

Habitat specificity of selected grassland fungi in Norway

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NØKKELOORD

Beitemarkssopp, seminaturlige enger, skog, andre habitater, Norge

SAMMENDRAG

132 taksa av sopp med regelmessig forekomst i seminaturlig eng av slektene *Camarophylloopsis*, *Clavaria*, *Clavulinopsis*, *Dermoloma*, *Entoloma*, *Geoglossum*, *Hygrocybe*, *Microglossum*, *Porpoloma*, *Ramariopsis* og *Trichoglossum* er valgt ut. Habitatspesifisiteten deres er undersøkt basert på 39818 norske funn. Ca. 80% av funnene er gjort i seminaturlige enger, ca. 10% i andre åpne habitater som parker, hager og veikanter, rikmyrer, kystlyngheier, åpen grunnlendt mark, fosse-enger, rasmarksenger og alpine habitater, mens 13% er funnet i ulike skogtyper (enkelte funn har angitt mer enn én naturtype, derfor blir summen over 100%). Av funnene i skog er minst 85% gjort i rike skogtyper (både løvskog og barskog), mens relativt få funn er gjort i fattige skoger. Ulikheter mellom artene

er undersøkt når det gjelder habitatspesifisitet. 70 taksa (53%) har mindre enn 10% av sine funn i skog, mens 23 (17%) har mer enn 20% av funnene i skog. De som har høyest frekvens i skog i Norge er for det meste også vanligst i skog i Sverige.

ABSTRACT

132 taxa of fungi regularly found in seminatural grasslands from the genera *Camarophylloopsis*, *Clavaria*, *Clavulinopsis*, *Dermoloma*, *Entoloma*, *Geoglossum*, *Hygrocybe*, *Microglossum*, *Porpoloma*, *Ramariopsis* and *Trichoglossum* were selected. Their habitat specificity was investigated based on 39818 records from Norway. Approximately 80% of the records were from seminatural grasslands, ca. 10% from other open habitats like parks, gardens and road verges, rich fens, coastal heaths, open rocks with shallow soil, waterfall meadows, scree meadows and alpine habitats, while 13% were found in different forest types (some records had more than one habitat type, the sum therefore exceeds 100%). Of all records in forests, at least 85% were from rich types (both deciduous and coniferous forests), while relatively few were from poor forests. Differences in habitat specificity between the taxa were analyzed. 70 taxa (53%) had less than 10% of their records in forests, while 23 (17%) had more than 20% of their records in forests. The taxa which had the highest frequency in forests in Norway are mostly the same as the most common species in forests in Sweden.

INTRODUCTION

The concept of grassland fungi could potentially be used about all fungi living in grasslands. However, here we use the term in a narrower sense, in accordance with several European authors (e.g. Nitare 1988, Griffith et al. 2013). According to this concept, grassland fungi are macrofungi confined to seminatural grasslands, which are regularly grazed (pastures) or mown (meadows), not or poorly manured, and not plowed (except possibly a long time ago). The concepts of “grassland fungi” and “waxcap grasslands” (used about seminatural grasslands rich in *Hygrocybe* species) were established a long time ago, and according to Griffith et al. (2013), they were given attention already in the 18th century. Grassland fungi form a taxonomically diverse group of seemingly ecologically related species from *Hygrocybe* (sensu lato), *Camarophylloopsis*, *Clavaria*, *Clavulinopsis*, *Dermoloma*, *Entoloma*, *Geoglossum*, *Microglossum*, *Porpoloma*, *Ramariopsis* and *Trichoglossum* (Nitare 1988, Noordeloos 1992, Jordal 1997, McHugh et al. 2000, Newton et al. 2003, Griffith et al. 2013). Here, we use the term grassland fungi to describe taxa from the genera mentioned above, often growing together in seminatural grasslands, and listed by at least two of the publications mentioned above. The genus *Tremellodendropsis* has been suggested to belong among the grassland fungi (Nitare 2014), but due to uncertainty about its ecology, we have chosen not to include this genus containing just one species in Norway, *T. tuberosa* (with 61 records). The group of grassland fungi comprises at least 150-160 species in Sweden and Norway (Nitare 1988, Jordal 2011, 2013); in the UK (also called “CHEGD” fungi - an acronym of group names) there are 180-200 species (Evans 2003, Griffith et al. 2013). Even small localities can be surprisingly rich in grassland fungi, with more than 50-60 species (Nitare 1988, Jordal 1997, McHugh et al. 2000, Evans

2003). The most species rich locality in the UK had 78 species, of which 34 were *Hygrocybe* spp. (Griffith et al. 2013). One Norwegian locality had 71 species, 32 of which were from *Hygrocybe* (Fadnes 2014), and one in Sweden had 76 species, 33 of these were *Hygrocybe* spp. (Pihl 1992). In one Swedish locality 36 species of *Hygrocybe* were recorded (Bergelin 2005). Additional 200-300 species of macrofungi from other genera occur in the same habitats (Arnolds and de Vries 1989, Aronsson and Hallingbäck 1995), but these species mostly seem to have other ecological preferences and are not treated here.

Different authors have pointed to the fact that many of the grassland fungi also can be found in other habitats, including forests (Boertmann and Rald 1991, Nitare 2000, Bendiksen et al. 2008, Boertmann 2010, Brandrud et al. 2015, Lorås and Eidissen 2011, Griffith et al. 2013). Outside Europe, e.g. in North America, the same (or closely related) species mostly occur in forests (both deciduous, coniferous and mixed), but can also be found in grasslands and swamps (e.g. Hesler and Smith 1963, Boertmann 2010, Lodge et al. 2013, Birkebak et al. 2013, Griffith et al. 2013).

Seminatural grasslands have declined dramatically in Norway. Since 1900, a loss of roughly 80-90% of the area is estimated for Norway (Jordal 2010). In Western Europe, a loss of 90% during the last 75 years is estimated (Griffith et al. 2013); in some countries the situation is even more dramatic (e.g. in the Netherlands; Arnolds 1988). Therefore it is important to know if the species living here can also survive in other habitats. Especially in the preparing of red lists (lists of threat status according to the IUCN classification) this information is important (Brandrud et al. 2015). Many of the grassland fungi are present on the red lists of several European countries (Griffith et al. 2013).

In Norway, public herbaria and NGOs have cooperated, especially during the last 20 years, to make records of fungi available in online databases. Now most data owners share records of fungi (and other groups of organisms) found in Norway in the same Internet solution, called "Species Map Service" (Artskart), comprising about 540000 fungal records (not including lichens) (Norwegian Biodiversity Information Centre and GBIF 2014).

The aim of this article is to compile information on known habitats of selected grassland fungi in Norway, and look for differences between species. By discussing the habitat specificity of the species we hope to improve the knowledge about them, which is also the basis for their conservation. However, we do not intend to emphasize in detail the response of the species to edaphic, climatic or other gradients beyond the habitats these gradients create (like calcareous forests or alpine snow beds).

MATERIAL AND METHODS

Taxonomy and nomenclature

Taxonomy and nomenclature follow the Norwegian taxon database (Norwegian Biodiversity Information Centre 2015), which for Basidiomycota largely follows Knudsen and Vesterholt (2012). The genus *Hygrocybe* s.l. was recently split into several genera (Lodge et al. 2013), but this is not yet implemented, awaiting more information and some species to be placed and combined in the appropriate genera. In many of the other genera there is also ongoing research by molecular methods (e.g. Arauzo and Iglesias 2014, Kautmanová et al. 2012, Morozova et al. 2014, Vila et al. 2013). Most new or recently redefined taxa are poorly known (with fewer than 10 records) and therefore excluded from this study.

Data extraction, processing and compilation

Data on records of taxa from the genera mentioned above have been extracted and downloaded from the Species Map Service (03.12.2014) and imported in a Microsoft Access database. Own unpublished data have been added. Records with information on uncertain determination were excluded. Records from before 1900 were removed because they were very few and had little information on habitats. Taxa not belonging among the grassland fungi (as defined above, e.g. many *Entoloma* spp.) were excluded. Ecological information on some of our own records has been added or improved. There has been searched for ecological information in five different fields (locality, ecology, habitat, substrate and notes). Records lacking ecological information, or with insufficient information, have been removed. Taxa with less than 10 records containing habitat information have been excluded from the study. We have included three varieties from *Hygrocybe* s.l., by some authors treated at species level.

Habitats are classified using nature types defined by Halvorsen et al. (2015) - called Nature in Norway (NiN 2.0), but some of the types had to be merged, e.g. grasslands which are not seminatural grasslands. The ecological information is used to classify each record in one of the following nature types: seminatural grassland, other grasslands (mostly lawns, parks, road verges), forests, sea shore meadows, heaths (oceanic *Calluna* heaths), rocks with shallow soil, waterfall meadows (created by spray from waterfalls), fens, scree meadows, and alpine habitats.

We made some criteria for handling insufficient habitat information. 'Forests' are sometimes actually seminatural grasslands in succession towards forest, but still with some grassland features intact. Halvorsen et al. (2015) define these cases to type by using degrees of "management intensity". 'Grazed



Figure 1. Some habitats treated in this study. A. In Holmvassdalen (Nordland: Grane) there is calcareous tall herb spruce forest with many grassland fungi. B. Calcareous low herb birch forest, Nordland: Hattfjelldal: Varnvatnet. C. Sea shore meadow between the sea and *Calluna* heath, grazed by sheep and with many grassland fungi, Hordaland: Bømlo Haverøya. D. Rocks with shallow soil, Oslo: Nakholmen. E. Scree meadow grazed by goats in Møre og Romsdal: Stranda: Norangsdalen. F. Dry seminatural grassland grazed by cows, Oppland: Vågå: Fellese. Photo B: GG, photos A and C-F: JBJ.



Figure 2. Grassland fungi in different habitats. A. *Hygrocybe lacmus* in poor, boreal birch forest, Møre og Romsdal: Sunndal: Bæverdalen. B. *Entoloma mougeotii* at the edge of a rich fen, Troms: Finnsnes. C. *Hygrocybe conica* in alpine snowbed 1450 m a.s.l., Møre og Romsdal: Sunndal: Råstu. D. *Hygrocybe aurantiosplendens* in calcareous birch forest, Nordland: Hattfjelldal: Raudvatnet. E. *Hygrocybe laeta* in a mossy spot in acid coastal *Calluna* heath, Møre og Romsdal: Smøla. F. *Porpoloma metapodium* in seminatural grassland, Sør-Trøndelag: Oppdal. Photo A, B, D: GG; photos C, E, F: JBJ.

forest' can be interpreted as forest, but can also be seminatural grassland with tree cover. If information was too scarce to make a final decision according to the definitions, we normally interpreted these cases as both forest and seminatural grassland. Half open pastures with some trees ("hagemark") were defined as seminatural grassland. In some cases of doubt we had to choose either the most probable nature type, two possible types where a final decision was difficult, or leave the record as "lacking sufficient ecological information" and thereby exclude it. Alpine habitats comprise more than one type in NiN 2.0, but the lack of detailed habitat information, combined with rather few records here, made us merge these types to one.

Statistical analysis

We wanted to investigate the habitat specificity of the different species and to look for differences between them. We assume that the probability of observing each species is equal among species and in all habitats, for a given sampling effort (but see discussion). Thus, if the habitat preferences of all species are similar, we would expect the frequency distribution of species records over all habitats to be equal among species. In order to test if this was the case, we used contingency tables and Chi-squared tests. For each species we compared the observed frequency in a given habitat (no. of records in the habitat/no. of records in total) with the expected frequency (no. of records in the habitat pooled over all species/no. of records in total pooled over all species and habitats). A significant test statistic (p -value < 0.050) suggests that the species has a higher/lower frequency of occurrence in the habitat than expected, i.e. than in the total dataset. Due to the low number of records in other habitats than seminatural grasslands and forests, analysis were only performed for these two habitats (with two exceptions; *Hygrocybe acutoconica*

and *H. conica*). When a record had two habitats given, we included two separate rows in the dataset for this record, one for each habitat.

RESULTS

Examples of habitats and species are shown in Figures 1-2.

Metadata

Totally about 43000 records from the mentioned genera were downloaded and about 4000 own, unpublished records were added. After the exclusion of species not belonging among the grassland fungi, rare and little known grassland species (< 10 records with habitat information), records from before 1900 (12 records) and records with uncertain determination, 42210 remained. Further, 2392 records lacking (sufficient) ecological information were excluded. Data from the remaining 39818 records of 132 taxa (129 species and 3 varieties) were analyzed and the results are presented in Tables 1-3 and in Figures 3-5. In *Hygrocybe* (sensu lato) there were 23773 records (59.7%) of 39 species and three varieties. There were 9117 records (22.9%) of 51 species of *Entoloma*. *Clavaria*, *Clavulinopsis* and *Ramariopsis* had totally 3829 records (9.6%) of 18 species. *Geoglossum*, *Microglossum*, and *Trichoglossum* had 2467 records (6.2%) of 14 species. Other genera (*Camarophylloopsis*, *Dermoloma*, *Porpoloma*) had 632 records (1.6%) of 7 species.

Table 1 shows the owners of the data used in this study. There were totally 28734 observations and 11084 herbarium collections. Two of the authors (JBJ, GG) have participated by the collecting of approximately 22500 of the records, 5500 of which are being stored as dried collections in the herbaria.

Table 1. Data owners with number of objects (dried specimens) and observations. N=total number of records. ¹3503 of the total number of records are unpublished. ²476 of the total number of records are unpublished. All other records were downloaded from Norwegian Biodiversity Information Centre & GBIF (2014).

Data owner	Objects	Observations	N
BioFokus	50	3468	3518
Ecofact		16	16
J.B. Jordal ¹		9090	9090
Miljøfaglig Utredning ²		6328	6328
Naturhistorisk Museum - UiO	9803	2943	12746
Norges sopp- og nyttevekstforbund		6785	6785
Norsk institutt for naturforskning		104	104
NTNU - Vitenskapsmuseet	743		743
Tromsø museum - Universitetsmuseet	339		339
Universitetsmuseet i Bergen - UiB	149		149
Total	11084	28734	39818

Figure 3 shows when the records have been collected. More than 96% were collected in/after 1990, i.e. the last 25 years. Therefore, e.g. conclusions on decline of the species over decades cannot be drawn based on the species records themselves, but have to depend on knowledge on decline of the habitats.

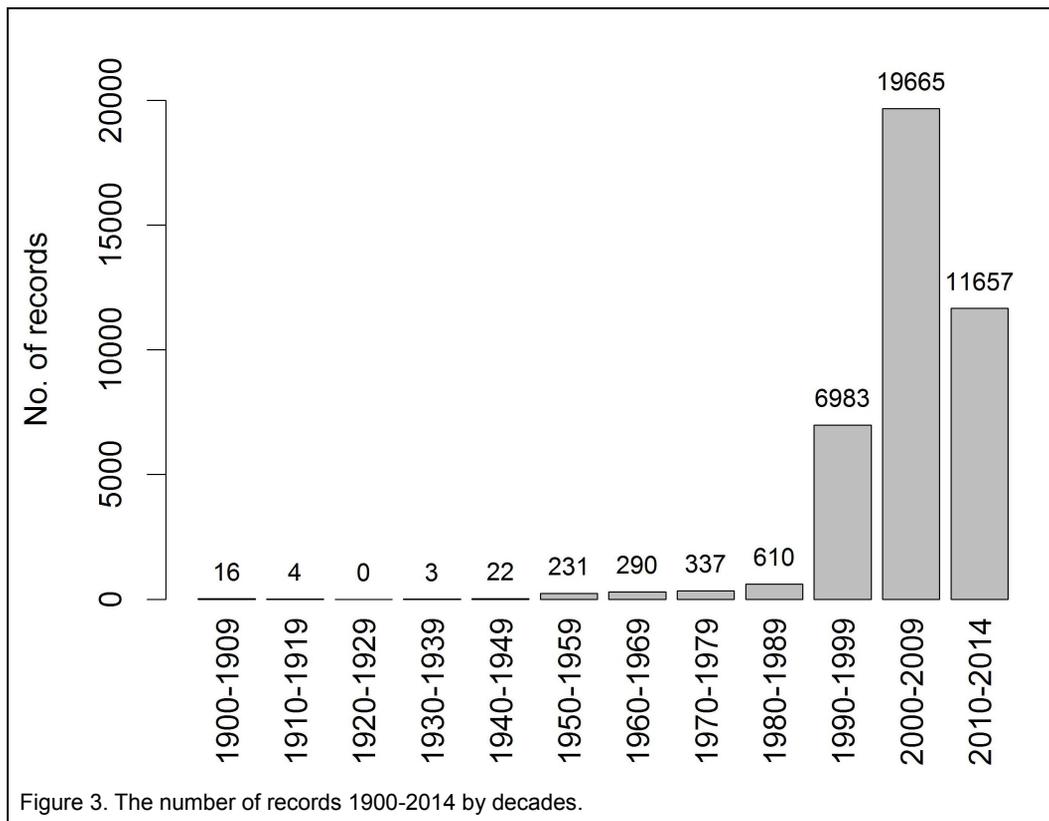
Habitats

Table 2 shows detailed information on the number of records of each species in the different habitats. For three records, three different habitats are given, whereas two different habitats are given for 1706 records. The remaining 38109 records have one habitat only. Some habitats are shown in Figure 1.

Seminatural grassland is generally the most important habitat, with 32034 records (80.5%) of (all) 132 species (Table 2). Most of the species also occur in other grasslands (*lawns*, *parks* and *road verges* which mostly are being mown). A total of 2147 records (5.4%) of 113 species are given from these habitats. *Sea shore meadows* (i.e. upper part, mostly the supralittoral zone which is only occasionally flooded by sea water) have 561 records (1.4%) of 88 species. *Sand dune meadows* have 188

records (0.5%) of 52 species. In *coastal Calluna heath* we find 351 records (0.9%) of 68 species. *Waterfall meadows* (created by the spray impact from waterfalls keeping trees away) are pretty rare, and have 24 records (0.1%) of 14 species. *Rocks with shallow soil*, often near the sea (and often grazed) have 487 records (1.2%) of 98 species. *Scree meadows* (kept open by snow avalanches in winter, often in combination with grazing in summer) have 64 records (0.2%) of 35 species. *Fens* (mostly at the edges of rich/calcareous fens) have 188 records (0.5%) of 52 species. In the *alpine region* most records are from different low alpine habitats, including seminatural grasslands, snowbeds and heaths (often described as grazed). The data include 240 records (0.6%) of 68 species from alpine habitats. *Forests* have 5246 records (13.2%) of 121 species. The term forest can include a wide variety of types, see below.

In summary, 91% of the records are found in open habitats – with 80.5% in seminatural grasslands. As 13% are from forests this sum up to 104%, due to some records coded for more than one habitat type.



Species occurrences in open habitats

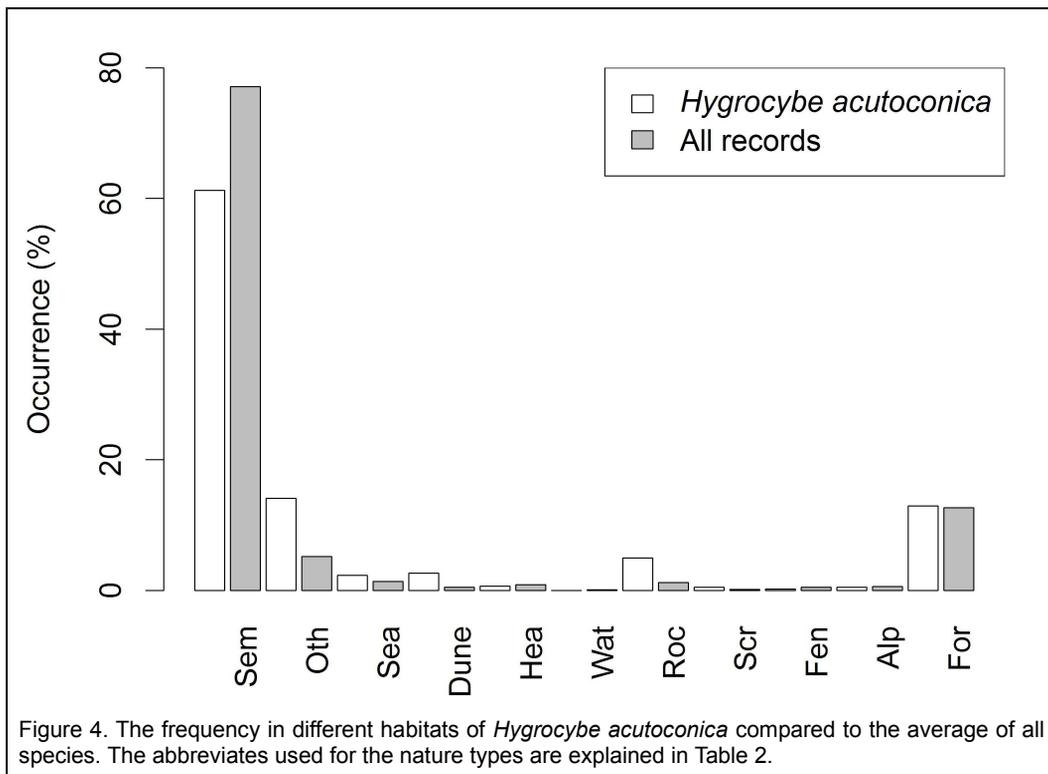
The most common species (both totally and in seminatural grasslands) were *Hygrocybe conica* (2516/1591), *H. pratensis* (1918/1593), *Hygrocybe virginea* (1724/1299) and *H. psittacina* (1408/1231), which is identical with the four most common species in the UK according to Griffith et al. (2013).

Table 3 shows the results of our statistical analysis of differences in habitat selection between the species. The species are grouped according to their frequency in forests.

Seminatural grasslands. A total of 11 species had significantly higher frequency ($p < 0.05$) of occurrence in seminatural grasslands than the total average: *Clavulinopsis helvola*, *Entoloma griseocyaneum*, *E. infula*, *Hygrocybe ceracea*, *H. flavipes*, *H. helobia*, *H. ingrata*,

H. laeta, *H. nitrata*, *H. psittacina* and *H. splendidissima* (Table 3). All were relatively common in the dataset, with > 300 records. 15 species had significantly lower frequency of occurrence in seminatural grasslands than the total average (Table 3). With one exception, all of these occurred more often in forests (see below).

Other grasslands. The majority of the investigated species can occur in grasslands like lawns, parks, gardens, old road verges etc. These habitats have much in common with seminatural grasslands if they are old and unmanured (not treated with fertilizer). *Hygrocybe acutoconica* was one of the most frequent species found in other grasslands. This species was significantly less frequent in seminatural grasslands ($p < 0.001$), but more



frequently observed than expected in other grasslands ($p < 0.001$), dune habitats ($p < 0.001$) and rocks with shallow soil ($p < 0.001$) (Figure 4).

Of the 88 species recorded in *sea shore meadows*, 14 had more than 10 records in this habitat. The most common were *Hygrocybe conica*, *H. virginea*, *H. russocoriacea*, *Entoloma sericeum*, *H. chlorophana*, *H. pratensis*, *H. ceracea*, *E. griseocyaneum*, *H. psittacina*, *H. coccinea*, *E. corvinum*, *Geoglossum cookeanum*, and *H. acutoconica* (Table 2). Some of these, like *H. russocoriacea*, *G. cookeanum* and *E. griseocyaneum* probably prefer calcareous shell bed areas. On the mostly acid rocks of western Norway, *H. russocoriacea* almost exclusively occurs on calcareous sandy soil near the sea.

The most common species recorded in *sand dune meadows* were *Entoloma corvinum*, *E. sericellum*, *E. sericeum*, *E. serrulatum*,

Geoglossum cookeanum, *Hygrocybe acutoconica*, *H. cantharellus*, *H. chlorophana*, *H. conica*, *H. psittacina*, *H. russocoriacea*, *H. virginea*, *Microglossum atropurpureum* and *Trichoglossum hirsutum*. Stabilized dunes have often been extensively grazed, and have many features in common with seminatural grasslands.

In *coastal Calluna heaths* the most common species was *Hygrocybe laeta* (25 records), which is sometimes also seen in burnt heath, where the vegetation the first years after burning is rather grass rich. Other species (8-17 records) were *Clavulinopsis helvola*, *C. luteoalba*, *Geoglossum difforme*, *Hygrocybe cantharellus*, *H. ceracea*, *H. chlorophana*, *H. coccinea*, *H. conica*, *H. flavipes*, *H. irrigata*, *H. pratensis*, *H. psittacina*, *H. punicea*, *H. reidii*, *H. splendidissima*, *H. virginea* and *Trichoglossum walteri*.

Many of the records on *rocks with shallow soil* were made on rocks near the sea shore. These habitats are sometimes grazed and occur in mosaic with pastures on deeper soil. Commonly found are e.g. *Hygrocybe acutoconica*, *H. conica*, *H. virginea*, *Entoloma prunuloides*, *H. coccinea*, *H. russocoriacea*, *H. pratensis*, *H. psittacina* and *E. mougeotii*. In the Oslofjord area there are many calcareous rocks with shallow soil and a rich flora and funga. These areas seem to stay open without overgrowing for a long time even without grazing or mowing (Halvorsen et al. 2015). A considerable amount of the records on rocks are from the Oslofjord area, and many of the species preferring strongly calcareous rocks are found here, like *Camarophylloopsis* spp., *Entoloma bloxamii*, *E. excentricum*, *E. incanum*, *Hygrocybe calciphila*, *H. colemaniana*, *H. mucronella* and *Microglossum olivaceum*. Some species with less than 10 Norwegian records (not included in our data) were also found here, like *Camarophylloopsis atropuncta* and *Entoloma fridolfingense*. Similar habitats also occur in some other parts of the country, like the coast of Nordland.

Records from *fens* with detailed habitat information were especially found at the edges of rich or intermediate fens. Most common was *Entoloma mougeotii* (23 records), regularly found at the edges of rich fens (Figure 2). Other species (4-11 records) are e.g. *Entoloma asprellum*, *E. caesiocinctum*, *E. formosum*, *E. poliopus*, *E. serrulatum*, *Geoglossum simile*, *Hygrocybe cantharellus*, *H. coccinea*, *H. conica*, *H. helobia*, *H. miniata*, *H. russocoriacea*, *H. virginea* and *Trichoglossum hirsutum*. Many of the fungi found in rich fens belong to the genus *Entoloma*. Species which are often also found in moist to wet places in seminatural grassland are e.g. *Geoglossum simile*, *Hygrocybe helobia* and *Trichoglossum hirsutum*.

The number of species recorded in *waterfall meadows* was low, due to the rarity of the

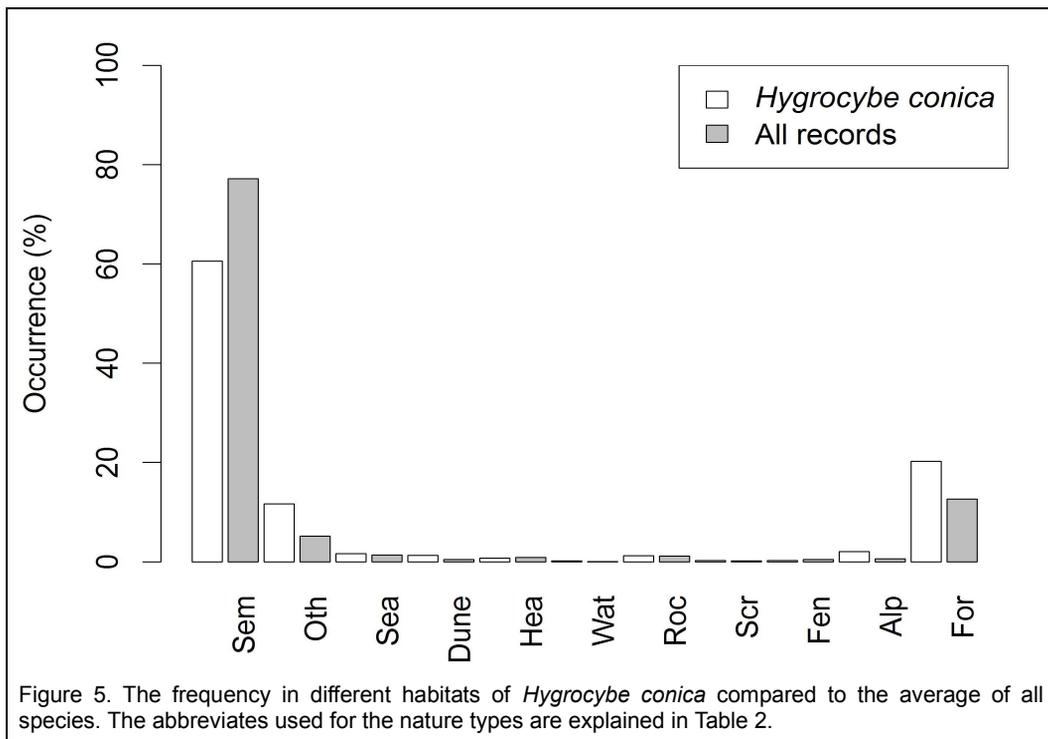
habitat. Species with >1 record were *Entoloma caesiocinctum*, *E. poliopus*, *Hygrocybe conica* and *H. reidii*, which all are widespread species.

The most abundant species in *scree meadows* were generally common species like *Hygrocybe conica*, *H. acutoconica*, *H. coccinea*, *Entoloma poliopus*, *E. serrulatum* and *E. sericeum*. Scree meadows – often grazed by domestic animals – differ only slightly from other pastures, but the soil layer may be interrupted or destroyed more often due to snow avalanches which often bring with them stones, trees, ice and gravel. The instability of the soil is a possible reason why scree habitats are generally poor in grassland fungi.

In *alpine habitats* the far most common species was *Hygrocybe conica* (49 records), which is rather frequent in snowbeds, and found up to 1450 m a.s.l in the middle alpine zone (Figures 2 and 5). Other species (4-11 records) were *Entoloma asprellum*, *E. caesiocinctum*, *E. corvinum*, *E. papillatum*, *E. prunuloides*, *E. sericellum*, *E. sericeum*, *E. serrulatum*, *E. turci*, *E. xanthochroum*, *Hygrocybe pratensis* and *H. virginea*. Grazed, rich snowbeds have many features in common with seminatural grasslands, and true seminatural grasslands can also occur in the low alpine zone (Moen 1999, Senn-Irlet et al. 1990).

Species occurrences in forests

A total of 121 species were recorded in forests, with 5246 records. In *Hygrocybe* (sensu lato), 3260 records (13.8%) were from forests. In *Entoloma*, 1067 records (11.7%) were from forests; in *Clavaria*, *Clavulinopsis* and *Ramariopsis* 508 records (13.9%); *Geoglossum*, *Microglossum*, and *Trichoglossum* had 234 records (9.5%) in forests, while other genera (*Camarophylloopsis*, *Dermoloma*, *Porpoloma*) had 51 records (8.3%) from forests. *Porpoloma* is rare in forests, the two other genera more frequent. For 33 species,



the frequency of occurrence in forest was lower than expected (Table 3). Some species were never found in forests, like *Entoloma velenovskyi* and *Geoglossum difforme*, whereas several species had < 5% of their records in forests, such as *Entoloma griseocyanum*, *E. infula*, *E. papillatum*, *Geoglossum glutinosum*, *Hygrocybe flavipes*, *H. helobia*, *H. ingrata*, *H. nitrata*, *H. ovina*, *H. turunda*, *H. vitellina*, *Porpoloma metapodium* and *Trichoglossum walteri*.

On the other hand, there were species with a considerable part of their records in forests. E.g. *Entoloma incanum*, *Hygrocybe cantharellus*, *Ramariopsis subtilis* and *Microglossum olivaceum* had more than 30% of their records in forests (Table 3). In the interval of 20-30% of the records in forest there were both species preferring calcareous soil like *Clavulinopsis umbrinella*, *Dermoloma cuneifolium*, *Entoloma bloxamii*, *E. mougeotii* and *H. mucronella*, and more indifferent species like *Hygrocybe*

coccinea, *H. conica* and *H. miniata*. Notable is for instance the difference in habitat preference between the closely related *H. flavipes* (0.6% in forests, less frequent than expected, $p < 0.001$) and *H. lacmus* (19.7% in forests, not significantly different from expected).

Hygrocybe conica constituted the majority of records in several habitat types. Figure 5 shows the observed frequency distribution of *H. conica* compared with the frequency distribution of all species over all habitats. Although the species was commonly found in semi-natural grasslands (ca. 60% of the records, significantly lower than expected, $p < 0.001$), it was overrepresented in other habitats, such as other grasslands, alpine habitats, sand dunes and forests (all $p < 0.001$). *H. conica* alone constituted about 10% of all records in forests, and about 20% of the records of this species was from different forest types.

Among the records from forests, we did a descriptive analysis of information on forest type. There was information on 1324 records said to be found in calcareous forests, that means 25.2% of all records in forests. There was information on 2273 (43.3%) records said to be found in broadleaved forests (mainly forests with *Ulmus*, *Fraxinus*, *Tilia* or *Corylus* as important trees). We also searched for the terms "rich" and "low herb" and for some plant species occurring in rich forests like *Hepatica nobilis* and *Galium odoratum*. Adding this to the information above, we got totally 4375 (83.4%) records found in calcareous or rich/low herb forest types including rich broadleaved forests (and exclusive poor oak forests). For grassland fungi growing in forests, these rich forest types are obviously important. In addition, a total of 489 records (9.3% of forest records) were from "grazed forests", which possibly in many cases also could have been counted as "rich".

There was also a smaller group of records found in more acid forests, like poor boreal deciduous forests and poor oak forests. The species diversity here seems to be rather low, mainly with widespread species, like *Hygrocybe cantharellus*, *H. conica* and *H. reidii* (see also Bendiksen et al. 2008, pp. 60-61). One of the rarer species repeatedly encountered in poor forests was *Hygrocybe lacmus* (Figure 2). *H. cantharellus* has occasionally been found on strongly decayed wood. This substrate has similarities with soil, containing humus and plant roots.

DISCUSSION

Data quality

Our data are based on collections and observations without comprehensive quality control, and there are obviously many possible sources of error. The quality of output data is never better than the quality of input data, and the data should be used with caution. Nevertheless,

many authors point to the big possibilities if such data are used carefully. The availability of open data sources like Species Map Service has made it possible to extract information that may be very useful in scientific work (e.g. Kauserud 2012). The amount of data from Norway can also be compared to 95585 records of 'CHEGD species' in a similar database in the UK according to Griffith et al. (2013), also used for extracting data.

Representativity of sampling

The majority of records in our data were from seminatural grasslands. This could be due to either higher sampling effort (more time spent searching) in seminatural grasslands than in other habitats, to higher detectability of the species in seminatural grasslands, or to higher occurrence of the species in seminatural grasslands. These factors probably influence the observed pattern, but their relative importance is difficult to entangle. We do not know the relative effort of sampling in different habitats. What we know is that there has been a considerable effort investigating seminatural grasslands during the last 25 years. The people sampling in grasslands also collect or note these fungi when searching in other habitats, like forests, but the sampling effort might be lower. The sampling effort in fens may have been lower than in grasslands and forests (Tor Erik Brandrud pers. comm.). Other examples of undersampled habitats might be rocks with shallow soils and scree meadows. However, as a whole we believe that the bias created by different sampling effort between habitats is rather similar between species. Therefore we think that the frequency in different habitats can be compared among species. However, non-significant results of habitat distribution for a species does not mean that a species does not prefer seminatural grassland, but that its distribution is not significantly different

from the overall average of all species in the dataset. This could partly be due to low sampling size (i.e. a low number of records). Knowledge on sampling effort in different habitats would be required to get more solid data on habitat specificity, although the results give some clear indications of relative habitat preferences for several species.

Another bias is related to differences in detectability due to size, colors and presence/lifetime of the carpophores. *Hygrocybe* spp. constitute 59.7% of the records, but only 31.8% of the taxa. These fungi are both big, colourful and possibly more frequently present (long lived, often with fruit bodies) compared to many other genera, and are probably oversampled due to this. Many *Entoloma*'s are smaller, brown, short lived and difficult to determine, while many taxa from *Clavaria*, *Clavulinopsis*, *Ramariopsis*, *Geoglossum*, *Trichoglossum* and *Microglossum* are small and easily overlooked. We think that the bias due to different detectability is rather similar between habitats and therefore not seriously affects the relative frequency between habitats when we compare the species.

Identification

An obvious source of error in the input data is the possibility of misidentifications. We have used a large amount of observations (72.5% of all data) where no control of the determination is possible. On the other hand, collections sent to herbaria are often not controlled either and may have a similar quality as the observations – the difference is only the possibility to control them. *Hygrocybe* s.l. is regarded as a rather well-known group with some exceptions (Boertmann 2010, Lodge et al. 2013). An ongoing Norwegian project on *Entoloma* spp. will probably contribute to changes in species limitations within this genus and even species new to science, but the results are not yet published

or used here. In this situation we have chosen a pragmatic approach. Some poorly understood and rarely collected taxa were initially excluded from the study. All records with information on uncertain determination (cf./aff.) were also excluded. Records of the selected species where the determination is considered valid by the providers of data were included. As two of the authors (GG, JBJ) are responsible for 56.5% of the records, we take our part of the responsibility for this. Generally, data on easily determined species can be trusted more than data on difficult ones.

Habitat information

Another kind of quality is related to the ecological information given in each record. We often had to make an interpretation of what was the meaning in the text describing the habitats, and there is still a potential of improving and standardizing the methods used. Generally, the quality is assumed to be quite good for our purpose. This is partly due to efforts by herbaria and NGOs during the last 20 years to improve the methods of people collecting fungi. As our own data comprise more than a half of the records used here, we were also able to control and improve the quality of the habitat data especially for the aim of this article. Nevertheless the results create many new questions. Based on our own observations, the typical habitat labelled "*Calluna* heath" is in fact often grassy or mossy spots in the heaths, a vegetation type with many features in common with pastures, but detailed information on this is often lacking. So "which species can actually grow in *Calluna* dominated vegetation?" is an example of many questions which may not be properly answered here.

Taxonomic notes

In most genera, several taxonomic problems are not yet solved, but this will not be discussed in detail here. The variation in/around e.g.

Hygrocybe virginea, *H. acutoconica* and *H. conica* is still not completely understood. What has been called *Hygrocybe pratensis* var. *pallida* is probably at least two separate species different from *H. pratensis* (Ellen Larsson pers. comm.). The genus *Entoloma* is very species rich, with sometimes subtle characters separating the species, which can also be variable depending on age of basidiomata and weather conditions (Noordeloos 1992, 2004). The subgenus *Cyanula*, which is important in grasslands, still awaits a comprehensive analysis by molecular methods. The same is the case in parts of Clavariaceae, where some groups have been treated recently (e.g. Kautmanová et al. 2012, Birkebak et al. 2013, Olariaga et al. 2015). In spite of some recent publications on earth tongues (e.g. Arauzo and Iglesias 2014), there are still unsolved problems in *Geoglossum*, *Trichoglossum* and *Microglossum*. Many of the new taxa and redefined species are not yet well understood or investigated in Norway. For example we use *Microglossum olivaceum* in a broad sense including *M. nudipes* which is recently discovered in Norway and Sweden (Kristiansen and Marstad 2015, Persson 2013). The problems with the delimitation of species should generally lead us to be careful about conclusions on ecological differences between closely related taxa. What we believed was one species or even a variety can turn out to comprise two or more species with ecological differences. On the other hand, seemingly separable species can turn out to be one species.

Selection of species

The selection of species is based on the definition of grassland fungi (see Introduction) and some criteria related to data quality (see Material and methods). Several poorly known species have been excluded from our analysis. Some of them are probably belonging among the grassland fungi, supported by data from

other European countries. Here we have to wait for more Norwegian data.

Notes on species and habitats

Generally, the selected species are regarded as grassland species all over Northern Europe (see Introduction). Our results (Tables 2 and 3) show that 83% of the species have less than 20% of their records from forests. For these species, open grassy habitats by far seem to be the most important in Norway. Only for the species with a high number of records, however, we can say this with more confidence. We have also included species with a considerable part of their known Norwegian population in forests. When living in seminatural grasslands, these species seem to have a similar ecology as the other species, also supported by these species listed among grassland fungi in other countries. But these species have a lower degree of habitat specificity. As a conclusion, we can regard the majority of species as having a rather high degree of habitat specificity, preferring seminatural grasslands and similar open, mostly grass- or herb-dominated habitats.

Hygrocybe acutoconica is deviating by having a higher frequency than expected in other grasslands (like road verges) and rocks with shallow soil (Figure 4). This pattern may be due to a preference for calcareous, mineral rich soil poor in humus (sand/clay), and may be shared by more species, e.g. some *Camarophylloopsis* spp., *Clavaria* spp. and *Entoloma incanum*. These species, however, have too few records to give significant results.

Hygrocybe species found by us to occur also in alpine habitats (but which are not true alpine species) are very much the same as reported from the alpine, subarctic or low arctic zone in Greenland, Scandinavia and the Alps (Boertmann 2010, Borgen and Arnolds 2004, Senn-Irlet et al. 1990), like *H. conica*, *H. nitrata*, *H. pratensis* and *H. virginea*.

The same is the case in *Entoloma*, compared with information from Northern Europe in Noordeloos (1992, 2004). As mentioned earlier, true seminatural grasslands can also occur in the low alpine zone (Moen 1999).

Nitare (2014) gives semi-quantitative information on the occurrence of 50 grassland fungi in forests in Sweden. In about 30-35 species there is a good to very good compliance between his results and ours, e.g. regarding most of the *Hygrocybe* spp. However, in some few species the results differ. Species not often observed in forests in Sweden are e.g. *H. miniata* (Table 3: 24.0% in forests in Norway) and *H. punicea* (29.6%). *H. punicea* is on the red list in Sweden but not in Norway, due to the seemingly different habitat specificity between the countries. On the other hand some species are more frequently found in Swedish than in Norwegian forests, like *Geoglossum fallax* (forest records in Norway: 6.3%), *G. glutinosum* (4.0%) and *Hygrocybe fornicata* (7.2%). Nitare (2000) lists 'grassland fungi' used to evaluate management priority of forests in Sweden. He mentions 20 *Hygrocybe* species. Most of these have more than 10% of their records in forests in our data. We find that there are striking similarities between Swedish and Norwegian data, indicating that there are real differences between species of grassland fungi with regard to their occurrence in forests in Scandinavia. Differences in available habitats, habitat quality or climate could possibly explain the observed differences between the two countries within some species.

In the literature, many forest localities with records of grassland fungi are described as moist and shady, often with naked soil (Nitare 2000, Hesler and Smith 1963), in strong contrast to open grassland habitats which are frequently sun exposed and with a dense layer of mosses, grasses and herbs. In our dataset, only 227 of the forest records

were noted on naked soil and additional 140 records on naked soil in tall herb vegetation. Many forest records were from sun exposed forests, but certainly often in regions with a moist climate. Generally, our data on forest vegetation are not very detailed, but the preference in most species for rich forest types seems to be clear (see results).

Boertmann (2010) also describes *Alnus* swamps as a *Hygrocybe* habitat. We found only 16 records of 10 common species (*Clavaria*, *Entoloma*, *Hygrocybe*) in our material describing wetland forests as habitat. The most abundant was *Hygrocybe cantharellus* with 7 records. This is probably a habitat of minor importance in Norway. The same is the case in Sweden (Johan Nitare pers. comm.).

Implications for nature management

The survival of these species is strongly influenced by the decline in seminatural grasslands, a habitat listed as vulnerable (VU) on the Norwegian red list for nature types (Lindgaard and Henriksen 2011). Forest constitutes an important habitat for 23 species (17.0%) having more than 20% of their records in forests. These species are less vulnerable to the loss of seminatural grasslands. This is taken into consideration in the revision of the Norwegian red list, and should be considered in general nature management. However, the forest types most important for these fungi – calcareous or rich/low herb forests – have also declined and cover limited areas, and some of these are also present on the Norwegian red list for nature types (as NT or VU, Lindgaard and Henriksen 2011). Some other open habitats of grassland fungi have also declined during the last decades. Sea shore meadows are exposed to regrowth or habitat destruction and are near threatened (NT, Lindgaard and Henriksen 2011). Coastal heaths (endangered – EN), sand dunes (VU) and waterfall meadows (NT) can also be

subject to regrowth or other changes in land use (Lindgaard and Henriksen 2011). Continued grazing of these habitats is probably important for the fungi. Rich fens have declined in many regions, and are classified as EN in the lowlands (Lindgaard and Henriksen 2011). Grassland fungi in Norway thus seem to have experienced more decline in their populations during the last 50-100 years than most other fungi (Jordal 2010), and therefore deserve high attention when it comes to management measures, like in other European countries (e.g. Arnolds 1988, Griffith et al. 2013, Newton et al. 2003, Nitare 1988).

Is habitat specificity influenced by nutritional strategy?

Knowledge on the nutritional strategy of the grassland fungi treated here could contribute to the understanding of their habitat selection and habitat specificity. This topic has been debated for a long time, some authors arguing that they must have some kind of mycorrhiza (e.g. Nitare 1988, 2014), while others think they are saprotrophs (e.g. Arnolds 1982). These fungi are very difficult to cultivate in the laboratory (Griffith et al. 2013, Lodge et al. 2013). Recent studies have shown that many of them have isotopic signatures indicating that they are neither ectomycorrhizal nor saprotrophic, but could have some kind of biotrophy (Griffith et al. 2002, Seitzman et al. 2011, Birkebak et al. 2013). There are further some recent observations of *Hygrocybe* hyphae, verified by DNA analysis, inside plant tissues and even inside plant cells, like in roots of herbaceous plants, and leaves and seeds of *Plantago lanceolata* (Halbwachs et al. 2013, Tello et al. 2014), indicating endophytic growth and suggesting a close biotrophic relation between grassland fungi and plants. *Hygrocybe coccinea* was also detected in pine trees and mistletoes in Germany and Austria (Persoh 2013), which is interesting in trying to answer the question why 'grassland

fungi' occur in forests. Most questions about their ecology are still unanswered (Lodge et al. 2013, Birkebak et al. 2013). Differences in habitat specificity between species of fungi shown in this paper might be due to differences in nutritional strategy, for instance which plant species they are able to make biotrophic relations to. This will be an exciting topic in the future.

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Table 2. Selected grassland fungi in Norway with ≥ 10 records, collected 1900-2014. RL=Norwegian red list status 2015, Loc=number of localities (calculated for redlisted species only), N=number of records, Sem=seminatural grasslands, Oth=other grasslands (e.g. lawns, parks, road verges), Sea=sea shore meadows, Dun=sand dune meadows, Hea=coastal heath, Wat=waterfall meadows, Roc= rocks with shallow soil, mostly near the sea, Scr=open scree meadows, Fen=fens, Alp=alpine habitats, For=different forest types, TOT=sum of records in all habitats; can exceed N because one record can contain information about more than one type of habitat, % For=the percent of records in forests in relation to N.

Species	RL	Loc	N	Sem	Oth	Sea	Dun	Hea	Wat	Roc	Scr	Fen	Alp	For	TOT	% For
<i>Camarophylloopsis foetens</i>	VU	38	56	42	2	0	1	0	0	4	0	0	0	9	58	16.1
<i>Camarophylloopsis hymenocephala</i>	EN	9	11	3	3	1	0	0	0	2	0	0	0	2	11	18.2
<i>Camarophylloopsis micacea</i>	EN	8	16	3	0	0	0	0	0	3	0	0	0	10	16	62.5
<i>Camarophylloopsis schulzeri</i>	NT	204	274	253	7	2	0	0	0	1	1	0	0	16	280	5.8
<i>Clavaria amoenoides</i>	VU	71	95	85	10	0	0	0	0	0	1	0	0	7	103	7.4
<i>Clavaria falcata</i>	LC		256	167	26	2	0	0	0	19	2	1	0	47	264	18.4
<i>Clavaria flavipes</i>	VU	92	103	94	6	0	0	0	0	1	0	0	0	8	109	7.8
<i>Clavaria fragilis</i>	LC		264	203	25	0	0	2	0	6	1	0	0	38	275	14.4
<i>Clavaria fumosa</i>	NT	144	191	161	5	0	0	0	0	2	0	0	0	31	199	16.2
<i>Clavaria greletii</i>	VU	9	11	6	2	0	1	0	0	1	0	0	0	2	12	18.2
<i>Clavaria pullei</i>	VU	11	15	12	1	0	0	0	0	0	0	0	0	2	15	13.3
<i>Clavaria rosea</i>	VU	19	24	11	14	0	1	0	0	0	0	0	0	1	27	4.2
<i>Clavaria zollingeri</i>	VU	162	235	206	7	1	0	0	0	2	0	0	0	26	242	11.1
<i>Clavulinopsis corniculata</i>	LC		625	462	40	10	0	0	1	14	1	3	2	114	647	18.2
<i>Clavulinopsis fusiformis</i>	VU	18	21	18	1	0	1	2	0	1	0	0	0	2	25	9.5
<i>Clavulinopsis helvola</i>	LC		848	757	30	11	2	10	1	3	0	0	0	64	878	7.5
<i>Clavulinopsis laeticolor</i>	LC		328	261	11	10	0	2	0	9	0	0	2	48	343	14.6
<i>Clavulinopsis luteoalba</i>	LC		440	377	14	4	0	8	0	3	0	0	2	48	456	10.9
<i>Clavulinopsis umbrinella</i>	NT	60	83	62	3	0	0	0	0	3	0	0	0	20	88	24.1
<i>Dermoloma cuneifolium</i>	VU	35	66	41	9	1	0	0	0	2	0	0	0	16	69	24.2
<i>Dermoloma pseudocuneifolium</i>	VU	14	21	15	1	0	0	0	0	1	2	0	0	5	24	23.8

Species	RL	Loc	N	Sem	Oth	Sea	Dun	Hea	Wat	Roc	Scr	Fen	Alp	For	TOT	% For
<i>Entoloma aethiops</i>	VU	9	14	12	0	0	0	0	0	1	0	0	2	2	17	14.3
<i>Entoloma ameides</i>	NT	25	34	25	3	1	0	0	0	0	0	0	0	9	38	26.5
<i>Entoloma anatinum</i>	VU	10	12	10	0	0	0	2	0	1	0	0	0	1	14	8.3
<i>Entoloma asprellum</i>	LC		340	270	9	4	0	2	0	1	0	5	6	60	357	17.6
<i>Entoloma atrocoeruleum</i>	NT	133	195	169	4	5	0	1	0	7	0	2	1	15	204	7.7
<i>Entoloma bloxamii</i>	VU	76	115	77	5	0	0	12	0	5	0	2	1	31	133	27.0
<i>Entoloma caeruleopolitum</i>	VU	63	77	75	1	0	0	0	0	0	0	0	1	1	78	1.3
<i>Entoloma caeruleum</i>	DD	13	20	12	0	0	0	0	0	0	0	2	0	6	20	30.0
<i>Entoloma caesiocinctum</i>	LC		364	243	11	0	4	2	5	1	3	10	5	110	394	30.2
<i>Entoloma chalybeum</i>	NT	166	209	174	9	4	2	2	0	5	0	0	1	22	219	10.5
<i>Entoloma cocles</i>	VU	39	45	43	0	0	0	1	0	1	0	0	0	3	48	6.7
<i>Entoloma coeruleoflocculosum</i>	VU	8	16	9	0	0	0	0	0	0	0	0	2	7	18	43.8
<i>Entoloma corvinum</i>	NT	234	289	239	11	14	3	3	0	1	0	2	5	30	308	10.4
<i>Entoloma cremeoalbum</i>	EN	4	11	11	0	0	0	0	0	0	0	0	0	0	11	0.0
<i>Entoloma cruentatum</i>	VU	10	13	12	0	0	0	0	0	0	0	0	0	1	13	7.7
<i>Entoloma cuspidiferum</i>	DD	9	16	15	0	0	0	0	0	0	0	0	0	1	16	6.3
<i>Entoloma cyanulum</i>	DD	10	12	8	1	0	0	0	0	0	0	1	0	2	12	16.7
<i>Entoloma excentricum</i>	VU	17	20	12	3	1	0	0	0	3	1	0	0	1	21	5.0
<i>Entoloma exile</i>	LC		269	237	8	3	0	2	1	1	1	3	2	21	279	7.8
<i>Entoloma formosum</i>	LC		234	169	22	2	1	3	0	1	0	4	2	44	248	18.8
<i>Entoloma fuscotomentosum</i>	NT	20	21	17	0	2	0	0	0	1	0	0	0	1	21	4.8
<i>Entoloma griseocyaneum</i>	NT	390	549	518	17	17	1	1	0	7	1	0	3	10	575	1.8
<i>Entoloma incanum</i>	NT	49	75	24	15	1	2	0	0	8	1	1	1	33	86	44.0
<i>Entoloma infula</i>	LC		328	302	4	2	0	1	0	1	1	2	2	18	333	5.5
<i>Entoloma jubatum</i>	NT	132	188	156	5	2	1	1	0	0	0	2	3	25	195	13.3

Species	RL	Loc	N	Sem	Oth	Sea	Dun	Hea	Wat	Roc	Scr	Fen	Alp	For	TOT	% For
<i>Entoloma kervernii</i>	VU	21	32	30	1	1	0	1	0	0	0	0	1	0	34	0.0
<i>Entoloma lividocyanulum</i>	LC		127	100	6	1	0	2	1	1	0	2	3	21	137	16.5
<i>Entoloma longistriatum</i>	LC		215	176	6	2	0	2	0	2	0	3	3	26	220	12.1
<i>Entoloma melanochroum</i>	VU	25	30	26	0	0	0	0	0	0	0	1	0	4	31	13.3
<i>Entoloma mougeotii</i>	NT	190	243	149	15	5	1	3	0	10	2	23	3	56	267	23.0
<i>Entoloma neglectum</i>	VU	12	13	8	3	0	0	0	0	0	1	0	0	1	13	7.7
<i>Entoloma papillatum</i>	LC		513	460	21	7	2	3	0	9	0	1	4	21	528	4.1
<i>Entoloma polioopus</i>	LC		561	472	8	7	2	6	3	8	3	5	5	55	574	9.8
<i>Entoloma polito flavipes</i>	NT	15	16	15	0	0	1	0	0	0	0	0	0	0	16	0.0
<i>Entoloma porphyrophaeum</i>	VU	81	100	93	3	1	1	0	0	0	0	0	1	9	108	9.0
<i>Entoloma pratulense</i>	VU	92	110	103	6	2	0	0	0	2	0	0	3	7	123	6.4
<i>Entoloma prunuloides</i>	NT	338	548	485	8	8	1	10	0	18	0	1	5	33	569	6.0
<i>Entoloma pseudocoelestinum</i>	VU	28	33	30	0	0	0	0	0	1	0	1	1	1	34	3.0
<i>Entoloma pseudoturci</i>	DD	23	27	25	0	1	0	0	0	0	1	0	1	1	29	3.7
<i>Entoloma queletii</i>	NT	24	37	26	0	0	0	0	0	5	0	1	2	7	41	18.9
<i>Entoloma rhombisporum</i>	VU	128	178	155	8	2	0	0	0	5	1	1	3	15	190	8.4
<i>Entoloma sacchariolens</i>	VU	9	12	11	0	0	1	0	0	0	0	0	2	0	14	0.0
<i>Entoloma scabropellis</i>	DD	13	15	12	1	1	0	0	0	1	0	0	0	1	16	6.7
<i>Entoloma sericellum</i>	LC		896	688	51	12	5	7	0	16	1	3	5	145	933	16.2
<i>Entoloma sericeum</i>	LC		954	803	73	25	10	6	0	5	3	1	7	53	986	5.6
<i>Entoloma serrulatum</i>	LC		543	399	24	12	4	3	0	12	3	8	7	100	572	18.4
<i>Entoloma sodale</i>	VU	13	18	13	2	0	0	0	0	1	0	2	2	2	22	11.1
<i>Entoloma turci</i>	NT	117	169	136	9	1	0	0	0	12	0	1	8	13	180	7.7
<i>Entoloma undatum</i>	LC		164	98	12	4	2	2	0	4	0	2	2	41	167	25.0
<i>Entoloma velenovskyi</i>	VU	31	38	36	2	0	0	0	0	1	0	0	1	0	40	0.0

Species	RL	Loc	N	Sem	Oth	Sea	Dun	Hea	Wat	Roc	Scr	Fen	Alp	For	TOT	% For
<i>Entoloma xanthochroum</i>	LC		60	55	1	0	0	0	0	0	0	1	6	3	66	5.0
<i>Geoglossum cookeanum</i>	NT	49	97	61	10	12	16	0	0	1	0	0	1	5	106	5.2
<i>Geoglossum difforme</i>	EN	22	77	74	1	4	1	8	0	0	0	0	0	0	88	0.0
<i>Geoglossum fallax</i>	LC		498	387	71	8	2	2	0	7	0	0	1	32	510	6.4
<i>Geoglossum glutinosum</i>	LC		339	284	36	4	0	4	0	5	0	0	0	14	347	4.1
<i>Geoglossum hakelieri</i>	EN	3	11	11	0	0	0	0	0	0	0	0	0	0	11	0.0
<i>Geoglossum simile</i>	NT	43	65	50	5	0	1	2	0	1	0	4	0	2	65	3.1
<i>Geoglossum starbaeckii</i>	LC		144	111	15	0	0	0	0	1	0	0	1	19	147	13.2
<i>Geoglossum uliginosum</i>	VU	15	28	26	1	0	0	0	0	0	0	1	0	1	29	3.6
<i>Geoglossum umbratile</i>	LC		379	265	71	5	2	1	0	4	0	0	1	35	384	9.2
<i>Hygrocybe acutoconica</i>	LC		567	370	85	14	16	4	0	30	3	1	3	78	604	13.8
<i>Hygrocybe aurantiosplendens</i>	NT	110	162	131	12	3	2	0	0	1	0	1	0	32	182	19.8
<i>Hygrocybe calciphila</i>	VU	27	31	20	3	2	0	0	0	8	0	0	1	0	34	0.0
<i>Hygrocybe calyptriformis</i>	EN	8	10	10	0	0	0	0	0	0	0	0	0	0	10	0.0
<i>Hygrocybe canescens</i>	EN	18	24	23	1	2	0	1	0	0	0	0	0	0	27	0.0
<i>Hygrocybe cantharellus</i>	LC		840	523	48	8	3	9	0	7	2	13	0	276	889	32.9
<i>Hygrocybe ceracea</i>	LC		1316	1179	47	18	1	6	0	6	1	0	2	85	1345	6.5
<i>Hygrocybe chlorophana</i>	LC		1281	1086	59	20	3	11	1	6	0	2	0	142	1330	11.1
<i>Hygrocybe citrinovirens</i>	EN	9	19	18	1	0	0	0	0	0	0	0	0	0	19	0.0
<i>Hygrocybe coccinea</i>	LC		1250	920	53	15	2	16	1	11	3	5	2	277	1305	22.2
<i>Hygrocybe colemanniana</i>	VU	139	238	215	12	5	0	0	0	4	0	0	1	13	250	5.5
<i>Hygrocybe conica</i>	LC		2516	1591	306	42	34	19	4	31	7	7	54	532	2627	21.1
<i>Hygrocybe flavipes</i>	NT	204	347	339	9	2	0	1	0	0	0	0	2	2	355	0.6
<i>Hygrocybe fornicata</i>	NT	206	317	286	17	1	0	0	0	3	0	0	2	24	333	7.6
<i>Hygrocybe glutinipes</i>	LC		237	204	18	2	0	1	0	1	0	0	0	21	247	8.9

Species	RL	Loc	N	Sem	Oth	Sea	Dun	Hea	Wat	Roc	Scr	Fen	Alp	For	TOT	% For
<i>Hygrocybe helobia</i>	LC		405	374	10	2	0	11	0	1	0	8	1	10	417	2.5
<i>Hygrocybe ingrata</i>	VU	222	340	329	5	4	0	1	0	0	0	0	4	10	353	2.9
<i>Hygrocybe insipida</i>	LC		721	599	27	10	0	6	0	3	0	0	0	90	735	12.5
<i>Hygrocybe intermedia</i>	VU	73	126	115	8	1	0	0	0	0	0	0	0	7	131	5.6
<i>Hygrocybe irrigata</i>	LC		549	478	12	5	0	8	0	1	0	1	0	59	564	10.7
<i>Hygrocybe lacmus</i>	NT	163	218	184	8	3	1	3	1	1	1	0	0	43	245	19.7
<i>Hygrocybe laeta</i>	LC		1228	1075	32	8	2	23	1	7	0	3	3	122	1276	9.9
<i>Hygrocybe miniata</i>	LC		533	340	48	8	3	1	0	5	0	17	6	135	563	25.3
<i>Hygrocybe mucronella</i>	NT	136	210	146	12	3	0	1	1	2	3	2	1	53	224	25.2
<i>Hygrocybe nitrata</i>	NT	567	887	838	19	7	1	5	0	1	0	0	3	31	905	3.5
<i>Hygrocybe ovina</i>	VU	119	201	191	4	5	1	1	0	0	0	0	0	9	211	4.5
<i>Hygrocybe phaeococcinea</i>	LC	194	249	218	30	3	0	2	0	0	0	0	0	10	263	4.0
<i>Hygrocybe pratensis</i>	LC		1918	1593	74	19	1	10	0	8	2	2	6	266	1981	13.9
<i>Hygrocybe pratensis</i> var. <i>pallida</i>	LC		77	73	2	1	0	0	0	0	3	0	0	4	83	5.2
<i>Hygrocybe psittacina</i>	LC		1408	1231	42	17	7	15	0	8	2	1	2	130	1455	9.2
<i>Hygrocybe punicea</i>	LC		861	591	22	7	0	13	0	4	1	0	1	269	908	31.2
<i>Hygrocybe quieta</i>	NT	289	480	408	11	3	1	3	0	4	1	0	3	69	503	14.4
<i>Hygrocybe reidii</i>	LC		1240	1057	24	10	1	11	2	7	2	2	0	170	1286	13.7
<i>Hygrocybe russocoriacea</i>	NT	244	442	379	11	25	9	13	0	13	0	5	2	26	483	5.9
<i>Hygrocybe spadicea</i>	EN	19	23	18	3	0	0	0	0	2	0	0	0	1	24	4.3
<i>Hygrocybe splendidissima</i>	VU	247	438	423	6	3	0	6	0	1	0	0	0	23	462	5.3
<i>Hygrocybe subpapillata</i>	VU	29	41	37	5	0	0	0	0	0	0	0	0	1	43	2.4
<i>Hygrocybe turunda</i>	VU	114	151	138	4	2	0	0	0	2	0	1	1	5	153	3.3
<i>Hygrocybe virginea</i>	LC		1724	1299	163	29	13	13	1	21	2	5	15	238	1799	13.8
<i>Hygrocybe virginea</i> var. <i>fuscescens</i>	LC		59	45	2	1	2	0	0	4	0	1	1	6	62	10.2

Species	RL	Loc	N	Sem	Oth	Sea	Dun	Hea	Wat	Roc	Scr	Fen	Alp	For	TOT	% For
<i>Hygrocybe virginea</i> var. <i>ochraceopallida</i>	LC		18	13	0	1	3	0	0	2	0	0	0	1	20	5.6
<i>Hygrocybe vitellina</i>	VU	40	71	67	1	1	0	2	0	1	0	0	1	1	74	1.4
<i>Microglossum atropurpureum</i>	VU	110	235	195	14	4	3	1	0	0	0	0	0	24	241	10.2
<i>Microglossum fuscorubens</i>	VU	57	75	40	3	5	1	0	0	7	0	0	0	21	77	28.0
<i>Microglossum olivaceum</i>	VU	49	100	44	11	2	1	0	0	3	0	0	0	41	102	41.0
<i>Porpoloma metapodium</i>	EN	96	188	178	4	2	0	2	0	0	0	0	0	3	189	1.6
<i>Ramariopsis crocea</i>	VU	31	37	7	1	0	0	0	0	2	1	0	0	27	38	73.0
<i>Ramariopsis kunzei</i>	LC		144	59	8	0	0	1	0	5	2	0	0	76	151	52.8
<i>Ramariopsis subtilis</i>	NT	85	109	55	7	0	0	0	0	3	0	0	0	50	115	45.9
<i>Trichoglossum hirsutum</i>	LC		217	146	21	7	5	2	0	3	1	9	1	34	229	15.7
<i>Trichoglossum walteri</i>	VU	121	202	185	7	4	0	10	0	0	0	0	0	6	212	3.0
TOTAL			39818	32034	2147	561	188	351	24	487	64	188	240	5246	41530	13.2
Percent			100	80.45	5.39	1.41	0.47	0.88	0.06	1.22	0.16	0.47	0.60	13.17		
Number of species			132	132	113	88	52	68	14	98	35	52	68	121		

Table 3. Overview of species with frequency of occurrence in seminatural grasslands or forest habitats which significantly deviated from the average, sorted alphabetically within 5% intervals of occurrences in forest. Asterisks refer to Chi-square tests of observed frequency against expected frequency of 77.1% of occurrences in seminatural grasslands and 12.6% of occurrences in forest. The analyses are based on 41530 unique species-habitat records (sum of TOT in Table 2), and consequently the frequencies reported here deviate slightly from the frequencies in Table 2 (evaluated based on N). · p < 0.10, * p < 0.05, p < 0.01, *** p < 0.001.

Species	Red list status	No. of records	% seminatural grassland	% forest
0-5% of records in forest				
<i>Entoloma caeruleopolitum</i>	VU	78	96.2	1.3 **
<i>Entoloma griseocyaneum</i>	NT	575	90.1 *	1.7 ***
<i>Entoloma papillatum</i>	LC	528	87.1 ·	4.0 ***
<i>Entoloma velenovskyi</i>	VU	40	90.0	0.0 *
<i>Geoglossum cookeanum</i>	NT	106	57.5 ·	4.7 *
<i>Geoglossum difforme</i>	EN	88	84.1	0.0 **
<i>Geoglossum glutinosum</i>	LC	347	81.9	4.0 ***
<i>Hygrocybe flavipes</i>	NT	355	95.5 **	0.6 ***
<i>Hygrocybe helobia</i>	LC	417	89.7 *	2.4 ***
<i>Hygrocybe ingrata</i>	VU	353	93.2 *	2.8 ***
<i>Hygrocybe nitrata</i>	NT	905	92.6 ***	3.4 ***
<i>Hygrocybe ovina</i>	VU	211	90.5	4.3 **
<i>Hygrocybe phaeococcinea</i>	LC	263	82.9	3.8 ***
<i>Hygrocybe turunda</i>	VU	153	90.2	3.3 **
<i>Hygrocybe vitellina</i>	VU	74	90.5	1.4 *
<i>Porpoloma metapodium</i>	EN	189	94.2 ·	1.6 ***
<i>Trichoglossum walteri</i>	VU	212	87.3	2.8 ***
5-10% in forest				
<i>Camarophylloopsis schulzeri</i>	NT	280	90.4 ·	5.7 **
<i>Clavulinopsis helvola</i>	LC	878	86.2 *	7.3 ***
<i>Entoloma exile</i>	LC	279	84.9	7.5 *
<i>Entoloma infula</i>	LC	333	90.7 *	5.4 ***
<i>Entoloma pratulense</i>	VU	123	83.7	5.7 *
<i>Entoloma prunuloides</i>	NT	569	85.2	5.8 ***

Species	Red list status	No. of records	% seminatural grassland	% forest
<i>Entoloma sericeum</i>	LC	986	81.4	5.4 ***
<i>Geoglossum fallax</i>	LC	510	75.9	6.3 ***
<i>Hygrocybe acutoconica</i>	LC	604	61.3 ***	12.9
<i>Hygrocybe ceracea</i>	LC	1345	87.7 **	6.3 ***
<i>Hygrocybe colemanniana</i>	VU	250	86.0	5.2 **
<i>Hygrocybe fornicata</i>	NT	333	85.9	7.2 **
<i>Hygrocybe intermedia</i>	VU	131	87.8	5.3 *
<i>Hygrocybe laeta</i>	LC	1276	84.2 *	9.6 **
<i>Hygrocybe psittacina</i>	LC	1455	84.6 *	8.9 ***
<i>Hygrocybe russocoriacea</i>	NT	483	78.5	5.4 ***
<i>Hygrocybe splendidissima</i>	VU	462	91.6 *	5.0 ***
15-20% in forest				
<i>Clavaria falcata</i>	LC	264	63.3	17.8 *
<i>Clavulinopsis corniculata</i>	LC	647	71.4	17.6 **
<i>Entoloma asprellum</i>	LC	357	75.6	16.8 *
<i>Entoloma formosum</i>	LC	248	68.1	17.7 *
<i>Entoloma sericellum</i>	LC	933	73.7	15.5 *
<i>Entoloma serrulatum</i>	LC	572	69.8	17.5 **
20-30% in forest				
<i>Clavulinopsis umbrinella</i>	NT	88	70.5	22.7 *
<i>Dermoloma cuneifolium</i>	VU	69	59.4	23.2 *
<i>Entoloma bloxamii</i>	VU	133	57.9	23.3 **
<i>Entoloma caesiocinctum</i>	LC	394	61.7 **	27.9 ***
<i>Entoloma mougeotii</i>	NT	267	55.8 **	21.0 ***
<i>Entoloma undatum</i>	LC	167	58.7 *	24.6 ***
<i>Hygrocybe coccinea</i>	LC	1305	70.5 *	21.2 ***
<i>Hygrocybe conica</i>	LC	2627	60.6 ***	20.3 ***
<i>Hygrocybe miniata</i>	LC	563	60.4 ***	24.0 ***
<i>Hygrocybe mucronella</i>	NT	224	65.2	23.7 ***

Species	Red list status	No. of records	% seminatural grassland	% forest
<i>Hygrocybe punicea</i>	LC	908	65.1 **	29.6 ***
<i>Microglossum fuscorubens</i>	VU	77	51.9 ·	27.3 **
30-40% in forest				
<i>Entoloma coeruleoflocculosum</i>	VU	18	50.0	38.9 *
<i>Entoloma incanum</i>	NT	86	27.9 ***	38.4 ***
<i>Hygrocybe cantharellus</i>	LC	889	58.8 ***	31.0 ***
> 40% in forest				
<i>Camarophylloopsis micacea</i>	EN	16	18.8 *	62.5 ***
<i>Microglossum olivaceum</i>	VU	102	43.1 **	40.2 ***
<i>Ramariopsis crocea</i>	VU	38	18.4 ***	71.1 ***
<i>Ramariopsis kunzei</i>	LC	151	39.1 ***	50.3 ***
<i>Ramariopsis subtilis</i>	NT	115	47.8 **	43.5 ***