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Ectomycorrhizal fungi in wood-pastures: Communities are determined by trees and soil properties, not by grazing

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Abstract

Traditional rural biotopes such as wood-pastures are species-rich environments that have been created by low-intensity agriculture. Their amount has decreased dramatically during the 20th century in whole Europe due to the intensification of agriculture. Wood-pastures host some fungal species that prefer warm areas and are adapted to semi-open conditions, but still very little is known about fungi in these habitats. We studied how management, historical land-use intensity, present grazing intensity, time since abandonment, and stand conditions affect the species richness and community composition of ectomycorrhizal fungi. We surveyed fruit bodies on three 10 m x 10 m study plots in 36 sites and repeated the surveys three times. Half of the sites were currently unmanaged but had a grazing history. We measured soil pH,

soil moisture and the basal area of different tree species, and interviewed landowners about grazing history. We found that the proportion of broadleaved trees, soil pH, and soil moisture are the major drivers of the communities of ectomycorrhizal fungi in boreal wood-pastures. Management or grazing intensity did not have significant effects on fungal species richness, whereas historical land-use intensity seemed to have a negative effect on species richness. To conclude, present stand conditions are the most important factors to evaluate when planning the conservation of ectomycorrhizal fungi living in semi-open forest habitats.

1. INTRODUCTION

Traditional rural biotopes are species-rich habitats that have been formed by low-intensity agriculture. Wood-pastures are forested traditional rural biotopes that have been grazed by domestic animals for up to hundreds of years. Long grazing history has notably changed their vegetation structure. Moreover, patchy grazing pressure and commonly performed selective logging have resulted in mosaic-like habitats where open, semi-open and closed patches alternate (Garbarino et al., 2011; Schulman et al., 2008; Vainio et al., 2001; WallisDeVries et al., 1998). In the boreal zone some wood-pastures have quite closed stand structure and they have also been called forest pastures (sensu Takala et al., 2014).

The area of traditional rural biotopes has decreased steeply during the 20th century in all European countries (Garbarino et al., 2011; Pykälä and Alanen, 2004). Land abandonment and farming intensification are the main reasons why biodiversity and the amount of these habitats have decreased. In Finland, traditional rural biotopes and many species adapted to these habitats are now threatened. Less than 1 % of

wood-pastures remain compared to the area in the 1950's, which was already much lower than in the 1800's (Rassi et al., 2010; Schulman et al., 2008).

Traditional rural biotopes host high biodiversity, which is proposed to be caused by management, high habitat heterogeneity, an intermediate disturbance regime, long grazing history, and variable soil properties (e.g. Benton et al., 2003; Cousins and Eriksson, 2002; Oldén et al., 2016; Paltto et al., 2011; Pykälä, 2003, 2001; Saarinen and Jantunen, 2005; Vujnovic et al., 2002). Currently grazed grasslands and wood-pastures have been shown to have higher plant species richness than abandoned ones (e.g. Dullinger et al., 2003; Oldén et al., 2016; Pykälä, 2003). Grazing benefits plant species richness by removing vegetation and breaking the soil surface, and this gives more space to weakly competitive species and thus increases species richness (Olf and Ritchie, 1998; Pykälä, 2001). The amount of light and soil temperature are increased by grazing (Olf and Ritchie, 1998; Pykälä, 2001), which improves the growth conditions for many fungal species (Nitare and Sunhede, 1993). Grazing has been proposed to benefit many fungal species (Jakobsson, 2005; Nauta and Jalink, 2001; Nitare and Sunhede, 1993). It has been found that while mowing increases grassland fungal species richness (Griffith et al., 2012), grazing provides a wider range of opportunities to fungal species than mowing (Nauta and Jalink, 2001). Grazing increases heterogeneity by creating a mosaic of vegetation and thus it creates various habitat patches for many species (Nauta and Jalink, 2001; Olf and Ritchie, 1998). According to the intermediate disturbance hypothesis it is expected that species richness is highest at intermediate grazing intensity, where habitat heterogeneity is also maximized (Grime, 1973; Milchunas et al., 1988; Mwendera et al., 1997; Vujnovic et al., 2002).

Most species-rich traditional rural biotopes have been grazed or mowed with traditional methods for a long time (Cousins and Eriksson, 2002; Mykkestad and Saetersdal, 2003; Pykälä, 2003). However, Oldén et al. (2016) did not find clear effects of historical land-use intensity on plant species richness in wood-pastures. In contrast, Lindborg and Eriksson (2004) found that historical landscape connectivity has a strong effect on plant species richness in semi-natural grasslands. Many characteristic grassland fungal species are dependent on continuous management that has lasted for decades (Arnolds, 2001).

Soil properties affect species richness and communities in traditional rural biotopes (Oldén et al., 2016; Raatikainen et al., 2007; Roem and Berendse, 2000). Vascular plant and bryophyte species richness has been shown to increase with increasing soil pH (Oldén et al., 2016; Roem and Berendse, 2000). Rousk et al. (2009) found that on arable managed land fungal growth was maximized at pH 4.5 and decreased both above and below that. Also, soil moisture has been shown to affect fungal communities (Kaisermann et al., 2015; McHugh and Schwartz, 2016). It is suggested that fungal populations are sensitive to soil moisture, and water treatments decrease fungal diversity (Kaisermann et al., 2015; McHugh and Schwartz, 2016).

Many of the fungal studies are focused on macrofungi species in grasslands (e.g. Arnolds, 2001; Nauta and Jalink, 2001; Öster, 2008). Fungal species from ectomycorrhizal and coprophilous species groups cannot fruit in mowed grasslands, but could have rich communities in grazed wood-pastures (Nauta and Jalink, 2001). Juutilainen et al. (2016) found that the species richness of wood-inhabiting fungi in wood-pastures was lower than in natural herb-rich forests, but wood-pastures hosted some red-listed species and other unique species that were not found in the other studied habitats. Only one study has focused on species of ectomycorrhizal fungi in

wooded meadows (Tedersoo et al., 2006). They found that communities of mycorrhizal fungi in managed and forested old wooded meadows differ, but species richness did not differ significantly.

The low number of studies on mycorrhizal fungi is alarming because they have an important role in ecosystems (Boddy et al., 2008). It is known that at least 95% of vascular plants have mycorrhizal associations (Moore et al., 2011). There are both specific and non-specific associations between mycorrhizal fungi species and their host trees (Molina et al., 1992; Moore et al., 2011). The reason for low number of fungal studies might be that they are difficult to identify and that there are few specialists who are able to conduct the studies (Boertmann, 1995; Watling, 1995).

In order to attain more knowledge on species of ectomycorrhizal fungi inhabiting wood-pastures, we studied the effects of management, grazing history, grazing intensity, time since abandonment and stand conditions on species richness and communities of ectomycorrhizal fungi in wood-pastures dominated by broadleaved, coniferous and mixed trees in the boreal zone. Based on earlier studies we hypothesized that grazing increases fungal species richness and has an effect on community composition, while species richness decreases after abandonment. We also hypothesized that high historical land-use intensity increases species richness, and that present intermediate grazing pressure creates highest species richness. Thus, our main questions were: (1) Do grazed sites have higher species richness than abandoned sites? (2) Does species richness increase with increasing historical land-use intensity? (3) Does the species richness increase with grazing intensity or does it peak with intermediate grazing intensity? (4) Does the species richness increase with time since abandonment or does it peak after abandonment? (5) Is there a difference between fungal communities among grazed and abandoned sites? and (6) How do the

present stand conditions affect species richness and community assembly in wood-pastures?

2. MATERIALS AND METHODS

2.1. Study sites

We confined our study to the province of Central Finland to reduce biological and geographical background variation in the data set. We studied 36 sites. The sites were located in 30 farms so in each farm there were one or two study sites. 32 of the sites were located in the Southern boreal and four in the Middle boreal vegetation zone (Ahti et al., 1968) (Figure 1a).

We conducted our study in broadleaved (birch-dominated, *Betula spp.*), coniferous (spruce-dominated, *Picea abies*), and mixed (with a coniferous-broadleaved mixture of *Picea abies*, *Pinus sylvestris*, *Betula spp.*, *Populus tremula*, *Alnus incana*, *Sorbus aucuparia* or a subset of these) wood-pastures, and in each of these three tree classes we included 12 sites. Half of the sites in each class were currently grazed and the other had been abandoned (not grazed currently but had been grazed during the recent history by domestic animals). Because our aim was to study the effects of grazing, we aimed to reduce the variation caused by different stand structure through selecting grazed and abandoned areas with similar tree densities (mature trunks/ha). We could not control the variation in growth site type (which varied from herb-rich to mesic heath) (see Hotanen et al., 2008) or the type of grazing animals because of the small number of potential sites. More information on the study sites is provided in Oldén et al. (2016).

Grazed sites were grazed yearly during the summer-autumn period by cattle, horses or sheep. The grazing regime and intensity varies between sites because they

are managed by private farmers. In most farms, grazing started in late May or in June and ended in September or when forage was depleted. Most farms use rotational grazing where the animals are moved to a new pasture when forage is depleted. The animals may graze the study site once or more times during the grazing season.

2.2. Data collection

At each study site we established three 10 m x 10 m square study plots based on the dominant tree species and the density of mature trees. Among all study sites, the study plots were at least 17 meters apart from each other. The whole selection procedure was conducted without paying any attention to the ground level vegetation, and during a season with almost no macrofungi producing fruit bodies (June-early July). Thus, other species than trees did not affect the study plot selection.

Within the study plots, we recorded fungi growing on the ground and on the surface of dead wood lying on the ground. We surveyed the ground very carefully by pushing plants aside, but did not turn over dead wood pieces to avoid affecting the fungal assemblage on the plots. We counted all the fruit bodies of stipitate ectomycorrhizal macrofungi.

We repeated the surveys three times among all the study sites. Ten of the birch-dominated study sites were surveyed three times during September-October in 2010. The remaining two birch-dominated sites as well as all mixed and spruce-dominated study sites were surveyed twice in August-September 2012 and once in September-October 2013. We identified fungi to species level at the site when possible, but collected specimens for microscopic identification if needed (altogether 1100 specimens). The abundance of each species in a plot was estimated by counting the number of fruit bodies. With fungi it is difficult to define which fruit bodies belong to one individual (Dahlberg and Mueller, 2011), so the fruit body count does not directly

reflect the number of individuals on the plot, but is more like a surrogate of the abundance of the species. While counting the fruit bodies we removed them from the ground to avoid counting the same fruit bodies during the next survey.

We separated mycorrhizal species from other species based on the ecological information provided in Knudsen and Vesterholt (2012), Kotiranta et al. (2009), and Kytövuori et al. (2005). Species that were reported in the literature to use both mycorrhizal and saprotrophic strategy (*Hydnum repandum*, *Hydnum rufescens* coll., etc.) were excluded except for *Paxillus involutus* that was reported to be mainly mycorrhizal. We included only species level data in the analyses. The nomenclature of agarics and boletoids follows Knudsen and Vesterholt (2012) and Aphylloporales Kotiranta et al. (2009). A few exceptions in the nomenclature are indicated by showing the author names in the species list (Table 1 in the Appendix B). These exceptions are situations where Nordic taxonomists currently disagree with the references that we used for nomenclature. The voucher specimens are preserved in the herbarium of the National History Museum of University of Jyväskylä (JYV) and in the personal collection of Kaisa Tervonen.

2.3. Background variables

Measuring historical land-use intensity proved to be complicated in the study area in Central Finland. It was not possible to reliably measure the age of each farm, because historical church records or cadastres do not specify the locations of the farms and properties. Agricultural records have only been collected from the 1920's onwards. In addition, in the 1800's free cattle grazing outside of fenced fields meant that cattle from different farms grazed in the forests surrounding villages (Jäntti, 1945). Thus, we created a surrogate for the historical land-use intensity by counting the number of surrounding farms (within one kilometer buffer zone around each site) in old cadastral

maps drawn in the 1850's and 1860's. We assumed that the number of surrounding farms correlates with historical grazing intensity and other traditional agricultural activities.

For the abandoned sites the landowners provided information about the year when the site had been abandoned. Time since abandonment varied between 7 and 42 years (calculated for year 2012 for all abandoned sites). We don't know the number of animals present in each of the sites but we evaluated grazing intensity at the end of grazing season (September or October 2012). It was evaluated in 2 m x 2 m subplots that were placed inside each corner of each study plot. Thus we had 12 subplots in each site. Grazing intensity was estimated as the proportion of clipped shoots out of all vascular plant shoots that had been at least 5 cm high. This measure was used in analyses as an average value for the whole study site. See more information about the measurements in Oldén et al. (2016). We note that even though the fungal species were surveyed in ten birch-dominated sites in 2010, the grazing intensity was measured also in these sites in 2012. Data on the carrying capacity or stocking rate of the pastures were not available, but based on our visual estimates the grazing intensity was usually at the same level between different years. Examples of vegetation in sites with different grazing intensities are shown in Figure 1b-d.

We also collected soil samples from each study plot in June 2013 to measure soil pH and soil moisture. The average value of the three plots was used for each study site in the analyses. See more information on the sampling in Oldén et al. (2016). Within the plots we measured the diameter at breast height (130 cm) of each tree that was at least 130 cm high. The diameters were used to calculate the basal area of trees. For each site, we calculated the proportion of broadleaved trees out of the

basal area of all trees. In addition, we calculated the species richness of trees in each site.

2.4. Statistical analyses

We conducted all the statistical analyses on site-level data and built separate models for all sites, grazed sites and abandoned sites. All statistical analyses were performed with R version 3.3.0 (R Core Team, 2016).

2.4.1. Tests among explanatory variables

We tested correlations between the continuous explanatory variables to find out possible collinearity in the statistical models (Spearman's rank correlation). Soil pH correlated significantly with soil moisture, tree species richness, and the proportion of broadleaved trees (Table 1 in the Appendix A). Also, time since abandonment correlated significantly with soil moisture and the proportion of broadleaved trees. Despite these correlations, we included these variables in the statistical models because we wanted to analyze their impacts on fungi simultaneously. However, the results must be interpreted with caution due to the correlations. In addition, the proportion of broadleaved trees correlated significantly and strongly with tree species richness, but we did not include these two variables in the same statistical models. The rest of the variables correlated only moderately or weakly with each other.

Moran's test was used to examine possible spatial autocorrelation. The test was done separately for two- and four-nearest-neighbor (2nn and 4nn) structures which were based on the distances between sites. We found that soil moisture and the historical land-use intensity are spatially autocorrelated within 2nn level. Time since abandonment was nearly significant within 4nn level. Results for variables with spatial autocorrelation should be taken with caution. Our sampling setup is probably

the main reason for observed autocorrelation. We had two study sites within some farms so those sites share the same farm-specific factors.

Wilcoxon tests revealed that the levels of continuous variables did not differ between grazed and abandoned sites.

2.4.2 General Linear Mixed Models

We analyzed the effect of management situation (grazed or abandoned), historical land-use intensity, grazing intensity, time since abandonment, and stand conditions on species richness with General Linear Mixed Models (GLMM). The response variable was the species richness of ectomycorrhizal fungi, explanatory discrete variable was management situation, and explanatory continuous variables were historical land-use intensity, soil moisture, soil pH, tree species richness, grazing intensity, and time since abandonment. We set the inventory time period (either 2010 or 2012+2013) variable as a random effect. The relationships between the response and explanatory variables were expected to be best described by linear and quadratic models. We allowed quadratic effects for soil pH, soil moisture, grazing intensity and time since abandonment.

We standardized all continuous variables to zero mean and unit variance to make their effect sizes comparable. We used Negative Binomial GLMM model and chose the best model based on Akaike's Information Criterion values. The first model with all sites was built for management situation, historical land-use intensity, soil pH, soil moisture, and tree species richness. Based on our study questions, we were primarily interested in the effects of management and historical land-use intensity, so we kept these variables in the model and compared all possible models where we varied the presence of soil pH, soil moisture and tree species richness. The second model was built for grazed sites similarly than for all sites, but without management

situation and with grazing intensity. In this model we kept historical land-use intensity and grazing intensity, while we found the best model with a subset of soil pH, soil moisture and tree species richness. The third model for abandoned sites always included historical land-use intensity and time since abandonment while we varied the presence of soil pH, soil moisture and tree species richness. The analyses were performed with the function “glmer.nb” from package “lme4” (Bates et al., 2015). See detailed information about GLMM from the Appendix A.

2.4.3. Bioenv-analyses and Nonmetric Multidimensional Scaling

We studied how management situation (grazed or abandoned), inventory time period (2010 or 2012+2013), historical land-use intensity, grazing intensity, time since abandonment, soil pH, soil moisture, and the proportion of broadleaved trees affect the community structure of ectomycorrhizal fungi. Again, we tested the effects separately for all sites, grazed sites, and abandoned sites. We used Chao’s dissimilarity index, which takes into account the number of unseen species (Chao et al., 2005; Oksanen et al., 2015). Our data is based on the observed fruit bodies and several species have probably not been observed on many sites. The different survey years could also have affected the likelihood of observing certain species on different sites. With Chao’s dissimilarities we conducted Bioenv-analysis to reveal the best subset of environmental variables that have the maximum correlation (Spearman) with the community dissimilarities. Because we included also categorical variables, we used Gower distance for calculating distances between the environmental variables. We used function “bioenv” from “vegan” package by Oksanen et al., (2015). We conducted Nonmetric Multidimensional Scaling (NMDS) to visualize the effects of environmental variables on ectomycorrhizal species composition (function “metaMDS” in “vegan”). We chose three-dimensional solutions. We overlaid the

ordination results with environmental factors whose location shows the average location of sites in that category, and with environmental vectors whose length shows the maximum correlations of the continuous environmental variables. In addition, we performed the same Bioenv-analyses and NMDS ordinations with the commonly used Bray-Curtis dissimilarities for comparison. All of the Bray-Curtis analyses are provided in the Appendix A.

3. RESULTS

In this study we recorded 14 831 fruit bodies among all sites, and 11 818 of them were identified to species level and were therefore taken into account in the analyses, including 4843 among grazed and 6975 among abandoned sites. We found 226 ectomycorrhizal fungi species out of which 167 species were found from grazed sites and 187 from abandoned sites. On average grazed sites hosted 9.3 species and abandoned sites 10.4 species.

The most common species in the data were *Lactarius tabidus* Fr. (28 sites/1296 fruit bodies), *Paxillus involutus* (Batsch: Fr.) Fr. (28 sites/333 fruit bodies) and *Laccaria laccata* (Scop.: Fr.) Berk. & Broome (25 sites/1045 fruit bodies). We recorded 16 species of special interest. Two of them are red-listed (NT) in Finland: *Cortinarius rubroviolipes* Bendiksen & K. Bendiksen (2 sites/14 fruit bodies) and *Inocybe hystrix* (Fr.) P. Karst. (1 site/4 fruit bodies). Three species are not evaluated (NE) in previous IUCN evaluation: *Naucoria submelinoides* (Kühner) Maire (1 site/37 fruit bodies), *Russula olivaceoviolascens* Gillet sensu Romagnes (3 sites/12 fruit bodies), and *Russula robertii* coll. J. Blum (1 site/4 fruit bodies). 11 species are either quite new to Finland or not yet published. See detailed species list from Table 1 in the Appendix B.

3.1 Species richness of ectomycorrhizal fungi

The only variable that had a significant effect on species richness among all as well as among grazed sites was the historical land-use intensity (negative effect) (Table 1, Figure 2e).

Among abandoned sites soil moisture (negative effect) and historical land-use intensity (negative effect) affected species richness. Among abandoned sites the species richness increased as time since abandonment increased, and there was also a nearly significant quadratic (humped) effect (Table 1, Figure 2j).

Inventory time period (used as a random effect) seems to have a great effect on species richness especially with abandoned sites: More species were observed in sites that were studied in 2012 and 2013 than in the ones that were studied in 2010 (Figure 2a-c).

3.2 Community structure of ectomycorrhizal fungi

When all sites were analyzed together, the proportion of broadleaved trees, soil pH, and soil moisture explained the community structure of ectomycorrhizal fungi (Table 2 in the Appendix A, Figure 3a with axes 1 and 2).

Among grazed sites the community structure was mostly explained by soil moisture and the proportion of broadleaved trees (Table 2 in the Appendix A, Figure 3b).

Among abandoned sites the community structure was explained by the proportion of broadleaved trees and soil pH (Table 2 in the Appendix A, Figure 3c). Birch-dominated and spruce-dominated wood-pastures were clearly separated in the NMDS ordination, while mixed wood-pastures had intermediate positions and overlapped with the others (Figure 3, symbol size represents the proportion of broadleaved trees, thus for example spruce dominated sites have small symbol).

For the three-dimensional NMDS ordinations the final stress values were 0.150 for all sites, 0.126 for grazed sites, and 0.104 for abandoned sites. The results for axes 1 and 2 are shown in Figure 3. Results for axis 3 are shown in Figure 1 in the Appendix A and they only emphasize the effect of the proportion of broadleaved trees.

4. DISCUSSION

4.1. Grazing-related variables did not have clear effects on the fungal communities

Historical land-use intensity (historical number of farms surrounding the site within 1km) was the most important factor affecting species richness of ectomycorrhizal fungi, but it did not impact community composition. High historical land-use intensity had a significant negative effect on species richness among all sites, grazed sites, and abandoned sites. This is surprising because one could expect that the biodiversity of traditional rural biotopes in general would increase with historical land-use intensity. For example, Lindborg and Eriksson (2004) found that historical landscape connectivity has a strong positive effect on the present species richness of plants in semi-natural grasslands. On the other hand, in our study of these same wood-pastures, we did not find significant impacts of historical land-use intensity on the species richness of either vascular plants or bryophytes (Oldén et al., 2016). One explanation is that many of the species of boreal wood-pastures are primarily forest species instead of grassland species. It seems possible that among ectomycorrhizal fungi there are more species that suffer from human impacts than those that benefit from them. In addition, grazing may not be the most important historical factor determining current fungal assemblages, but instead other practices related to forestry and agriculture may

have negative impacts on local fungal diversity. Finally, we assumed that historical land-use intensity correlates with historical grazing intensity, but it may not correlate with the overall length of grazing history or the grazing intensity during the recent decades.

Management situation had no effect on fungal species richness, which is in contrast to our hypothesis. Management did not have a clear effect on community composition either. It seems that the communities of ectomycorrhizal fungi are not affected by grazing, although some individual species may respond to it. Instead, vascular plants and bryophytes had higher species richness in the currently grazed sites of this same setup (Oldén et al., 2016), indicating that grazing does have ecological impacts in these boreal wood-pastures.

Present grazing intensity did not have any significant effect on species richness. Thus, our result does not support our hypothesis that species richness would be highest at intermediate grazing intensity. With vascular plants there are several studies that show highest species richness with intermediate grazing pressure (Mwendera et al., 1997; Vujanovic et al., 2002), also in these same sites (Oldén et al., 2016). However, data on the stocking rates of grazers in these sites was not available, and our one-time estimation of grazing intensity may not be a comprehensive estimate of all the effects that grazers have on fungi throughout the grazing season and different years. In addition, our results might be affected by the consumption of fruit bodies by the grazers during the study. It is known, and we also noticed ourselves, that the grazers eat fruit bodies (Warren and Mysterud, 1991). It is possible that in sites with high grazing intensity the grazers consumed more fruit bodies, and thus fewer species were observed. However, the grazers may also purposefully seek for some fruit bodies over other food items (Bjugstad and Dalrymple, 1968), and in that case grazing

intensity does not correlate with the number of consumed fruit bodies. Grazing intensity had no clear effects on fungal community composition either. Together with the fact that management situation did not affect fungal species richness or community composition, it is clear that trees and soil properties impact fungal communities much more than grazing.

Time since abandonment had a positive and also slightly humped effect on species richness, but it had no clear effect on community composition. Thus, according to our results species richness increases slightly with time since abandonment, which is opposite to our hypothesis. Many ectomycorrhizal species may benefit from the increasing number of young trees during the first decades after abandonment, especially if the young trees increase the number of tree species that are available for mycorrhizal symbiosis. In time an abandoned wood-pasture develops towards an old-growth forest, which can offer habitats for species that are dependent on them (Bonsdorff et al., 2014). However, we note that more studies are needed on this topic, especially because the positive effect in our data can be caused by a few long-ago abandoned sites that are biodiversity hotspots due to other properties than grazing.

4.2. Soil moisture affects species richness and community composition

Our result reveals that soil moisture affects the species richness of ectomycorrhizal fungi. It is also one of the main drivers of ectomycorrhizal fungi community composition. We found that high soil moisture in wood-pastures results in low species richness of ectomycorrhizal fungi. However, the effect was significant only among abandoned sites. Our recent study revealed that bryophyte species richness increases with soil moisture in wood-pastures, but vascular plant species richness does not show

any clear responses (Oldén et al., 2016). Thus, different species groups respond differently to soil moisture in wood-pastures.

It is clear that fungal species need moisture to grow, but one could think that the mycelium of mycorrhizal fungi cannot grow properly if the soil is too moist. However, Kennedy and Peay (2007) found that with increasing soil moisture plant species with ectomycorrhizal associations had greater shoot biomass and photosynthesis than non-mycorrhizal plants. McHugh and Schwartz (2016) instead showed that water treatment decreased fungal diversity. Thus, our result supports the observation of McHugh and Schwartz (2016).

4.3. The proportion of broadleaved trees is the main driver of community composition

The proportion of broadleaved trees had the strongest effect on the community composition of ectomycorrhizal fungi. Our result was expected, because it is known that there are specific and non-specific associations between mycorrhizal fungi species and their host trees (Molina et al., 1992; Moore et al., 2011). For example, the fungal communities in spruce-dominated sites differed strongly from other sites, which is reasonable because spruce was often the only tree species present in the plots.

Surprisingly, tree species richness did not have a significant effect on species richness of ectomycorrhizal fungi. Since many ectomycorrhizal species are specialized to certain hosts, increasing tree species richness should increase ectomycorrhizal species richness, through the higher number of suitable hosts for different species. One reason why we did not find a significant effect might be that the difference cannot be detected in such a small scale due to high overall beta diversity

of fungal communities on small spatial scales (Abrego et al., 2014). The difference might be discovered on a larger scale.

4.4. Soil pH affects community composition

Soil pH had a strong effect on community composition of ectomycorrhizal fungi, but it did not impact species richness. Soil pH correlated strongly with the proportion of broadleaved trees: Most of the sites with high soil pH (max 4.9) are birch-dominated herb-rich forests, while most of the low-pH sites (min 3.1) are heath forests dominated by spruces or mixed trees.

Vascular plant and bryophyte species richness has been shown to increase with increasing soil pH (Oldén et al., 2016; Roem and Berendse, 2000). According to Rousk et al. (2009) fungal growth was maximized at pH 4.5 and decreased both above and below that. On the other hand, fungal biomass was highest at pH 6 but decreased with both increasing and decreasing pH (Rousk et al., 2009). Thus it could be assumed that in our quite acidic sites species richness would increase with soil pH, but we did not find significant effects on fungal species richness.

4.5. Survey year affected our results

Fungal surveys were conducted in 10 of the 12 birch-dominated sites on three visits during 2010. Two birch-dominated sites and all mixed and spruce-dominated sites were visited twice during 2012 and once during 2013. Autumn 2010 was quite dry and this could affect our results. In 2010 the numbers of detected fruit bodies were quite similar at the first and second survey visits compared to years 2012-2013, but much lower at the third survey visit. Another source of bias is that many fungal species do not produce fruit bodies every year (Straatsma et al., 2001), and thus a higher species richness can be observed in sites that have been studied during two different years, even though the number of survey visits is the same.

These study design problems have somewhat affected our results. Thus, we cannot really be sure how strongly the communities of birch-dominated sites differ from others, and how much the survey years have affected it. However, the effect of the year should be small in the Bioenv-analyses where we used Chao's dissimilarity index, which should take into account the unseen species (Chao et al., 2005; Oksanen et al., 2015). We also corrected for the effect of the survey year in the General Linear Mixed Models by using inventory time period (2010 or 2012+2013) as a random effect.

It is also known that studies that are only based on fruit bodies do not reveal the whole fungal community, because of the species that do not produce fruit bodies every year (Abrego et al., 2016; Ovaskainen et al., 2013; van der Linde et al., 2012). However, we argue that even a quite large proportion of undetected species should not mask the potential effects of management situation, for example.

5. CONCLUSIONS

Communities of ectomycorrhizal fungi in wood-pastures are determined by soil properties and tree species composition. Based on our results, grazing-related variables do not impact the communities of ectomycorrhizal fungi in boreal wood-pastures, but (currently grazed and abandoned) wood-pastures may still differ in their species composition from the forests that have no grazing history. Decisions on the management and conservation of wood-pastures should be based on other species groups that respond more clearly to management (such as vascular plants and bryophytes, see Oldén et al. 2016). However, some ectomycorrhizal species or the communities of saprotrophic fungi may still respond to grazing in wood-pastures. More studies are needed to reveal these subjects.

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Table 1. Variables from the best models from GLMM analyses (best models chosen based on the lowest AIC values) for ectomycorrhizal species richness for all sites, grazed sites, and abandoned sites. Management is a categorical variable (grazed or abandoned). For the continuous variables grazing intensity, time since abandonment, soil pH, and soil moisture both linear and quadratic (^{2}) effects were analyzed, whereas for the historical land-use intensity (the number of farms surrounding the site within 1km in the 1850s-60s) and trees species richness only linear effects were analyzed. Inventory time period was set as a random effect. Variables marked with $^+$ were always kept in the models irrespective of their significance.

All sites				
	Estimate	Std. Error	z value	P
(Intercept)	3.402	0.127	26.723	<2e-16 ***
+Management: Grazed	-0.123	0.129	-0.958	0.338
+Farms	-0.149	0.065	-2.275	0.0229 *
pH				
pH ^{2}				
Moisture	-0.100	0.069	-1.458	0.145
Moisture ^{2}				
TreesSR				
Grazed sites				
	Estimate	Std. Error	z value	P
(Intercept)	3.340	0.089	37.440	<2e-16 ***
+Farms	-0.176	0.077	-2.300	0.0217 *
+Grazing	-0.067	0.077	-0.870	0.386
Grazing ^{2}				
pH				
pH ^{2}				
Moisture				
Moisture ^{2}				
TreesSR				
Abandoned sites				
	Estimate	Std. Error	z value	P
(Intercept)	3.106	0.169	18.412	<2e-16 ***
+Farms	-0.184	0.093	-1.980	0.0477 *
+Abandonment	1.165	0.529	2.200	0.0278 *
Abandonment ^{2}	-0.497	0.254	-1.958	0.0502 .
pH				
pH ^{2}				
Moisture	-0.316	0.128	-2.467	0.0136 *

Moisture²

TreesSR

***=p<0.001, **=p<0.01, *=p<0.05, .=p<0.10

686

687

688 Figure 1. a) The 36 study sites located in Central Finland in the southern boreal and the
689 middle boreal vegetation zones. Examples of vegetation in sites of different grazing
690 intensity: b) heavy grazing, c) intermediate grazing, and d) no grazing (abandoned).

692

693 Figure 2. Responses of ectomycorrhizal fungi species richness to inventory time period (ITP)

694 among a) all sites, b) grazed sites, c) abandoned sites, d) management among all sites,

695 e) the number of farms surrounding the site within 1km in the 1850s-60s (historical

696 land-use intensity), f) soil pH, g) soil moisture (% content from the ground), h) tree

697 species richness, i) grazing intensity among grazed sites (% of clipped shoots), and j)

698 time since abandonment (years) for abandoned sites. The fitted linear and quadratic
699 curves represent significant or nearly significant effects from the GLMM analyses.

701

Figure 3. Nonmetric Multidimensional Scaling (NMDS) for the community structure of ectomycorrhizal fungi species among a) all sites, b) grazed sites, and c) abandoned sites with axes 1 and 2. Analyses were done with Chao's dissimilarity index. For the categorical variables inventory time period (ITP1 in 2010, ITP0 in 2012-2013) and management (M1 for grazed sites, and M0 for abandoned sites) the location represents the average location of sites in that category. The arrows represent the direction and strength of the a posteriori correlations between the site locations and the continuous environmental variables: the historical land-use intensity (Farms), soil moisture, soil pH, the proportion of broadleaved trees (Broa), grazing intensity on grazed sites, and time since abandonment on abandoned sites. Symbol size represents the proportion of broadleaved trees.

Appendix A for Tervonen et al.: Ectomycorrhizal fungi in wood-pastures: Communities are determined by trees and soil properties, not by grazing

Authors: Kaisa Tervonen, Anna Oldén, and Panu Halme

1. Detailed information about GLMM
2. NMDS with Bray-Curtis dissimilarity index

Table 1. Correlations between the environmental variables.

Table 2. Results from the Bioenv analyses for mycorrhizal fungi species.

Figure 1. NMDS for the community structure of mycorrhizal fungi species among all, grazed, and abandoned sites with Chao. (Axes 1 and 3)

Figure 2. NMDS for the community structure of mycorrhizal fungi species among all, grazed, and abandoned sites with Bray-Curtis. (Axes 1 and 2)

Figure 3. NMDS for the community structure of mycorrhizal fungi species among all, grazed, and abandoned sites with Bray-Curtis. (Axes 1 and 3)

1. Detailed information about GLMM

In the General Linear Mixed Models (GLMM) we compared models by using as family Poisson or Negative Binomial and decided the best model based on Akaike's Information Criterion values. The selected family was Negative Binomial. We used “bobyqa” as optimizer in the models. We set iteration number to 100 000 with function “glmerControl”. One of the models for grazed site model had “Hessian warning”. We double-checked the results with R’s convergence -help five step instructions to see that with many different optimizers the estimates for the models were similar. Therefore we could trust our results.

2. NMDS with Bray-Curtis dissimilarity index

When analyzing the data with Bray-Curtis dissimilarity index the correlations from Bioenv-analyses were almost the same, but it seems that with Chaos’s index the analysis finds a stronger effect of the proportion of broadleaved trees instead of pH (Table 2 in the Appendix). The NMDS ordinations with Chao’s and Bray-Curtis indexes are somewhat similar (Bray-Curtis NMDS ordinations in the Appendix Figure 2 and 3).

Table 1. Correlations between the environmental variables.

All sites					
	Farms	Moisture	pH	Broadleaved	
Moisture	-0.170				
pH	-0.024	-0.356 *			
Broadleaved	0.024	0.023	0.554 ***		
TreesSR	-0.045	-0.182	0.525 **	0.466 **	
Grazed sites					
	Farms	Moisture	pH	Broadleaved	TreesSR
Moisture	-0.306				
pH	0.183	-0.560 *			
Broadleaved	-0.016	-0.127	0.581 *		
TreesSR	0.010	-0.339	0.592 **	0.287	
Grazing	-0.010	0.034	0.104	0.113	-0.060
Abandoned sites					
	Abandonment	Farms	Moisture	pH	Broadleaved
Farms	-0.176				
Moisture	0.502 *	-0.166			
pH	0.095	-0.288	-0.137		
Broadleaved	0.469 *	0.019	0.152	0.583 *	
TreesSR	0.151	-0.034	0.067	0.682 **	0.717 ***

***=p<0.001, **=p<0.01, *=p<0.05

Table 2. Results from the Bioenv analyses of variables that affect mycorrhizal fungi community. Results are given for both Chao's and Bray-Curtis dissimilarity indexes. Spearman rank correlation was used in the analyses. Inventory time period (DITP: 2010 or 2012 and 2013) and management (Dmana: grazed or abandoned sites) are set as a dummy variables. The proportion of broadleaved trees are represented as "Broadleaved" and the historical land-use intensity as "Farms".

Chao		
All sites		
Size	Variables	Correlation
1	Broadleaved	0.314
2	pH, Broadleaved	0.400
3	pH, Moisture, Broadleaved	0.432
4	DITP, pH, Moisture, Broadleaved	0.365
5	Dmana, DITP, pH, Moisture, Broadleaved	0.338
6	Dmana, DITP, pH, Moisture, Broadleaved, Farms	0.311
Grazed sites		
Size	Variables	Correlation
1	Moisture	0.288
2	Moisture, Broadleaved	0.427
3	pH, Moisture, Broadleaved	0.424
4	pH, Moisture, Broadleaved, Grazing	0.389
5	pH, Moisture, Broadleaved, Farms, Grazing	0.353
6	DITP, pH, Moisture, Broadleaved, Farms, Grazing	0.278
Abandoned sites		
Size	Variables	Correlation
1	Broadleaved	0.417
2	pH, Broadleaved	0.505
3	pH, Moisture, Broadleaved	0.483
4	DITP, pH, Moisture, Broadleaved	0.438
5	DITP, pH, Moisture, Broadleaved, Farms	0.372
6	DITP, pH, Moisture, Broadleaved, Farms, Abandonment	0.318
Bray-Curtis		
All sites		
Size	Variables	Correlation
1	pH	0.313
2	pH, Broadleaved	0.397
3	pH, Moisture, Broadleaved	0.441
4	pH, Moisture, Broadleaved, Farms	0.375
5	Dmana, DITP, pH, Moisture, Broadleaved	0.334
6	Dmana, DITP, pH, Moisture, Broadleaved, Farms	0.309
Grazed sites		
Size	Variables	Correlation
1	Moisture	0.282
2	Moisture, Broadleaved	0.361
3	pH, Moisture, Broadleaved	0.360
4	pH, Moisture, Broadleaved, Grazing	0.344
5	pH, Moisture, Broadleaved, Farms, Grazing	0.311

6	DITP, pH, Moisture, Broadleaved, Farms, Grazing	0.225
Abandoned sites		
Size	Variables	Correlation
1	pH	0.414
2	pH, Broadleaved	0.541
3	pH, Moisture, Broadleaved	0.526
4	DITP, pH, Moisture, Broadleaved	0.473
5	DITP, pH, Moisture, Broadleaved, Farms	0.397
6	DITP, pH, Moisture, Broadleaved, Farms, Abandonment	0.329

Figure 1. Nonmetric Multidimensional Scaling (NMDS) for the community structure of mycorrhizal fungi species among a) all sites, b) grazed sites, and c) abandoned sites with axes 1 and 3. Analyses were done with Chao's dissimilarity index. For the categorical variables inventory time period (ITP1 in 2010, ITP0 in 2012-2013) and management (M1 for grazed sites, and M0 for abandoned sites) the location represents the average location of sites in that category. The arrows represent the direction and strength of the a posteriori correlations between the site locations and the continuous environmental variables: the historical land-use intensity (Farms), soil moisture, soil pH, the proportion of broadleaved trees (Broa), grazing intensity on grazed sites, and time since abandonment on abandoned sites. Symbol size represents the proportion of broadleaved trees.

Figure 2. Nonmetric Multidimensional Scaling (NMDS) for the community structure of mycorrhizal fungi species among a) all sites, b) grazed sites, and c) abandoned sites with axes 1 and 2. Analyses were done with Bray-Curtis dissimilarity index. For the categorical variables inventory time period (ITP1 in 2010, ITP0 in 2012-2013) and management (M1 for grazed sites, and M0 for abandoned sites) the location represents the average location of sites in that category. The arrows represent the direction and strength of the a posteriori correlations between the site locations and the continuous environmental variables: the historical land-use intensity (Farms), soil moisture, soil pH, the proportion of broadleaved trees (Broa), grazing intensity on grazed sites, and time since abandonment on abandoned sites. Symbol size represents the proportion of broadleaved trees.

Figure 3. Nonmetric Multidimensional Scaling (NMDS) for the community structure of mycorrhizal fungi species among a) all sites, b) grazed sites, and c) abandoned sites with axes 1 and 3. Analyses were done with Bray-Curtis dissimilarity index. For the categorical variables inventory time period (ITP1 in 2010, ITP0 in 2012-2013) and management (M1 for grazed sites, and M0 for abandoned sites) the location represents the average location of sites in that category. The arrows represent the direction and strength of the a posteriori correlations between the site locations and the continuous environmental variables: the historical land-use intensity (Farms), soil moisture, soil pH, the proportion of broadleaved trees (Broa), grazing intensity on grazed sites, and time since abandonment on abandoned sites. Symbol size represents the proportion of broadleaved trees.

Appendix B for Tervonen et al.: Ectomycorrhizal fungi in wood-pastures: Communities are determined by trees and soil properties, not by grazing

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Table 1. List of ectomycorrhizal fungi species found in this study. The nomenclature of agarics and boletoids follows Knudsen and Vesterholt (2012) and Aphylloporales Kotiranta et al. (2009). For a few *Cortinarius* spp., *Inocybe* spp. and *Russula* spp. species the authors have been mentioned. They are species names that specialists want to use or species that are not yet published (ined.) The IUCN status follows Bonsdorff et al. (2010), and not evaluated (NE) species Von Bonsdorff (2012). “NEW” species are species that have not been yet published or are quite new species to Finland. The number of observations among grazed (18), abandoned (18) and all sites (36) are also given.

Species	IUCN	Grazed	Aband	All
<i>Amanita battarrae</i>	LC	0	1	1
<i>Amanita fulva</i>	LC	6	4	10
<i>Amanita muscaria</i> var. <i>muscaria</i>	LC	9	5	14
<i>Amanita muscaria</i> var. <i>regalis</i>	LC	0	2	2
<i>Amanita olivaceogrisea</i>	LC	5	3	8
<i>Amanita porphyria</i>	LC	8	7	15
<i>Amanita rubescens</i> f. <i>rubescens</i>	LC	4	2	6
<i>Amanita virosa</i>	LC	0	1	1
<i>Boletus edulis</i> coll.	LC	6	4	10
<i>Cantharellus cibarius</i>	LC	5	7	12
<i>Chalciporus piperatus</i>	LC	7	8	15
<i>Chroogomphus rutilus</i> var. <i>rustilus</i>	LC	0	2	2
<i>Cortinarius acutus</i>	LC	1	3	4
<i>Cortinarius alboviolaceus</i>	LC	2	3	5
<i>Cortinarius alnetorum</i>	LC	1	1	2
<i>Cortinarius anomalus</i> coll.	LC	4	8	12
<i>Cortinarius anthracinus</i>	LC	3	4	7
<i>Cortinarius armeniacus</i>	LC	1	2	3
<i>Cortinarius armillatus</i>	LC	0	5	5
<i>Cortinarius aurantiomarginatus</i>	LC	0	1	1
<i>Cortinarius balaustinus</i>	LC	0	1	1
<i>Cortinarius biformis</i> coll.	LC	1	3	4
<i>Cortinarius bolaris</i>	LC	0	2	2
<i>Cortinarius borgsjoeënsis</i>	LC	0	1	1
<i>Cortinarius brunneus</i> coll.	LC	2	10	12
<i>Cortinarius bulliardii</i> coll.	LC	1	1	2
<i>Cortinarius camphoratus</i>	LC	2	4	6
<i>Cortinarius caperatus</i>	LC	2	4	6
<i>Cortinarius caput-medusae</i> coll.	LC	1	0	1
<i>Cortinarius casimiri</i>	LC	10	12	22

<i>Cortinarius causticus</i>	LC	0	1	1
<i>Cortinarius cf. disjungendus</i>	LC	2	1	3
<i>Cortinarius cf. gossypinus</i>	LC	1	0	1
<i>Cortinarius cf. privignatus</i>	LC	1	0	1
<i>Cortinarius cf. suberi</i>	LC	0	2	2
<i>Cortinarius cinnamomeus</i>	LC	1	4	5
<i>Cortinarius collinitus</i>	LC	2	5	7
<i>Cortinarius colus</i>	LC	0	1	1
<i>Cortinarius colymbadinus</i>	LC	0	2	2
<i>Cortinarius croceus</i> var. <i>croceus</i>	LC	3	4	7
<i>Cortinarius decipiens</i> var. <i>decipiens</i>	LC	1	1	2
<i>Cortinarius delibutus</i> coll.	LC	1	5	6
<i>Cortinarius depressus</i> coll.	LC	1	1	2
<i>Cortinarius duracinus</i> coll.	LC	0	2	2
<i>Cortinarius erubescens</i>	LC	0	2	2
<i>Cortinarius flexipes</i> coll.	LC	7	11	18
<i>Cortinarius gentilis</i>	LC	2	6	8
<i>Cortinarius hedyaromaticus</i> C. Cripps & O.K. Mill.	NEW	1	0	1
<i>Cortinarius hemitrichus</i>	LC	1	2	3
<i>Cortinarius Hinnulei</i>	LC	1	0	1
<i>Cortinarius illuminus</i>	LC	1	0	1
<i>Cortinarius impolitus</i> Kauffman	LC	3	4	7
<i>Cortinarius laniger</i>	LC	0	2	2
<i>Cortinarius lilacinopusillus</i>	LC	0	1	1
<i>Cortinarius limonius</i>	LC	1	0	1
<i>Cortinarius lucorum</i>	LC	1	0	1
<i>Cortinarius malachius</i>	LC	1	0	1
<i>Cortinarius malicorius</i>	LC	1	1	2
<i>Cortinarius mucosus</i>	LC	0	1	1
<i>Cortinarius multififormis</i> coll.	LC	1	3	4
<i>Cortinarius obtusus</i> coll.	LC	1	1	2
<i>Cortinarius pansa</i>	NEW	0	1	1
<i>Cortinarius parvannulatus</i> coll.	LC	2	2	4
<i>Cortinarius pholideus</i>	LC	1	3	4
<i>Cortinarius raphanoides</i>	LC	3	10	13
<i>Cortinarius rubroviroleipes</i>	NT	2	0	2
<i>Cortinarius rusticus</i>	LC	0	1	1
<i>Cortinarius sanguineus</i> var. <i>sanguineus</i>	LC	2	4	6
<i>Cortinarius saniosus</i>	LC	2	4	6
<i>Cortinarius semisanguineus</i>	LC	1	1	2
<i>Cortinarius spilomeus</i>	LC	0	4	4
<i>Cortinarius stillatitius</i>	LC	1	2	3
<i>Cortinarius subtortus</i>	LC	1	1	2
<i>Cortinarius tortuosus</i>	LC	1	0	1
<i>Cortinarius traganus</i> f. <i>traganus</i>	LC	1	5	6
<i>Cortinarius triumphans</i>	LC	6	3	9

<i>Cortinarius trivialis</i>	LC	1	1	2
<i>Cortinarius turmalis</i>	LC	0	1	1
<i>Cortinarius umbrinolens</i>	LC	2	2	4
<i>Cortinarius uraceus</i>	LC	0	1	1
<i>Cortinarius venustus</i>	LC	1	2	3
<i>Cortinarius violilamellatus</i>	LC	1	0	1
<i>Craterellus cornucopioides</i>	LC	1	3	4
<i>Craterellus sinuosus</i>	LC	0	1	1
<i>Gomphidius glutinosus</i>	LC	2	4	6
<i>Hebeloma birrus</i>	LC	12	1	13
<i>Hebeloma mesophaeum</i>	LC	1	2	3
<i>Hebeloma theobrominum</i>	LC	2	0	2
<i>Hygrophorus agathosmus</i>	LC	2	3	5
<i>Hygrophorus erubescens</i>	LC	0	1	1
<i>Hygrophorus hedrychii</i>	LC	0	2	2
<i>Hygrophorus korhonenii</i>	LC	1	2	3
<i>Hygrophorus olivaceoalbus</i>	LC	4	8	12
<i>Hygrophorus pustulatus</i>	LC	4	1	5
<i>Inocybe acuta</i>	LC	1	1	2
<i>Inocybe aff. grammata</i>	NEW	1	0	1
<i>Inocybe aff. napipes</i>	NEW	1	0	1
<i>Inocybe armeniaca</i> Huijsman	LC	0	1	1
<i>Inocybe calamistrata</i>	LC	0	1	1
<i>Inocybe castanea</i>	LC	5	9	14
<i>Inocybe cf. griseoscabrosa</i>	NEW	0	1	1
<i>Inocybe cf. humilis</i> (J. Favre & E. Horak) Estre-Rav. & Vila	LC	2	2	4
<i>Inocybe cf. squarrosa</i>	LC	0	1	1
<i>Inocybe cinnamomea</i> var. <i>cinnamomea</i>	LC	4	8	12
<i>Inocybe curvipes</i>	LC	1	0	1
<i>Inocybe flavella</i>	LC	1	0	1
<i>Inocybe flocculosa</i>	LC	4	5	9
<i>Inocybe fuscidula</i> var. <i>fuscidula</i>	LC	0	1	1
<i>Inocybe geophylla</i>	LC	11	13	24
<i>Inocybe grammata</i>	LC	0	1	1
<i>Inocybe hystrix</i>	NT	0	1	1
<i>Inocybe lacera</i> coll.	LC	2	1	3
<i>Inocybe leptophylla</i>	LC	1	0	1
<i>Inocybe lilacina</i>	LC	3	6	9
<i>Inocybe lindrothii</i> (P. Karst.) Vauras & E. Larss.	LC	3	2	5
<i>Inocybe maculata</i>	LC	0	1	1
<i>Inocybe mixtilis</i>	LC	5	2	7
<i>Inocybe napipes</i>	LC	3	3	6
<i>Inocybe nitidiuscula</i>	LC	1	3	4
<i>Inocybe proximella</i>	LC	1	1	2
<i>Inocybe rimosa</i> coll.	LC	1	1	2

<i>Inocybe rivularis</i>	LC	1	1	2
<i>Inocybe sindonia</i>	LC	0	1	1
<i>Inocybe soluta</i>	LC	1	0	1
<i>Inocybe sp1.</i>	NEW	1	0	1
<i>Inocybe sp2.</i>	NEW	0	1	1
<i>Inocybe subcarpta</i>	LC	1	0	1
<i>Inocybe subnudipes</i>	LC	0	1	1
<i>Inocybe terrigena</i>	LC	0	1	1
<i>Laccaria laccata</i>	LC	14	11	25
<i>Laccaria tortilis</i>	LC	1	0	1
<i>Lactarius aurantiacus</i>	LC	1	0	1
<i>Lactarius camphoratus</i>	LC	3	10	13
<i>Lactarius deterrimus</i>	LC	2	5	7
<i>Lactarius flexuosus</i> var. <i>flexuosus</i>	LC	3	3	6
<i>Lactarius fuliginosus</i>	LC	1	3	4
<i>Lactarius glyciosmus</i>	LC	11	11	22
<i>Lactarius helvus</i>	LC	0	2	2
<i>Lactarius lacunarum</i>	LC	1	0	1
<i>Lactarius mammosus</i>	LC	1	0	1
<i>Lactarius necator</i>	LC	13	11	24
<i>Lactarius obscuratus</i>	LC	2	2	4
<i>Lactarius rufus</i>	LC	2	3	5
<i>Lactarius sphagnetii</i>	LC	0	1	1
<i>Lactarius spinosulus</i>	LC	1	3	4
<i>Lactarius tabidus</i>	LC	13	15	28
<i>Lactarius torminosus</i>	LC	5	6	11
<i>Lactarius trivialis</i>	LC	4	5	9
<i>Lactarius uvidus</i>	LC	0	1	1
<i>Lactarius vietus</i>	LC	5	9	14
<i>Leccinum scabrum</i>	LC	7	2	9
<i>Leccinum variicolor</i>	LC	2	3	5
<i>Leccinum versipelle</i>	LC	0	1	1
<i>Leucocortinarius bulbiger</i>	LC	1	0	1
<i>Naucoria bohemica</i>	LC	3	1	4
<i>Naucoria celluloderma</i>	LC	1	0	1
<i>Naucoria escharioides</i>	LC	1	1	2
<i>Naucoria salicis</i>	LC	1	1	2
<i>Naucoria submelinoides</i>	NE	0	1	1
<i>Paxillus filamentosus</i>	LC	0	1	1
<i>Paxillus involutus</i>	LC	16	12	28
<i>Phaeocollybia arduennensis</i>	LC	1	0	1
<i>Phaeocollybia</i> cf. <i>festiva</i>	LC	1	0	1
<i>Ramaria eosanguinea</i>	LC	0	1	1
<i>Russula adusta</i> coll.	LC	1	2	3
<i>Russula aeruginea</i> coll.	LC	8	2	10
<i>Russula alnetorum</i>	LC	1	0	1

<i>Russula ancillaris</i> Ruots. & Vauras ined.	NEW	2	0	2
<i>Russula aquosa</i>	LC	9	6	15
<i>Russula atrorubens</i>	LC	4	6	10
<i>Russula aurea</i>	LC	0	1	1
<i>Russula betularum</i>	LC	10	11	21
<i>Russula cessans</i> coll.	LC	3	0	3
<i>Russula chloroides</i> coll.	LC	4	2	6
<i>Russula claroflava</i>	LC	5	5	10
<i>Russula consobrina</i>	LC	1	4	5
<i>Russula crassipes</i> Ruots. & Vauras ined.	NEW	3	1	4
<i>Russula decolorans</i>	LC	2	3	5
<i>Russula emetica</i> coll.	LC	0	1	1
<i>Russula fennoscandica</i> Ruots. & Vauras ined.	NEW	0	5	5
<i>Russula foetens</i>	LC	4	2	6
<i>Russula globispora</i>	LC	0	2	2
<i>Russula gracillima</i>	LC	7	3	10
<i>Russula grisescens</i>	LC	2	2	4
<i>Russula integriformis</i>	LC	1	0	1
<i>Russula intermedia</i>	LC	3	6	9
<i>Russula medullata</i>	LC	1	0	1
<i>Russula nana</i>	LC	1	1	2
<i>Russula nauseosa</i>	LC	0	3	3
<i>Russula nitida</i> coll.	LC	5	3	8
<i>Russula olivaceoviolascens</i> Gillet sensu Romagnes	NE	2	1	3
<i>Russula paludosa</i>	LC	2	1	3
<i>Russula pelargonia</i> coll.	LC	4	2	6
<i>Russula pubescens</i>	LC	0	1	1
<i>Russula puellaris</i>	LC	1	2	3
<i>Russula pyrenaica</i> J. Blum	NEW	0	1	1
<i>Russula renidens</i> coll.	LC	1	1	2
<i>Russula rhodopus</i>	LC	2	2	4
<i>Russula risigallina</i> var. <i>risigallina</i>	LC	0	1	1
<i>Russula robertii</i> coll.	NE	0	1	1
<i>Russula roseipes</i>	LC	1	0	1
<i>Russula sanguinea</i>	LC	2	0	2
<i>Russula sapinea</i>	LC	1	0	1
<i>Russula sardonica</i>	LC	1	1	2
<i>Russula turci</i>	LC	1	1	2
<i>Russula velenovskyi</i> coll.	LC	6	7	13
<i>Russula versicolor</i> coll.	LC	0	2	2
<i>Russula vesca</i>	LC	7	5	12
<i>Russula vinosa</i>	LC	3	3	6
<i>Russula vinososordida</i>	LC	1	1	2
<i>Russula violaceoincarnata</i>	LC	3	4	7
<i>Russula vitellina</i>	LC	4	3	7

<i>Russula xerampelina</i> coll.	LC	4	1	5
<i>Suillus luteus</i>	LC	1	1	2
<i>Thelephora palmata</i>	LC	1	1	2
<i>Tricholoma albobrunneum</i>	LC	1	0	1
<i>Tricholoma columbetta</i>	LC	0	1	1
<i>Tricholoma fulvum</i>	LC	7	2	9
<i>Tricholoma inamoenum</i>	LC	2	6	8
<i>Tricholoma saponaceum</i> var. <i>saponaceum</i>	LC	1	1	2
<i>Tricholoma stans</i>	LC	0	1	1
<i>Tricholoma stiparophyllum</i>	LC	4	5	9
<i>Tricholoma vaccinum</i>	LC	0	1	1
<i>Tricholoma virgatum</i>	LC	0	2	2
<i>Xerocomus badius</i>	LC	1	0	1
<i>Xerocomus subtomentosus</i> coll.	LC	4	1	5

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