist of presence-only data sets (Zaniewski et al., 2002), museum data being the prime example, suffering from several drawbacks, however. The most critical step is sampling of the data (Hirzel and Guisan, 2002). The 'presence record' provided by museums can give useful information on species distributions and ecology though.

Museum data has been used in modelling habitat suitability, e.g. Reutter et al. (2003) modelling habitat-suitability maps on the basis of reclassified museum material for *Apodemus* species from the Alps, and there is an ongoing debate and development on modelling tools using museum data (e.g. Hirzel et al. 2002, Engler et al. 2004, Elit and Graham et al. 2006, Hirzel et al. 2006)

The present study is an attempt to explain observed distributional patterns from herbarium data by using Generalised linear models (GLM) and ordination. A total of 10735 specimens of 83 selected species accessioned in the four Norwegian University herbaria were included in the study, their identification verified, UTM coordinates (WGS84) assigned, and the species recorded as present or absent in a grid of 14972 squares of 5x5 km, covering Norway. The obtained species distribution patterns in Norway were then related to an extensive dataset of 81 environmental variables recorded for Norway (Bakkestuen et al. in prep) in the same grid system. GLM and principal component analysis (PCA) were used to investigate the relationships between the distribution patterns and environmental factors in order to reveal which variables that accounts most for the species distribution patterns.

A further aim of the study was to examine the conceptual value of mycogeographical elements. The obtained distribution patterns were therefore subjectively grouped and referred to seven mycogeographical elements. These elements were *a priori* obtained from analyses of the observed patterns and represent a refinement of previously defined mycogeographical elements in Norway (Eckblad 1981, Gulden et al. 1996). Due attention was paid to the species occurrence in neighbouring countries and the rest of Europe when species were referred to the various elements. Results from the GLM analyses and the PCA ordination were then compared for the different elements to find the environmental parameters that mostly accounted for the various elements, or if there in fact were any parameters that could explain the elements.

The selected study area, Norway (Fig. 1), is well suited as a model system for ecological mycogeography. Norway is spanning the latitudes 58° - 71° and longitudes 4° - 32°, has a long coastline and a weakly continental inland, high mountains and a varied geology and topography. Thus, Norway embraces extensive ecological gradients in a rather small area (Moen 1999).

Norway and northern Europe in general, is probably the region in the world where the fungi, as well as the flora, are most thoroughly investigated. In Norway, about 5900 macrofungi have been recorded (Aarnes 2002).

Basically this study is an attempt to find answers to questions like: Which environmental variables govern the distribution of macrofungi in Norway? How do we best group the species in mycogeographical units – and do such geographical elements contribute to the understanding of distribution? Essential here is the question: do the same environmental variables govern each member of a mycogeographical unit? This study is a first attempt to explore mycogeographical patterns on a regional scale by means of Generalised linear models (GLM) and ordination.



Figure 1. Map of Europe showing the study area, Norway.

MATERIALS AND METHODS

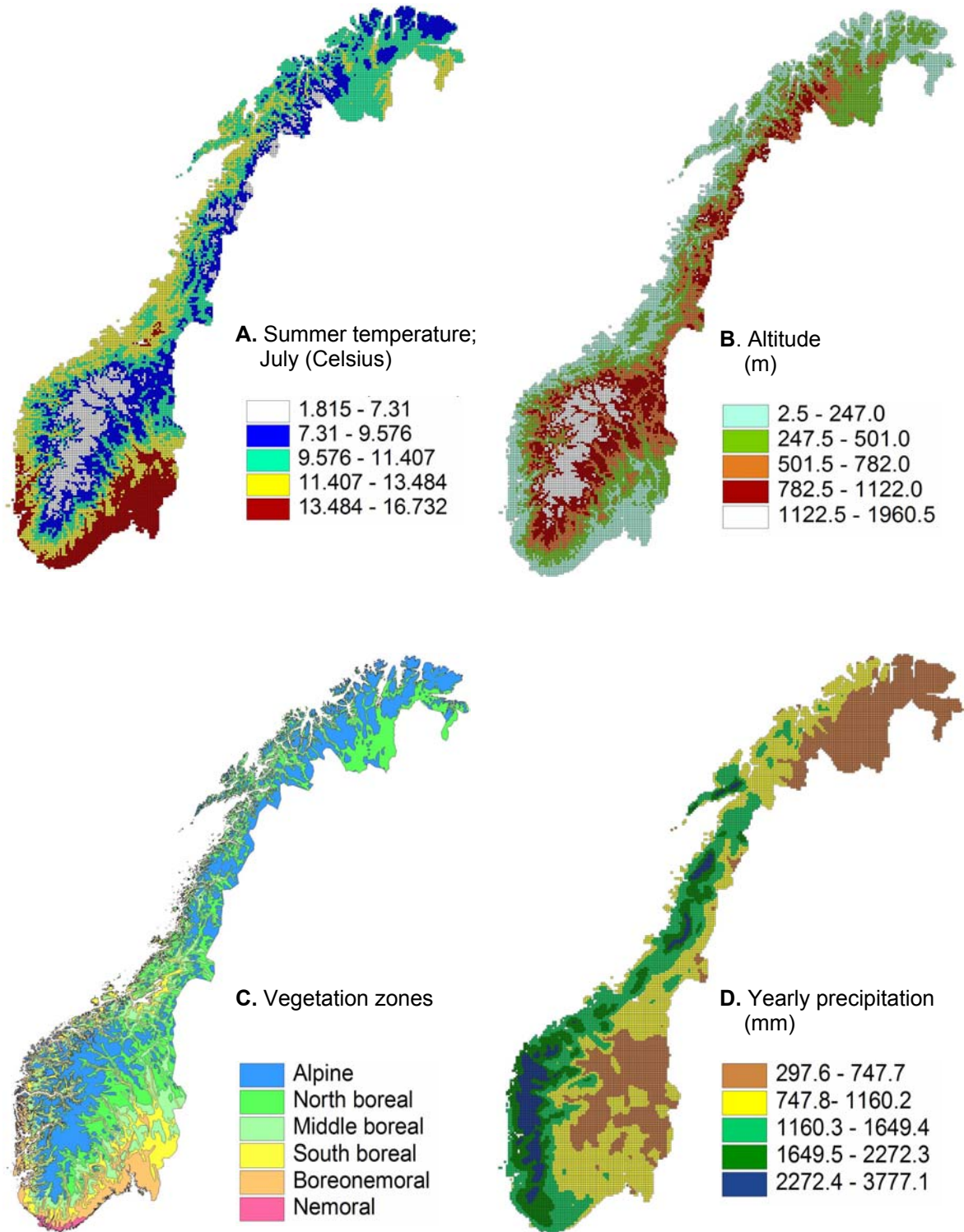
The study area

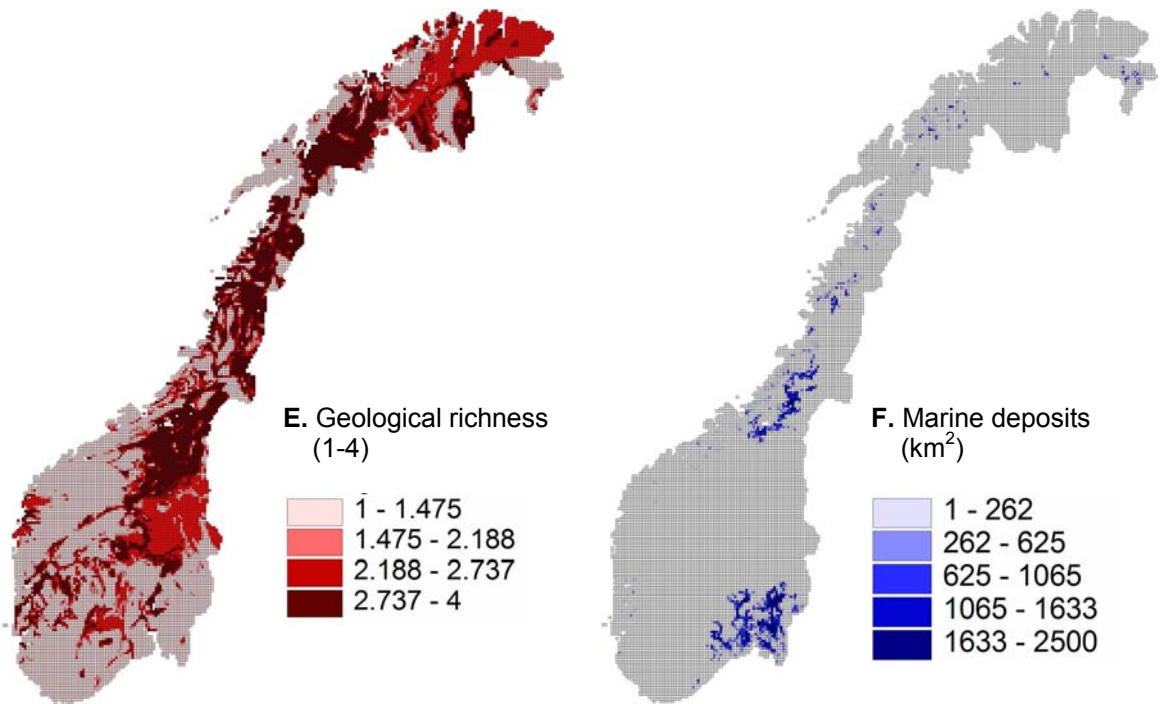
Norway is positioned to the east of the Atlantic Ocean, making up the northwest extreme of the Eurasian continent. Due to Atlantic winds and the Gulf Stream, the climate in Norway is more favourable than expected from the high latitude. Several fungi reach their northernmost known distribution in Norway. There is a marked gradient in temperature and related parameters with increasing latitude and elevation (Fig. 2 A and B). The vegetation zones range from nemoral in the southernmost part, boreonemoral in the Oslofjord area and on south-exposed localities in the western fjords, to alpine and sub arctic (Fig. 2 C) in the highest mountains and the extreme north, respectively. All eight vegetation zones of North Europe occur in Norway and the zones from the nemoral to mid-boreal occur further north in Norway than in any other part of the world (Moen 1999). The other marked gradient is from oceanic to continental climates (Fig. 2 D). Here Norway spans a range from strongly oceanic to slightly continental (Moen 1999). The oceanic west coast experiences small annual amplitudes in temperature and it rains all seasons, with maximum annual precipitation in mid-fjord districts generally up to 3500 mm (local maximum values of 6000 mm). The continental interior has high annual temperature amplitudes, with hot, dry summers and cold winters.

Norway is dominated by the mainly siliceous Precambrian bedrock of the Baltic Shield in Fennoscandia (Sigmond et al. 1984), and the western mountain chain consisting of metamorphic bedrock and sedimentary rocks (Fig. 2 E). Bedrock from the shield is dominating both in northern and southern Norway. The mountain chain provides a varied geology in what today is western and central Norway. In small areas in the southeast, there are almost unaltered Cambro-Silurian sedimentary rocks as well as an area with Permian eruptives, giving rise to more fertile ground.

Glacial erosion has created the alpine landscapes in Norway, the characteristic U-shaped valleys and fjords, and the island landscape along the south and west coast. Most sediments/deposits in Norway are of glacial, glaciofluvial, glaciolacustrine or glaciomarine origin, almost solely from the latest ice age, ending around 10,000 years BP (Andersen, 2001). Block-fields dominate in the middle and high alpine zones. Coarse tills cover large parts of the inland, but areas with shallow quaternary deposits are also common (Klemsdal & Sjulsen 1986). Fine grained tills, glaciofluvial, glaciolacustrine and glaciomarine deposits (Fig. 2 F) are found in valley bottoms and coastal areas. The resulting soils, a product of parent materials, climate, biota, exposition and time (Jenny 1941), consequently shows great variation. Podzol-types of soil profiles dominate in coniferous forests, whereas brown soils dominate the southern deciduous forests (Låg, 1979).

Figure 2 A – F. Maps of Norway showing (A) summer temperatures, (B) altitudinal classes, (C) vegetation zones, (D) yearly precipitation, (E) geological richness and (F) marine deposits, respectively. **Map sources:** (A) After Aune (1993a); (B) After Statens kartverk (the Norwegian Mapping Authority); (C) After Moen (1999); (D) After Aune (1993a); (E) From Bakkestuen et al (in prep); (F) After Thoresen (1991).





Human activity has influenced the Norwegian landscapes since the end of the last ice age. Both in South-Norway and in the northernmost county, Finnmark, archaeologists have documented human settlements as old as 11 500 years BP (Østmo and Hedager, 2005). After the introduction of farming between 6000 and 3500 B.P. (Høeg 2000, Almås 2004), practically all areas below the timberline have been strongly influenced by human activities. Also mountain areas in the low- and mid alpine vegetation zones are to a great extent influenced, especially by summer farming and domestic grazing (Bryn and Daugstad 2001). Below the upper limit of glaciomarine deposits, and on fertile soils of Cambro-Silurian origin, Norway is close to 100% a cultural landscape. The traditional agriculture with domestic animal grazing, outfield hay-making and collection of fodder probably raised the biodiversity (Norderhaug 1996), whereas modern agriculture, forestry and urbanization (e.g Ihse 1995, Robinson and Sutherland 2002) tends to reduce it again. The mechanisation and specialisation of post WW2 agriculture and the on-going restructuring of the agricultural landscape to larger, industrial units have strongly diminished the traditional agriculture (Puschmann et al. 2006).

From an ecological perspective, including Sweden and the northern parts of Finland in the study area would have been more logical, giving a study area naturally delineated by the Norwegian Sea and the Baltic Sea, corresponding better with the distribution of the majority of the species. Fungi do not recognize political borders, and with a few exceptions the species in this study show a continuous distribution across the borders between Norway and Sweden, Finland and/or Russia. Environmental variables with latitudinal and/or altitudinal gradients are equally well represented within the current study area, while environmental variables with a longitudinal/continental-oceanic gradient would have been longer and probably improved by the discussed extension

The macrofungi

To represent the Norwegian funga of macromycetes (macrofungi), 83 species (Appendix 1) were selected among 200 species included in a preceding field survey, with its main

purpose to document the diversity and distribution of macrofungi in Norway¹. Species were selected for the study that fulfilled the criteria that they were: (i) fairly well known among Norwegian amateur mycologists, and (ii) well circumscribed and easy to identify, (iii) providing a good representation of different taxonomic and ecological groups, and (iv) adequately representing different known patterns of distribution.

A total of 10735 specimens of the 83 selected species were accessioned in the four Norwegian University herbaria; Oslo (O), Bergen (B), Trondheim (TRH) and Tromsø (TROM). The identification of all specimens was verified using macroscopic and microscopic traits and relevant literature, mainly: Breitenbach & Kränzlin (1984, 1986, 1991, 1995, 2000), Hansen & Knudsen (1992, 1997, 2000), Ryvarde & Gilbertson (1993, 1994), Boertmann (1995), and Heilmann-Clausen et al. (1998). Fungal names are given according to the taxon list of the Mycological Herbarium in Oslo (O) <http://www.nhm.uio.no/botanisk/sopp/index.html>. UTM coordinates (WGS84) were assigned by the collectors in some cases (< 10%) and for the rest of the collection by me, to all specimens using the GIS based program (freeware) 'Norgesglasset' (<http://ngis2.statkart.no/norgesglasset/default.html>) (Roed 2002). UTM coordinates were used to generate presence/absence data for 14972 5×5 km grid squares (UTM zone belt 33) covering Norway. The herbaria data are strictly speaking presence-only data. Since the selected species are well known and most of them have been collected for >100 years (some only for decades though) the data were treated as presence/absence.

The mycogeographical elements

My efforts in controlling species identifications and assigning geographical coordinates did result in 83 distribution maps for macrofungi in Norway. The different mycogeographical elements proposed in this study came from comparing and classifying the obtained distribution maps supplemented with information on recognised distribution of the species in neighbouring countries, most important Great Britain (GB), Finland (FI), Sweden (SE) and Denmark (DK), and continental Europe (C Europe), especially the mountainous Switzerland (SW), obtained from literature (e.g. Ryman and Holmåsén 1984, Breitenbach and Kränzlin 1984/86/91/95/2000, Hansen and Knudsen 1992/97/2000, Ryvarde and Gilbertson 1993/94, Cortecuisse 1994, Heilmann-Clausen et al. 1998; (Appendix 2)) and online material (Appendix 2). Definitions of the Norwegian mycogeographical elements are shown in Table 1, with distribution maps of example species for the different elements. The seven mycogeographical elements thus defined for Norway compare to some extent with the vegetation zones in Norway (Fig. 2 C) as depicted in Moen (1999, map 69). The elements are to some degree also based on previously recognised mycogeographical elements in Norway (Eckblad 1981, Gulden et al. 1996, Gulden et al. 2001), and constitute a further development of these.

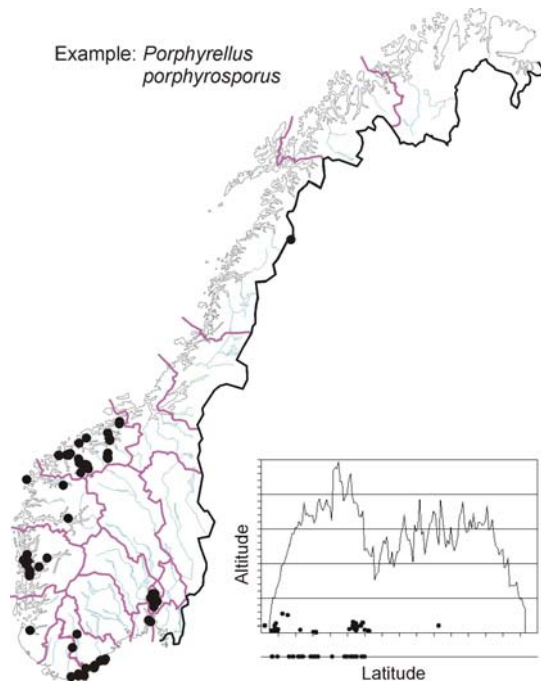
A priori, the 83 selected species were thus grouped into the seven mycogeographical elements and a group of ubiquitous species. In some cases patterns in Norway could be almost identical, but deviating patterns in the rest of Europe suggested placement in different units, e.g. species belonging in the Mid-Boreal – western (MBo – w) and in the Boreal – Montane (Bo – M) elements often had similar patterns in Norway. The 83 species were also grouped according to how widespread they appeared on the maps, as restricted, intermediate and common/widespread, respectively.

¹ Kartlegging av storsopp i Norge (mapping of Norwegian macromycetes (Timmermann 1995)) (1988 -). A joint project among Norwegian mycologists, professionals and amateurs.

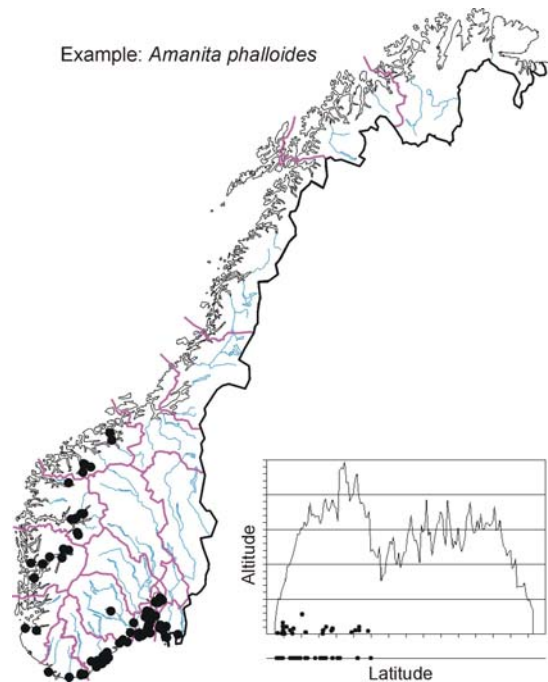
The explanatory variables

A total of 81 explanatory variables were initially included in the study. Excluding the variables for proximity to roads and other human structures, 75 explanatory variables were included in the final analyses (Table 2). The term ‘explanatory’ is used in a strictly statistical sense for predictor variables that may potentially account for variation in response variables in generalised linear models (GLM; McCullagh and Nelder, 1989; Crawley 2005). The 75 variables were furthermore grouped according to the categories; ‘Topography’ (10 variables), ‘Energy’ (10), ‘Humidity’ (20), ‘Temperature’ (13), ‘Rich ground’ (2), ‘Forest’ (1), ‘Continentality’ (3), ‘Other’ (7) and ‘Missing area’ (9) (Table 2). The categories ‘Temperature’ and ‘Energy’ are related, the difference being that the ‘Temperature’ category contains the monthly and yearly mean temperatures, while ‘Energy’ includes derived parameters like duration of the growing season, the amount of favourable locations, etc. The category ‘Missing area’ represents the amount of the grid squares including sea, i. e. without values for the explanatory variables in the grid squares, and is used to detect potential sources of error in the analyses.

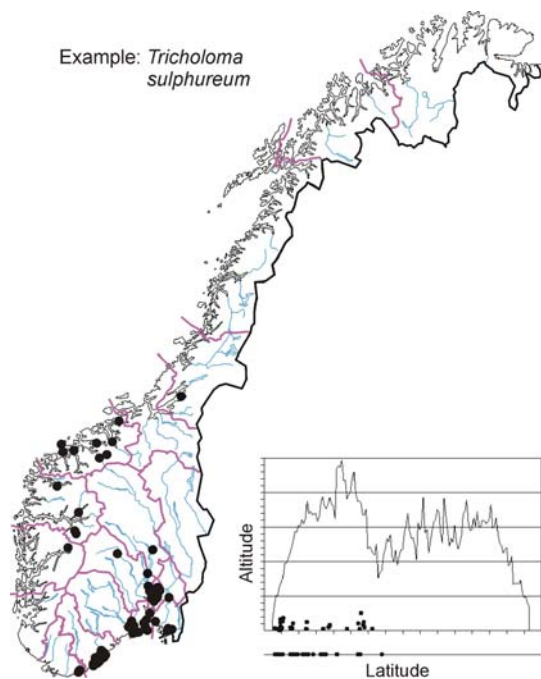
Table 1. Description of the mycogeographical elements made for this study, based on current knowledge of the species distributions in Norway and neighbouring countries to the west, east and south, most important Great Britain (GB), Finland (FI), Sweden (SE) and Denmark (DK), and continental Europe (C Europe), especially the mountainous Switzerland (SW), estimated from literature studies and online material (**Appendix 2**). Typical distributions for the different mycogeographical elements are shown by example species, with distribution maps and profiles of distribution versus altitude; Y-axis: altitude, 0-2400 m alt; X-axis: latitudes 58° - 71°. Dots on the x-axis = finds without information on altitude.



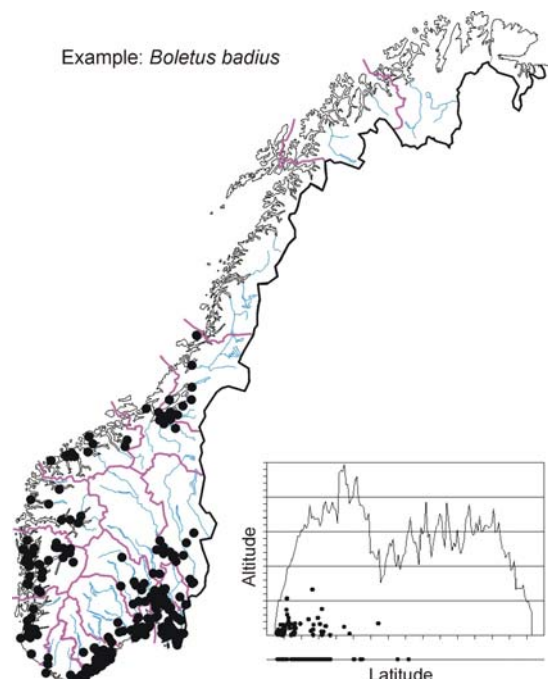
Atlantic (Atl): In Norway with a coastal distribution, extending almost to the inner, rather continental parts of the western fiords, northwards to C Norway and upwards to 500- 600 m asl., some species more restricted both inlands and upwards. Typically species associated with deciduous forests. In FI, SE and DK absent or rare (southern), in GB mostly in southern and lower parts. In C Europe mainly western and colline-montane.



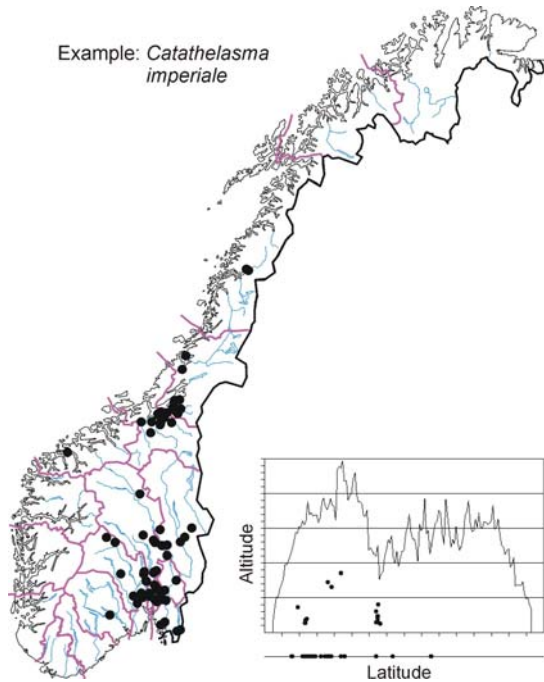
Nemoral-Boreonemoral (Ne-Bne): In Norway with a southern coastal distribution, reaching the inner fiord regions, extending up to 400 m asl. Typically species associated with deciduous forests. In FI and GB absent or southern, in DK occasional to common. In C Europe common in the lowlands and up to submontane altitudes.



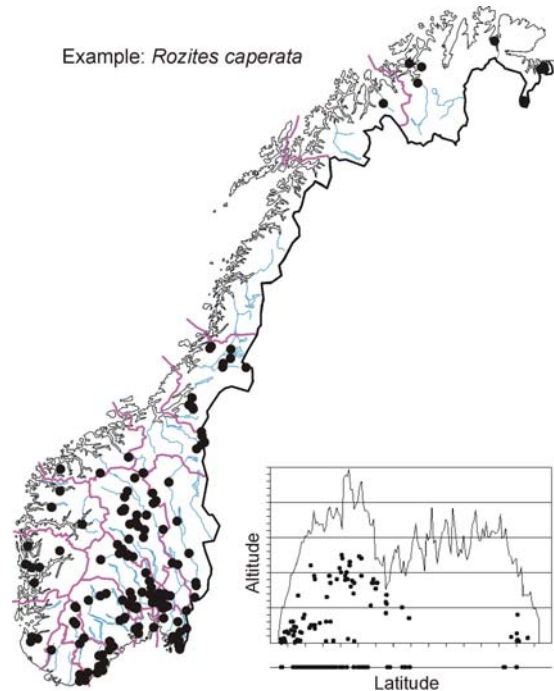
South-Boreal (S-Bo): In Norway common in SE from the coast to the inland valleys, in the W mainly in inner fiord districts, extending to C Norway or locally favorable sites further north, up to 600 m asl. Occurring in southern to central parts of FI, common/occ in DK, i GB southern (absent or rare in Scotland and Ireland). In C Europe mostly common, extending to montane/subalpine regions.



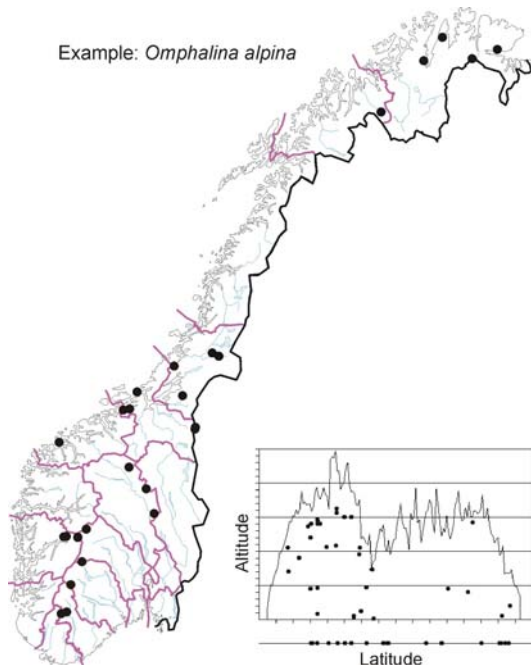
Mid-Boreal, western (MBo-w): Common both in W and E Norway, extending far northwards – some of them to Troms, up to ca 800 m alt. in S Norway. Many coniferous forest species associated with spruce and pine. In FI often rare, north to central parts, occasional or common in DK, and in GB mostly occurring in England, Scotland and Ireland. In C Europe common up to montane-subalpine regions.



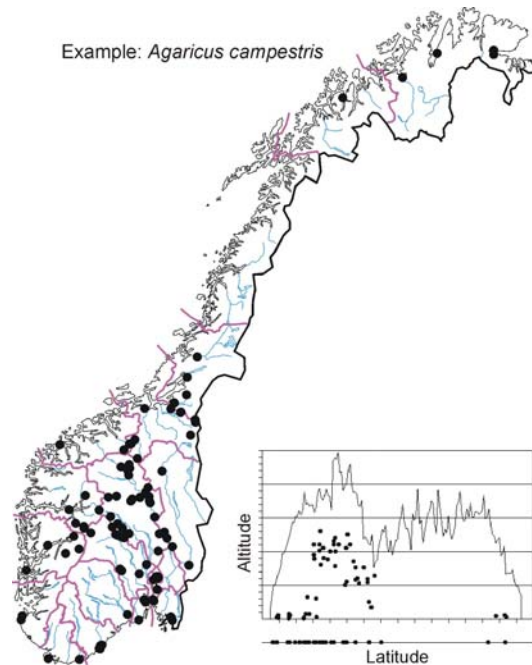
Boreal-Montane (Bo-M): In Norway eastern, extending northwards mostly to C Norway, some north to Troms, fairly common up to ca 600-800 m alt; typically coniferous forest species, many confined to spruce. In FI mostly common in the whole country, in DK and GB mostly rare or absent (some on the red list, some only in Scotland). In C Europe most common in eastern parts and at colline to montane altitudes.



Boreal-Subalpine (Bo-SA): In Norway common in the inland and eastern parts, also in the far north, absent or rare towards west, some extending to 1300 m asl, i.e. well above the timberline. In FI common in all parts, in DK absent or rare, in GB absent or rare (many in Scotland only, absent or rare in Ireland, and many on the red list). In C Europe mainly occurring in eastern and (colline) montane to subalpine regions.



Arctic-Alpine (A-A): In Norway in alpine and subarctic regions in southern as well as the northern parts, occasionally down to sea level on the W coast. In FI alpine, absent or rare in DK and GB (mostly present in Scotland only), occurring in the N Atlantic islands and Greenland. In C Europe in alpine regions and rarely on the W coast.



Ubiquitous species, (Ubi): In Norway typically from the far south to the very north, and also at higher elevations (*A. campestris* registered at 1300 m asl). Widespread species, without any clear pattern of distribution. Seemingly able to grow wherever the substrate is agreeable for the species. Strictly speaking not a mycogeographical element.

Statistical Analysis

Statistical analyses were done with the R software package Version 2.2.0 for windows (Anonymous 2005, © R Foundation for Statistical Computing, 2005) and generalised linear models (GLM; McCullagh and Nelder, 1989; Myers et al. 2002; Venables and Ripley 2002; Crawley 2005). GLM were chosen as they are flexible modelling tools suitable to investigate the relationships between binomial data (recorded as presence/absence) for response variables and predictor variables; in this study presence/absence data for each of the 83 species as response variables and the 81/75 environmental variables as predictor variables (explanatory variables).

Parameters β_i in nested GLM models were tested (null hypothesis: $\beta_i = 0$, against the two-tailed alternative) by the F-statistic

$$F = \frac{(D_{i-1} - D_i) df_i}{D_i (df_i - df_{i-1})}$$

where D_{i-1} and D_i are the deviances of models M_{i-1} and M_i , respectively (deviance is -2 times the summed log-likelihood of a model), and df_i and df_{i-1} are the degrees of freedom remaining after fitting models i and $i-1$. The F -test was chosen because it compensates for under- or overdispersion (scale parameter $\theta_i \neq 1$ in models; Myers et al. 2002).

To accomplish the computer intensive analyses, scripts for [automated] GLM analysis, programmed in R Version 2.2.0 for Windows, were used (Ruden, 2006) (Online material 1 and 2). The analyses were run on a supercomputer managed by the computing center, USIT, at UiO, the University of Oslo, accessed via a personal computer. Logistic regression (GLM with logit link function and binomial error) was performed for each of the 83 species by a two-step procedure. First, the response of each species to each of the 81, respectively 75 explanatory variables was modelled (Online material 1), performing $83 \times 81 = 6723$, respectively 6225 single GLMs. F values for all models (Online material 3) were used to quantify the extent to which the occurrence of the species in question could be 'explained' by the variable in question. Secondly, multi-predictor logistic models for each response variable were built (Online material 2) by including predictor variables and their interactions in order of decreasing F (and p) values. Checks were made at each stage that terms already in the model remained strongly contributing (based upon the criterion F value > 4) when new terms were added. Among models with the lowest number of degrees of freedom for included terms and to which no more terms could be added with $F > 4$, the model with lowest residual deviance was considered as best from a statistical point of view. The high number of explanatory variables required a strict criterion ($F > 4$) to avoid predictors to be included just because of their high numbers. Based on the same argument, only explanatory variables with $p < 0.01$ was included in the models for the respective species (Online material 4).

The fraction of variation explained (as percentage of the null deviance) in each of the 83 multi-predictor GLM models was related to species frequency (Nos. of grid squares with observations) in a regression analysis. Fraction of variation explained versus frequency was compared between distribution types (restricted, intermediate, or widespread/scattered) using boxplots.

A 'species F -values matrix' of F -values from the GLM analyses of single explanatory variables for each species was constructed, and Principal Component Analysis (PCA; Pearson 1901, ter Braak and Prentice, 1988) was used to detect structures in this matrix. PCA will find axes which are linear combinations of explanatory variables, explaining as much as possible of the variation in F -values for the respective species.

Since F -values from GLM analysis were strongly right-skewed I transformed them prior to PCA analysis in order to comply with demands for normal distribution of errors. The F values for the 75 explanatory variables for the 83 species were weighted (transformed) to a scale (after weighting) with minimum = 1 for $F = 4$ and maximum = 100 for $F = 698.130$ by the power function (van der Maarel 1979, Økland 1990a):

$$Y_{ij}' = f(y) = a * y_{ij}^w$$

where y_{ij} is the original F value of species for the combination of explanatory variable (i) and species (j), w is the weighting parameter, a is a ranging scalar determining the absolute limits for F after weighting, and y_{ij}' is the weighted F value. Hence, I obtained the following values for a and w :

$$a = 4^{-w}$$

$$w = \frac{\ln 100}{\ln (f_{\max}/4)} = \frac{\ln 100}{\ln (100/4)} = 0.892$$

$$a = 4^{-w} = 4^{-0.892} = 0.290$$

The weighted (transformed) ‘species/explanatory variables F -value’ matrix’ (Online material 3) was submitted to PCA analysis with the expectation that species grouping together in the ordination have their distribution affected by the same explanatory variables, and that explanatory variables grouping together (have parallel vectors) affect the species along a common ecological gradient (complex gradient). These complex gradients were furthermore expected to be of different importance for the respective species according to ecology and distribution (Økland, 1990a)

Table 2. Explanatory variables. From Bakkestuen in prep.

Id: Identification number for the explanatory variable, used in ordination analysis (PCA). **Explanatory variables:** Name of the variable. **Abbreviation:** Short version of variable name. **Category:** Assumed type of variable. **Unit** and **Resolution** of the value for the variable are listed. **Zonalstat** gives the zonal statistics (**Range**, **Mean** and **SD**) for the variable. For calculations and references see 'Appendix 3'.

Categories are abbreviated as follows: Topography = **Topo**, Energy = **E**, Missing area = **MA**, Humidity = **Hum**, Temperature = **Temp**, Rich ground = **RichG**, Continental = **Cont**, Other = **O**, Forest = **F**

Id	Explanatory variable	Abbreviation	Category	Unit	Resolution	Zonalstat	Range	Mean	SD
1	Elevation	Elev	Topo	m	100x100 m	mean	0.0 – 1821.0	410.8	380.2
2	Elevation – Relative relief	Elev – RelRef	Topo	m	100x100 m	Range	0.0 – 2184	552.9	415.6
3	Slope	Slope	Topo	°	100x100 m	mean	0.0 – 28.5	6.86	5.65
4	Slope: sum	SlopeSum	Topo	°	100x100 m	sum	0 – 293533	70694	58225
5	Slope – Terrain variation	SlopeTerrVar	Topo	°	100x100 m	std	0.0 – 18.9	5.8	4.1
6	TRI – Terrain ruggedness	TRI – TerrRugg	Topo	index	100x100 m	mean	0.0 – 164.5	37.4	31.3
7	TRI – Terrain ruggedness : sum	TRI – TerrRuggSum	Topo	index	100x100 m	sum	0 – 1693923	385545	322597
8	Plan curvature	PlanCurv	Topo	index	100x100 m	mean	0.0 – 361.3	60.7	51.6
9	Profile curvature	ProfileCurv	Topo	index	100x100 m	mean	0.0 – 784.1	62.8	57.8
10	Curvature	Curv	Topo	index	100x100 m	mean	-0.0118 – 0.0792	0.001	0.003
11	Radiation heat index	Rad – HeatInd	E	categorical	100x100 m	mean	-0.112 – 0.110	-0.0001	0.0184
12	Aspect unfavourability	AspUnFav	E	°	100x100 m	mean	39.5 – 147.7	84	10.2
13	Missing area 1 – 12	MisArea 1 – 12	MA	m ²	100x100 m	fraction	-	-	-
14	Annual precipitation	P-Ann	Hum	mm	1x1 km	mean	311.1 – 3681.7	1104.3	560
15	January precipitation	P-Jan	Hum	mm	1x1 km	mean	11.2 – 373.8	98.3	60.4
16	February precipitation	P-Feb	Hum	mm	1x1 km	mean	7.9 – 280.2	74.1	44.5
17	March precipitation	P-Mar	Hum	mm	1x1 km	mean	9.7 – 326.8	77.3	49.5
18	April precipitation	P-Apr	Hum	mm	1x1 km	mean	5.9 – 211.3	56.8	30.1
19	May precipitation	P-May	Hum	mm	1x1 km	mean	17.6 – 155.9	57.7	23.9
20	June precipitation	P-Jun	Hum	mm	1x1 km	mean	24.4 – 209.9	69.8	25.1
21	July precipitation	P-Jul	Hum	mm	1x1 km	mean	35.1 – 206.8	87.6	25.4
22	August precipitation	P-Aug	Hum	mm	1x1 km	mean	37.8 – 259.4	95.7	36.5
23	September precipitation	P-Sep	Hum	mm	1x1 km	mean	24.7 – 422.7	125.2	68.9
24	October precipitation	P-Oct	Hum	mm	1x1 km	mean	23.3 – 499.9	135.2	75.8

Id	Explanatory variable	Abbreviation	Category	Unit	Resolution	Zonalstat	Range	Mean	SD
25	November precipitation	P-Nov	Hum	mm	1x1 km	mean	18.0 – 393.4	114.4	69.3
26	December precipitation	P-Des	Hum	mm	1x1 km	mean	10.8 – 400.9	112	71.8
27	Missing area 14 – 26	MisArea 14 – 26	MA	m ²	1x1 km	fraction	-	-	-
28	Annual temperature	T-Ann	Temp	°C	1x1 km	mean	-5.7 – 7.6	1.3	3.05
29	January temperature	T-Jan	Temp	°C	1x1 km	mean	-17.2 – 2.6	-6.91	4.82
30	February temperature	T-Feb	Temp	°C	1x1 km	mean	-16.7 – 2.3	-6.77	4.56
31	March temperature	T-Mar	Temp	°C	1x1 km	mean	-12.4 – 3.1	-4.23	3.65
32	April temperature	T-Apr	Temp	°C	1x1 km	mean	-8.0 – 5.4	-0.58	2.94
33	May temperature	T-May	Temp	°C	1x1 km	mean	-3.4 – 11.1	4.31	2.99
34	June temperature	T-Jun	Temp	°C	1x1 km	mean	0.24 – 15.6	8.4	2.77
35	July temperature	T-Jul	Temp	°C	1x1 km	mean	2.8 – 16.6	10.54	2.39
36	August temperature	T-Aug	Temp	°C	1x1 km	mean	4.2 – 16.0	10.36	2.1
37	September temperature	T-Sep	Temp	°C	1x1 km	mean	-0.3 – 12.4	6.35	2.47
38	October temperature	T-Oct	Temp	°C	1x1 km	mean	-4.7 – 9.5	2.35	3.05
39	November temperature	T-Nov	Temp	°C	1x1 km	mean	-10.8 – 6.0	-2.68	3.82
40	December temperature	T-Des	Temp	°C	1x1 km	mean	-15.5 – 3.9	-5.56	4.51
41	Missing area 28 – 40	MisArea 28 – 40	MA	m ²	1x1 km	fraction	-	-	-
42	Annual evapotranspiration	Evapotrans	E	mm	1x1 km	mean	7.3 – 933.2	364.5	158.2
43	Annual runoff	Runoff	Hum	mm	1x1 km	mean	392.6 – 4963.8	1494	740.6
44	Runoff corrected annual precipitation	Runoff Precorr	Hum	mm	1x1 km	mean	127.5 – 6944.28	1135.781	757.6245
45	Missing area 42 – 44	MisArea 42 – 44	MA	m ²	1x1 km	fraction	-	-	-
46	Growing season	GS	E	days	1x1 km	mean	11.9 – 226.0	130.2	40.2
47	Growing Degree Days	GDD	E	°C	1x1 km	mean	10.1 – 1496.4	554.7	323.6
48	Missing area 46 – 47	MisArea 46 – 47	MA	m ²	1x1 km	fraction	-	-	-
49	# days with precipitation threshold 0.1 mm	Rdd100	Hum	days	1x1 km	mean	95.2 – 250.9	195.4	23.4
50	# days with precipitation threshold 1.0 mm	Rdd010	Hum	days	1x1 km	mean	69.8 – 204.4	137.1	31.3
51	# days with precipitation threshold 10.0 mm	Rdd001	Hum	days	1x1 km	mean	2.24 – 108.1	28.9	20.8
52	Missing area 49 – 51	MisArea 49 – 51	MA	m ²	1x1 km	fraction	-	-	-
53	Geological richness	GeoRich	RichG	categorical	~ 5x5 km	mean	1 – 4	1.771432	0.807422
54	Area proportion 53	MisArea 53	MA	m ²	~ 5x5 km	fraction	-	-	-
55	# days snow-covered	Snowdays	Hum	days	1:7 mil	mean	37 – 232	152.8	55.3

Id	Explanatory variable	Abbreviation	Category	Unit	Resolution	Zonalstat	Range	Mean	SD
56	Last day with snow cover	Lastsnow	Hum	days	1:7 mil	mean	82 – 174	123	21.8
57	Sun radiation January	Rad-Jan	E	Wh/ m ²	1:7 mil	mean	25 – 375	158.8	123.7
58	Sun radiation April	Rad-Apr	E	Wh/ m ²	1:7 mil	mean	2625 – 3875	3161	378.5
59	Sun radiation July	Rad-Jul	E	Wh/ m ²	1:7 mil	mean	3750 – 5750	4446.3	450.7
60	Sun radiation October	Rad-Oct	E	Wh/ m ²	1:7 mil	mean	350 – 1350	793.4	252.9
61	Missing area 55 – 60	MisArea 55 – 60	MA	m ²	1:7 mil	fraction	-	-	-
62	Distance to coastline	DistCoast	Cont	m	100x100 m	mean	0 – 210477.3	34897.5	43210.7
63	Distance to ocean base line	DistOcean	Cont	m	100x100 m	mean	0 – 296516.1	105318.2	64616.12
64	Conrad continentality	Conrad	Cont	categorical	1x1 km	mean	2.3407 – 36.0944	17.01842	7.093122
65	Missing area 64	MisArea 64	MA	m ²	1x1 km	fraction	-	-	-
66	Marine deposits	MarDep	RichG	km ²	1:1 mil	mean	0 – 2500	486.0	537.3
67	Sea	Sea	O	km ²	N50 - vector	mean	0 – 2500	972.2	746.6
68	Lake	Lake	O	km ²	N50 - vector	mean	0 – 2280	133.2	205.0
69	River	River	O	km ²	N50 - vector	mean	0 – 932	184.8	92.7
70	Glacier	Glacier	O	km ²	N50 - vector	mean	0 – 2250	257.8	453.5
71	Glacial deposits	GlacDep	O	km ²	1:1 mil	mean	0 – 2500	848.5	750.0
72	Mire	Mire	O	km ²	N50 - vector	mean	0 – 2066	156.6	220.7
73	Forest	Forest	F	m ²	N50 - vector	mean	4401 – 11121327	4461963	3190462
74	Avalanche/landslide/rockfall deposits	AvalDep	O	km ²	1:1 mil	mean	0 – 1746	201.9	212.8
75	Southfacing slope	S – Slope	E	km ²	100x100m	mean	0 – 2161	558.6	292.5

RESULTS

The species distribution maps

The different species distribution maps clearly showed typical patterns of distributions, with the two main differences being along latitudinal/altitudinal and coast-inland gradients. The distribution maps were used together with literature and online material (Appendix 2) to define the mycogeographical elements presented in Table 1, as well as in assigning the species to the mycogeographical elements (Table 3). Distribution maps for the 83 species are presented in Appendix 6.

Modelling the species distributions by GLM

Through GLM analyses with environmental variables as explanatory and species occurrences as responses, models for the 83 species were generated. The GLM correlations for all species are presented in ‘Online material 4’ at Bioportal, Institute of biology, UiO: http://www.bioportal.uio.no/onlinemat/online_material.php. When all the 81 explanatory variables were included in the GLM analysis, variables in the category ‘Road’ (proximity to Roads, etc.) turned out to be most frequently included in the GLM models. Approximately 25 % of the included variables in this primary analysis belonged to the category ‘Road’, while variables in the categories ‘Temperature’ and ‘Topography’ made up 18.7 % and 14.5 % of the included variables, respectively.

All further analyses were done employing the reduced dataset of 75 explanatory variables, excluding the variables in the category ‘Road’ (Table 2). One to seven variables in addition to seven interaction terms were included in the models for the 83 species, based upon the criterion F value > 4 (cf. materials and methods). The highest numbers of explanatory variables included in the models were 14, 9 and 8 variables, for *Fomitopsis rosea*, *Plicatura nivea* and *Marasmius oreades*, respectively. For 10 species only one explanatory variable was included in the model (Table 3). Models for the species showed generally a large degree of variation (Online material 4) but the level of categories patterns emerged.

Overall, variables in the category ‘Temperature’ were most frequently included in the models (28.75 %), followed by ‘Topography’ (15.74 %), ‘Energy’ (15.74 %), ‘Humidity’ (14.57 %) and ‘Rich ground’ (9.31 %) (Fig. 3 A). The most frequently included explanatory variables were the ‘Topography’ variable *Elevation - Relative relief* (27 times included), the ‘Temperature’ variables *T-Jun* (23), *T-May* (18) and *T-Jul* (10), the ‘Energy’ variables *Aspect unfavourability* (10) and *Growing Degree Days* (10) and the ‘Rich ground’ variable *Geology richness* (21) (Table 4). Explanatory variables related to ‘Temperature’ were frequently included in the models for species belonging to all the predefined mycogeographical elements, with temperature variables for the summer showing a trend from early summer/southern distributions to later summer/northern distributions (Fig. 3 B). *T-May* was most frequently included in models for species belonging to the most southerly and coastal elements, ‘Nemoral – Boreonemoral’ and ‘Atlantic’, while *T-Jun* and *T-Jul* were more frequently included for the more northerly mycogeographical elements. Furthermore, *T-Sep* was in addition frequently included in models for species belonging to the most northern-continental element – ‘Boreal – Subalpine’ (B – Subalp). All the Temperature variables were frequently included in species models for the ‘Arctic – Alpine’ element.

The frequency of explanatory variables in the categories ‘Energy’ (e.g. *Growing Degree Days*) and ‘Topography’ (*Elevation – Relative relief*) increased from species with a more northerly to species with a more southerly distributional tendency, while it was more or less the other way around for variables in the category ‘Humidity’.

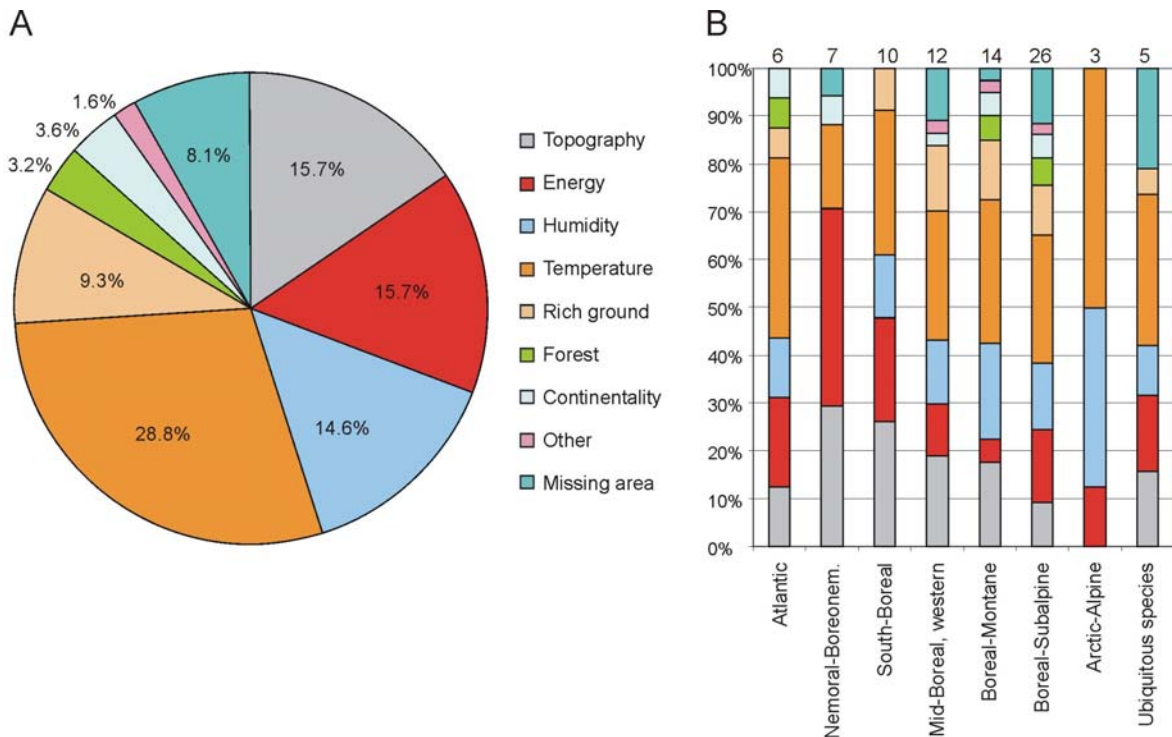


Figure 3 A and B. Diagrams showing the proportion of explanatory variables from various categories, included ($p < 0,01$) in the models for **(A)** all species collectively, and **(B)** species grouped in mycogeographical elements. Upper row of numbers refers to number of species assigned to the respective elements.

The ‘Atlantic’ (Atl) element and the ‘Ubiquitous’ (Ubi) group did not fit into these latitudinal and altitudinal trends (Fig. 3 B).

Different categories of explanatory variables were more prevalent in some of the predefined mycogeographical elements than in others (Fig. 3 B), and some specific explanatory variables characteristically were included for species belonging to some mycogeographical elements (Table 4). The ‘Atlantic’ mycogeographical element was distinguished by having winter temperature variables (*T-Jan* and *T-Feb*) and snow conditions (*Snowdays* and *Lastsnow*) as explanatory variables included in the models for some species. For species in the ‘Nemoral – Boreonemoral’ (Ne – Bn) element, explanatory variables of the category ‘Energy’ (*Growing Degree Days* and *Aspect unfavourability*), followed by ‘Topography’ were most frequently included in the respective species models. The explanatory variable *Slope* was significant for two species in this element only. In the four boreal mycogeographical elements, *Geology richness* (category ‘Rich ground’) was a frequently included explanatory variable, but no single category of variables dominated. In the ‘Mid boreal – western’ (MBo – w), ‘Boreal – Montane’ (Bo – M) and ‘Boreal – Subalpine’ (B – Subalp) elements, all categories of explanatory variables were represented. Species in the mycogeographic elements ‘South Boreal’ (SB) and ‘Mid boreal – western’ had *Elevation – Relative relief*, *T-May*, *T-Jun*, *Geology richness* and *Growing Degree Days* in common as frequently included explanatory variables. The difference between the two was mainly that ‘South Boreal’ in addition included precipitation variables early and late in the summer season (*P-Apr*, *P-May* and *P-Nov*), while ‘Mid boreal-western’ included *P-Jul*, *Aspect unfavourability* and temperature variables from midsummer and onwards (*T-Jul* through *T-Oct*).

Table 3. Species: numbers, ecology, distribution and explanatory variables included in the models for the species.

Id: Identification number for the taxa, used in ordination analysis (PCA, species). **Taxon:** Scientific name according to the taxon list at the Mycological herbarium in Oslo (O), example species for the respective mycogeographical elements in bold letters. **N:** Number of specimens. **#:** Number of grid squares with specimen. **%:** Fraction of variation explained by the model (GLM). **Nutr:** Mode of nutrition (saprotrophic, mutualistic or parasitic). **Element:** Mycogeographical element. **Occ:** Type of occurrence; restricted (1), intermediate (2) and widespread/scattered (3). **Explanatory variables:** The explanatory variables included in the models for the species (GLM; $p < 0,01$).

Mycogeographical elements are abbreviated as follows: Atl: Atlantic; **Ne-Bne:** Nemoral – Boreonemoral; **SBo:** South-Boreal; **MBo-w:** Mid-Boreal – western; **Bo-M:** Boreal – Montane; **Bo-SA:** Boreal – Subalpine; **A-A:** Arctic – Alpine. In addition species were classified as ubiquitous (**Ubi**).

Id	Taxon	N	#	%	Nutr	Element	Occ	Explanatory variables
1	<i>Agaricus campestris</i>	175	139	5.05	s	Ubi	3	-Runnoff, GeoRich, -AsplUnFav, MarDep
2	<i>Albatrellus ovinus</i>	218	157	29.85	m	Bo-SA	3	T-Jun, -Sea, -P-Nov, Rad-Oct
3	<i>Albatrellus syringae</i>	64	43	10.52	m	Bo-SA	3	-Runnoff, T-Jun, -T-Aug
4	<i>Amanita pantherina</i>	138	75	47.06	m	SBo	1	GDD, Elev-RelRef, -P-Apr
5	<i>Amanita phalloides</i>	116	74	41.57	m	Ne-Bne	1	T-May, Elev-RelRef, -DistCoast, Rad-Oct, -(T-May x Elev-RelRef)
6	<i>Amanita virosa</i>	307	212	26.69	m	Bo-SA	3	GDD, Elev-RelRef, -Rad-Jan, MisArea 49 - 51, Evapotrans, -TRI – TerrRugg
7	<i>Auricularia mesenterica</i>	167	77	34.09	p	Atl	1	T-May, Elev-RelRef, Snowdays, -(T-May x Elev-RelRef)
8	<i>Boletus badius</i>	291	198	32.46	m	MBo-w	3	T-May, MisArea 53, GeoRich, Elev-RelRef, T-May x T-Des
9	<i>Boletus luridus</i>	72	50	35.84	m	MBo-w	2	T-Jun, GeoRich, SlopeSum, -(GeoRich x Mire)
10	<i>Calocybe gambosa</i>	246	88	49.60	s	SBo	1	T-Jun, GeoRich, SlopeSum, -P-Nov
11	<i>Catathelasma imperiale</i>	88	70	24.79	m	Bo-M	3	T-Jun, GeoRich, MisArea 53, -P-Nov, -T-Jul
12	<i>Clavicornia pyxidata</i>	207	140	39.82	s	Bo-M	2	T-Jul, Rad-Oct, TRI – TerrRugg, Forest
13	<i>Collybia fusipes</i>	23	12	59.79	s	Ne-Bne	1	T-Mar
14	<i>Cortinarius bolaris</i>	100	77	31.74	m	MBo-w	2	T-May, P-Jul, MisArea 46 -47, -(T-May x DistCoast)
15	<i>Cortinarius percomis</i>	58	46	24.77	m	Bo-M	1	T-Jun
16	<i>Cortinarius rubellus</i>	283	187	27.86	m	Bo-SA	3	T-May, Elev, -Curv, Forest x P-Jul
17	<i>Cortinarius rubicundulus</i>	125	86	26.06	m	Atl	2	T-May, Forest, GeoRich, Elev-RelRef
18	<i>Cystolepiota seminuda</i>	38	31	24.71	s	MBo-w	2	T-Jul, -T-Sep, Elev-RelRef, T-Jul x T-Sep
19	<i>Entoloma sinuatum</i>	42	22	30.18	m	SBo	1	GDD
20	<i>Fistulina hepatica</i>	136	85	41.04	p	Ne-Bne	1	Elev-RelRef, -AsplUnFav
21	<i>Fomitopsis pinicola</i>	687	426	23.73	p	Bo-SA	3	T-Jun, Snowdays, -(T-Jun x MisArea 42 – 44), DistOcean x Elev-RelRef, MisArea 42 - 44 x T-Aug
22	<i>Fomitopsis rosea</i>	303	185	34.82	p	Bo-SA	2	Rad-Jul, DistOcean, Forest, P-Des, T-Apr, Rad-Oct, DistCoast, -(Rad-Jul x T-Apr), Rad-Jul x DistCoast, -(P-Des x Rad-Oct), P-Des x DistCoast, -(GlacDep x Rad-Oct), Rad-Jul x GlacDep, SlopeTerrVarx GlacDep

Id Taxon	N	#	%	Nutr	Element	Occ	Explanatory variables
23 <i>Ganoderma lucidum</i>	131	95	29.71	p	SBo	2	T-May, SlopeSum, Rad-Apr
24 <i>Geronema chrysophyllum</i>	106	79	30.01	s	Bo-SA	2	MisArea 64
25 <i>Gymnopilus junonius</i>	59	38	42.56	s	Ne-Bne	1	GDD, SlopeSum
26 <i>Gyrodon lividus</i>	65	49	26.05	m	SBo	2	T-May, GeoRich, Elev-RelRef, -T-Jan
27 <i>Gyroporus castaneus</i>	27	19	42.77	m	Ne-Bne	1	GDD
28 <i>Gyroporus cyanescens</i>	90	69	25.14	m	SBo	2	T-May, -(T-May x DistCoast)
29 <i>Holwaya mucida</i>	49	39	28.71	s	Atl	1	Rad-Apr, -DistCoast
30 <i>Hygrocybe cinnopallida</i>	14	13	3.02	s	A-A	3	-T-Jul*(p<0.05)
31 <i>Hygrocybe irrigata</i>	117	82	25.24	s	MBo-w	2	T-Mar, -Rdd100, Lastsnow, T-Mar x Lastsnow, T-Mar x T-Nov
32 <i>Hygrocybe nitrata</i>	177	108	14.63	s	Ubi	3	Elev-RelRef, T-May, -T-Jun, -T-Sep, Lastsnow
33 <i>Hygrocybe punicea</i>	294	188	15.77	s	Bo-M	3	GlacDep, P-Jul
34 <i>Hygrocybe vitellina</i>	17	15	45.07	s	Atl	1	T-Feb, -T-Jan
35 <i>Hygrophorus camarophyllus</i>	121	108	19.91	m	Bo-SA	3	T-Jun, MisArea 14 - 26, - HeatIndex, -AspUnFav, Elev-RelRef, -Runnoff, Rad-Jan x Runnoff, T-Jun x Rad-Jan
36 <i>Hygrophorus discoideus</i>	97	66	29.82	m	Bo-M	2	T-Jun, GeoRich, P-Apr
37 <i>Hygrophorus gliocyclus</i>	67	44	31.43	m	Bo-SA	2	GeoRich, T-Apr, -T-Sep, -Rad - HeatIndex, -(Runnoff x GeoRich), T-Apr x Rad - HeatIndex
38 <i>Hygrophorus karstenii</i>	88	72	11.82	m	Bo-SA	3	T-Jun, P-Aug, -T-Jul
39 <i>Hygrophorus russula</i>	41	32	50.76	m	Ne-Bne	1	GDD, Rad-Apr, Slope
40 <i>Hypoholoma fasciculare</i>	212	135	32.69	s	MBo-w	3	T-May, Elev-RelRef, T-Oct, MisArea 53, GeoRich, -(T-Oct x GeoRich)
41 <i>Hypocreopsis lichenoides</i>	23	13	44.24	s	Bo-M	1	T-Jul,
42 <i>Laccaria amethystina</i>	289	173	33.30	s	MBo-w	3	GDD, -DistCoast, MisArea 14 - 26, Elev-RelRef x DistCoast
43 <i>Lactarius hygginus</i>	153	121	10.30	m	Ubi	3	T-Jun, GeoRich, MisArea 53
44 <i>Lactarius lignyotus</i>	167	124	24.80	m	Bo-SA	3	T-Jun, MisArea 42 - 44, GeoRich
45 <i>Lactarius pyrogalus</i>	134	102	29.71	m	MBo-w	3	GDD, Elev-RelRef, GeoRich, GlacDep
46 <i>Lactarius repaesentaneus</i>	212	174	5.92	m	Bo-SA	3	Rad-Oct, Forest, -(Rad-Oct x Curv), -(Rad-Oct x Forest), Forest x GDD
47 <i>Lactarius volernus</i>	83	59	36.12	m	SBo	1	T-May, Evapotrans, Elev-RelRef
48 <i>Leccinum pseudoscabrum</i>	129	70	32.20	m	Ne-Bne	1	T-Ann, Slope, -AspUnFav, MisArea 1 - 12, -(Slope x T-Nov), -(T-Ann x T-Nov)
49 <i>Limacella guttata</i>	76	58	31.88	m	Bo-M	2	T-Jul, GeoRich, -P-Aug, Elev-RelRef
50 <i>Macrolepiota procera</i>	65	46	36.05	s	MBo-w	2	T-Aug, Elev-RelRef, -P-Jul, -AspUnFav
51 <i>Marasmius oreades</i>	231	147	34.33	p	Bo-M	3	T-Aug, -P-Apr, Elev-RelRef, -Forest, GeoRich, DistOcean, -(T-Aug x Elev_Rel.relieff), Elev_Rel.relieff x Forest
52 <i>Marasmius siccus</i>	28	19	39.34	s	Bo-SA	2	SlopeTerVar, -(P-Aug x Runoff Preccorr)
53 <i>Melanoleuca verrucipes</i>	8	7	19.19	s	Bo-SA	2	T-May

Id	Taxon	N	#	%	Nutr	Element	Occ	Explanatory variables
54	<i>Melastiza scotica</i>	25	20	31.83	s	MBo-w	1	GeoRich
55	<i>Microstoma protracta</i>	71	54	22.50	s	Bo-SA	2	-Runoff, T-May, GeoRich, -T-Sep, -Mire
56	<i>Neolectia vitellina</i>	28	19	32.97	s	Bo-SA	1	-T-Aug, Forest, T-Jun x T-Aug
57	<i>Omphalina alpina</i>	143	120	7.50	m	A-A	3	-T-Jun, GS, -P-Mar
58	<i>Omphalina grossula</i>	21	20	35.02	s	SBo	1	T-Jun, Rad-Jan
59	<i>Omphalina hudsoniana</i>	181	130	11.19	m	A-A	3	-T-May, T-Sep, -P-Nov, P-May, -(T-May x P-May)
60	<i>Phaeolus schweinitzii</i>	131	96	20.61	s	Ubi	3	GDD, Elev-RelRef, -P-May, -AspUnFav
61	<i>Pholiota astragalina</i>	110	88	19.77	s	MBo-w	3	T-May, Elev-RelRef, Snowdays
62	<i>Pholiota flammans</i>	158	116	22.87	s	Bo-SA	3	T-Jun, Elev-RelRef, Evapotrans
63	<i>Pholiota heterocita</i>	56	50	6.73	p	Bo-SA	3	T-Jul
64	<i>Phyllotopsis nidulans</i>	99	87	15.85	s	Bo-SA	3	T-Jun, -T-Sep, MisArea 46-47, -P-Jun, T-Ann, GeoRich x T-Ann
65	<i>Pleurocybella porrigens</i>	289	198	32.27	s	MBo-w	3	MisArea 28 - 40, -AspUnFav, P-May x evapotrans, T-May x AspUnFav
66	<i>Plicatura nivea</i>	161	93	26.41	s	Bo-SA	3	T-Jul, Elev-RelRef, -P-Oct, MisArea 14 - 26, -Mire, -DistOcean, -GeoRich, P-Oct x DistOcean, T-Jul x P-Jan
67	<i>Plicaturopsis crispa</i>	200	134	22.30	s	Bo-M	3	DistCoast, Rad-Apr, AspUnFav, DistCoast x Rad-Apr
68	<i>Pluteus leoninus</i>	27	22	29.53	s	Bo-M	1	T-Jun
69	<i>Porphyrellus porphyrosporus</i>	69	51	27.86	m	Atl	1	T-Ann, -T-Okt, Rad-Oct
70	<i>Pseudoplectania nigrella</i>	112	89	27.66	s	Bo-M	2	T-Jun, -T-Sep, Elev-RelRef
71	<i>Psilocybe magnivelaris</i>	64	53	15.36	s	Bo-SA	3	GeoRich, MarDep, -(Mire x Elev)
72	<i>Pulcherrimum caeruleum</i>	25	17	39.13	s	Atl	1	-Lastsnow, -AspUnFav
73	<i>Rozites caperatus</i>	327	264	6.08	m	Bo-SA	3	Rad-Oct, -Runoff, GeoRich, MisArea 42 - 44, -(Rad-Oct x MisArea 42 - 44)
74	<i>Sistotrema confluens</i>	114	81	28.32	s	SBo	2	T-Jun, Elev-RelRef, -(T-Jun x Elev-RelRef)
75	<i>Suillus flavidus</i>	142	115	10.81	m	Bo-SA	3	T-May, -DistCoast, Forest
76	<i>Tapinella atrotomentosa</i>	300	211	32.31	s	Ubi	3	T-Jun, Elev-RelRef, Rad-Oct, -(Elev-RelRef x PlanCurv)
77	<i>Thelephora palmate</i>	112	90	26.02	s	Bo-M	3	T-Jun, -PlanCurv, Elev-RelRef
78	<i>Tremiscus helvelloides</i>	89	67	32.60	s	Bo-SA	2	GeoRich, MisArea 53
79	<i>Tricholoma aestuans</i>	82	72	18.15	m	Bo-M	3	T-Jun, Elev-RelRef, MarDep
80	<i>Tricholoma colossus</i>	87	59	29.43	m	Bo-M	2	P-Jun, -(T-May x P-Jun)
81	<i>Tricholoma nauseosum</i>	30	24	37.28	m	Bo-SA	2	T-Jul, -P-Aug, S - Slope, -MisArea 1 - 12, -(P-Aug x MisArea 1 - 12), -(P-Aug x S - Slope)
82	<i>Tricholoma sulphureum</i>	130	84	30.54	m	SBo	2	Elev-RelRef, -(P-Jun x AspUnFav)
83	<i>Tubaria confragosa</i>	104	85	11.89	s	Bo-SA	3	GeoRich, Forest, Elev x Elev-RelRef

The ‘Boreal – Montane’ element showed the lowest proportion of explanatory variables in the category ‘Energy’. Species belonging to the ‘Boreal – Subalpine’ mycogeographic element was distinguished by having late summer temperatures variables, *Annual runoff*, *Geology richness*, *Rad-Oct* and *Forest* frequently included as explanatory variables. Species categorized in the ‘Arctic – Alpine’ (Arct – Alp) element most often included variables in the category ‘Humidity’. Species belonging to the ‘Ubiquitous’ group, frequently included *Elevation* and *Radiation – Heath Index* as significant explanatory variables (Table 4), and had the highest proportion of variables in the category ‘Missing area’ included in the species models (Fig. 3 B).

Table 4. Explanatory variables included ($p < 0.01$) in the models for species assigned to the different elements. Variables of the category ‘Missing area’ and variables included only once or not at all are with one exception* omitted.

Id	Exp. Var	Category	Total	Atl	Ne-Bne	S-Bo	MBo-w	Bo-M	Bo-SA	A-A	Ubi
				6 sp	7 sp	10 sp	12 sp	14 sp	26 sp	3 sp	5 sp
2	Elev-RelRef	Topo	27	2	2	5	6	5	4		3
3	Slope	Topo	2		2						
5	SlopeSum	Topo	4		1	2	1				
11	Rad - HeatInd	E	4						2		2
12	AspUnFav	E	10	1	2		2	1	2		2
18	P-Apr	Hum	2			1		1			
19	P-May	Hum	2							1	1
20	P-Jun	Hum	2					1	1		
21	P-Jul	Hum	3				2	1			
22	P-Aug	Hum	3					1	2		
25	P-Nov	Hum	4			1		1	1	1	
28	T-Ann	Temp	3	1	1				1		
29	T-Jan	Temp	1*	1							
30	T-Feb	Temp	1*	1							
31	T-Mar	Temp	2		1		1				
32	T-Apr	Temp	2						2		
33	T-May	Temp	18	2	1	4	4		4	1	2
34	T-Jun	Temp	23			3	1	7	8	1	3
35	T-Jul	Temp	10				1	4	4	1	
36	T-Aug	Temp	4				1	1	2		
37	T-Sep	Temp	7				1	1	3	1	1
38	T-Oct	Temp	2	1			1				
42	Evapotrans	E	3			1			2		
43	Runoff	Hum	5						4		1
47	GDD	E	10		4	2	2		1		1
49	Rdd100	Hum	1				1				
53	GeoRich	Rich G	21	1		2	5	4	8		1
55	Snowdays	Hum	4	1			1		1		1
56	Lastsnow	Hum	2	1			1				
57	Rad-Jan	E	2			1			1		
58	Rad-Apr	E	4	1	1	1		1			
60	Rad-Oct	E	8	1	1			1	4		1
62	DistCoast	Cont	6	1	1		1	1	2		
63	DistOcean	Cont	2					1	1		
66	MarDep	Rich G	2					1	1		
71	GlacDep	O	2				1	1			
73	Forest	F	8	1				2	5		

The variables 29 and 30, T-Jan and T-Feb, are included as explanatory in the model for one Atlantic species only, are not excluded from the table.

The fraction of variation explained

The fraction of variation explained (as percentage of the null deviance) in each of the 83 multi-predictor GLM models varied from 3% up to 60%, averaging 27.65% (Table 3). Nine species models had higher than 40% fraction of variation explained, fifty three species models were in the range 20-40%, fourteen in the range 10-20%, and six lower than 10%. In a regression analysis, the fraction of variation explained was related to how widespread the species are (using the three categories widespread/scattered, intermediate and restricted occurrence) and the species frequencies (Nos. of grid squares with observations). The fraction of variation explained was significantly related to how widespread the species are ($p < 0.05$), where widespread/scattered species had a lower fraction of variation explained (average % 19.55), compared to species with a restricted distribution (average % 38.49) (Fig. 4 A). In addition, the fraction of variation explained was significantly negatively related with the number of records ($p < 0.05$) of the species (Fig. 4 B).

High fractions of explained variance were observed for *Collybia fusipes* (60%), *Hygrophorus russula* (52%) and *Hygrocybe vitellina* (45%). These three species are all rare in Norway, having restricted and concentrated distributions (recorded in 12, 32 and 13 grid squares, respectively). The species *Calocybe gambosa* and *Amanita pantherina*, which are restricted but locally frequent (recorded in 88 and 75 grid squares, respectively) also had high fractions of explained variance (50% and 47%, respectively). Species with low fraction of explained variance (<10%) included both common and rare species, all with widespread or scattered distributions in Norway. The common and widespread species *Agaricus campestris* and *Rozites caperata* (registered in 139 and 264 grid squares, respectively) had 5% and 6% fraction of explained variance, respectively. The rare and scattered species *Hygrocybe citrinopallida*, recorded in 13 grid squares, had a fraction of explained variance of only 3%.

PCA of the GLM modelling results

The ordination of the species/explanatory variables F -values matrix, obtained from the 6225 GLM models where the responses of each species to each of the 75 explanatory variables were inferred (Online material 1), gave axis that were easily interpreted in ecological terms, with eigenvalues accounting for 60.40%, 9.15%, 3.57% and 2.50% of the total variation on the first four axes, respectively.

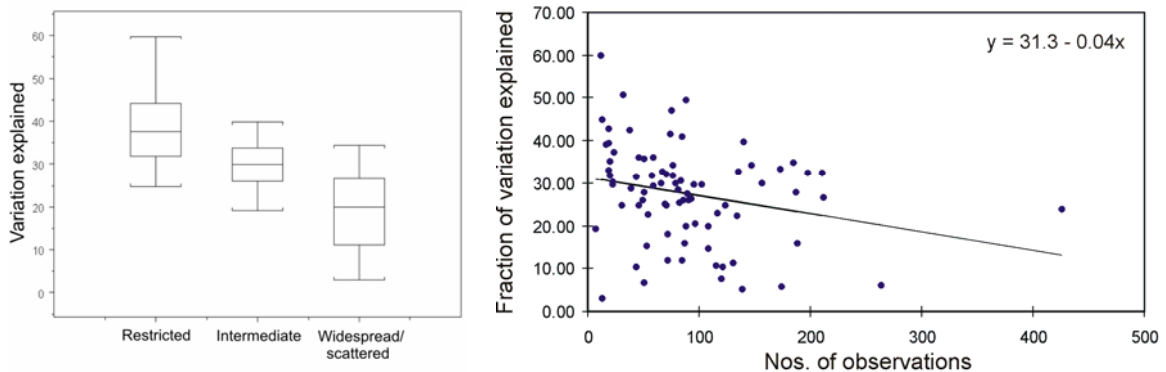


Figure 4. (A) Boxplot showing fraction of variation explained by the GLM-models versus distribution pattern (restricted, intermediate, or widespread/scattered). Species were grouped in the three categories based on their distribution maps in Norway (Appendix 6). (B) Linear regression showing the significant relationship ($p < 0.05$) between fraction of variation explained by the GLM-models versus species frequency (Nos. of grid squares with observations).

Noteworthy, the F -values which are ordinated all have positive figures, only denoting the strength of the species-variables correlations. Whether a species shows attraction or aversion for a variable will not be shown, it will be positioned only according to the strength of the F -value. Some clustering of species according to the predefined mycogeographical elements was present in the 'species version' PCA diagram (Fig. 5), but the various elements overlapped considerably as well. Coordinates for all species along the first (PC1), second (PC2) and third (PC3) axes are shown in appendix 4. Species with low scores for the first axis belonged to the 'Boreal – Subalpin' and 'Atlantic' elements or the 'Ubiquitous' group, while high scores were obtained by species of all mycogeographical elements (Fig. 5). The 'Boreal – Subalpine' species *Marasmius siccus* and *Psilocybe magnivelaris* and the ubiquitous *Agaricus campestris* made up the low-score end of the first axis (Fig. 6). Species classified as 'Atlantic' obtained high scores along the second axis, with maximum reached for *Hygrocybe vitellina*, while Boreal – Subalpine species obtained low scores, with least for *Albatrellus syringae* and *Microstoma protractum*. Species of the Midboreal – western and the Boreal – Montane elements spread along this axis. In the main cluster in the PCA ordination diagram were representatives of all mycogeographical elements, except the 'Arctic – Alpine', which made up a small individual cluster (Fig. 6).

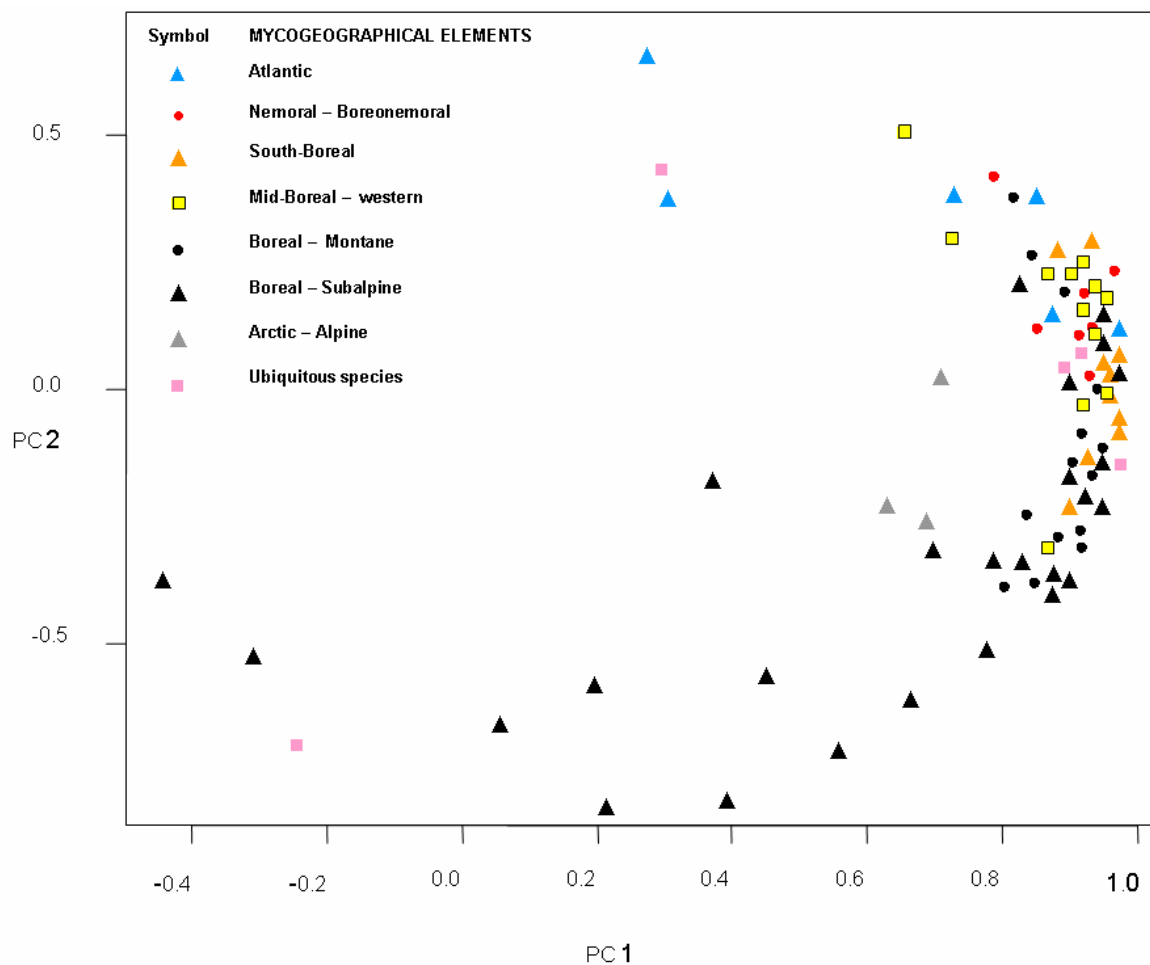


Figure 5. PCA ordination of the 'species/explanatory variables F -values matrix', with symbols for the respective mycogeographical elements showing species along the first (PC1) and second (PC2) axes. The species grouped to some extent according to the pre-defined elements, but some elements overlapped considerably.

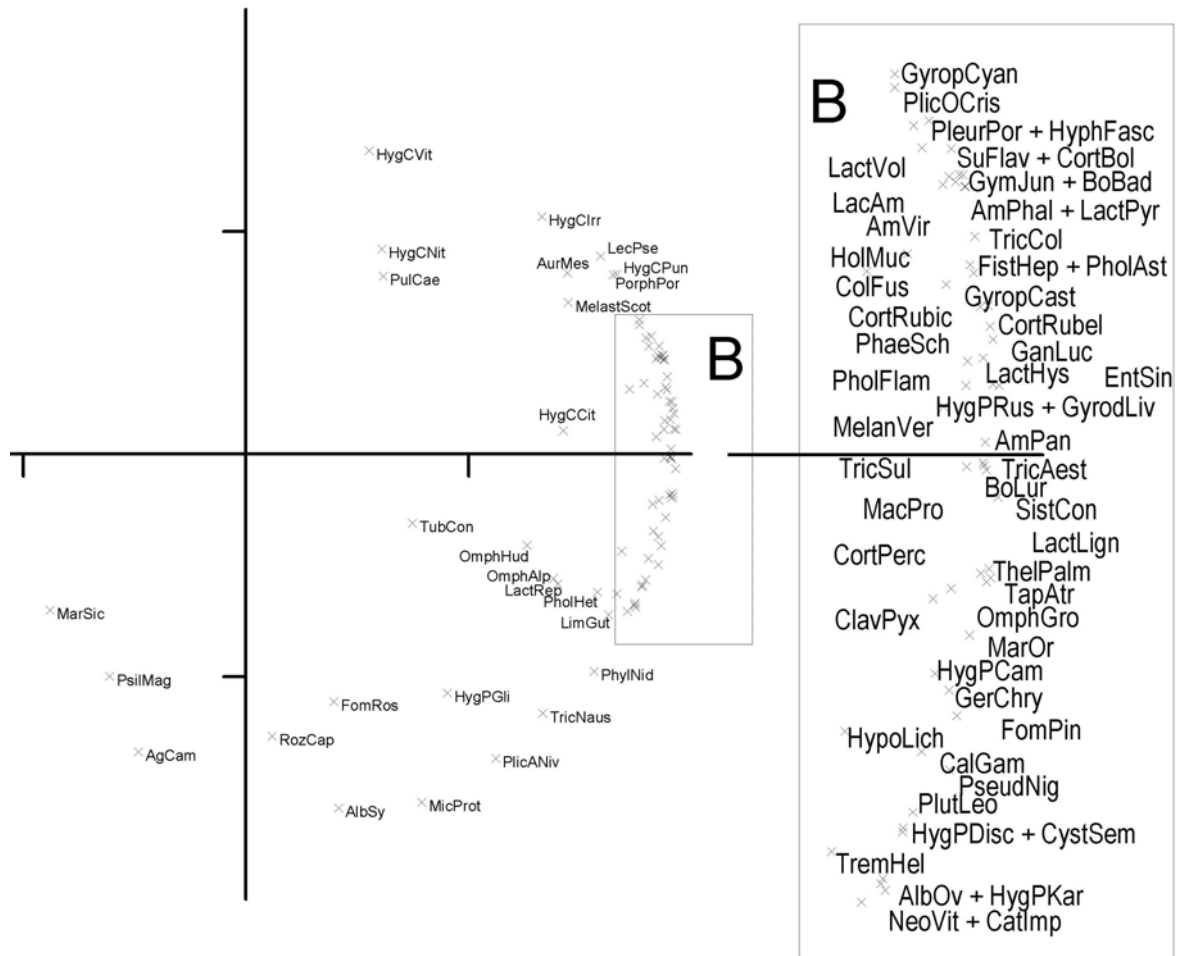


Figure 6. PCA ordination of the species/explanatory variables matrix of *F*-values, showing species along the first (PC1) and second (PC2) axes. See **appendix 1** for explanation of abbreviated species names. Coordinates for all species along axis PC1, PC2 and PC3 are found in **appendix 4**.

PCA ordination with explanatory variables as output of the matrix of *F*-values (the ‘variables version’ of the ordination) gave axes (PC1, PC2 and PC3) that are well interpretable in environmental terms. Coordinates for all variables along PC1, PC2 and PC3 are given in appendix 5. The ordination diagrams in figures 7 A, 7 B and 8 show the distribution of the explanatory variables along axes PC1, PC2 and PC3. Conjugated variables are not shown.

Temperature variables for the months April through September (*T-Apr – T-Sep*), were strongly and positively correlated with PC1, as were the *Growing Degree Days* (GDD) and *Growing season* (GS). The first PC axis, PC1, is therefore interpreted as a gradient of summer temperatures.

Three groups of variables had high, positive loadings on PC2 (Fig. 7 A). Highest loadings were obtained for the winter months November through March (*T-Nov – T-Mar*). The variables *Distance to coastline* (DistCoast) and *Distance to ocean base line* (DistOcean) and *# days snow-covered* (Snowdays) and *Last day with snow cover* (Lastsnow) were also strongly affiliated with the positive end of PC2. In contrast, the variables *Annual runoff* (Runoff) and *Runoff corrected annual precipitation* (Runoff Precorr) had high, negative loadings on the second axis. *Marine deposits* (MarDep) and *Forest* (Forest) showed a marked negative correlation with PC2, having vectors parallel to those of *Annual runoff* and *Runoff corrected annual precipitation*. The second axis, PC2,

mainly recording a gradient of winter temperatures/continentality and runoff, is therefore interpreted as a gradient of continentality.

Along PC3 (Fig. 7 B) a cluster of precipitation variables (*Annual precipitation* (P-Ann), and *precipitation* variables for all months of the year (except June and December) and *# days with precipitation threshold 0.1 mm* (Rdd100), in the category 'Humidity', obtained high positive loadings, and the four *Sun radiation* variables (Rad-Jan, Rad-Apr, Rad-Jul, Rad-Oct) in the category 'Energy' obtained low loadings. The third axis, PCA3, a gradient of humidity and radiation is also interpreted as a gradient of continentality. Variables in the categories 'Topography' and 'Missing Area', all have short vectors not contributing much to any of the three first axes.

The explanatory variables did not consequently group according to variable category (Figs. 7 A and B). The Temperature variables were separated on two axes, the summer *Temperature* variables contributing to the PC1 gradient of summer temperatures, and the winter *Temperature* variables contributing to the PC2 gradient of winter temperatures and runoff. The vectors for the variables in the category 'Energy' pointed diagonally in opposite directions, with *Growing Degree Days* and the *Sun radiation* variables positive along PC1 and negative along PC2, while the other were slightly negative along PC1, slightly positive along PC2 (Appendix 5). Variables in the category 'Humidity' clustered together and define PC3 as a gradient of humidity, at the exception of *Annual runoff* and *Runoff corrected annual precipitation* and *# days snow-covered* and *Last day with snow cover* contributing to PC2 with negative and positive vectors, respectively. Variables in the categories 'Topography', 'Other' and 'Missing area' clustered together, close to zero on all axes, apart from the variable *Elevation* being a positive outlier on axis one (Appendix 5). The category 'Continental' was split along PC2, *Distance to coastline* and *Distance to ocean base line* both with a strong positive correlation, the index-variable *Conrad continentality* with a slightly negative correlation. The category 'Rich ground' was also split along PC2; with *Geology richness* (GeoRich) close to zero and *Marine deposits* (MarDep) negative (Appendix 5). The variable *Forest* is given status as a category on its own.

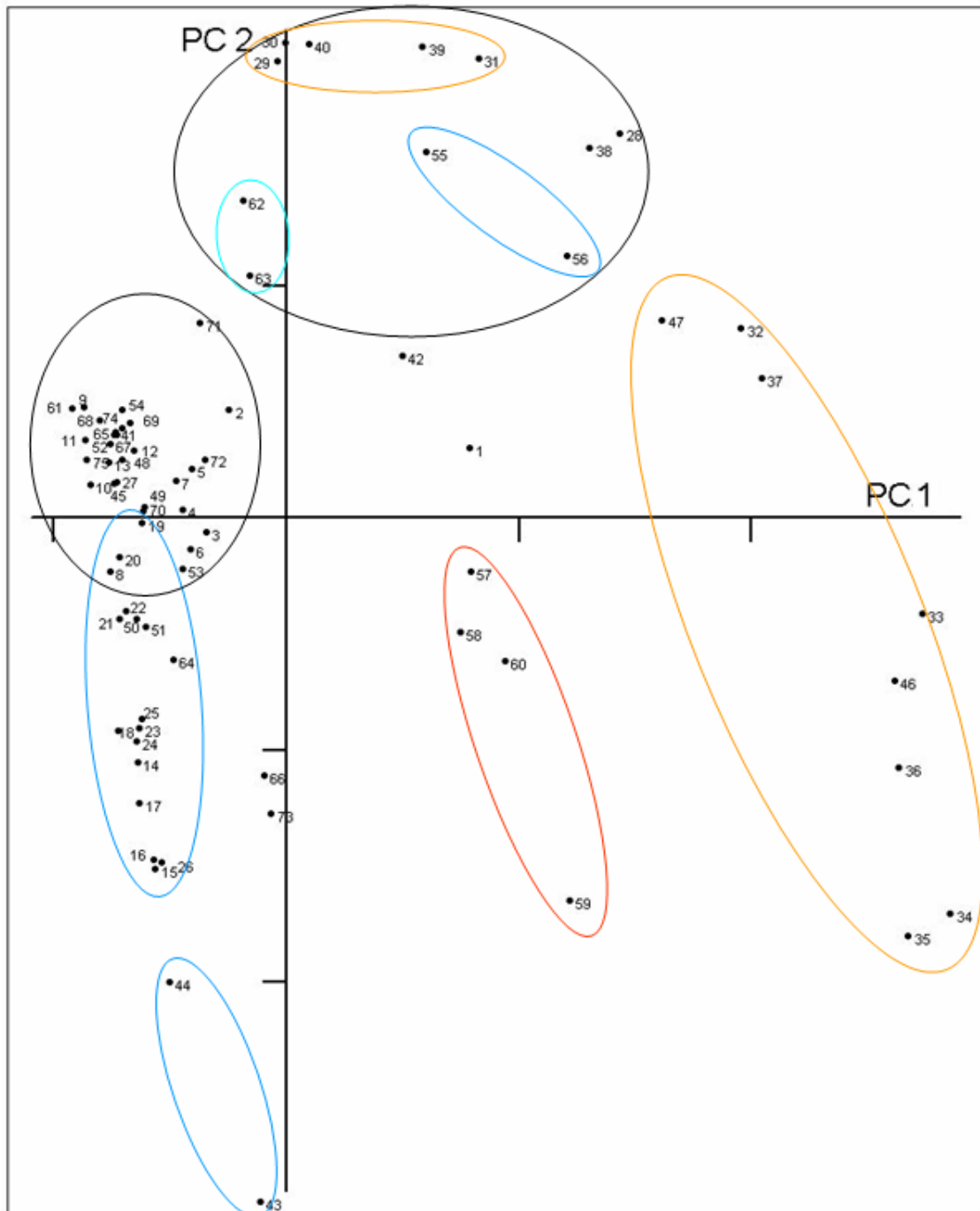
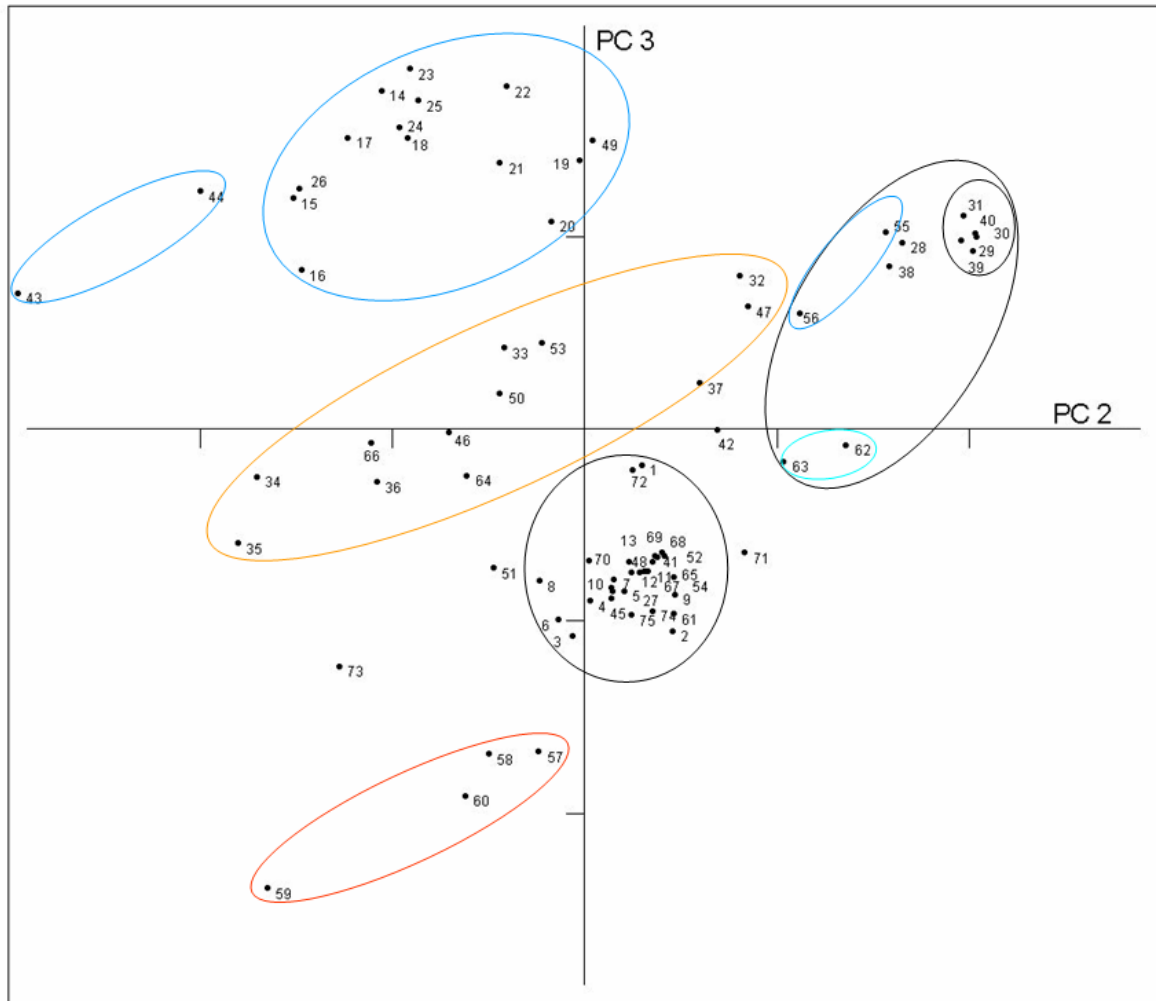


Figure 7 A and B. Diagram of PCA ordination of the 'species/explanatory variables of *F*-values matrix' from the GLM modelling showing the endpoints of vectors of the explanatory variables (**A**) along the first (PC1) and second (PC2) axes and (**B**) along the second (PC2) and third (PC3) axes, as numbered dots. Numbers, names and axis coordinates for axes PC1, PC2 and PC3 for all explanatory variables are shown in appendix 5. Circles show vector endpoints for variables being decisive for the gradients expressed by the three PC axes. Conjugated variables are not shown. **A.** Explanatory variables along axes one and two show that PC1 is dominated by summer temperature variables, *Growing Degree Days* and *Growing Season*, endpoints of vectors encircled in orange (big orange circle). PC2 is dominated by winter temperatures (small orange circle), variables of the category 'Continentality' (turquoise circle) and *Snowdays* and *Lastsnow* (blue circle) in the positive end of axis two, all encircled in black, and the variables *Runoff* and *Runoff Precorr* in the category 'humidity', encircles in blue at the negative end. The big black circle shows mainly variables belonging to the categories 'Topography' and 'Missing Area', all close to origo and not contributing much too either axes. The two figures left, the red and the blue slim oval, which dominates PC3, is described in figure B.



B. Explanatory variables dominating PC2 (this time horizontal) are recognisable as circles with the same colour coding; winter temperatures (small orange circle), variables of the category 'continentality' (turquoise circle) and *Snowdays* and *Lastsnow* (blue circle) in the positive end of the second axis, all encircled in black, and the variables *Runoff* and *Runoff Precorr* in the category 'humidity', at the negative end. PC3 is dominated by precipitation variables and other variables in the category 'Humidity', encircled blue (the big one) at the positive end of the third axis, and radiation variables in the category 'Energy', encircled red, at the negative end. The dominating orange circle close to origo shows the rest-values of the variables dominating PC1 (Summer temperature variables, *Growing Degree Days* and *Growing Season*). The black circle shows the same variables as in figure A, mainly variables belonging to the categories 'Topography' and 'Missing Area', still close to origo and not contributing much too any axes.

DISCUSSION

In this study I have used herbarium data and general linear models (GLM) to analyze fungal distribution patterns and to investigate which environmental variables account for species' distributions. PCA ordination was used to identify underlying structures in the results, to aid in explaining. To my knowledge, this is the first time fungal herbarium data have been used in such analyses, and the study demonstrates that herbarium data can be used to answer questions within the fields of ecology and biogeography. However, great caution must be taken when employing herbarium data in this manner. Some specimens are accessioned with the wrong taxon identity in herbaria. For instance, in this study it was discovered that 30 specimens of *Lactarius dryadophilus* were accessioned as *Lactarius repraesentaneus*. Furthermore, molecular phylogenetics has shown that cryptic species commonly occur within fungal morphotaxa (e.g. Kauserud et al. 2006, 2007). Treating cryptic species with divergent ecological and distributional patterns as one unit will certainly lead to false interpretations (see below). Another aspect is that herbarium data are not sampled according to strict predefined sampling strategies, but are presence-only data, and may give a highly skewed picture of species distributions and ecology depending on where the collectors have been. Since the species studied here are morphologically well known and the time-span for registering has been more than 100 years, the data were treated as presence/absence.

In the initial GLM analyses, various infrastructure variables in the category 'Road' (distance to nearest road, etc.) were most frequently included in the species models as explanatory variables. This is probably because collectors most often sample fungi in close vicinity to roads. This result indicates that fungal distribution patterns observed with herbarium accessions to some extent are explained by human behaviour, as summarized by Smith and Weber (1980) in one sentence: '*Mushrooms are where you find them*'. Variables in the category 'Road' were not included in the main analyses, since the superior aim of the study was to evaluate the fungal distribution patterns in the light of natural environmental variables.

The overall most important explanatory variables

The interpreted environmental complex gradients from the PCA ordination are to a large degree congruent with recognised main regional environmental gradients in Norway (Bakkestuen et al. in press), indicating that the systematic division of vegetation into zones and sections by Moen (1999) actually describes the most important regional variation governing the distribution of species. These results indicate that there is an underlying structure in the herbarium data for the species occurrences used in this study, which support the idea of using GLM models to predict species occurrences. The importance of temperature conditions is reflected in the first PCA axis (Fig. 7 A), with eigenvalue 60.40%. This axis is interpreted as a 'complex gradient' of summer temperature variables, *growing-degree days* (GDD) and *growing sum* (GS). The importance of humidity- and temperature/energy were reflected by the second and third PCA axes (Fig. 7 B), both interpreted as gradients of continentality. The cluster of variables in the category 'Topography' is close to zero, not contributing much to any of the three first axes (Fig. 7A and B), reflecting a minor contribution from these variables.

Presence models from the GLM analyses for the respective species generally included variables in the categories 'Temperature', 'Energy', 'Humidity' and 'Topography' and the variable *Geological richness*. Variables in the category 'Topography' are primarily considered of indirect influence by altering conditions for variables of presumably more direct physiological significance and by increasing the total environmental variability (and thus the numbers of niches). Noteworthy, the GLM analyses

might oversimplify the relationships between fungal distribution patterns and environmental variables. When the single explanatory variable that accounts most for the fungal distribution is included in the model, other correlated variables accounting for almost equally much are not necessarily included, since the next iteration of calculations uses the 'rest-variation' as starting point, finding the variable explaining the most of this. *Hygrocybe vitellina*, with only *T-Feb* as included, exemplifies the problem. *F*-values for the neighbouring months are almost as high (cf. Online material 3), reflecting the species dependence on above zero winter temperatures in general. The fact that *T-Feb* was included in the model might indicate that the risk of sub zero (lethal) temperatures are highest in February though.

Overall, the various temperature variables were most frequently included in the models (28.8%) and indicate that fungal distribution patterns to a large extent are governed by temperature conditions, generally known to be one of the cardinal factors that determine the distribution of many fungi. The majority of fungi are mesophilic, which grow in temperature conditions between 5 and 37°C (Hudsen 1986, Dix and Webster 1995), with optima between 20 and 25°C. Temperatures in the months of May, June and July were especially frequently included in species distribution models. Many of the investigated species form mycorrhiza or are otherwise dependant on plant growth. Plant growth is generally strongly related to air temperature, especially during the early growing season (Menzel 2002, Sparks and Menzel 2002), which indirectly influences the fungi.

Environmental variables in the category 'Energy' (radiation, growing degree days per season, etc.) were also frequently included in the species models (15.7%). Of these variables, *Growing degree days* (GDD) and *Growing season* (GS) are strongly related to the temperature variables. The number of growing degree days (GDD) per season was included in the models for ten species, mainly southerly ones. This probably reflects that for the southern species in particular (northern hemisphere perspective), the northern distribution limit to a large degree depends on temperatures- and temperature related variables in the growing season (Lange 1974, Eckblad 1981). Radiation variables, mainly in October (*Rad-Oct*), were included for eight species, probably due to their influence on soil temperature (Petersen 1977). This influence will probably be highly variable at both regional and local levels, being highest in non-forested areas and stronger at higher elevations and favourable aspects.

Variables in the category 'Humidity' were also often included in the models (14.6%). According to Cooke and Whipps (1993), access to water is probably the single most important environmental factor affecting growth. One could ask why variables in this category not are included even more often. Since the GLM models are based on average values for environmental variables (30 years normal period 1961 - 1990) they will not necessarily have high predictive power on presence based on i.e. precipitation, since it probably is the driest periods/year and not the average that actually is critical for the distribution of the fungi.

It is tempting to speculate that the selected species only to a small degree are limited by humidity under the generally moist conditions encountered during the Norwegian growing season. Most fungi grow best at higher water potentials, in the range of 0 to -1 MPa, but do not immediately desiccate and die at lower levels: Most wood-living fungi even grow at levels down to -4 MPa (Carlile and Watkinson 1996). Furthermore, at a resolution of 5x5 km, with a generally varied topography and high precipitation values, the preferred water potentials might potentially occur somewhere in a square. One might argue that the variables included (precipitation values, snow conditions, runoff etc) may not adequately represent the humidity experienced by fungal mycelium, which is determined by the ground/substrate humidity at the very local level. It seems obvious that the

distribution of fungi depends on micro-ecology as well as macro-ecology (Petersen 1995) (see below).

The frequent inclusion of 'Topography' variables in the species models (15.7%), and the inclusion of the variable *Elevation – Relative relief* as the most frequently of all variables (27 times), can best be explained as an indirect influence. A varied topography may increase the odds of favourable conditions for variables of presumably more direct physiological significance, like 'Temperature'- and 'Humidity' variables. By increasing the total environmental variability and thus the numbers of niches available, a varied topography will increase the probability of occurrence.

The variable *Geological richness (GeoRich)*, which is a categorical variable, was included in 21 species models. Most species with *GeoRich* included in their model are calciphilous, like *Calocybe gambosa* and *Catathelasma imperiale*, or prefer fertile soils, like *Agaricus campestris*. A few species well known from acidic soils in Norway, e.g. *Lactarius lignyotus* and *Rozites caperatus*, also had *Geological richness*, included in their models, and are probably strictly linked to the least rich range. However, some species considered calciphilous, e.g. *Cortinarius percomis* (Nitare 2000), did not have *GeoRich* included in their models. This result is most likely due to the scale of 5x5 km being too coarse meshed to represent relatively rare species with their preferred habitat found scattered as small patches, resulting in low predictive power of the models.

Since temperature variables were shown to be of utmost importance, one might speculate that global warming could have large impacts on fungal distribution patterns and on biodiversity in Norway. With a warmer climate it seems obvious that the fungi may shift towards more southerly species and species now inhabiting alpine areas might suffer reductions in habitat area, encountering increasingly unstable conditions as well as a smaller surface area available as it becomes necessary to move upslope. Studies on fungal communities' responses to temperature changes in the mesophilic range have emphasized the importance of temperature fluctuations in shaping community structure and indicate that small changes in temperature can markedly stimulate growth (Jensen 1969, Weidensaul and Wood 1984). Skaugen and Tveito (2004) concluded in their scenario for Norway for the period 2021–2050 that the thermal growing season and growing degree-day sum (GDD) within the growing season (GS) will increase. (Fig. 7A and B) Høgda et al. (2001) found that the GS increased between 1982 and 1998, especially along the southern coast of Norway, where some of the most southerly species in Norway have their only known distribution and global northern limit. An example of a fungus influenced by this factor (GS) could be the Nemoral – Boreonemoral *Collybia fusipes*, which is dependent upon *Quercus* forests of long continuity (Brandrud et al 2000). The species was registered in Norway for the first time in 1976. In the 80's it was registered three more times, and it has been registered 22 times since then (data from the Mycological herbarium in Oslo, accessed 01.02.2007). This adds credibility to the speculations of Jordal et al. (2004) that some species could be relicts from the warmer postglacial period and are rarely or not producing sporocarps under (the) existing climatic conditions. Such species will be favoured by the climatic shift. And probably become more frequent in the future. Furthermore, it indicates that increased summer temperatures already influence the biodiversity of the Norwegian fungi. Alternatively, the explanation of the increase in observations of *Collybia fusipes* is simply sampling bias; mycologists now being increasingly aware of rare species with interestingly restricted distributions.

Do species in predefined mycogeographical elements respond to the same variables?

The PCA plot in figure 5 showed that species within predefined mycogeographic elements to some degree clustered together, indicating that they respond to the same environmental

variables. However, there was also great overlap between the elements in the PCA plot. Some of the elements clustered, mainly the 'Nemoral – Boreonemoral', the South-Boreal and the Arctic – Alpine, and some elements spread out, especially the Atlantic and the 'Boreal – Subalpine'. PCA axis 1, interpreted as a gradient of temperature-variables and GDD, illustrate well that most fungi have quite similar temperature preferences (Dix and Webster 1995), and also shows ecologically meaningful differences between mycogeographic elements. The southerly elements are clustered at the positive end of axis one, while the most continental species of the 'Boreal – Subalpine' element are found at the negative end.

To which degree species in the respective elements correlate with specific environmental variables varies – and to some degree it varies systematically according to mycogeographical element. Interestingly, no 'Humidity' variables were included for any Nemoral – Boreonemoral species. This could be because these rather southerly species presumably are drought resistant and do not experience humidity levels within their Norwegian distribution range as limiting. The Arctic – Alpine element at the other extreme, show a high proportion of variables in the category 'Humidity', related directly to the risk of desiccation in alpine environments as well as indirectly to temperature in the growing season (Petersen 1977) because cloud formation influences radiation. The fact that the number of species in arctic-alpine environments decrease with latitude, (which is correlated with decreasing seasonal length (Borgen in press)), confirms the temperature dependence.

Within the boreal mycogeographic elements, the number of precipitation variables included in the species models increased in the more northern elements, including also late summer and autumn months. This probably reflects the generally lower precipitation values inland, in the Boreal – Montane and Boreal – Subalpine elements, with correspondingly increased risk of drought stress. The predominant coarse moraine in the same areas may add to the risk of desiccation. The trend within the temperature variables for all elements except the Ubiquitous group parallels that of precipitation. The length of the growing season is probably more limiting with increasing latitude and altitude, an argument used by Lange (1977) to explain the marked difference in the funga on the southern and northern side of *Limes Norlandicus*. The trend observed in variables in the category 'Energy', except for the Atlantic element and the Ubiquitous group, is mainly caused by the variable growing degree days (GDD), the effective temperature sum ($>5^{\circ}\text{C}$) indicating the intensity of the GS (Carter 1988). GDD is often included for Nemoral – Boreonemoral species, then progressively more seldom for the more northerly elements. This supports the general opinion that the most southerly species in Norway are limited by temperature related variables (Eckblad 1981, Gulden et al. 1996, Brandrud et al. 2000). These south-north trends indicate that the species constitute a macrofungal gradient correlated with the temperature gradient.

Species within mycogeographical elements also vary with respect to their strength of relationships with explanatory variables. Interestingly, the more southerly elements and the 'Arctic – Alpine' element were the most homogenous. These elements are those who experience the most extreme environmental conditions and the steepest gradients. Species in the 'Nemoral – Boreonemoral' element, almost all included variables related to high temperatures/energy input in the growing season. The 'Arctic – Alpine' species critically dependent on temperature and humidity, balance between high radiation and subsequently high enough soil temperature for growth and production of sporocarps, but at the risk of desiccation and visa versa. This situation is elegantly described by Petersen (1977) stating: "...the macromycetes in The Arctic live as between Scylla and Charybdis". The 'Atlantic' element is also characterized by extreme steep environmental gradients, and is –

if split in two by introducing a hyper-oceanic element, – also homogeneous. The different distribution pattern, ecology and GLM model for *Hygrocybe vitellina* compared to the other species assigned to the ‘Atlantic’ element, supports Jordals (2002) idea of establishing a separate ‘hyper-oceanic’ mycogeographical element for this (type of) species. Its GLM model included mild temperatures in February (Online material 4), i.e. avoiding sub-zero temperatures. Other species are probably favoured by high summer temperatures combined with ‘oceanic’ conditions, like *Pulcherricium caeruleum* (Ryvarden 2002). This species GLM model included an early snowmelt and a favourable aspect as predictive variables (Online material 4), both contributing to a long growing season, and a favourable aspect also results in higher maximum temperatures. The two species have seemingly different ecological preferences and show no overlap in known distribution, but clearly belong in the ‘Atlantic’ mycogeographical element.

The ‘Boreal – Subalpine’ element serves as an example of a heterogeneous element, consisting mostly of widespread species with generally low to medium high fractions of variation explained (see below). This mycogeographic element covers a large part of inland Norway and do not include very steep environmental gradients. At a 5 x 5 km scale the grid may not capture the ecologically significant variables, thus giving less good predictions and a possibly false impression of a heterogeneous element. On the other hand, that the ‘Boreal – Subalpine’ element might be less homogeneous, considering the huge area covered and the differences in distribution between the most extreme species included in the element. The PCA confirms the general impression of the ‘Boreal – Subalpine’ element as widespread, with species spanning the entire PC1 and most of PC2.

The low number of species in some elements calls for caution in evaluating the results from the GLM analyses. For example, in the ‘Arctic-Alpine’ element only three species were included.

The explanatory power of the GLM models

The fraction of variation explained varied from 3% to 60% in the 83 species models, averaging 27.7%. More of the variation was typically accounted for in species with a restricted distribution compared to widespread species. This agrees well with Elith and Graham et al. (2006) concluding that species deemed to be specialists by the distribution tend to be better predicted than generalists in modelling studies. More of the variation was also explained in uncommon compared to common species, but this might be just because the specialists also are the uncommon one. Species with the highest fraction of variation explained (40% - 60%) typically have a restricted, mainly southerly distribution in Norway, or exclusively coastal. The Atlantic species *Hygrocybe vitellina* considered hyper- oceanic and limited by sub-zero temperatures had the variable *T-Feb* as explanatory in its GLM model. The two South-Boreal species *Amanita pantherina* and *Calocybe gambosa* and the six Nemoral – Boreonemoral species *Amanita phalloides*, *Collybia fusipes*, *Fistulina hepatica*, *Gyroporus castaneus*, *Gymnopilus junonius* and *Hygrophorus russula* are all confined to the warmest regions, and presumably temperature limited. All species included GDD or temperature variables from months early in the growing season in their GLM models and generally few other variables, except for *F. hepatica* whose distribution was better explained by topographic variables. This appears to be a general trend.

An additional explanation is the correlation of fraction of variation explained with the rate of change in the environmental gradients, discussed by Elith et al. (2006). By comparing results from the same modelling methods from topographically different areas they concluded that steep environmental gradients, e.g. steep topographic gradients, result in higher fractions of variation explained. The same phenomenon is observed in this study,

with species with a coastal distribution having a high proportion of their variation explained and more continental species having a relatively low proportion of variation explained. The species discussed above all have coastal distributions with the steepest environmental gradients and the greatest proportion of variation explained.

Sampling bias inherent in the herbarium data may influence results strongly. With a more representative distribution, a higher fraction of variation explained could be expected. With rare species there is a higher risk of operating with misleading patterns, because their recorded occurrence may to a higher extent be determined by the sampling rather than by their real distribution, leading to lower fractions of variation explained. A 'false absence' could significantly reduce the quality of a model, as opposed to common species where the number of occurrences would counteract the effect of a few 'false absences' (Engler *et al.* 2004). This could be the case for rare species with a scattered distribution, like *Hygrocybe citrinopallida* (3.0%), having the lowest fraction of variation explained as well as low figures recorded. The species might not be rare in its preferred habitat though, as often observed when studying pasture fungi, e.g. many species of *Hygrocybe* (Jordal 1997). On the other hand, rare species with a restricted distribution often attract great attention, resulting in a more representative picture of the actual distribution than can be expected for widespread common species, which may be considered as too trivial to report and thus not that representatively collected. This artefact may contribute to explain why the fraction of variation explained is negatively correlated with how widespread the species are.

It is worth noting that many potentially important environmental variables were not included in the analyses because these data were not available. This includes edaphic factors, which probably would be very useful at a much finer scale and distributional data for important host trees such as *Picea abies*, *Pinus sylvestris*, *Populus tremula*, *Betula pubescens*, etc. Adding the mycorrhizal partner/host species as explanatory variable presumably would have resulted in higher fractions of variation explained for most host specific mycorrhizal, saprotrophic and parasitic fungal species. One could speculate why the fungi not follow its symbiont species/host/substrate throughout its distribution range (Eckblad 1981). Is it for historical or ecological reasons, and in the latter case; which environmental variables limits its distribution? One example might be *Collybia fusipes* (60%) which is only found in the Nemoral vegetation zone in Norway, while its obligate host *Quercus* sp. in Norway reaches the South-Boreal zone (Elven 2005). Performing GLM on both the tree and the fungal species, with the associated species included as an explanatory variable, would presumably give some interesting answers concerning ecological preferences of mycorrhizal species of fungi. Used on parasitic species and their respective host trees it might also shed light on parasite-host relationships.

Cryptic speciation has been shown to be a common phenomenon within basidiomycete morphotaxa (e.g. Kausserud *et al.* 2006, 2007). For some widespread species with low fraction of variation explained, especially those with several mycorrhizal partners, e.g. *Lactarius repraesentaneus* and *Rozites caperatus*, one might suspect that the occurrence of cryptic species could be a cause to the poor explanatory power of the GLM models. The same phenomenon could explain the low fraction of variation explained in parasitic and saprotrophic species such as *Pholiota heteroclita* and *Agaricus campestris*. All the four mentioned species are common and widespread in Norway and are found from sea level to montane altitudes. All four species show a similar bimodal distribution along the altitude gradient indicating a possible temperature- and/or symbiont/host differentiation in two ecotypes. However, one can not conclude from the herbarium data, but the hypotheses should rather be investigated by multi-locus phylogenetic analyses as described in Taylor *et al.* (2000).

In this regional study the geographic unit was 5x5 km squares. However, fungal distribution patterns are certainly also governed by ecological factors that vary on a more restricted spatial level. Soil humidity and soil temperature at micro level are decisive for growth and production of sporocarps in arctic-alpine areas according to Petersen (1977), and obviously also in other habitats. Bendiksen et al. (2004) demonstrated that while the vegetational gradients were more strongly correlated with macroscale topographic variables, the fungal gradients were more strongly correlated with soil pH and nitrogen content, indicating that fungi are especially dependent upon microscale ecology. A timely question is to which degree the explanatory power is influenced by grid-size.

Conclusions and perspectives

In this study, the distribution pattern of 83 selected macrofungi in Norway were mapped and related to a dataset of 81 environmental variables through GLM analyses in order to reveal which environmental variables that mainly accounts for the species distributions. Initial analyses showed that infrastructure variables like distance to roads were of great importance, indicating that a significant bias is introduced due to the 'unsystematic' sampling of herbarium data. Among the natural explanatory variables, temperature conditions were shown to be of great importance for explaining many species distribution. PCA ordination of *F*-values from the GLM analyses strongly supported that temperature conditions (and other variables closely related to the temperature conditions) are the main structuring factors of the Norwegian 'macrofunga'. The results indicate that global warming probably will have great impact on the Norwegian fungi and that many species distributions probably will be altered significantly. Other important variables frequently included in the GLM models accounting for species distributions were either related to continentality; humidity, length of growing season, or they reflected the topography; primarily acting indirectly by favouring other factors of direct physiological influence. The analyses indicate that species a priori categorized into various mycogeographic elements to a certain degree were structured by the same environmental variables. However, great overlap also occurred between elements, reflecting that macrofungi to a large degree are influenced by the same underlying factors. Interestingly, the distribution of infrequent species with a limited distribution could be better predicted by the GLM models compared to common widespread species. Sampling bias in favour of the rare and interesting species must be considered, but is not necessary to explain the effect. The species in question all have a most southerly or south-westerly distribution in Norway, thus restricted to coastal areas with steep topographic and correspondingly steep environmental gradients. This typically confines the species to limited areas with marked environmental characteristics as opposed to surrounding areas – leading to a high fraction of variations explained.

This work shows that herbarium data in the future can be used in novel ways to analyze topics within ecology and biogeography. For example, the future effects of global warming on species diversity and species distribution can be predicted in modelling studies implementing empirical herbarium data. The occurrence and distribution of rare and threatened species can be better understood, which will be a valuable tool in conservation biology. Using GLM modelling, the most likely places of finding threatened species can be predicted. Different questions should be addressed with studies on different scales, and with adequate sets of explanatory variables, e.g. edaphic factors and symbiont/host trees should be included to gain insight into fungal microhabitat ecology and parasite-host interactions, respectively.

THE MYCOGEOGRAPHICAL ELEMENTS

Introduction

Plotting localities for the applied material (the Norwegian herbarium collections) resulted in widely different distribution patterns. Mycogeographical elements were defined (Table 1, page 13-14) according to the observed distribution patterns in Norway and current knowledge about the distribution of the species in Europe from the literature sources indicated in the Material and Methods chapter (unless otherwise stated). For each element an example species was chosen to illustrate a typical distribution for the element. A presentation and discussion of the obtained elements follows, with species assigned to the different elements listed in Tabs. 5 – 12. Maps of recorded distributions in Norway for all 83 species are presented in Appendix 6.

To analyse and discuss the results obtained from the GLM modelling for all 83 species is beyond the scope of this thesis. I have chosen to examine the GLM models (Table 13) for the (somewhat arbitrarily, pre-GLM) selected example species for each geographical element. The highly variable fraction of variation explained, from 3% to 60% and averaging 28% must be taken into account when analysing the GLM models for the species. Models for all species are found in ‘Online material 4’, at ‘Bioportal: http://www.biportal.uio.no/onlinemat/online_material.php

Description of the mycogeographical elements

The Atlantic element (Atl) (Distribution maps 1-6, Appendix 6)

The Atlantic element is characterized by coastal distributions extending north to C Norway and upwards up to 500-600 m asl. The included species are absent or rare in Finland, Sweden and Denmark; in Great Britain they are mostly southern, and on the continent they are mainly western and colline-montane. Typically the species are associated with deciduous trees. The element has only six species (among the 83 selected species), and they have considerably different distribution patterns.

Table 5. *The Atlantic mycogeographical element*, with numbers, ecology, type of occurrence and explanatory variables included in the models for the species.

Id: Identification number for the taxa, used in ordination analysis (PCA, species). **Taxon:** Scientific name according to the taxon list at the Mycological herbarium in Oslo (O), the example species for the mycogeographical element in bold letters. **N:** Number of collections. **#:** Number of grid squares with collections. **%:** Fraction of variation explained by the model (GLM). **Nutr:** Mode of nutrition (saprotrophic, mutualistic or parasitic). **Occ:** Type of occurrence; restricted (1), intermediate (2) and widespread/scattered (3). **Explanatory variables:** The explanatory variables included in the models for the species (GLM; $p < 0,01$).

Id	Taxon	N	#	%	Nutr	Occ	Explanatory variables
7	<i>Auricularia mesenterica</i>	167	77	34.09	p	1	T-May, Elev-RelRef, Snowdays, -(T-May x Elev-RelRef)
17	<i>Cortinarius rubicundulus</i>	125	86	26.06	m	2	T-May, Forest, GeoRich, Elev-RelRef
29	<i>Holwaya mucida</i>	49	39	28.71	s	1	Rad-Apr, -DistCoast
34	<i>Hygrocybe vitellina</i>	17	15	45.07	s	1	T-Feb, -T-Jan
69	<i>Porphyrellus porphyrosporus</i>	69	51	27.86	m	1	T-Ann, -T-Okt, Rad-Oct
72	<i>Pulcherricium caeruleum</i>	25	17	39.13	s	1	-Lastsnow, -AspUnFav

The example species, *Porphyrellus porphyrosporus*, has a coastal distribution in S Norway, does not occur in Finland and is fairly common in Great Britain, but deviates from what normally will be expected of an Atlantic species by having a mainly colline-montane occurrence in continental Europe. *Pulcherricium caeruleum* has a clear-cut Atlantic distribution in Europe, but a very restricted occurrence in Norway, being confined to a small area near the SW coast. It has its nearest known occurrence in S England and southern Europe and belongs to a thermophilous, subtropical group of species occurring in coastal Norway (Ryvarden 2002). *Hygrocybe vitellina* is restricted in Norway to the outermost W-coast, apparently by sub- zero winter temperatures, and is considered hyperatlantic (Jordal 2002). *Auricularia mesenterica* and *Cortinarius rubicundulus* deviate slightly from the idealized pattern by extending relatively far inland, *Holwaya mucida* by apparently being unknown in Great Britain.

The species in the Atlantic element are with one exception restricted in occurrence, and have medium to high fractions of variation explained.

The Nemoral – Boreonemoral element (Ne-Bne) (Distribution maps 7-13, Appendix 6)

The element is characterized by southern, coastal distribution patterns, reaching the inner fjord districts and extending up to 400 m asl. In Finland and Great Britain the species are absent or southern, in Denmark occasional to common; on the continent they are common in the lowlands and extend up to submontane altitudes. Typically the species are associated with deciduous trees.

The seven Norwegian species in the Nemoral – Boreonemoral element show quite congruent patterns of distribution; four species (*Fistulina hepatica*, *Gymnopilus junonius*, *Gyroporus castaneus* and *Leccinum pseudoscabrum*) with a distribution pattern similar to that of the reference species, *Amanita phalloides* and the two other species mainly differing in being more rare. The reference species *A. phalloides* has a coastal distribution in S Norway, in the West preferring inner fjord regions and in the East not extending further inland than to sites slightly North of Oslo, extending up to 300 m asl. It has a very restricted southern distribution in Finland, is common in England and Denmark as well as in the lowlands of continental Europe where it extends up to submontane altitudes. Typically it is a species associated with deciduous forests; its distribution in Sweden follows *Quercus sp.* north to the *Limes Norlandicus* (Larson 1997). *Collybia fusipes*, deviates from the general pattern of the element by being restricted to the most southern part of the country. *Hygrophorus russula* – with a distribution in Norway like a less common version of the reference species – deviates by apparently being absent from Denmark and extremely rare in Great Britain, possibly extirpated.

Table 6. *The Nemoral – Boreonemoral mycogeographical element*

Id	Taxon	N	#	%	Nutr	Occ	Explanatory variables
5	<i>Amanita phalloides</i>	116	74	41.57	m	1	T-May, Elev-RelRef, -DistCoast, Rad-Oct, -(T-May x Elev-RelRef)
13	<i>Collybia fusipes</i>	23	12	59.79	s	1	T-Mar
20	<i>Fistulina hepatica</i>	136	85	41.04	p	1	Elev-RelRef, -AspUnFav
25	<i>Gymnopilus junonius</i>	59	38	42.56	s	1	GDD, SlopeSum
27	<i>Gyroporus castaneus</i>	27	19	42.77	m	1	GDD
39	<i>Hygrophorus russula</i>	41	32	50.76	m	1	GDD, Rad-Apr, Slope
48	<i>Leccinum pseudoscabrum</i>	129	70	32.20	m	1	T-Ann, Slope, -AspUnFav, MisArea 1 - 12, -(Slope x T-Nov), -(T-Ann x T-Nov)

The species of the Nemoral – Boreonemoral element are all restricted in their occurrences and show a high fraction of variation explained by the GLM models.

The South Boreal element (S-Bo) (Distribution maps 14-23, Appendix 6)

This element includes species common in south-eastern parts, from the coast to the inland valleys, in the W occurring mainly in inner fjord districts, extending northwards to C Norway or to locally favourable sites further North, up to 600 m asl. Distributions in Finland are southern, extending to central parts, in Denmark widespread, in Great Britain southern (absent or rare in Scotland and Ireland), and on the continent mostly widespread extending to montane/subalpine regions.

The example species, *Tricholoma sulphureum*, has a distribution pattern strictly according to the element definition except for not being found higher than 250 m asl. in Norway.* [in 2003, and not included in the original set of data, the species was found at 600 m in S Norway (Aust-Agder)]. Most of the ten species in the element follow this pattern closely; the most notable exception is *Calocybe gambosa*, which is solely eastern, the species not being found in western Norway. *Calocybe gambosa*, being strictly calciphilous and showing a distinct pattern of distribution, points to the need for a refinement of the mycogeographical elements by adding an element or sub-element based on edaphic characters. Interestingly, in Sweden the species in this element show rather different distribution patterns; most species have a distribution reaching north of *Limes Norlandicus* along the eastern coast, while some species are limited to the area south of *Limes Norlandicus* (e.g. *C. gambosa* and *E. sinuatum*) or are utterly limited, restricted to the south-easternmost parts (e.g. *G. cyanescens*).

The species in the South Boreal element all show intermediate or restricted occurrence types, and correspondingly medium to high fractions of variation explained.

Table 7. *The South Boreal mycogeographical element*

Id	Taxon	N	#	%	Nutr	Occ	Explanatory variables
4	<i>Amanita pantherina</i>	138	75	47.06	m	1	GDD, Elev-RelRef, -P-Apr
10	<i>Calocybe gambosa</i>	246	88	49.60	s	1	T-Jun, GeoRich, SlopeSum, -P-Nov
19	<i>Entoloma sinuatum</i>	42	22	30.18	m	1	GDD
23	<i>Ganoderma lucidum</i>	131	95	29.71	p	2	T-May, SlopeSum, Rad-Apr
26	<i>Gyrodon lividus</i>	65	49	26.05	m	2	T-May, GeoRich, Elev-RelRef, -T-Jan
28	<i>Gyroporus cyanescens</i>	90	69	25.14	m	2	T-May, -(T-May x DistCoast)
47	<i>Lactarius volemus</i>	83	59	36.12	m	1	T-May, Evapotrans, Elev-RelRef
58	<i>Omphalina grossula</i>	21	20	35.02	s	1	T-Jun, Rad-Jan
74	<i>Sistotrema confluens</i>	114	81	28.32	s	2	T-Jun, Elev-RelRef, -(T-Jun x Elev-RelRef)
82	<i>Tricholoma sulphureum</i>	130	84	30.54	m	2	Elev-RelRef, -(P-Jun x AspUnFav)

The Mid boreal-western element (MBo-w) (Distribution maps 24-35, Appendix 6)

This element includes species that are well represented in W Norway, showing no preference for eastern parts (where most collecting has taken place), extending far northwards along the coast and to altitudes around 800 m. Many species are associated with the coniferous forests. The species of the element are limited to southern and central parts in Finland and are often rare; in Denmark they are occasional or common, and in Great Britain common, also occurring in Scotland and Ireland. The element has a

somewhat oceanic character. In continental Europe their distribution is rather variable, many species preferring montane to subalpine regions.

The example species, the mycorrhizal *Boletus badius*, associated with spruce and pine, is common both in W and E Norway, extending northwards to Nordland, and up to ca 660 m altitude in S Norway; it strictly follow the element definition. Most of the 12 species in this element have a fairly identical distribution pattern in Norway, with *Melastiza scotica* as the most western species, being rare in inland eastern area, and *Cystolepiota seminuda* as the most continental and northern, being rare in coastal areas in western Norway, but probably both species are under-sampled. A few species deviate from the defined pattern in the other countries as well; *Melastiza scotica* not being found in Finland, which makes sense compared to its western distribution in Norway, *Pleurocybella porrigens* being rare in Denmark, and *Pholiota astragalina* being very rare in Great Britain, and reaching further north in Finland. Most species in this element show a preference for the montane-subalpine regions in C Europe, one exception being *Laccaria amethystina* that is common also in lowland areas. The patterns of the species in Great Britain are divided approximately half and half between species preferring higher elevations in Scotland (e.g. *P. porrigens* and *M. scotica*) or the lowlands in England (e.g. *C. seminuda* and *L. amethystina*).

The Mid boreal-western element comprises mostly intermediate to widespread occurrence types and generally shows intermediate fractions of variation explained.

Table 8. *The Mid boreal-western mycogeographical element*

Id	Taxon	N	#	%	Nutr	Occ	Explanatory variables
8	<i>Boletus badius</i>	291	198	32.46	m	3	T-May, MisArea 53, GeoRich, Elev-RelRef, T-May x T-Des
9	<i>Boletus luridus</i>	72	50	35.84	m	2	T-Jun, GeoRich, SlopeSum, GeoRich x Mire
14	<i>Cortinarius bolaris</i>	100	77	31.74	m	2	T-May, P-Jul, MisArea 46 -47, -(T-May x DistCoast)
18	<i>Cystolepiota seminuda</i>	38	31	24.71	s	2	T-Jul, -T-Sep, Elev-RelRef, T-Jul x T-Sep
31	<i>Hygrocybe irrigata</i>	117	82	25.24	s	2	T-Mar, -Rdd100, Lastsnow, T-Mar x Lastsnow, T-Mar x T-Nov T-May, Elev-RelRef, T-Okt, MisArea 53, GeoRich, -(T-Okt x GeoRich)
40	<i>Hypholoma fasciculare</i>	212	135	32.69	s	3	GDD, -DistCoast, MisArea 14 – 26, Elev-RelRef x DistCoast
42	<i>Laccaria amethystina</i>	289	173	33.30	s	3	GDD, Elev-RelRef, GeoRich, GlacDep
45	<i>Lactarius pyrogalus</i>	134	102	29.71	m	3	GDD, Elev-RelRef, GeoRich, GlacDep
50	<i>Macrolepiota procera</i>	65	46	36.05	s	2	T-Aug, Elev-RelRef, -P-Jul, -AspUnFav
54	<i>Melastiza scotica</i>	25	20	31.83	s	1	GeoRich
61	<i>Pholiota astragalina</i>	110	88	19.77	s	3	T-May, Elev-RelRef, Snowdays MisArea 28 - 40, -AspUnFav, P-May x evapotrans, T-May x AspUnFav
65	<i>Pleurocybella porrigens</i>	289	198	32.27	s	3	T-May x AspUnFav

The Boreal – Montane element (Bo-M) (Distribution maps 36-49, Appendix 6)

The element includes south-eastern or eastern distribution types, extending northwards mostly to C Norway; some species extending northwards to Troms. They are fairly common up to 600-800 m asl and are typically coniferous forest species, mainly confined to spruce. In Finland they tend to be common throughout, in Denmark they are mostly absent or rare, and so also in Great Britain where many are on the Red List. On the continent they are most common in eastern parts and have colline-montane distributions. The example species, *Catathelasma imperiale*, has a distribution pattern strictly according to the element definition, but its occurrence in Finland is very restricted – probably reflecting its requirement for calcareous rocks. Eight of the fourteen species in the element follow this markedly eastern pattern closely, with some variation as to northern extension and maximum altitude. One species, *Hypocreopsis lichenoides* is very rare, confined to the

southernmost parts of eastern Norway and probably in the process of spreading (Eckblad 1981). *Thelephora palmata*, *Tricholoma aestuans* and *T. colossus* are found at some localities along the western fiords, presumably drier and hotter. These species all follow the standard pattern for the element by being absent, rare or occasional in Denmark, and Great Britain, and being most common in eastern parts of continental Europe. The three species *Plicaturopsis crispa*, *Hygrocybe punicea* and *Marasmius oreades* likewise deviate from the main pattern by being well represented in western parts, in fact being quite widespread in Norway. Of these *P. crispa* is rare in Denmark and England, widespread but rare in Finland and on the continent, thus following the European pattern of this element quite closely. *Marasmius oreades* is typically not found in Ireland, is also absent from the outer western coast in Norway, and reaches montane to subalpine elevations in continental Europe, but it deviates considerably from the boreal-montane pattern by being common in England and Denmark. *Hygrocybe punicea*, which almost reach the timber-line in Norway is widely distributed in Europe, mainly montane on the continent, and has a circumpolar boreal distribution. Its restricted distribution in Finland to rather southern parts, and its wide occurrences in Denmark and Great Britain, indicate that the species perhaps should be included in the Mid-boreal western element.

The Boreal – Montane element comprises great variation as to species occurrence types and shows generally intermediate fractions of variation explained.

Table 9. *The Boreal – Montane mycogeographical element*

Id	Taxon	N	#	%	Nutr	Occ	Explanatory variables
11	<i>Catathelasma imperiale</i>	88	70	24.79	m	3	T-Jun, GeoRich, MisArea 53, -P-Nov, -T-Jul
12	<i>Clavicornona pyxidata</i>	207	140	39.82	s	2	T-Jul, Rad-Oct, TRI - TerrRugg, Forest
15	<i>Cortinarius percomis</i>	58	46	24.77	m	1	T-Jun
33	<i>Hygrocybe punicea</i>	294	188	15.77	s	3	GlacDep, P-Jul
36	<i>Hygrophorus discoideus</i>	97	66	29.82	m	2	T-Jun, GeoRich, P-Apr
41	<i>Hypocreopsis lichenoides</i>	23	13	44.24	s	1	T-Jul
49	<i>Limacella guttata</i>	76	58	31.88	m	2	T-Jul, GeoRich, -P-Aug, Elev-RelRef
51	<i>Marasmius oreades</i>	231	147	34.33	p	3	T-Aug, -P-Apr, Elev-RelRef, -Forest, GeoRich, DistOcean , -(T-Aug x Elev_Rel.relieff), Elev_Rel.relieff x Forest
67	<i>Plicaturopsis crispa</i>	200	134	22.30	s	3	DistCoast, Rad-Apr, AspUnFav, DistCoast x Rad-Apr
68	<i>Pluteus leoninus</i>	27	22	29.53	s	1	T-Jun
70	<i>Pseudoplectania nigrella</i>	112	89	27.66	s	2	T-Jun, -T-Sep, Elev-RelRef
77	<i>Thelephora palmate</i>	112	90	26.02	s	3	T-Jun, -PlanCurv, Elev-RelRef
79	<i>Tricholoma aestuans</i>	82	72	18.15	m	3	T-Jun, Elev-RelRef, MarDep
80	<i>Tricholoma colossus</i>	87	59	29.43	m	2	P-Jun, -(T-May x P-Jun)

The Boreal – Subalpine element (Bo-SA) (Distribution maps 50-75, Appendix 6)

The difference between this and the previous element is slight, mainly expressed by the species extending further north and to higher elevations, some also beyond the timber-line. They are common in the whole of Finland and absent or rare in Denmark and Great Britain.

The example species, *Rozites caperatus*, is a very common species in Norway, especially in the inland, both in the boreal forests and in the montane areas, deviating from the element definition by not being rare in the western parts of the country. The 26 species in the Boreal – Subalpine element show some variation in distribution in Norway, with *Psilocybe magnivelaris* representing the most northerly distribution, *Marasmius siccus* the

most northerly and continental (inland), *Neolecta vitellina* the most southerly and *Fomitopsis rosea* the most easterly distribution. *Melanoleuca verrucipes* is so rare it is difficult to evaluate its distribution, and like *Albatrellus syringae* it is most likely antropochore and spreading (Mathiassen et al. 1999, Smith 1997). The other 19 species are generally widespread – some at the verge of being ubiquitous – and show distribution patterns similar to that of the reference species, *R. caperatus*. Looking at the distribution in Europe the picture is more uniform, with only a few deviating species: *Fomitopsis pinicola* is common in Denmark, *Microstoma protractum* is rare in Finland, but widespread; neither of them has a distribution that fits better with another element.

The species of the Boreal – Subalpine element mainly show intermediate or widespread occurrence types, and correspondingly, medium to low fractions of variation explained.

Table 10. The Boreal – Subalpine mycogeographical element

Id	Taxon	N	#	%	Nutr	Occ	Explanatory variables
2	<i>Albatrellus ovinus</i>	218	157	29.85	m	3	T-Jun, -Sea, -P-Nov, Rad-Oct
3	<i>Albatrellus syringae</i>	64	43	10.52	m	3	-Runnoff, T-Jun, -T-Aug GDD, Elev-RelRef, -Rad-Jan, MisArea 49 - 51, Evapotrans, -TRI – TerrRugg
6	<i>Amanita virosa</i>	307	212	26.69	m	3	
16	<i>Cortinarius rubellus</i>	283	187	27.86	m	3	T-May, Elev, -Curv, Forest x P-Jul T-Jun, Snowdays, -(T-Jun x MisArea 42 – 44), DistOcean x Elev-RelRef, MisArea 42 - 44 x T-Aug
21	<i>Fomitopsis pinicola</i>	687	426	23.73	p	3	Rad-Jul, DistOcean, Forest, P-Des, T-Apr, Rad-Oct, DistCoast, -(P-Des x Rad-Oct), Rad-Jul x DistCoast, -(P-Des x Rad-Oct), P-Des x DistCoast, -(GlacDep x Rad-Oct), Rad-Jul x GlacDep, SlopeTerrVarx GlacDep
22	<i>Fomitopsis rosea</i>	303	185	34.82	p	2	T-Jun, MisArea 14 - 26, -HeatIndex, -AspUnFav, Elev-RelRef, -Runnoff, Rad-Jan x Runnoff, T-Jun x Rad-Jan
24	<i>Gerronema chrysophyllum</i>	106	79	30.01	s	2	GeoRich, T-Apr, -T-Sep, -Rad - HeatIndex, -(Runnoff x GeoRich), T-Apr x Rad - HeatIndex
35	<i>Hygrophorus camarophyllus</i>	121	108	19.91	m	3	T-Jun, -P-Aug, -T-Jul
37	<i>Hygrophorus gliocyclus</i>	67	44	31.43	m	2	
38	<i>Hygrophorus karstenii</i>	88	72	11.82	m	3	T-Jun, MisArea 42 - 44, GeoRich
44	<i>Lactarius lignyotus</i>	167	124	24.80	m	3	Rad-Oct, Forest, -(Rad-Oct x Curv), -(Rad-Oct x Forest), Forest x GDD
46	<i>Lactarius repraesentaneus</i>	212	174	5.92	m	3	SlopeTerrVar, -(P-Aug x Runoff Preccorr)
52	<i>Marasmius siccus</i>	28	19	39.34	s	2	
53	<i>Melanoleuca verrucipes</i>	8	7	19.19	s	2	T-May
55	<i>Microstoma protracta</i>	71	54	22.50	s	2	-Runnoff, T-May, GeoRich, -T-Sep, -Mire
56	<i>Neolecta vitellina</i>	28	19	32.97	s	1	-T-Aug, Forest, T-Jun x T-Aug
62	<i>Pholiota flammans</i>	158	116	22.87	s	3	T-Jun, Elev-RelRef, Evapotrans
63	<i>Pholiota heteroclita</i>	56	50	6.73	p	3	T-Jul
64	<i>Phyllotopsis nidulans</i>	99	87	15.85	s	3	T-Jun, -T-Sep, MisArea 46 -47, -P-Jun, T-Ann, GeoRich x T-Ann T-Jul, Elev-RelRef, -P-Oct, MisArea 14 - 26, -Mire, -DistOcean, -GeoRich, P-Oct x DistOcean, T-Jul x P-Jan
66	<i>Plicatura nivea</i>	161	93	26.41	s	3	
71	<i>Psilocybe magnivelaris</i>	64	53	15.36	s	3	GeoRich, MarDep, -(Mire x Elev) Rad-Oct, -Runnoff, GeoRich, MisArea 42 - 44, -(Rad-Oct x MisArea 42– 44)
73	Rozites caperatus	327	264	6.08	m	3	
75	<i>Suillus flavidus</i>	142	115	10.81	m	3	T-May, -DistCoast, Forest
78	<i>Tremiscus helvelloides</i>	89	67	32.60	s	2	GeoRich, MisArea 53 T-Jul, -P-Aug, S - Slope, -MisArea 1 - 12, -(P-Aug x MisArea 1 – 12), -(P-Aug x S – Slope)
81	<i>Tricholoma nauseosum</i>	30	24	37.28	m	2	
83	<i>Tubaria confragosa</i>	104	85	11.89	s	3	GeoRich, Forest, Elev x Elev-RelRef

The Arctic – Alpine element (A-A) (Distribution maps 76-78, Appendix 6)

This element includes species distributed in alpine and subarctic parts of Norway and with occasional finds on the West coast. In Finland they have an alpine-subarctic distribution, in Denmark they are absent or rare, and in Great Britain they tend to be present in Scotland only. The species are also common in the North Atlantic islands and in the Arctic. On the continent they occur in alpine regions and occasionally at sea level on north-western coasts.

The example species for the Arctic-Alpine element, *Omphalina alpina*, has a distribution pattern well in accordance with the element definition. Of the two other species, *Omphalina hudsoniana* differs in being extremely rare on Svalbard, lacking on Iceland and in being found more often in lowland areas, including Denmark. *Hygrocybe citrinopallida* is a seemingly very rare species in Norway, found scattered in arctic and alpine habitats on the mainland and on Svalbard. It generally seems to follow the typical distribution for the element, but with a fairly wide distribution in Great Britain, being recorded in Wales, northern Ireland, and England in addition to Scotland.

The three species in the Arctic – Alpine element are all widespread or scattered and show a low fraction of variation explained by the GLM models.

Table 11. *The Arctic – Alpine mycogeographical element*

Id	Taxon	N	#	%	Nutr	Occ	Explanatory variables
30	<i>Hygrocybe citrinopallida</i>	14	13	3.02	s	3	-T-Jul *(p<0,05)
57	<i>Omphalina alpina</i>	143	120	7.50	m	3	-T-Jun, GS, -P-Mar
59	<i>Omphalina hudsoniana</i>	181	130	11.19	m	3	-T-May, T-Sep, -P-Nov, P-May, -(T-May x P-May)

The Ubiquitous group (Ubi) (Distribution maps 79-83, Appendix 6)

This group is strictly speaking not a mycogeographical element. The five species assigned to the ubiquitous group are all widespread, with distribution patterns according to their substrate requirements. The saprotrophic example species *Agaricus campestris* is distributed all over Norway from sea level to 1300m asl.

All species in the group are by definition widespread, and with the exception of *Tapinella atrotomentosa*, that is restricted by its substrate being decaying coniferous roots and stumps, they have a low fraction of variation explained by the GLM models.

Table 12. *The Ubiquitous group*

Id	Taxon	N	#	%	Nutr	Occ	Explanatory variables
1	<i>Agaricus campestris</i>	175	139	5.05	s	3	-Runnoff, GeoRich, -AspUnFav, MarDep
32	<i>Hygrocybe nitrata</i>	177	108	14.63	s	3	Elev-RelRef, T-May, -T-Jun, -T-Sep, Lastsnow
43	<i>Lactarius hygginus</i>	153	121	10.30	m	3	T-Jun, GeoRich, MisArea 53
60	<i>Phaeolus schweinitzii</i>	131	96	20.61	s	3	GDD, Elev-RelRef, -P-May, -AspUnFav
76	<i>Tapinella atrotomentosa</i>	300	211	32.31	s	3	T-Jun, Elev-RelRef, Rad-Oct, -(Elev-RelRef x PlanCurv)

GLM models for the example species

Porphyrellus porphyrosporus (Atl)

The presence of *Porphyrellus porphyrosporus*, the example species for the Atlantic mycogeographical element, is determined primarily by annual mean temperature (*T-Ann*) and October radiation (*Rad-Oct*, Table 13A). The negative correlation with October temperature is merely a correction term, modifying the influence of *T-Ann*, due to forward selection.

Looking at the distribution map (Tab. 1), *P. porphyrosporus* is confined to areas with warm summers and mild winters. Ecological references point out its association with *Fagus sylvatica*, a nemoral species. The species is in the cluster showing high loadings along axes 1 in the PCA plot, close to *T-Ann* (Fig. 8), confirming the general importance of temperature and *T-Ann*. A fraction of variation explained of 27.86%, close to the average 27.65%, is not impressive, but given the ecologically meaningful GLM result is considered a good indication that the model is realistic. Winter temperatures, which generally are supposed to be highly indicative of Atlantic patterns, are not especially indicated by the GLM modelling, but probably contribute generously to *T-Ann*.

Amanita phalloides (Ne-Bne)

The GLM model predicts the presence of *Amanita phalloides* when temperatures in May (*T-May*) are high, when there is a high degree of differences of elevation in the area (*Elev-RelRef*), the distance to the sea (*DistCoast*) is short, and there is high radiation in October (*Rad-Oct*) (Table 13 B). This corresponds well with the distribution map of the species (Tab. 1) with regard to *T-May*, *DistCoast* and *Rad-Oct*, and also for the less obvious *Elev-RelRef*, which is necessarily high for coastal areas, especially along the West coast and in the inner fjord area with its steep elevation gradient. The importance of *Elev-RelRef* is presumably indirect, by heightening the values of variables of physiological importance to the species, like the temperature- and temperature-related variables *T-May* and *Rad-Oct*. The negative correlation with the combined effect *T-May* x *Elev-RelRef* is a correction term due to forward selection, moderating the positive correlation with the two variables on their own. *Amanita phalloides* is associated with *Fagus* and *Quercus*, and has a Nemoral center of distribution in Europe, but in Norway it is also found also in the Boreonemoral zone. It does not follow *Quercus* to its northern limit of distribution in Norway though, indicating that its northward distribution is temperature limited. The northern global limit of distribution of *A. phalloides* is in the inner fjord areas on the Norwegian West coast (Brandrud et al. 2000), generally explained by the special climatic conditions; a long growing season due to the oceanic influence, and high summer temperatures due to the almost continental summer conditions in the innermost fjord areas (Gulden et al. 2001).

References to its ecology and distribution supports the GLM model for the species, and with a high a fraction of variation explained (41.57%), the model probably gives a good prediction on the presence probability of *A. phalloides*.

Tricholoma sulphureum (S-Bo)

A high degree of elevation differences in the area (*Elev-RelRef*) and nothing/little of the combined effect of precipitation in June and an unfavorable aspect - (*P-Jun* x *AspUnFav*), are the main variables determining presence probability for *Tricholoma sulphureum* according to the GLM model (Table 13 C). The variable *AspUnFav* records the deviation from SW inclination – meaning that a species with a negative value for this variable actually is positively correlated with a presumably favorable aspect facing SW; in the case

of *T. sulphureum* it shuns NE-facing slopes with precipitation in June. *Tricholoma sulphureum* is mainly known from deciduous forests in calcareous areas in Norway. The distribution map and the altitude-latitude diagram of *T. sulphureum* (Table 1) show a species confined to low altitude in southern and western Norway, areas with a moderate to very steep altitudinal gradient, thus giving plenty of areas with a generally high degree of differences of elevation and a favorable aspect. This though, is no causal effect, but the assumption that *Elev-RelRef* and $-(P-Jun \times AspUnFav)$ influence the physiologically decisive ground humidity and temperature in a way positive for a species with a southerly, presumably temperature limited distribution often prevailing in calcareous areas is possible. The effect might also be indirect through the deciduous trees, the mycorrhizal partners of *T. sulphureum* needing a high sum of Growing Degree Days (*GDD*) (or some other temperature-related variable) most often found in the lower parts of southern and western Norway, but not attainable in NE-facing slopes. A fraction of variation explained at a moderate 30.54 % is not a strong support for a model this obscure. The model is good argument for including more, ecologically meaningful variables, notably edaphic factors and the distribution of the relevant species of trees.

Boletus badius (MBo-w)

The GLM model yields high probabilities of presence of *Boletus badius* when temperatures in May (*T-May*) are high and there is a high degree of elevational relief in the area (*Elev-RelRef*). The ‘grid-square-bias’ variable *MissArea53* indicates that the variable *GeoRich* (nr 53) is wrongly included and the combined effect of temperatures in May and in December ($T-May \times T-Dec$) is a correction term for *T-May* (Table 13 D). *Boletus badius* is found in the southern half of Norway, and high temperatures in May will be prevalent in the coastal range of its distribution, but the species is also common inland and found to an altitude of approximately 800 meters. With a distribution in Norway spanning steep coastal areas to flat inland areas, the level of *Elev-RelRef* will vary throughout its range. *Boletus badius* is common in coniferous forests, rare in deciduous forests and grows mainly on acid soil. It is reasonable for a species restricted to the southern half of Norway to be predicted by high temperatures in May, but apart from that the model does not give any good predictions. The moderate (30.54%) fraction of variation explained is not a strong support for the model.

Catathelasma imperiale (Bo-M)

The ‘grid-square-bias’ variable *MissArea53* indicates that values for the variable *GeoRich* (nr 53) is missing in some grid squares with the species registered is probably a ‘borderline effect’, caused by some of the squares with *Catathelasma imperiale* being cut by the Swedish border. Excluding this variable and comfortably accepting *GeoRich* in the model, knowing the species to be calciphilous, leaves *Catathelasma imperiale* to be predicted by high temperatures in June and little precipitation in November according to the GLM model (Table 13 E). High temperatures in June being positive for this eastern, slightly continental species makes sense, likewise a dry November, implying a clear sky with higher radiation and thus higher soil temperatures prolonging the growing season. Assuming the correlation with *GeoRich* is caused by the species’ affinity to category 4 (the richest) of this variable, we end up with an ecologically reasonable model for predicting presence probability for *Catathelasma imperiale*, but with a moderately low fraction of variation explained.

Rozites caperatus (Bo-SA), *Omphalina alpina* (A-A), *Agaricus campestris* (Ubi)

With fractions of variation explained of 6.08 %, 7.50 % and 5.05 %, respectively, a discussion of the GLM model versus the species' known distributions and ecology would be nonsense (for *Rozites caperata* (Table 13 F), *Omphalina alpina* (Table 13 G) and *Agaricus campestris* (Table 13 H)). Seemingly meaningful as well as absurd correlations may appear at random. See above (The explanatory power of the GLM models) for a discussion on fractions of variation explained.

Table 13 A – H. Species models from the GLM for the example species for the respective mycogeographical elements. All other species GLM models are found in 'Online material 4'.

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 ('p < 0.01 used as criteria for inclusion in species models and for further calculations). Significant variables in bold.

A: (Id. 69) Porphyrellus porphyrosporus (Atl):			
Coefficients (first first):	Estimate	Pr(> z)	Signif. codes
(Intercept)	-1.850e+01	1.55e-06	***
T-Ann	4.113e+00	7.25e-08	***
T-Octt	-2.497e+00	0.000106	***
Rad-Oct	4.701e-03	1.89e-06	***
Lastsnow	2.205e-02	0.390333	
TRI	-4.417e-02	0.058867	.
Lastsnow x TRI	5.432e-04	0.010938	*
Null deviance:	681.40 on 14971 df		
Residual deviance:	491.55 on 14965 df		
AIC:	505.55		
Fraction of variation explained:	27.86		
B: (Id. 5) Amanita phalloides (Ne-Bne):			
Coefficients:	Estimate	Pr(> z)	Signif. codes
(Intercept)	-2.471e+01	< 2e-16	***
T-May	1.456e+00	9.58e-09	***
Elev-RelRef	8.911e-03	2.58e-08	***
DistCoast	-1.844e-04	2.09e-05	***
Rad-Oct	6.674e-03	1.74e-06	***
T-May x Elev-RelRef	-6.905e-04	8.25e-05	***
Null deviance:	933.49 on 14971 df		
Residual deviance:	545.47 on 14966 df		
AIC:	557.47		
Fraction of variation explained:	41.57		

C: (Id. 82) Tricholoma sulphureum (S-Bo):

Coefficients:	Estimate	Pr(> z)	Signif. codes
(Intercept)	-8.977e+00	0.00382	**
GDD	3.424e-03	0.03099	*
P-Jun	-1.570e-02	0.75489	
Elev-RelRef	3.615e-03	< 2e-16	***
AspUnFav	5.368e-02	0.08538	.
P-Jun x AspUnFav	-1.436e-03	0.00549	**
GDD x P-Jun	6.163e-05	0.02755	*
Null deviance:	1027.93 on 14971 df		
Residual deviance:	731.95 on 14965 df		
AIC:	745.95		
Fraction of variation explained:	30.54		

D: (Id: 8) Boletus badius (MBo-w):

Coefficients:	Estimate	Pr(> z)	Signif. codes
(Intercept)	-2.192e+01	< 2e-16	***
T-May	1.864e+00	5.07e-12	***
MisArea 53	2.967e-07	0.00680	**
T-Des	-3.171e-01	0.03853	*
GeoRich	4.064e-01	4.85e-05	***
Elev-RelRef	1.399e-03	0.00124	**
T-May x T-Des	5.494e-02	0.00183	**
T-May x MisArea 53	-2.396e-08	0.03603	*
Null deviance:	2097.7 on 14971 df		
Residual deviance:	1437.8 on 14964 df		
AIC:	1453.8		
Fraction of variation explained:	32.46		

E: (Id. 11) Catathelasma imperiale (Bo-M):

Coefficients:	Estimate	Pr(> z)	Signif. codes
(Intercept)	-8.508e+00	6.72e-05	***
T-Jun	2.477e+00	1.27e-07	***
GeoRich	9.007e-01	8.36e-10	***
MisArea 53	8.947e-08	0.00222	**
T-Aug	-3.675e-01	0.50786	
P-Nov	-1.147e-02	0.00101	**
T-Jul	-1.740e+00	0.00305	**
Null deviance:	880.10 on 14971 df		
Residual deviance:	661.92 on 14965 df		
AIC:	675.92		
Fraction of variation explained:	24.79		

F: (Id. 73) Rozites caperatus (Bo-SA):

Coefficients:	Estimate	Pr(> z)	Signif. codes
(Intercept)	-1.051e+01	3.89e-12	***
Rad-Oct	6.066e-03	4.09e-05	***
Runoff	-6.551e-04	2.43e-08	***
GeoRich	3.131e-01	0.000172	***
MisArea 42 - 44	1.994e-07	0.001007	**
Rad-Oct x MisArea 42 - 44	-1.687e-10	0.005003	**
Null deviance:	2615.1 on 14971 df		
Residual deviance:	2456.1 on 14966 df		
AIC:	2468.1		
Fraction of variation explained:	6.08		

G: (Id. 57) Omphalina alpina (A-A):

Coefficients:	Estimate	Pr(> z)	Signif. codes
(Intercept)	-1.9313299	0.000375	***
T-Jun	-1.0404820	3.10e-13	***
Elev	-0.0006085	0.069103	.
GS	0.0522729	1.26e-07	***
P-Mar	-0.0144368	5.56e-06	***
Null deviance:	1397.4 on 14971 df		
Residual deviance:	1292.6 on 14967 df		
AIC:	1302.6		
Fraction of variation explained:	7.5		

H: (Id: 1) Agaricus campestris (Ubi):

Coefficients:	Estimate	Pr(> z)	Signif. codes
(Intercept)	-4.4747407	2.58e-09	***
Runoff	-0.0007092	2.40e-05	***
GeoRich	0.5310910	7.99e-07	***
AspUnFav	-0.0158913	0.007211	**
MarDep	0.0007460	0.000516	***
Rad-Oct	0.0007845	0.039886	*
Null deviance:	1549.5 on 14971 df		
Residual deviance:	1471.2 on 14966 df		
AIC:	1483.2		
Fraction of variation explained:	5.05		

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APPENDICES

Appendix 1. Taxa with author names according to the Mycological Herbarium in Oslo (O)
<http://www.nhm.uio.no/botanisk/sopp/index.html>. Authors are cited according to Kirk and Ansell 1992. "Abbrev" refers to the abbreviated form used in **figures 6** and **appendix 3**.

Taxon with author name	Abbrev	Taxon with author name	Abbrev
<i>Agaricus campestris</i> L. : Fr.	AgCam	<i>Laccaria amethystina</i> Cooke	LacAm
<i>Albatrellus ovinus</i> (Schaeff. ex Fr.) Kotl. & Pouzar	AlbOv	<i>Lactarius hygginus</i> (Fr. : Fr.) Fr.	LactHys
<i>Albatrellus syringae</i> (Parmasto) Pouzar	AlbSy	<i>Lactarius lignyotus</i> Fr.	LactLign
<i>Amanita pantherina</i> (DC. : Fr.) Krombh.	AmPan	<i>Lactarius pyrogalus</i> (Bull. : Fr.) Fr.	LactPyr
<i>Amanita phalloides</i> (Vaill. : Fr.) Link	AmPhal	<i>Lactarius repraesentaneus</i> Britzelm.	LactRep
<i>Amanita virosa</i> (Fr.) Bertillon	AmVir	<i>Lactarius volemus</i> (Fr. : Fr.) Fr.	LactVol
<i>Auricularia mesenterica</i> (Dicks. : Fr.) Pers.	AurMes	<i>Leccinum pseudoscabrum</i> (Kallenb.) Sutara	LecPse
<i>Boletus badius</i> (Fr.) Fr.	BoBad	<i>Limacella guttata</i> (Pers. : Fr.) Konrad & Maubl.	LimGut
<i>Boletus luridus</i> Schaeff. : Fr.	BoLur	<i>Macrolepiota procera</i> (Scop. : Fr.) Sing.	MacPro
<i>Calocybe gambosa</i> (Fr.) Donk	CalGam	<i>Marasmius oreades</i> (Bolton : Fr.) Fr.	MarOr
<i>Catathelasma imperiale</i> (Fr.) Sing.	CatImp	<i>Marasmius siccus</i> (Schwein. : Fr.) Fr.	MarSic
<i>Clavicornia pyxidata</i> (Pers. : Fr.) Doty	ClavPyx	<i>Melanoleuca verrucipes</i> (Fr. in Qué.) Singer	MelanVer
<i>Collybia fusipes</i> (Bull. : Fr.) Qué.	ColFus	<i>Melastiza scotica</i> Graddon	MelastScot
<i>Cortinarius bolaris</i> (Pers. : Fr.) Fr.	CortBol	<i>Microstoma protracta</i> (Fr.) Kanouse	MicProt
<i>Cortinarius percomis</i> Fr.	CortPerc	<i>Neolecta vitellina</i> (Bres.) Korf & J. K. Rogers	NeoVit
<i>Cortinarius rubellus</i> Cooke	CortRubel	<i>Omphalina alpina</i> (Britzelm.) Bresinsky & Stangl	OmphAlp
<i>Cortinarius rubicundulus</i> (Rea) A. Pers.	CortRubic	<i>Omphalina grossula</i> (Pers.) Singer	OmphGro
<i>Cystolepiota seminuda</i> (Lasch) Bon	CystSem	<i>Omphalina hudsoniana</i> (H.S. Jenn.) H.E. Bigelow	OmphHud
<i>Entoloma sinuatum</i> (Pers.:Fr.) P. Kumm.	EntSin	<i>Phaeolus schweinitzii</i> (Fr.) Pat.	PhaeSch
<i>Fistulina hepatica</i> (Schaeff. : Fr.) With.	FistHep	<i>Pholiota astragalina</i> (Fr.) Singer	PholAst
<i>Fomitopsis pinicola</i> (Sw. : Fr.) P. Karst.	FomPin	<i>Pholiota flammans</i> (Batsch : Fr.) P. Kumm.	PholFlam
<i>Fomitopsis rosea</i> (Alb. & Schwein. : Fr.) P. Karst.	FomRos	<i>Pholiota heteroclita</i> (Fr. : Fr.) Qué.	PholHet
<i>Ganoderma lucidum</i> (Curtis : Fr.) P. Karst.	GanLuc	<i>Phyllotopsis nidulans</i> (Pers. : Fr.) Singer	PhylNid
<i>Gerronema chrysophyllum</i> (Fr.) Singer	GerChry	<i>Pleurocybella porrigens</i> (Pers. : Fr.) Singer	PleurPor
<i>Gymnopilus junonius</i> (Fr. : Fr.) P.D. Orton	GymJun	<i>Plicatura nivea</i> (Sommerf. : Fr.) P. Karst.	PlicANiv
<i>Gyrodon lividus</i> (Bull. : Fr.) Sacc.	GyrodLiv	<i>Plicaturopsis crispa</i> (Pers. : Fr.) D.A. Reid	PlicOCris
<i>Gyroporus castaneus</i> (Bull. : Fr.) Qué.	GyropCast	<i>Pluteus leoninus</i> (Schaeff. : Fr.) P. Kumm.	PlutLeo
<i>Gyroporus cyanescens</i> (Bull. : Fr.) Qué.	GyropCya	<i>Porphyrellus porphyrosporus</i> (Fr. & Hök) E. J. Gilbert	PorphPor
<i>Holwaya mucida</i> (Schulzer) Korf & Abawi	HolMuc	<i>Pseudoplectania nigrella</i> (Pers. : Fr.) Fuckel	PseudNig
<i>Hygrocybe citrinopallida</i> (A. H. Sm. & Hesler) Kobayasi	HygCCit	<i>Psilocybe magnivelaris</i> (Peck) Høil.	PsilMag
<i>Hygrocybe irrigata</i> (Pers. : Fr.) Bon	HygCirr	<i>Pulcherricium caeruleum</i> (Lam.) Parmasto	PulCae
<i>Hygrocybe nitrata</i> (Pers.:Fr.) Wünsche	HygCNit	<i>Rozites caperatus</i> (Pers. : Fr.) P. Karst.	RozCap
<i>Hygrocybe punicea</i> (Fr.) P. Kumm.	HygCPun	<i>Sistotrema confluens</i> Pers.	SistCon
<i>Hygrocybe vitellina</i> (Fr.) P. Karst. (sensu Boertmann)	HygCVit	<i>Suillus flavidus</i> (Fr. : Fr.) J. Presl	SuFlav
<i>Hygrophorus camarophyllum</i> (Alb. & Schw. : Fr.) Dumée, Grandjean & Maire	HygPCam	<i>Tapinella atrotomentosa</i> (Batsch : Fr.) Sutara	TapAtr
<i>Hygrophorus discoideus</i> (Pers. : Fr.) Fr.	HygPDisc	<i>Thelephora palmate</i> Scop. : Fr.	ThelPalm
<i>Hygrophorus gliocyclus</i> Fr.	HygPGli	<i>Tremiscus helvelloides</i> (DC. : Fr.) Donk	TremHel
<i>Hygrophorus karstenii</i> Sacc. & Cub.	HygPKar	<i>Tricholoma aestuans</i> (Fr.) Gillet	TricAest
<i>Hygrophorus russula</i> (Schaeff. : Fr.) Qué.	HygPRus	<i>Tricholoma colossus</i> (Fr.) Qué.	TricCol
<i>Hypholoma fasciculare</i> (Huds. : Fr.) P. Kumm.	HyphFasc	<i>Tricholoma nauseosum</i> (A. Blytt) Kytöv.	TricNaus
<i>Hypocreopsis lichenoides</i> (Tode. ex Fr.) Seaver *	HypoLich	<i>Tricholoma sulphureum</i> (Bull. : Fr.) P. Kumm.	TricSul
		<i>Tubaria confragosa</i> (Fr.) Harmaja	TubCon

Appendix 2. References on material used for estimating the species distributions

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Appendix 3. Explanatory variables; Calculations and References

Id: Identification number for the explanatory variables, used in ordination analysis (PCA). **Abbreviation:** Short version of explanatory variables name. **Explanation / Calculation and Reference** gives a simple description of the calculations behind the variable values and the reference for the background material, formulas or variable values, respectively. Shading/hone mark variables calculated from the same raw material, map, program etc.

Id	Abbreviation	Calculation / Explanation	Reference
1	Elev	Calculated from the "100 meter resolution digital elevation model" (DEM) from the National Map Authorities: mean in each grid square	Statens kartverk (the National Map Authorities)
2	Elev – RelRef	"range", the difference between maximum and minimum elevation in each grid square	
3	Slope	calculated as the maximum elevation difference from a target cell to any of its neighbouring squares	
4	SlopeSum	sum of all slope values in each grid squares (an expression of <i>terrain diversity</i>)	
5	SlopeTerrVar	Standard deviation of slope in each grid square (an expression of <i>terrain variability</i>)	
6	TRI – TerrRugg	Calculated by the standard procedure in ArcView GIS 9.0 (ESRI 2005)	ESRI, 2005
7	TRI – TerrRuggSum		
8	PlanCurv	Calculated by standard option in ArcView Spatial Analyst 2.0 (ESRI 1999). (The Curvature request calculates the curvature of a surface at each cell center, and optionally, the slope and aspect)	ESRI, 1999
9	ProfileCurv		
10	Curv		
11	Rad – HeatInd	Calculated by the following formulae: $\tan(\text{slope}) \times \cos(\text{aspect})$	Bakkestuen, V., Stabbetorp, O.E., Erikstad, L. & Eilertsen, O. (In press.). Vegetation composition, gradients and environment relationships of birch forest in six monitoring reference areas in Norway. – Sommerfeltia 31.
12	AspUnFav	Expressed as deviation from SSW (225gradians/202,5grades)	Økland, T., 1996. Vegetation-environment relationships of boreal spruce forest in ten monitoring reference areas in Norway. – Sommerfeltia 22: 1-349.
13	MisArea 1 – 12		
14	P-Ann		Tveito, O. E., Førland, E. J., Dahlström, B., Elomaa, E., Frich, P., Hanssen-Bauer, I.,
15	P-Jan		Jónsson, T., Madsen, H., Perälä, J., Rissanen P. and Vedin, H., 1997. Nordic
16	P-Feb		precipitation maps. – DNMI-Report 22/97 KLIMA, 22 pp.
17	P-Mar		
18	P-Apr		
19	P-May		
20	P-Jun		

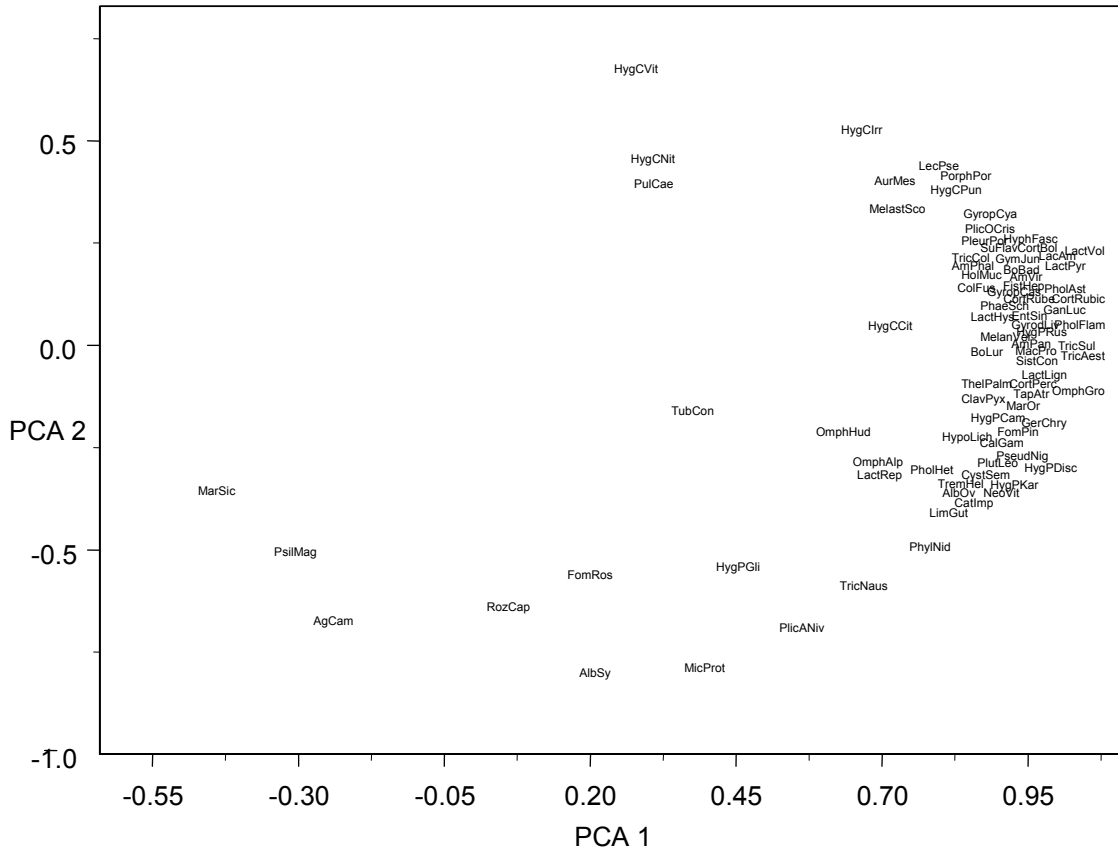
Id	Abbreviation	Calculation / Explanation	Reference
21	P-Jul		Tveito, O. E., Førland, E. J., Dahlström, B., Elomaa, E., Frich, P., Hanssen-Bauer, I., Jónsson, T., Madsen, H., Perälä, J., Rissanen P. and Vedin, H., 1997: Nordic precipitation maps. – DNMI-Report 22/97 KLIMA, 22 pp.
22	P-Aug		
23	P-Sep		
24	P-Oct		
25	P-Nov		
26	P-Des		
27	MisArea 14 – 26		
28	T-Ann		Tveito, O. E., Førland, E. J., Heino, R., Hanssen-Bauer, I., Alexandersson, H., Dahlström, B., Drebb, A., Kern-Hansen, C., Jónsson, T., Vaarby Laursen, E. and Westman, Y., 2000: Nordic temperature maps. – DNMI Report 09/00 Klima: 1-55.
29	T-Jan		
30	T-Feb		
31	T-Mar		
32	T-Apr		
33	T-May		
34	T-Jun		
35	T-Jul		
36	T-Aug		
37	T-Sep		
38	T-Oct		
39	T-Nov		
40	T-Des		
41	MisArea 28 – 40		
42	Evapotrans		Beldring, S., Roald, L. A. & Voksø, A., 2002. Avrenningskart for Norge.
43	Runoff		Årsmiddelværdier for avrenning 1961-1990. – NVE-Dokument 2-2002. 49 pp.
44	Runoff Precorr		
45	MisArea 42 – 44		
46	GS		Skaugen, T. E. and Tveito, O. E., 2002: Growing degree-days – Present conditions and scenario for the period 2021-2050. – DNMI-rapport Klima 2002 2: 1-54.
47	GDD		
48	MisArea 46 – 47		
49	Rdd100		Tveito, O. E., Førland, E. J., Alexandersson, H., Drebb, A., Jónsson, T. and Vaarby - Laursen, E., 2001: Nordic climate maps – DNMI-Report 06/01 KLIMA, 29 pp.
50	Rdd010		
51	Rdd001		

Id	Abbreviation	Explanation / Calculation	Reference
52	MisArea 49 – 51		
53	GeoRich	Calculated from the geology richness map (Sigmond 1985), classified in to 4 classes with increasing importance of nutrient availability to biota	Sigmond, E. M. O., 1985: Brukenveiledning til Berggrunnskart over Norge. Nasjonalatlas for Norge. – Statens kartverk, Hønefoss. 1-64. (in Norwegian)
54	MisArea 53		
55	Snowdays		Bjørnbæk, G., 1993: Snø 1:7 mill. Det norske meteorologiske institutt. Nasjonalatlas for Norge. Kartblad 3.1.4. – Statens kartverk, Hønefoss. (in Norwegian).
56	Lastsnow		
57	Rad-Jan		Aune, B., 1993a: Klima. Nasjonalatlas for Norge. – Statens kartverk, Hønefoss. 1-64. (in Norwegian)
58	Rad-Apr		
59	Rad-Jul		
60	Rad-Oct		
61	MisArea 55 – 60		
62	DistCoast	Measurements based on the digital map series N250 (1:250 000) from the National Map Authorities:	Statens kartverk (the National Map Authorities)
63	DistOcean	distance from the sea distance from the open ocean (from the outer edge of the continental shelf)	
64	Conrad	$k = \frac{1.7A}{\sin(\phi + 10^\circ)} - 14,$ where A is the difference between the mean temperature (°C) of the warmest and coldest months and ϕ is the latitude of the place in question. The continentality index of Conrad entered further analysis as sample square mean	Conrad, V., 1946: Methods in Climatology – Harvard University Press, 296–300.
65	MisArea 64		
66	MarDep	Calculated from National Atlas of Norway 2: Landforms, bedrock and surficial deposit	Solliid and Torp, 1984
67	Sea	Amount is based on the digital map series N50 from the National Map Authorities	Statens kartverk (the National Map Authorities)
68	Lake		
69	River		
70	Glacier		
71	GlacDep	Calculated from National Atlas of Norway 2: Landforms, bedrock and surficial deposit	Solliid and Torp, 1984
72	Mire	Amount is based on the digital map series N50 from the National Map Authorities	Statens kartverk (the National Map Authorities)
73	Forest		
74	AvailDep	Calculate from National Atlas of Norway 2: Landforms, bedrock and surficial deposit	Solliid and Torp, 1984
75	S – Slope	Calculated from the '100 meter resolution digital elevation model' (DEM) from the National Map Authorities	Statens kartverk (the National Map Authorities)

Appendix 4. PCA ordination of the 'species/explanatory variables F value matrix'. (A) Diagram of PCA axes 1 and 2. (B) Diagram of PCA axes 2 and 3. (C) Coordinates for all species along axes PC1, PC2 and PC3

A. Diagram PC1 and PC2

Nr, species name and coordinates below.



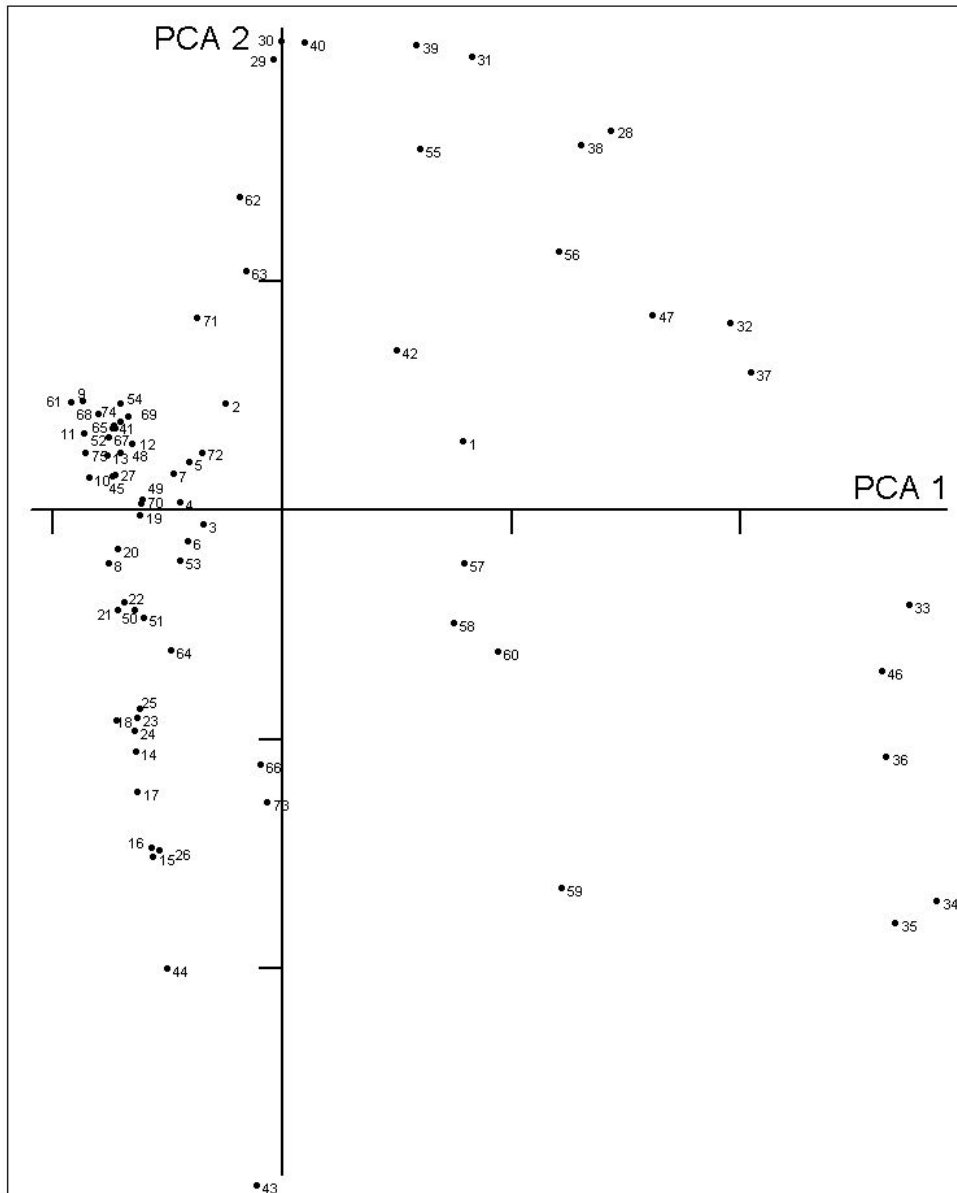
C. Coordinates for all species along PC1, PC2 and PC3

Id	Explanatory variabel	PC1	PC2	PC3	Id	Explanatory variabel	PC1	PC2	PC3
	Elev	0.79	0.30	-0.19	39	T-Nov	0.59	2.03	0.93
2	Elev-RelRef	-0.24	0.46	-1.05	40	T-Des	0.1	2.04	1.02
3	Slope	-0.34	-0.06	-1.07	41	AreaProp 28-40	-0.73	0.37	-0.66
4	SlopeSum	-0.44	0.03	-0.90	42	Evapotrans	0.5	0.70	0.00
5	SlopeTerrVar	-0.41	0.21	-0.84	43	Runoff	-0.11	-2.94	0.71
6	TRI - TerrRugg	-0.41	-0.13	-0.99	44	Runoff Precorr	-0.5	-2.00	1.24
7	TRI - TerrRuggSum	-0.47	0.16	-0.78	45	AreaProp 42-44	-0.73	0.15	-0.88
8	PlanCurv	-0.75	-0.23	-0.79	46	GS	2.62	-0.70	-0.02
9	ProfileCurv	-0.86	0.47	-0.86	47	GDD	1.62	0.85	0.64
10	Curv	-0.84	0.14	-0.83	48	AreaProp 46-47	-0.7	0.25	-0.75
11	Rad - HeatInd	-0.86	0.34	-0.74	49	Rdd100	-0.6	0.05	1.51
12	AspUnFav	-0.65	0.29	-0.75	50	Rdd010	-0.64	-0.44	0.19
13	AreaProp 1-12	-0.76	0.24	-0.69	51	Rdd001	-0.6	-0.47	-0.72
14	P-Ann	-0.64	-1.05	1.76	52	AreaProp 49-51	-0.7	0.38	-0.67
15	P-Jan	-0.56	-1.51	1.20	53	GeoRich	-0.44	-0.22	0.45
16	P-Feb	-0.57	-1.47	0.83	54	AreaProp 53	-0.7	0.47	-0.77
17	P-Mar	-0.63	-1.23	1.52	55	Snowdays	0.6	1.57	1.03
18	P-Apr	-0.72	-0.91	1.52	56	Lastsnow	1.21	1.13	0.60
19	P-May	-0.61	-0.02	1.40	57	Rad-Jan	0.8	-0.23	-1.68
20	P-Jun	-0.72	-0.17	1.08	58	Rad-Apr	0.75	-0.49	-1.69
21	P-Jul	-0.71	-0.43	1.39	59	Rad-Jul	1.22	-1.65	-2.39
22	P-Aug	-0.69	-0.40	1.78	60	Rad-Oct	0.94	-0.62	-1.91
23	P-Sep	-0.63	-0.90	1.88	61	AreaProp 55-60	-0.92	0.47	-0.96
24	P-Oct	-0.64	-0.96	1.57	62	DistCoast	-0.18	1.37	-0.08
25	P-Nov	-0.62	-0.86	1.71	63	DistOcean	-0.15	1.04	-0.17
26	P-Des	-0.53	-1.48	1.25	64	Conrad	-0.48	-0.61	-0.24
27	AreaProp 14-26	-0.72	0.15	-0.84	65	AreaProp 64	-0.73	0.36	-0.69
28	T-Ann	1.44	1.66	0.97	66	MarDep	-0.09	-1.11	-0.07
29	T-Jan	-0.04	1.97	0.98	67	Sea	-0.75	0.32	-0.74
30	T-Feb	0	2.04	1.00	68	Lake	-0.8	0.42	-0.66
31	T-Mar	0.83	1.98	1.11	69	River	-0.67	0.41	-0.64
32	T-Apr	1.96	0.82	0.80	70	Glacier	-0.61	0.03	-0.68
33	T-May	2.74	-0.41	0.42	71	GlacDep	-0.37	0.84	-0.64
34	T-Jun	2.86	-1.70	-0.25	72	Mire	-0.35	0.25	-0.21
35	T-Jul	2.68	-1.80	-0.59	73	Forest	-0.06	-1.27	-1.23
36	T-Aug	2.64	-1.08	-0.28	74	AvalDep	-0.72	0.36	-0.95
37	T-Sep	2.05	0.60	0.24	75	S - Slope	-0.85	0.25	-0.97
38	T-Oct	1.31	1.59	0.85					

Appendix 5. PCA ordination of the 'species/explanatory variables *F*-value matrix', showing explanatory variables. **(A)** Diagram of PCA axes 1 and 2. **(B)** diagram of PCA axes 2 and 3. **(C)** Coordinates for all explanatory variables along PC1, PC2 and PC3.

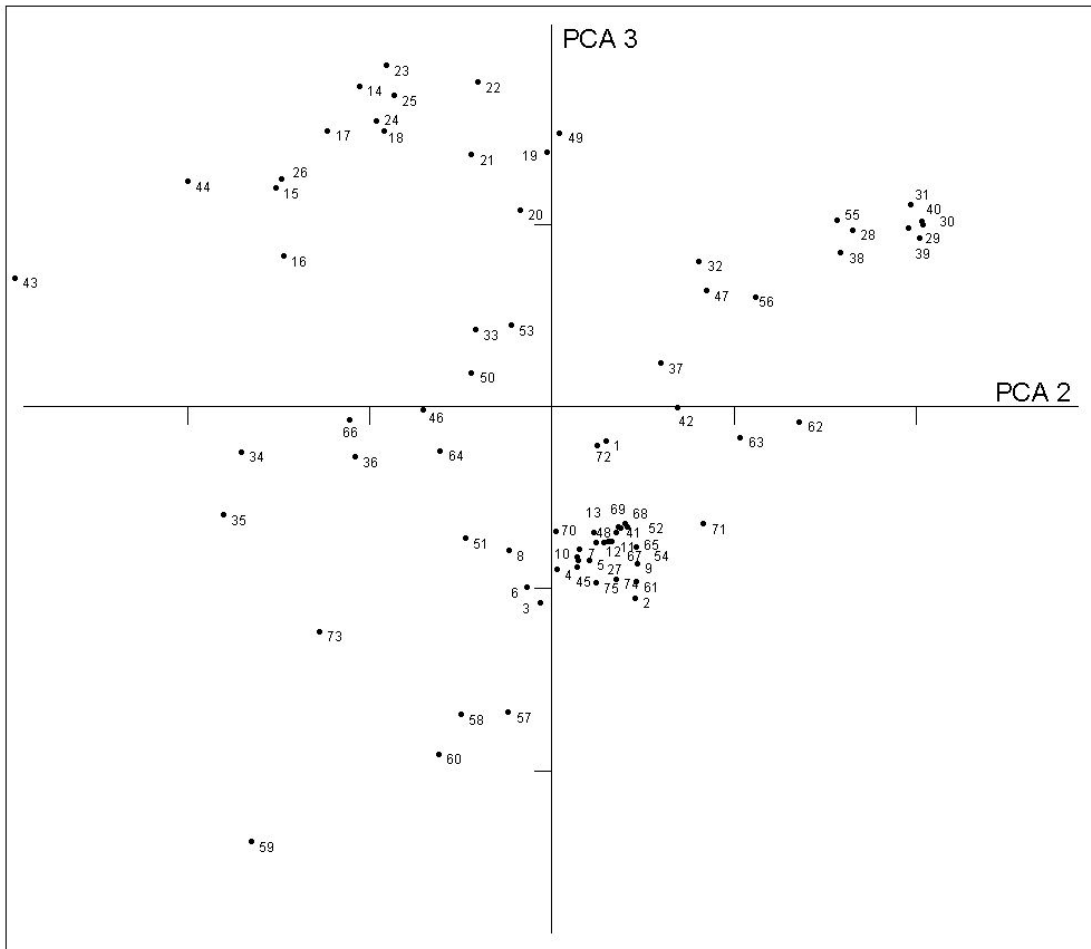
A. Diagram of PC1 and PC2

Conjugated vectors are not shown. Nr, variable name and coordinates below.



B. Diagram of PC2 and PC3

Conjugated vectors are not shown. Nr, variable name and coordinates below.

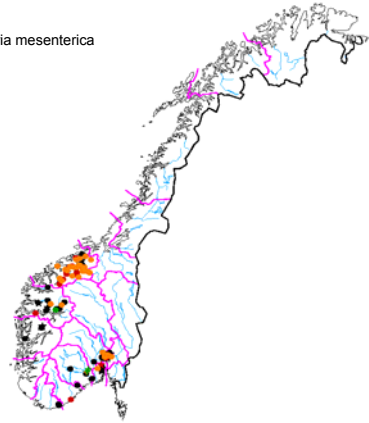


C. Coordinates for all explanatory variables along PC1, PC2 and PC3

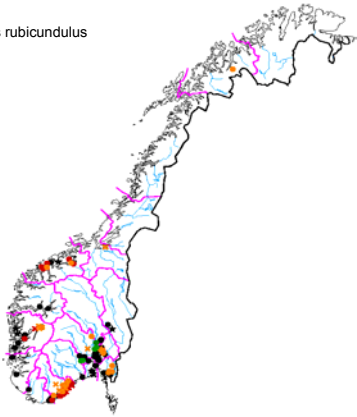
Id	Explanatory variabel	PC1	PC2	PC3	Id	Explanatory variabel	PC1	PC2	PC3
	Elev	0.79	0.30	-0.19	39	T-Nov	0.59	2.03	0.93
2	Elev-RelRef	-0.24	0.46	-1.05	40	T-Des	0.1	2.04	1.02
3	Slope	-0.34	-0.06	-1.07	41	AreaProp 28-40	-0.73	0.37	-0.66
4	SlopeSum	-0.44	0.03	-0.90	42	Evapotrans	0.5	0.70	0.00
5	SlopeTerrVar	-0.41	0.21	-0.84	43	Runoff	-0.11	-2.94	0.71
6	TRI - TerrRugg	-0.41	-0.13	-0.99	44	Runoff Precorr	-0.5	-2.00	1.24
7	TRI - TerrRuggSum	-0.47	0.16	-0.78	45	AreaProp 42-44	-0.73	0.15	-0.88
8	PlanCurv	-0.75	-0.23	-0.79	46	GS	2.62	-0.70	-0.02
9	ProfileCurv	-0.86	0.47	-0.86	47	GDD	1.62	0.85	0.64
10	Curv	-0.84	0.14	-0.83	48	AreaProp 46-47	-0.7	0.25	-0.75
11	Rad - HeatInd	-0.86	0.34	-0.74	49	Rdd100	-0.6	0.05	1.51
12	AspUnFav	-0.65	0.29	-0.75	50	Rdd010	-0.64	-0.44	0.19
13	AreaProp 1-12	-0.76	0.24	-0.69	51	Rdd001	-0.6	-0.47	-0.72
14	P-Ann	-0.64	-1.05	1.76	52	AreaProp 49-51	-0.7	0.38	-0.67
15	P-Jan	-0.56	-1.51	1.20	53	GeoRich	-0.44	-0.22	0.45
16	P-Feb	-0.57	-1.47	0.83	54	AreaProp 53	-0.7	0.47	-0.77
17	P-Mar	-0.63	-1.23	1.52	55	Snowdays	0.6	1.57	1.03
18	P-Apr	-0.72	-0.91	1.52	56	Lastsnow	1.21	1.13	0.60
19	P-May	-0.61	-0.02	1.40	57	Rad-Jan	0.8	-0.23	-1.68
20	P-Jun	-0.72	-0.17	1.08	58	Rad-Apr	0.75	-0.49	-1.69
21	P-Jul	-0.71	-0.43	1.39	59	Rad-Jul	1.22	-1.65	-2.39
22	P-Aug	-0.69	-0.40	1.78	60	Rad-Oct	0.94	-0.62	-1.91
23	P-Sep	-0.63	-0.90	1.88	61	AreaProp 55-60	-0.92	0.47	-0.96
24	P-Oct	-0.64	-0.96	1.57	62	DistCoast	-0.18	1.37	-0.08
25	P-Nov	-0.62	-0.86	1.71	63	DistOcean	-0.15	1.04	-0.17
26	P-Des	-0.53	-1.48	1.25	64	Conrad	-0.48	-0.61	-0.24
27	AreaProp 14-26	-0.72	0.15	-0.84	65	AreaProp 64	-0.73	0.36	-0.69
28	T-Ann	1.44	1.66	0.97	66	MarDep	-0.09	-1.11	-0.07
29	T-Jan	-0.04	1.97	0.98	67	Sea	-0.75	0.32	-0.74
30	T-Feb	0	2.04	1.00	68	Lake	-0.8	0.42	-0.66
31	T-Mar	0.83	1.98	1.11	69	River	-0.67	0.41	-0.64
32	T-Apr	1.96	0.82	0.80	70	Glacier	-0.61	0.03	-0.68
33	T-May	2.74	-0.41	0.42	71	GlacDep	-0.37	0.84	-0.64
34	T-Jun	2.86	-1.70	-0.25	72	Mire	-0.35	0.25	-0.21
35	T-Jul	2.68	-1.80	-0.59	73	Forest	-0.06	-1.27	-1.23
36	T-Aug	2.64	-1.08	-0.28	74	AvalDep	-0.72	0.36	-0.95
37	T-Sep	2.05	0.60	0.24	75	S - Slope	-0.85	0.25	-0.97
38	T-Oct	1.31	1.59	0.85					

The Atlantic element
Distribution maps 1-6

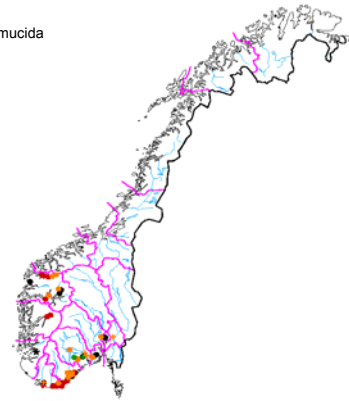
Map 1. *Auricularia mesenterica*



Map 2. *Cortinarius rubicundulus*



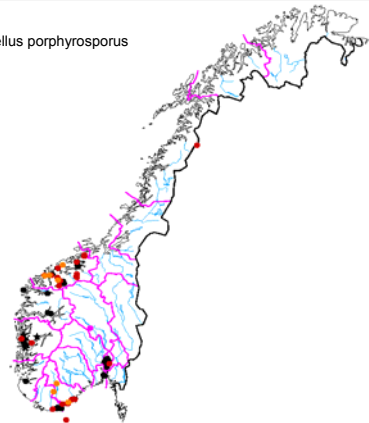
Map 3. *Holwaya mucida*



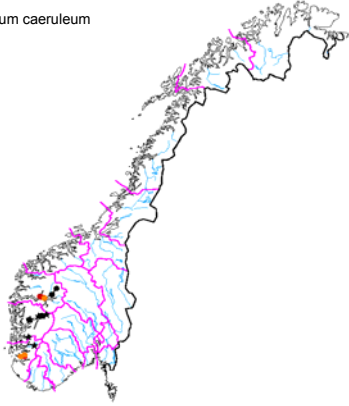
Map 4. *Hygrocybe vitellina*



Map 5. *Porphyrellus porphyrosporus*

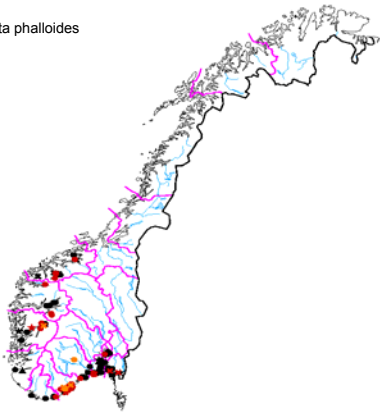


Map 6. *Pulcherricium caeruleum*

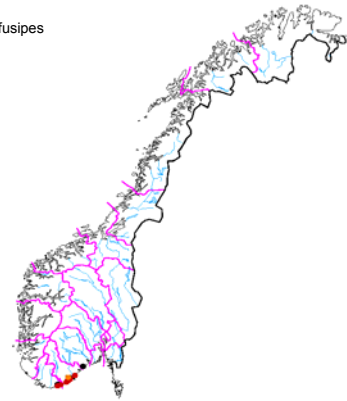


The Nemoral – Boreonemoral element
Distribution maps 7-13

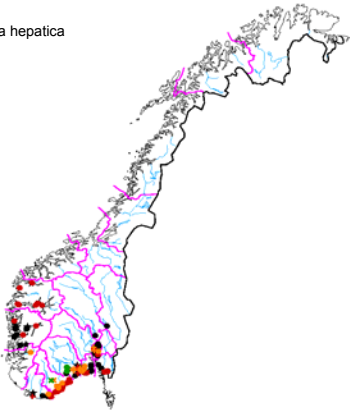
Map 7. *Amanita phalloides*



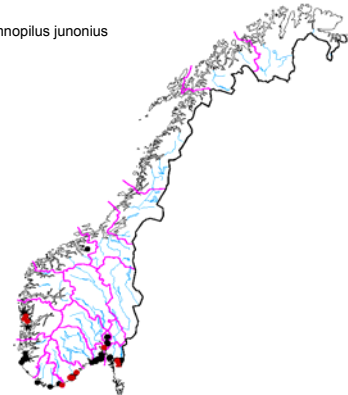
Map 8. *Collybia fusipes*



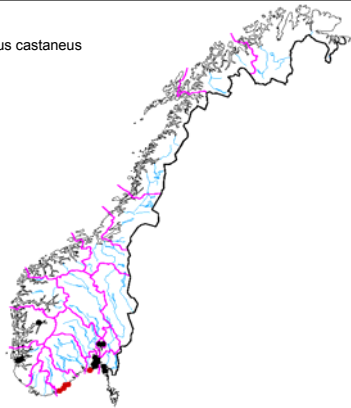
Map 9. *Fistulina hepatica*



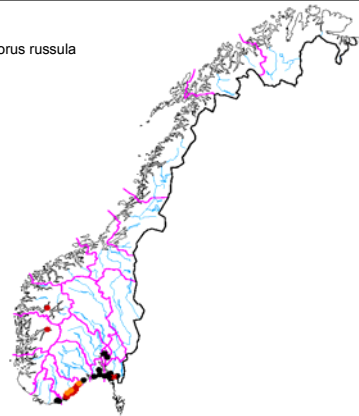
Map 10. *Gymnopilus junonius*



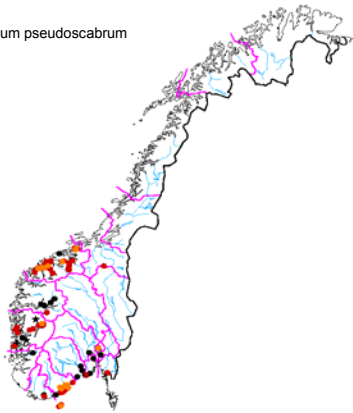
Map 11. *Gyroporus castaneus*



Map 12. *Hygrophorus russula*

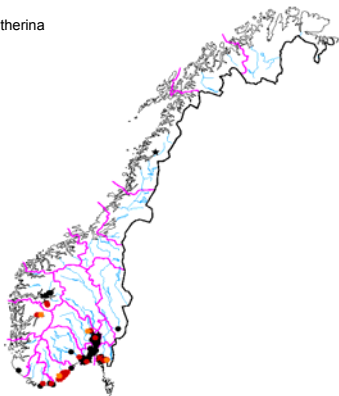


Map 13. *Leccinum pseudoscabrum*

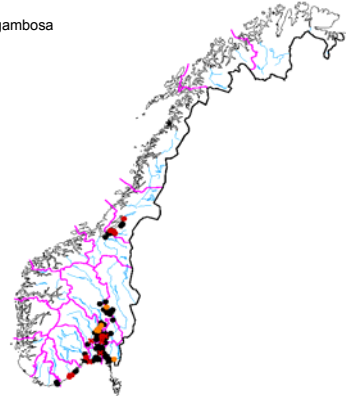


The South Boreale elemen
Maps 14-23

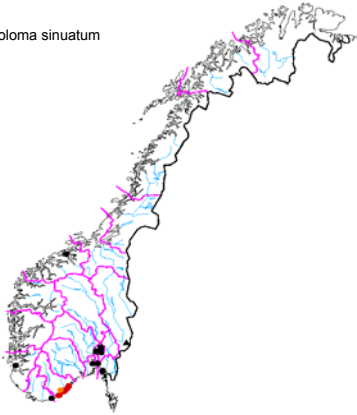
Map 14. *Amanita pantherina*



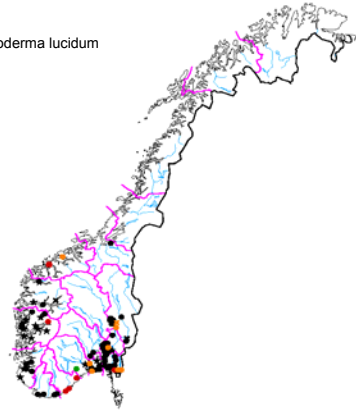
Map 15. *Calocybe gambosa*



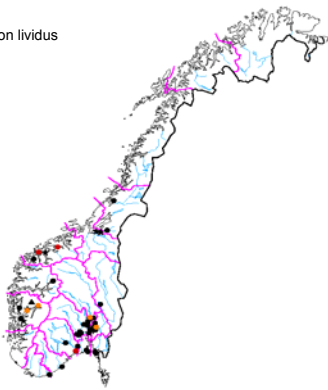
Map 16. *Entoloma sinuatum*



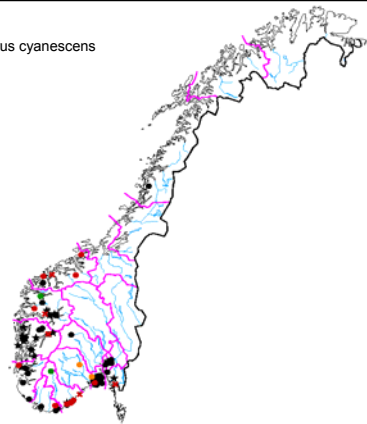
Map 17. *Ganoderma lucidum*



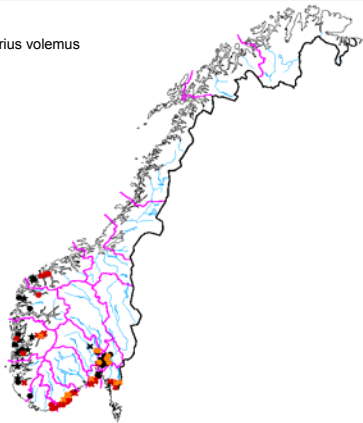
Map 18. *Gyrodon lividus*



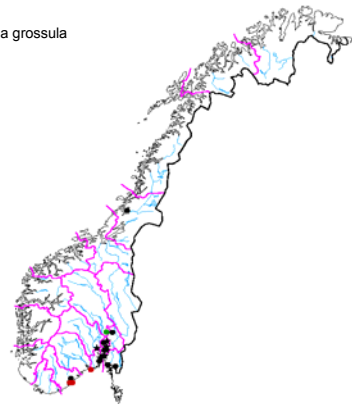
Map 19. *Gyroporus cyanescens*



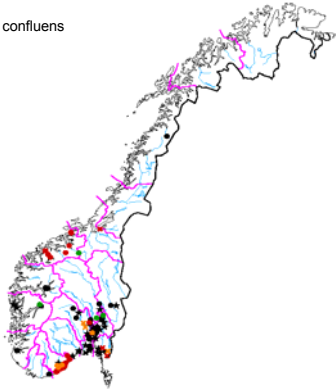
Map 20. *Lactarius volemus*



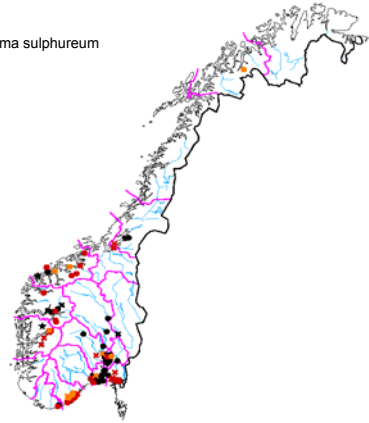
Map 21. *Omphalina grossula*



Map 22. *Sistotrema confluens*

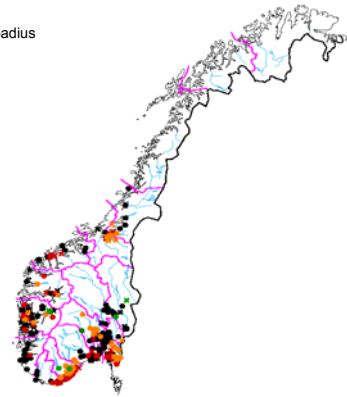


Map 23. *Tricholoma sulphureum*

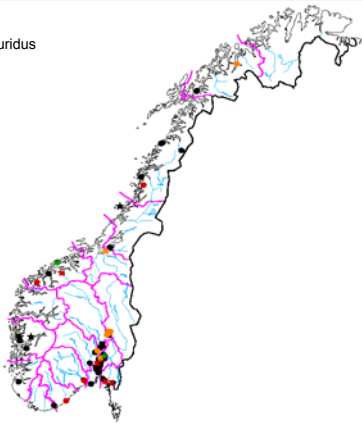


The Mid Boreale-western element
Maps 24-35

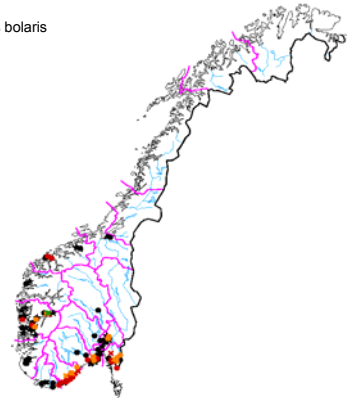
Map 24. *Boletus badius*



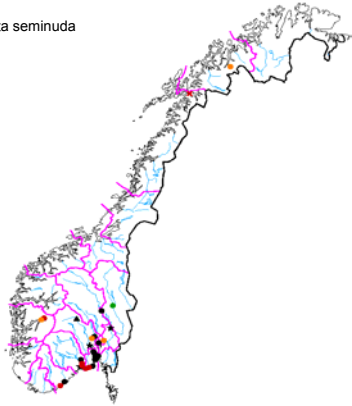
Map 25. *Boletus luridus*



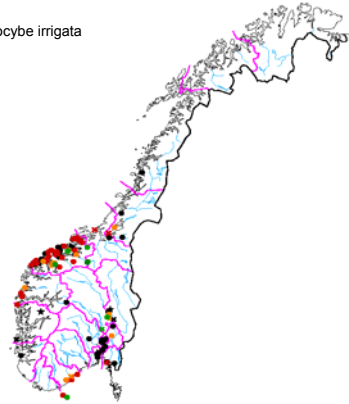
Map 26. *Cortinarius bolaris*



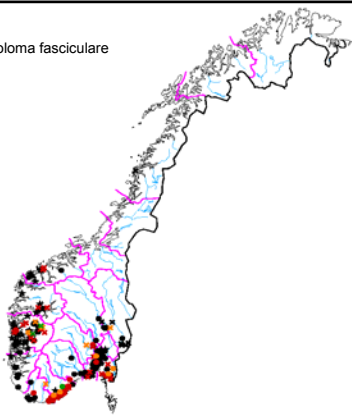
Map 27. *Cystolepiota seminuda*



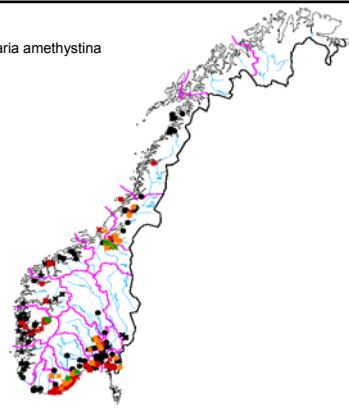
Map 28. *Hygrocybe irrigata*



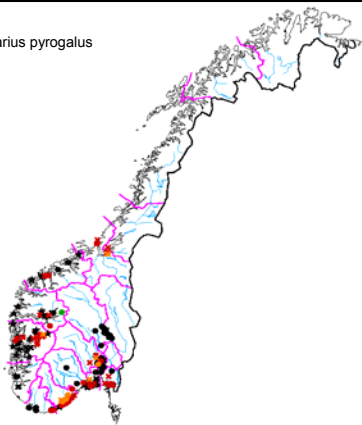
Map 29. *Hypholoma fasciculare*



Map 30. *Laccaria amethystina*



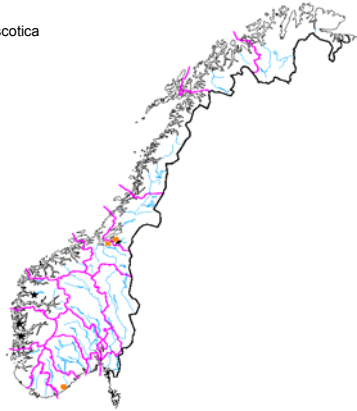
Map 31. *Lactarius pyrogalus*



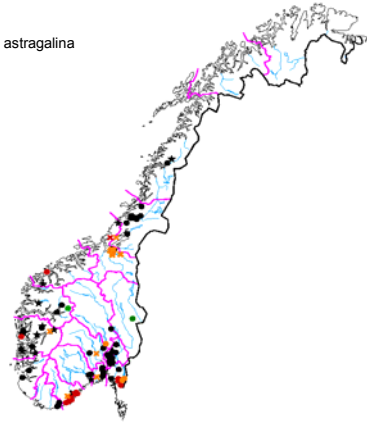
Map 32. *Macrolepiota procera*



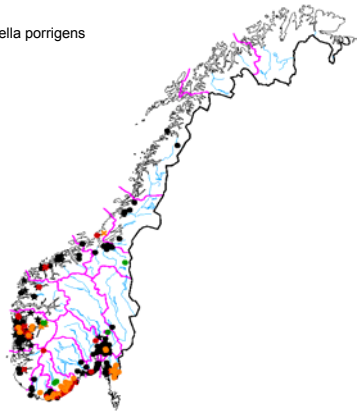
Map 33. *Melastiza scotica*



Map 34. *Pholiota astragalina*

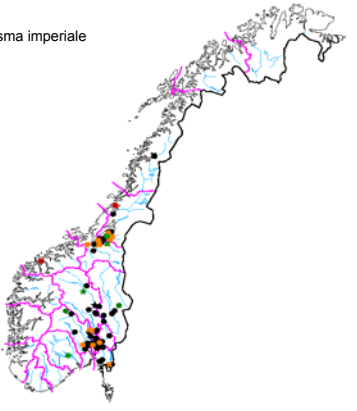


Map 35. *Pleurocybella porrigens*

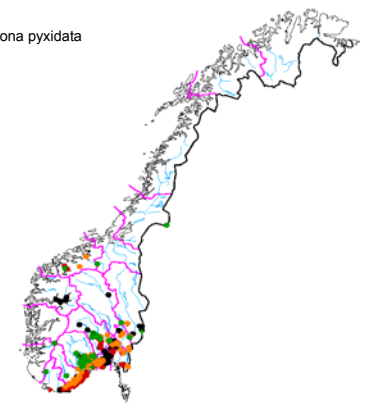


The Boreal – Montane element
Maps 36-49

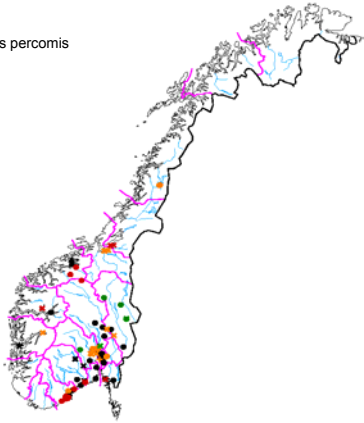
Map 36. *Catathelasma imperiale*



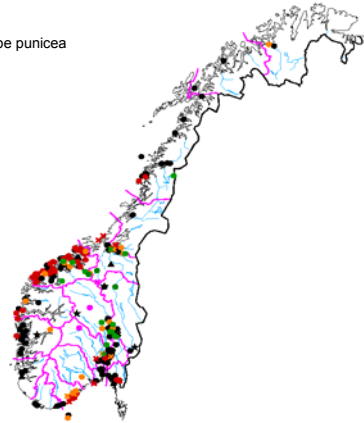
Map 37. *Clavicornia pyxidata*



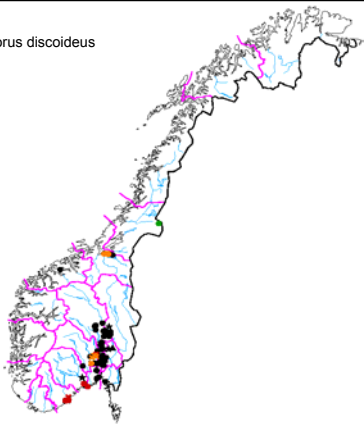
Map 38. *Cortinarius percomis*



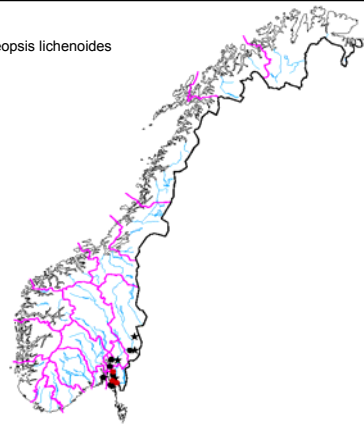
Map 39. *Hygrocybe punicea*



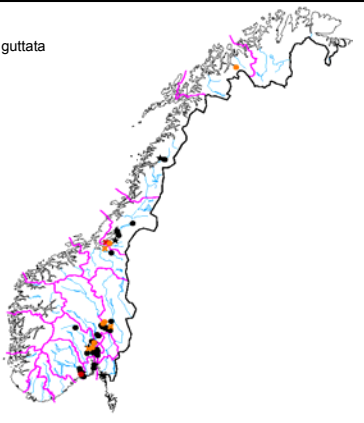
Map 40. *Hygrophorus discoideus*



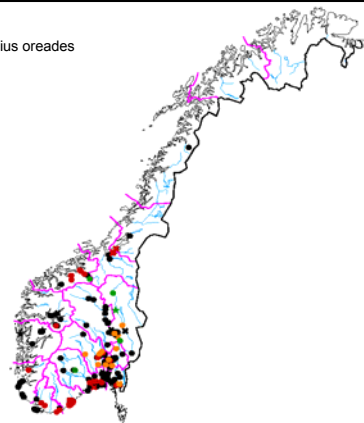
Map 41. *Hypocreopsis lichenoides*



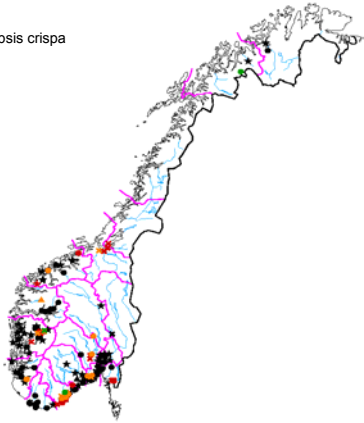
Map 42. *Limacella guttata*



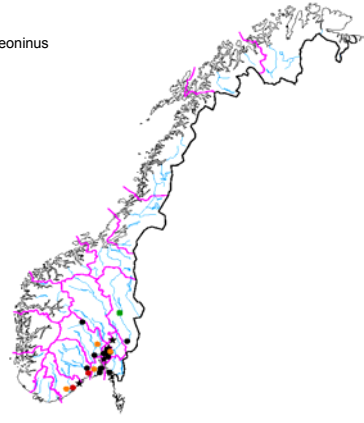
Map 43. *Marasmius oreades*



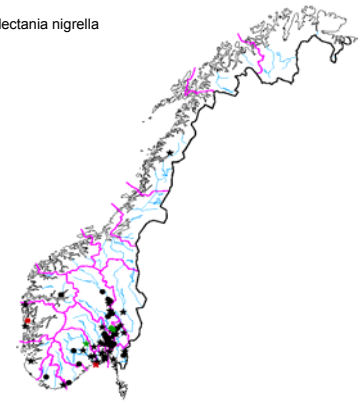
Map 44. *Plicaturopsis crispa*



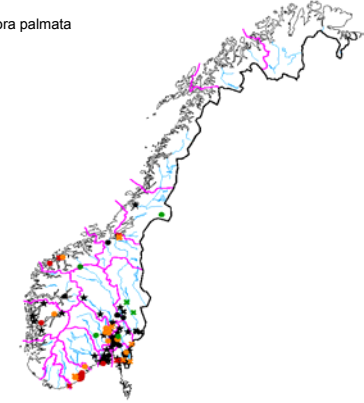
Map 45. *Pluteus leoninus*



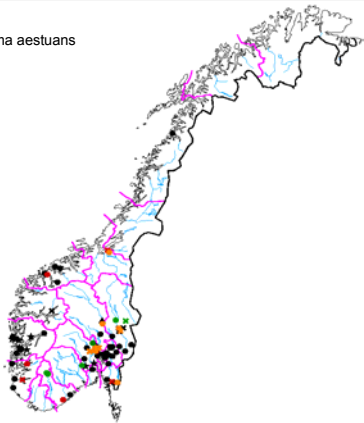
Map 46. *Pseudoplectania nigrella*



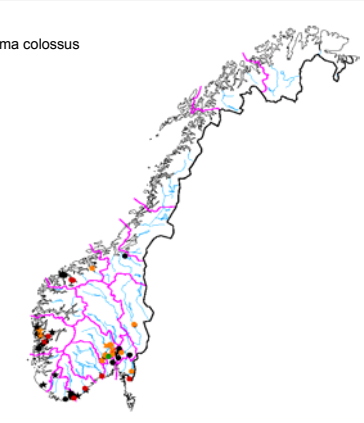
Map 47. *Thelephora palmata*



Map 48. *Tricholoma aestuans*

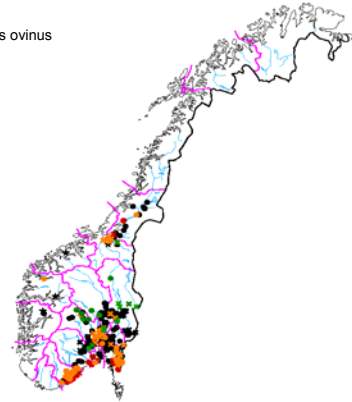


Map 49. *Tricholoma colossus*

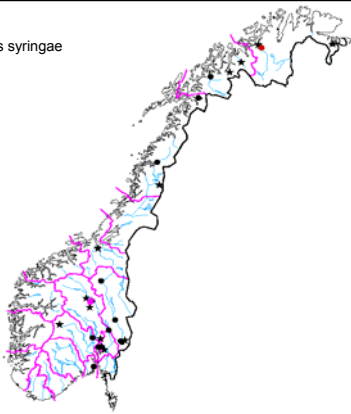


The Boreal – Subalpine element
Maps 50-75

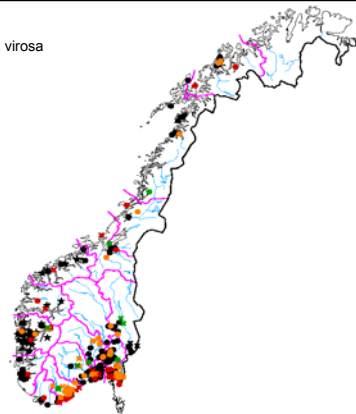
Map 50. *Albatrellus ovinus*



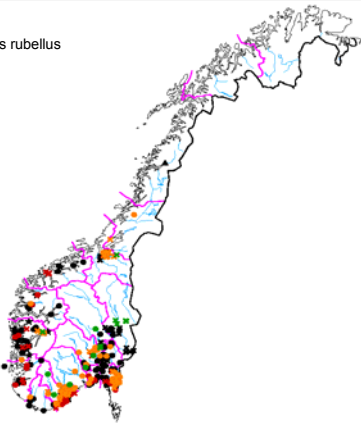
Map 51. *Albatrellus syringae*



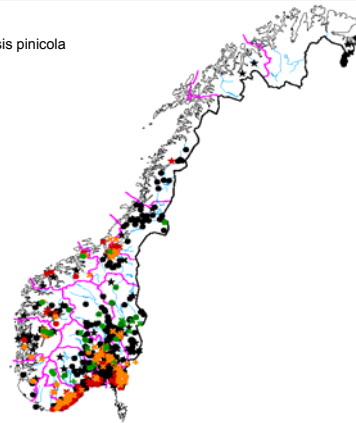
Map 52. *Amanita virosa*



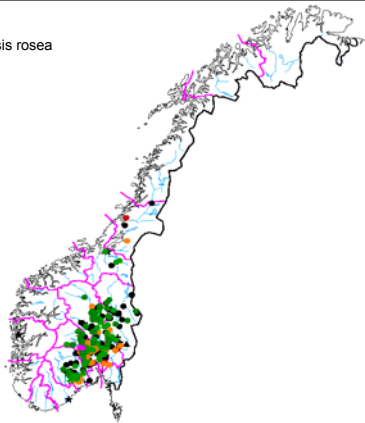
Map 53. *Cortinarius rubellus*



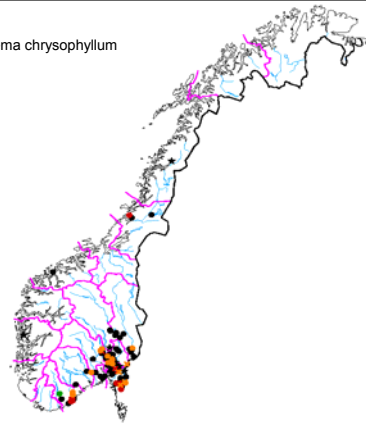
Map 54. *Fomitopsis pinicola*



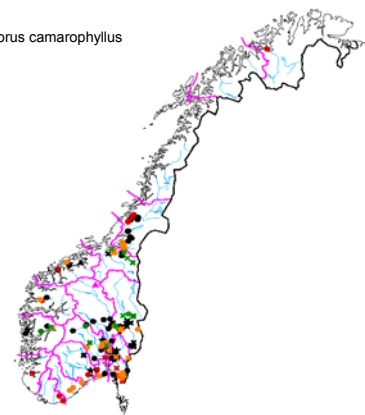
Map 55. *Fomitopsis rosea*



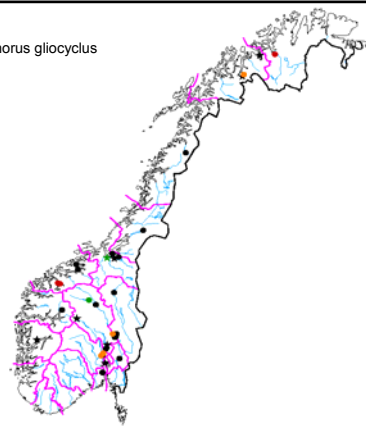
Map 56. *Gerronema chrysophyllum*



Map 57. *Hygrophorus camarophyllus*



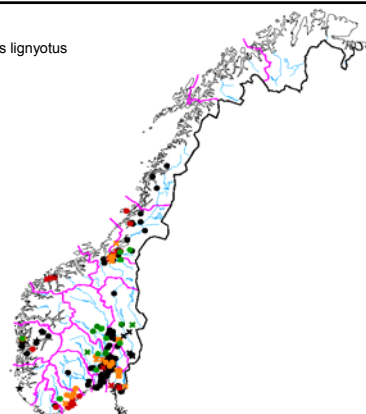
Map 58. *Hygrophorus gliocyclus*



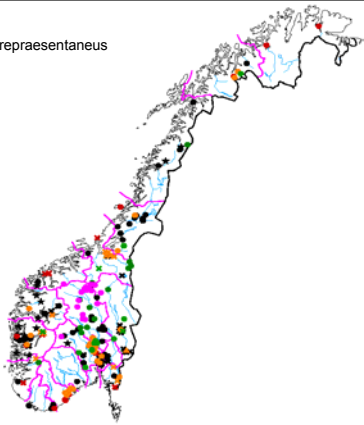
Map 59. *Hygrophorus karstenii*



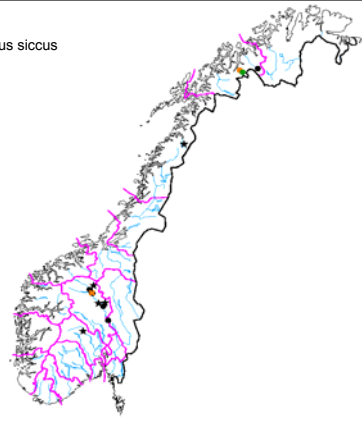
Map 60. *Lactarius lignyotus*



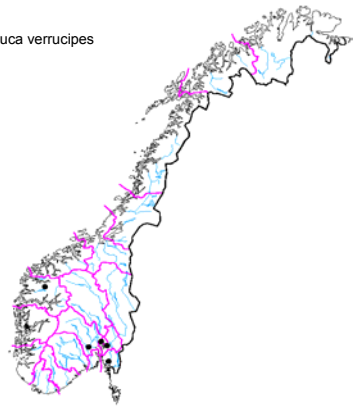
Map 61. *Lactarius repraesentaneus*



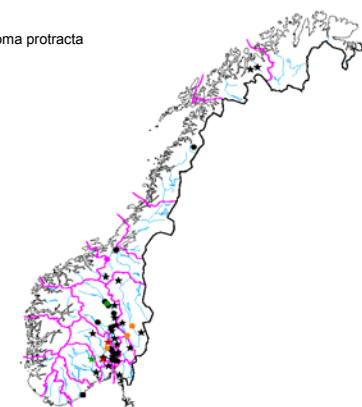
Map 62. *Marasmius siccus*



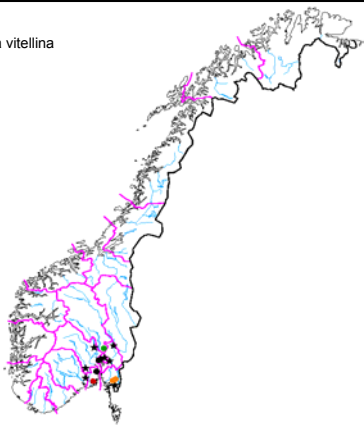
Map 63. *Melanoleuca verrucipes*



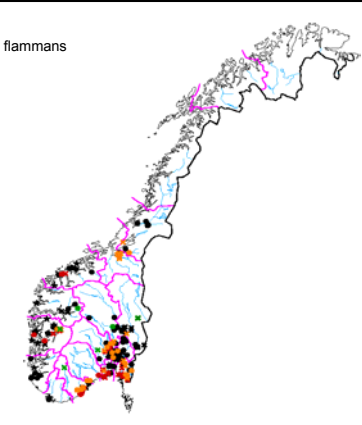
Map 64. *Microstoma protracta*



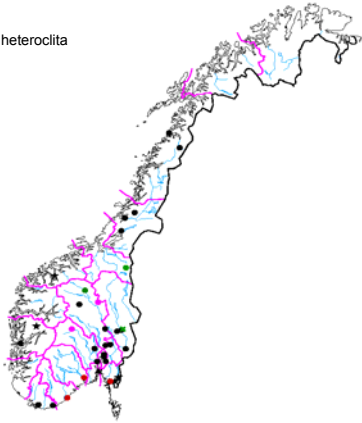
Map 65. *Neolecta vitellina*



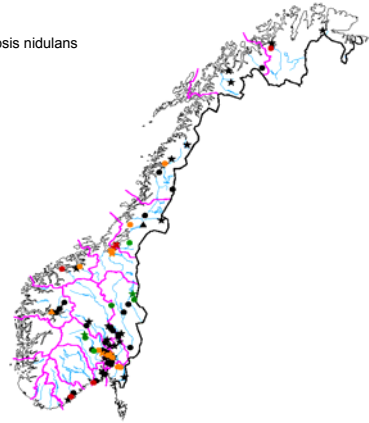
Map 66. *Pholiota flammans*



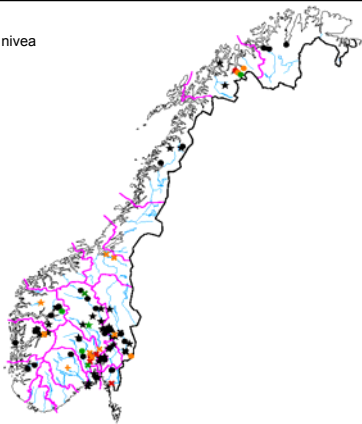
Map 67. *Pholiota heteroclitia*



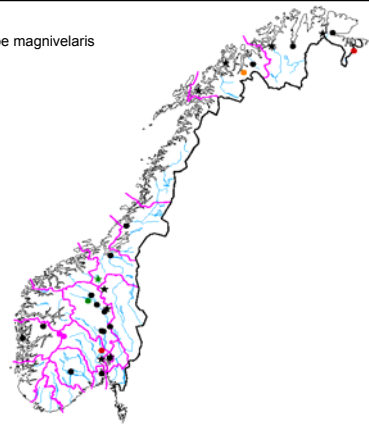
Map 68. *Phyllotopsis nidulans*



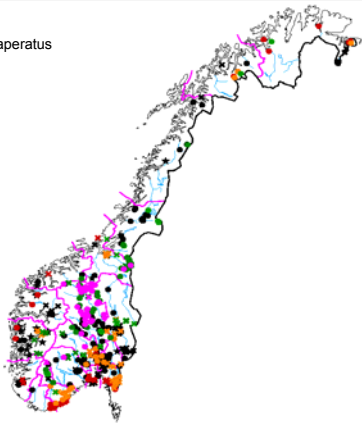
Map 69. *Plicatura nivea*



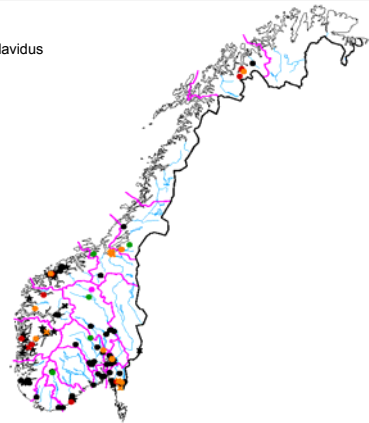
Map 70. *Psilocybe magnivelaris*



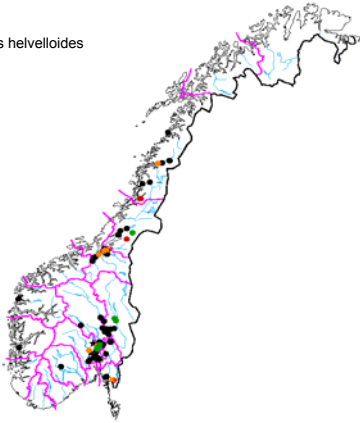
Map 71. *Rozites caperatus*



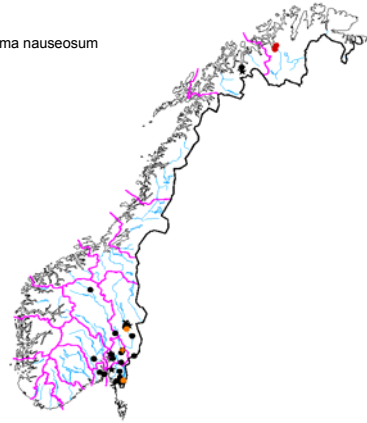
Map 72. *Suillus flavidus*



Map 73. *Tremiscus helvelloides*



Map 74. *Tricholoma nauseosum*

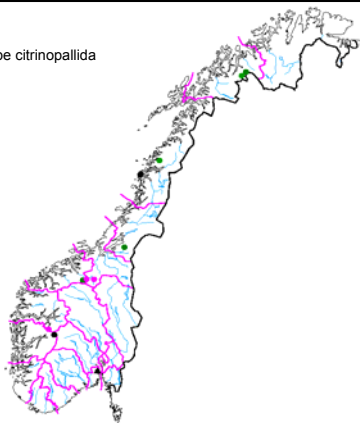


Map 75. *Tubaria confragosa*

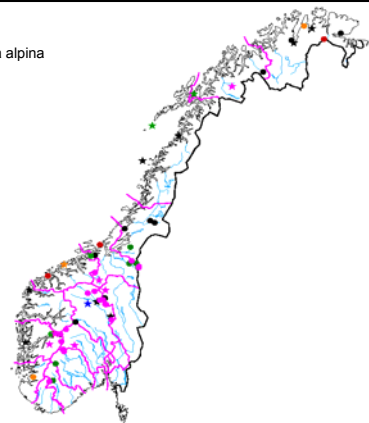


The Arctic – Alpine element
Maps 76-78

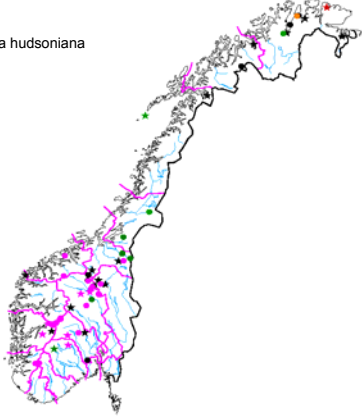
Map 76. *Hygrocybe citrinopallida*



Map 77. *Omphalina alpina*

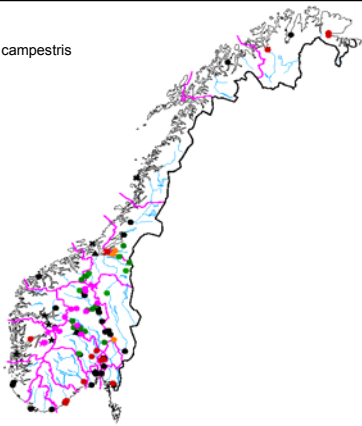


Map 78. *Omphalina hudsoniana*

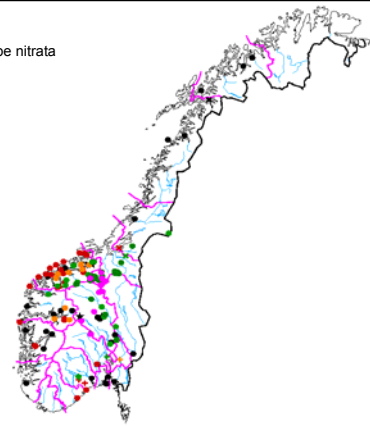


The Ubiquitous group
Maps 79-83

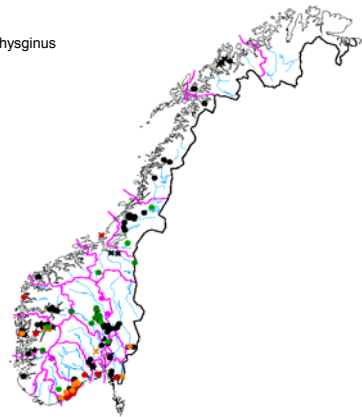
Map 79. *Agaricus campestris*



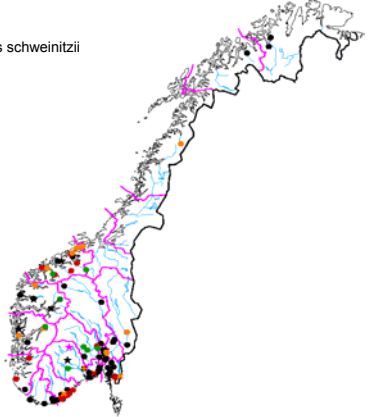
Map 80. *Hygrocybe nitrata*



Map 81. *Lactarius hysginus*



Map 82. *Phaeolus schweinitzii*



Map 83. *Tapinella atrotoментosa*

