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The effect of grazing history on fungal diversity in broadleaved wood pastures

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ABSTRACT

Traditional rural biotopes such as wood pastures are species rich habitats which have been created by extensive agriculture. In all European countries both the quality and quantity of traditional rural biotopes have drastically decreased during the past century because of increasing farming intensity. This decline is causing a threat to many species, but very little is known about the conservation ecology of fungi living in wood pastures. Considering vascular plants, it is known that sites with long management history have higher species richness compared to abandoned sites. It is also known that species richness is highest with intermediate grazing intensity. In this study I investigated if there is a difference in fungal species richness between presently grazed and presently ungrazed sites. I also investigated the effect of grazing history on fungal species richness and community assembly. In addition, I studied the effect of current grazing intensity on fungal species richness. All my study sites were broadleaved wood pastures in Central Finland. I studied 12 sites of which 6 were presently grazed by domestic animals and 6 were presently not, but had been grazed in the past. Grazing history of the study sites varied between 40-205 years, and considering sites which were presently ungrazed, the time after abandonment varied between 5-40 years. I focused on the agarics, boletoids, ramarioid fungi, Gasteromycetes, Pezizomycetes, and stipitate polypores. I conducted both sample plot surveys and time constrained surveys on each study site and repeated the surveys three times. Overall, I found 313 fungi species in this study. I found out that presently grazed sites do not have more fungal species than presently ungrazed sites. Instead, my results suggest that fungal species richness increases with grazing history duration and sites with long grazing history have a similar community structure even if they are presently ungrazed. I also suggest that with intermediate grazing intensity species richness is the greatest. I conclude that it is very important to know detailed management history when prioritizing management for sites. Moreover, targeting for optimal grazing intensity for sites may be important.

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TIIVISTELMÄ

Perinnebiotoopit, kuten metsälaitumet, ovat perinteisen karjatalouden muovaamia lajirikkaita elinympäristöjä. Perinnebiotooppien määrä on 1900-luvun aikana laskenut rajusti koko Euroopassa maatalouden muuttuessa yhä intensiivisemmäksi. Perinnebiotooppien vähäinen määrä uhkaa monien lajien säilymistä, mutta vain vähän tiedetään metsälaitumilla esiintyvien sienilajien ekologiasta. Putkilokasveilla tehdyissä tutkimuksissa on havaittu, että pitkän hoitohistorian omaavilla kohteilla on suurempi lajimäärä verrattuna hoitamattomiin kohteisiin. On myös todettu, että keskimääräisen laidunnusintensiteetin kohteilla on suurin putkilokasvilajimäärä. Tässä tutkimuksessa selvitin eroavatko laidunnetut kohteet sienilajimäärältään laiduntamattomista kohteista. Selvitin myös kuinka laidunnushistorian pituus vaikuttaa sienilajien lajimäärään ja yhteisörakenteeseen. Lisäksi tarkastelin kuinka nykyinen laidunpaine vaikuttaa lajimäärään. Kaikki tutkimusalueeni sijaitsivat lehtimetsälaitumilla Keski-Suomessa. Vertailin kahtatoista kohdetta, joista kuusi oli tutkimushetkellä laidunnuksessa ja kuusi ei ollut. Kohteiden kokonaislaidunnushistoria vaihteli 40-205 vuoteen ja laiduntamattomilla kohteilla tauon pituus vaihteli 5-40 vuoteen. Tutkin kohteilta kaikki jalalliset suursienet, kuten helttasienet, tatit ja haarakkaat. Tein kohteilla inventoinnit kolmella aarin kokoisella koelalla ja lisäksi tein aikarajoitteisen inventoinnin. Tein inventoinnit kolme kertaa syksyn 2010 aikana. Tutkimuksessani havaitsin kaiken kaikkiaan 313 sienilajia. Tutkimuksessa havaitsin, että sienten lajimäärään ei vaikuta onko kohde laidunnuksessa sillä hetkellä vai ei. Sen sijaan kohteen kokonaislaidunnushistorian kasvaessa lajimäärä kasvaa ja kohteet, joilla on pitkä laidunnushistoria ovat yhteisörakenteeltaan samankaltaisia, vaikkeivät sillä hetkellä olisi laidunnuksessa. Havaitsin myös, että keskimääräisen laidunpaineen omaavilla kohteilla oli suurin lajimäärä. Johtopäätöksenä on, että on tärkeää selvittää kohteiden laidunnushistoria kun priorisoidaan kohteiden hoitoa. Lisäksi on tärkeää selvittää kullekin kohteelle sopiva laidunpaine.

Contents

1. INTRODUCTION

Human activities have decreased the biological diversity in most habitat types worldwide. Typically, increasing human impact is mostly negative on the biodiversity values of the habitat (Foley et al. 2005, Young et. al. 2005). However, traditional low-intensity agriculture has also created habitats which have high biological diversity and also high diversity of species that are threatened by local and global extinctions (Bignal & McCracken 1996, Plieninger et al. 2006). These habitats are called traditional rural biotopes (Bignal & McCracken 1996, Jutila 1999, Plieninger et al. 2006).

Traditional rural biotopes are classified into several types based on their soil conditions and vegetation (Schulman et al. 2008). Wood pastures are forests which have been grazed by domestic animals for a long time, up to hundreds of years, and that have a substantially changed vegetation structure due to the grazing pressure and selective logging. In general they are semi-open habitats, where open and closed patches alternate (WallisDeVries et al. 1998, Vainio et al. 2001, Garbarino et al. 2011). In Finland, wood pastures are classified into three categories: deciduous wood pastures, mixed wood pastures, and coniferous wood pastures (Schulman et al. 2008).

In all European countries the area of traditional rural biotopes has drastically decreased during the 20th century (Pykälä & Alanen 2004, Garbarino et al. 2011). Nowadays, increasing farming intensity and land abandonment are the major threats for the biological diversity in these habitats (Pykälä 2001, Plieninger et al. 2006, Stoate et al. 2009). Due to these reasons traditional rural biotopes and a great number of species inhabiting these habitats are threatened in Finland (Schulman et al. 2008, Rassi et al. 2010). It has been proposed that these biotopes have high biological diversity mostly due to long duration of rural management history, an intermediate disturbance regime, high resource availability, and high habitat heterogeneity (e.g. Pykälä 2001, Benton et al. 2003, Lindborg & Eriksson 2004, Saarinen & Jantunen 2005, Pykälä 2007, Paltto et al. 2011).

Duration of rural management history greatly affects species richness (Pykälä 2003, Lindborg & Eriksson 2004). Traditional rural biotopes that have highest species richness usually have a long history with traditional management methods such as grazing or mowing (Cousins & Eriksson 2002, Myklestad & Sætersdal 2003, Pykälä 2003). According to Pykälä (2003) species richness of vascular plants is lower in abandoned grasslands than in grazed grasslands and when managed again vegetation recovery is slow. Pykälä (2003) also discovered that grassland and indicator vascular plant species richness was significantly higher in grazed sites. Long grazing history is known to have many positive effects on vascular plant species richness e.g. decline of resource competition, decline of nutrients, increased light availability and higher soil pH (e.g. Olff & Ritchie 1998, Ewald 2000, Pykälä 2007). However, it is also known that historical landscape connectivity has a strong positive effect on species richness in semi-natural grasslands (Lindborg & Eriksson 2004). According to Lindborg & Eriksson (2004) connectivity of landscapes 50 and 100 years ago explains present vascular plant species richness. In contrast, present-day landscape connectivity was not connected to species richness. This is why, the present species richness in traditional rural biotopes is not only determined by the management history, but also by the landscape history as a whole.

Numerous studies with grassland plants show that livestock grazing often increases plant species richness (e.g. Dullinger et al. 2003, Luoto et al. 2003, Pykälä 2003), but if grazing is too intensive it can decrease species richness (Milchunas et al.1988, van Wieren 1995). Livestock grazing causes disturbance by removing vegetation and also breaking the soil surface (Olff & Ritchie 1998, Pykälä 2007). Disturbance due to grazing has been

noticed to increase richness of plant species in productive traditional rural biotopes by removing plant biomass of dominant plant species and thus reducing competition (Olff & Ritchie 1998, Pykälä 2001, Dullinger et al. 2003). According to the intermediate disturbance hypothesis it is expected that when disturbance frequency is at medium intensity, species richness is highest (Grime 1973). Very strong disturbance keeps environment in early stage of succession (change of community in time in certain environment), where are few species, and rare or light disturbance allows the strongest competitors to dominate. This is why intermediate disturbance hypothesis predict that species richness is highest in intermediate disturbance level (Townsend et al. 2003). Several researchers have discovered that intermediate disturbance caused by grazing in semi-natural grasslands results in the highest plant species richness (Mwendera et al. 1997, Vujnovic et al. 2002, Pöyry et al. 2006). Grazing at low to intermediate intensity has been discovered to foster the heterogeneity in managed grasslands (Raatikainen et al. 2007).

Even though livestock grazing has a great impact on vascular plant species richness, there are many other environmental variables that affect species richness, too (Raatikainen et al. 2007). According to Raatikainen et al. (2007) cations, nutrients, especially phosphorus and water soluble salts significantly affect vascular plant species compositional variation. They also detected that in abandoned grassland's, species composition often changed rapidly due to tall vegetation, nutrient-enrichment, and increased productivity. Globally, it is expected that species richness increases with productivity, but it is not always the case (Evans et al. 2005). In traditional rural biotopes it has been shown that plant species richness decreases after fertilization in grasslands (Janssens et al. 1998, Myklestad & Sætersdal 2003, Stevens et al. 2004, Kleijn et al. 2009) even though primary production increases with fertilizers (Pykälä 2001, Schaffers 2002). Schaffers (2002) discovered that when biomass or productivity increases, the species richness of vascular plants, bryophytes, and lichens decreases in semi-natural vegetation types. Grazing can mitigate the effect of nutrient-enrichment in grasslands which is caused by humans, by removing biomass (Pykälä 2007).

Environmental heterogeneity also has a great impact on farmland species richness (Benton et al. 2003, Raatikainen et al. 2007). Because of increasing agricultural intensity environmental heterogeneity and species richness have decreased (Benton et al. 2003). Habitat is space where species live (Townsend et al. 2003) and it has been proposed that grazing creates a mosaic of vegetation and this creates various habitat patches for species living in these biotopes (Nauta & Jalink 2001). Raatikainen et al. (2007) have discovered that grassland soil heterogeneity (e.g. range of pH, number of soil types, range of stoniness) and habitat characters (e.g. solar radiation, moisture, stoniness) correlated with plant species composition. They revealed that soil heterogeneity explains 13.7 % and habitat characters 16.5 % of the total variation in plant species richness. Traditional management of grasslands has been suggested to maintain heterogeneity of soils, e.g. range of pH (Raatikainen et al. 2007). Traditional grazing has been noticed to increase soil pH (Ewald 2000, Pykälä 2000), which instead adds heterogeneity compared to surrounding ungrazed environment. According to Ewald (2000), it seems that plant species that require high soil pH favor pastures. According to Roem & Berendse (2000) vascular plant species richness increased with soil pH (almost up to 8).

Grazing also benefits many fungal species. Low soil nutrient concentration is proposed to be important for many vascular plants but also for grassland fungal species (Jakobsson 2005, Raatikainen et al. 2007). Grazing decreases the amount of nutrients and litter in soil (Pykälä 2007) and this benefits many fungal species (Jakobsson 2005). Grazing increases the amount of light at ground level and soil temperature (Olff & Ritchie 1998, Pykälä 2001) which makes growth circumstances better for fungal species and

therefore many fungal species occur in traditional rural biotopes (Nitare & Sunhede 1993). According to Arnolds (2001) characteristic grassland fungal species depend on continuous management over decades. Mowing has been showed to increase grassland fungal species richness (Griffith et al. 2012), but according to Nauta & Jalink (2001) grazing gives opportunities for a wider range of fungal species than mowing. Ectomycorrhizal and coprophilous fungal species cannot fruit in mowed grasslands but have potentially rich communities in grazed wood pastures (Nauta & Jalink 2001). Even these few studies have been made, fungi living in traditional biotopes are still very poorly known. Many of these studies have focused on macrofungi living in grasslands (e.g. Arnolds 2001, Nauta & Jalink 2001, Öster 2008) and Tedersoo et al. (2006) studied ectomycorrhizal fungi in only one wooded meadow by DNA-sampling. The very low number of studies is quite surprising because according to Boertmann (1995) fungi might even be better indicators of valuable traditional rural biotopes than vascular plants, which are commonly used as indicators.

Fungi play an important role as ecosystem engineers in many habitats because they are responsible for decaying organic matter and form mycorrhizal relationships with many plant species. Decomposer fungi release nutrients to the environment from dead organic matter and after that nutrients are again available for plants (Boddy et al. 2008). Mycorrhizal fungi live in two-way beneficial mutualistic associations with their host plants by transporting nutrients (Smith & Read 2008). In spite of their crucial role in the ecosystems, the ecology and conservation biology of fungi is very poorly known. For example, it has been recently argued that if some environmental change would cause a mass extinction in some of these important but inconspicuous species groups, it could remain unnoticed in spite of the fatal consequences on global ecosystem functioning (Griffith 2012). One reason for poor knowledge and scarcity of field studies is that many fungal species are difficult to identify and there is a lack of specialist researchers who are able to conduct the studies (Öster 2008). Fungi are also quite difficult to survey because of their low perceptivity and the ephemeral occurrence of their visible part, the fruit bodies. For example, some agaric genera produce fruit bodies during quite short, unpredictable periods, and not even every year. It has been shown that to detect the majority of the local species pool, the surveys must be continued for many years and even then some species will probably been overlooked (Straatsma et al. 2001, Geml et al. 2009).

To conclude, there is evidence that richness of vascular plant species increases with the length of grazing history (Pykälä 2003, Lindborg & Eriksson 2004) and that species richness is highest at intermediate grazing disturbance (Grime 1973, Mwendera et al. 1997, Pöyry et al. 2006). These issues have been rarely studied on fungi in traditional rural biotopes and not at all in wood pastures, even though fungi are an ecologically important part of the biodiversity in these biotopes. To fill this gap in knowledge, I studied the effects of grazing history and present grazing pressure on fungal species richness in deciduous wood pastures in the boreal zone. Based on the earlier knowledge on the general biodiversity effects of grazing, I hypothesized that the grazing increases fungal species richness and changes community composition. I also hypothesized that a prolonged grazing history increases species richness and that the sites with intermediate current grazing pressure have highest species richness. Thus, my aim was to answer the following questions: (1) Is there higher fungal species richness in presently grazed sites than in presently ungrazed sites? (2) Does fungal species richness increase with longer grazing history? (3) How similar are fungal communities in grazed and ungrazed sites? (4) Does the fungal species richness peak in intermediately grazed sites?

2. MATERIAL AND METHODS

2.1. Study sites

I limited my study to birch-dominated wood pastures locating in the province of Central Finland to reduce biological and geographical background variation in the data set. Thus, my study sites were 12 birch-dominated (*Betula sp.*) wood pastures located in Central Finland in the southern boreal vegetation zone (Ahti et al. 1968) (Figure 1). All of the study sites had been grazed by domestic animals during their recent history. Six study sites were currently grazed and six were not. One currently grazed site was grazed by sheep (site number 12, see Table 1), one by horses and cows (site number 1, see Table 1), and others by cows. Most of the sites are situated near farms and four of the currently grazed wood pastures were owned by cattle farmers. Three study sites were located in nature reserves. Previous and present land use was recorded by interviewing land owners; from literature (Kivelä 2000); and earlier site inventory material acquired from The Centre for Economic Development, Transport and the Environment for Central Finland (Kivelä 1993-1996). In addition, in each site, soil profiles were studied to find out if the traditional slash and burn farming method had been used in the study sites in the past. This revealed that all of the study sites had been slash and burn cultivated. Study sites situated in three biogeographical provinces: Savonia australis, Tavastia australis, and Tavastia borealis (Hämet-Ahti et al. 1998).

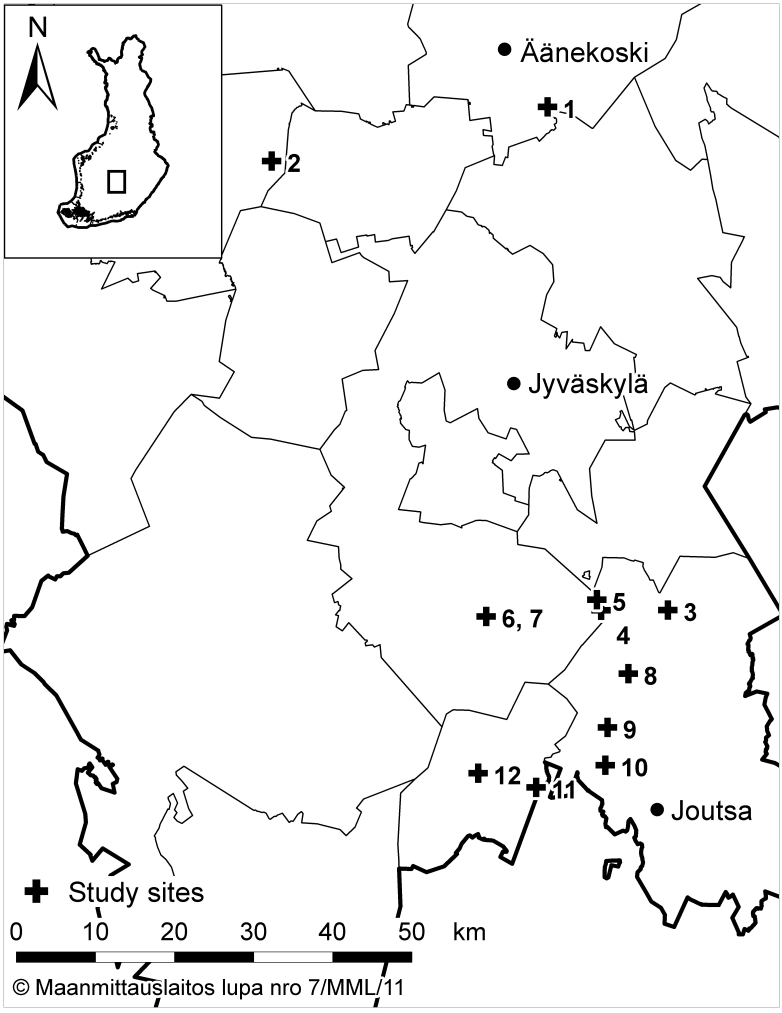


Figure 1. 12 study sites located in Central Finland in three biogeographical provinces.

The grazing history of the study sites varied substantially. For example, in one of the currently grazed sites, the grazing had just started again after a five year break (site number 12, see Table 1). On the other hand, two sites had been grazed without any breaks for 80-90 years. Considering the sites which were not currently grazed, the time period since the last grazing year varied extensively. The detailed grazing history of each study site is given in Table 1.

The size of the studied wood pastures varied, too. This study focused on wood pastures with birches as the dominant species. Because the area dominated by birch was mosaically embedded in the wood pastures, it was difficult to determine the total area of birch dominated wood pasture. Also it was quite difficult in some cases to delineate a large enough area with birch as the dominant tree species. The aim was to survey sites with as similar birch densities (mature trunks/ha) as possible. In practice it turned out to be rather difficult and thus I could not control the variation of forest site type which then varied from herb-rich to mesic heath site types (Hotanen et al. 2008).

Table 1. Characterization of the 12 study sites. Study site, town, biogeographical province, forest type, traditional rural biotope value, present grazing status, total grazing history, and years without grazing (since the last grazed year) are presented. Sa = Savonia australis, Ta = Tavastia australis, and Tb = Tavastia borealis. Traditional rural biotope values are (abbreviation follows Vainio et al. 2001): V = national, M = provincial, P = local. M and P are separated further to three groups: M-, M, M+ and P-, P, P+. The total grazing history is the sum of the years when the study site was grazed. It was calculated from the approximated starting year of grazing to the last grazed year so that estimated number of years with no grazing has been reduced from the sum.

Study site	Town	Biogeo-graphical province	Forest type	Traditional rural biotope value	Present grazing status	Total grazing history (years)	Years without grazing
1	Äänekoski	Tb	Herb-rich heath	V	Yes	155	0
2	Multia	Tb	Herb-rich	M-	Yes	205	0
3	Joutsa	Ta	Mesic heath	M	Yes	93	0
4	Jyväskylä	Ta	Herb-rich heath	P	Yes	90	0
5	Joutsa	Sa	Herb-rich	P-	No	40	30
6	Jyväskylä	Ta	Herb-rich	P	No	100	25
7	Jyväskylä	Ta	Herb-rich heath	P+	No	127	5
8	Joutsa	Sa	Mesic heath	P	No	40	20
9	Joutsa	Sa	Mesic heath	P	No	40	10
10	Joutsa	Sa	Herb-rich	M	Yes	80	0
11	Luhanka	Ta	Mesic heath	P-	No	50	40
12	Luhanka	Ta	Herb-rich heath	M	Yes	185	0

2.2. Data collection

Due to different long-term human activities in wood pastures, such as firewood logging, the variation in the dominant tree species cover, both between and within the wood pastures, is very high. If this variation is not controlled, it would be very difficult to see the potential effect of grazing history and intensity, because the dominant tree species would override the effects. Therefore, my aim was to find birch-dominated areas with as similar

mature tree densities as possible to establish sample plots. At each study site I established three 10 m x 10 m square sample plots. Thus, I first walked through the wood pastures to visually delineate suitable areas and then established three sample plots based on the density of mature birches. I marked the south-west corners of the sample plots with sticks. In all study sites, the sample plots were at least 10 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 no macrofungi producing fruit bodies (a very hot and dry June-early July period). Thus, I could effectively avoid the local species assemblage affecting the sample plot selection.

Within the sample plots, I recorded the fungi from the ground and from the surface of dead wood laying on the ground. I surveyed the ground very carefully and pushed large plants aside to find fruit bodies underneath them. However, I did not turn over dead wood pieces to avoid affecting the fungal assemblage on the plots. I counted all the fruit bodies of the agarics, boletoids, ramarioid fungi, Gasteromycetes, Pezizomycetes, and stipitate polypores. These groups were selected because they are ecologically important mycorrhizal fungi and litter decomposers and include species considered to be adapted to half-open areas (Jakobsson 2005). Moreover, other Ascomycetes were not recorded to avoid increasing the work load to an intolerable level.

To get reliable information about the fungi in the wood pastures, I conducted the surveys three times in all the study sites during September-October in 2010. I identified fungi to species level under the field conditions when possible, or collected specimens for microscopic identification. In the majority of surveys, I was assisted by Mika Toivonen who is a specialist in the identification of Agarics. All fruit bodies were counted as one occurrence because in fungi it is difficult to define which fruit body belongs to one individual (Dahlberg & Mueller 2011). After counting the fruit bodies I placed them outside the sample plots. However, for short-living species which were very abundant I did not always remove the fruit bodies from the plots. Therefore, I did not count the fruit bodies of these species in the next survey if the fruit bodies showed signs of decay because of the risk that they were counted during the previous survey.

In addition to the surveys conducted in the sample plots, I conducted a one hour time constrained survey (TCS) (Stokland & Sippola 2004) on the birch-dominant part of the study sites during the first and the second visit. In this TCS, the target species groups were the same as in the sample plot surveys, but naturally the accuracy of the time constrained survey was not as high as in sample plot surveys. During the TCS survey, I walked through the birch dominated area and identified fungi or collected specimens of all fungi that I could not identify. In this TCS survey I estimated the abundances of the detected species on a scale from one to three (1 = one group of fruit bodies, 2 = two distinctively separate groups of fruit bodies, 3 = more than two distinctively separate groups of fruit bodies). The one hour survey means effective survey time and therefore, for example, notifications for collected specimens were recorded after the survey had ended.

I collected altogether 1151 specimens for microscopic identification. Several specialists helped with the identification of the most difficult specimens in some genera (e.g. *Inocybe, Coprinus, Psathyrella*). I did not identify specimens of boletoids and the agaric genera *Clitocybe* and *Entoloma* to species level because they are microscopically very difficult to identify. Nomenclature of agarics and boletoids follows Knudsen & Vesterholt (2008), Gasteromycetes and Pezizomycetes Salo et al. (2006), and Aphylloporales Kotiranta et al. (2009). The voucher specimens are preserved in the herbarium of National History Museum of University of Jyväskylä (JYV) and in my personal collection.

I organised agarics and boletoids into two groups according to their preferred habitats. Species with traditional rural biotopes as their preferred habitats according to the current specialist knowledge are referred to as traditional rural biotope fungi (TRBF). I also recorded the species which were new for the biogeographical province and grouped mycorrhizal and saprotrophic fungi. All these groupings are according to Kytövuori et al. (2005). Near threatened (NT) species is according to von Bonsdorff et al. (2010) and data deficient (DD) and not evaluated (NE) species according to von Bonsdorff (2012).

2.3. Background variables

I measured some background variables from the sample plots to get more information of the soil characteristics in the study sites and growth circumstances of fungi.

I conducted a vegetation survey in summer 2010 in the study sites which I used to identify forest site type of the study sites (Hotanen et al. 2008). Some of the sites which had been grazed for a long time were difficult to classify to any of the existing forest site types. I used the 10 m x 10 m plots delineated for fungal surveys as the basis for the plant surveys. I had five 1 m x 1 m square plots within each of the 10 m x 10 m plots. I also identified three most dominant bryophyte species from the 1 m x 1 m squares because they are an important group for identifying forest site types.

I also evaluated the grazing intensity by using two ordinal scale variables (present grazing intensity, bare soil) when I was conducting the fungal surveys. The present grazing intensity variable was classified to four categories (1 = no traces of grazing, 2 = some traces of grazing, 3 = traces of grazing is seen in (almost) the whole plot area, 4 = vegetation grazed short). The area of soil without vegetation cover (bare soil) was classified in three categories (1 = ground is covered by vegetation, but some footsteps of domestic animals can be seen, 2 = some patches of bare soil can be seen in some places, for example footpath, 3 = at least about 1/3 of the ground area is bare due to animal trampling). For analyses I used these ordinal scale variables as continuous variables. I calculated the average value for each study site by combining all sample plots and inventory times. I also calculated average values for each sample plot on each study site by combining inventory times.

2.4. Statistical analyses

2.4.1. Effects of present grazing status and grazing history on fungal species richness

All the analyses were conducted with four separate target species groups as dependent variables: all fungi, TRBF, mycorrhizal fungi, and saprotrophic fungi. There were some species that were not included in the analyses and they are listed in Appendix 1. Some species were included only in genus level because these were thought to belong to one species in field conditions but while making microscopical studies of collections, they were determined as two different species. Also species which were found to be both mycorrhizal and saprotrophic were not included in either mycorrhizal or saprotrophic fungi groups.

I determined the effect of present grazing status on (1) species richness in the sample plots, (2) species richness on TCS, and (3) total fungal species richness (1 and 2 together). I separated species richness by inventories for getting some information of different inventory methods. I used one-way ANOVA to analyze present grazing status effect. I conducted 12 one-way ANOVA analyses with different inventory types and target species groups. Fungal species richness was entered as a dependent factor and present grazing status as an independent factor.

I determined the effect of total grazing history on the above mentioned three categories. I used linear regression analysis to analyze the effect of grazing history. Fungal species richness was entered as a dependent factor, total grazing history as an independent factor. I conducted 12 linear regression analyses with different inventory types and target species groups.

One-way ANOVA and linear regression analyses were performed by using PASW 18.0 statistics program (SPSS Inc.).

2.4.2. Fungal community structure in the study sites

I examined graphically the similarity of species composition between study sites with different present grazing status and total grazing histories with Nonmetric Multidimensional Scaling (NMS ordination). I also examined the similarity of species composition between forest site types. I did all of these NMS ordinations with and without coprophilous fungal species to reveal the effect of this very specialized group. Coprophilous fungal species can only occur in grazed sites because there is dung from domestic animals and these species are likely to heavily affect results. To reveal the difference between presently grazed and ungrazed sites without the impact of dung, I also tested the effect of total grazing history without coprophilous fungal species.

NMS ordination does not assume linear relationships among variables and is appropriate when data include many zeros (McCune & Grace 2002). I used the data of fruit body counts of each species in each study site across all the sample plots and surveys. I removed the species which occurred only in one study site from the data. I also conducted a logarithmic transformation on the occurrence data because there were two very abundant species. These two species made data very skewed. In the main matrix I included logarithmic fruit body counts of each species in the study sites. The second matrix included present grazing status, total grazing history, and forest site type in each of the study sites. I used NMS autopilot to find the best solution at each dimensionality and minimum final stress. I used Sörensen (Bray-Curtis) distance measure to count distance matrix of the study sites, which is recommended by McCune & Grace (2002). In the final solutions there were three dimensions.

I analyzed the effect of the present grazing status and the effect of the forest site type on the species composition in the study sites with Multi-response Permutation Procedure (MRPP). MRPP is a nonparametric procedure for testing for no difference between groups. NMS ordination and MRPP analyses were performed by using PC-ORD.

2.4.3. Effects of grazing intensity on fungal species richness

I determined grazing intensity by two different ordinal scale variables (present grazing intensity, bare soil). I analyzed the relationship between present grazing intensity or amount of bare soil and species richness in the sample plots. I used curve regression analysis (fitted curves: cubic, linear, quadratic) to analyze the effect of present grazing intensity and linear regression analysis to reveal the effect of ground erosion. Best fitted curve was selected (cubic). Fungal species richness was entered as a dependent factor, present grazing intensity or ground erosion as an independent factor. Curve regression and linear regression analyses were performed by using PASW 18.0 statistics program (SPSS Inc.).

3. RESULTS

3.1. General results

Altogether, 313 fungal species were identified in the studied deciduous wood pastures (Appendix 1). I recorded altogether 13 299 fruit bodies in the sample plots and 1280 occurrences (one species had a maximum of three occurrences per survey) during the TCS. The species richness of target species groups separated by study sites is presented in Table 2. The species richness of target species groups separated by present grazing status is presented in Table 3.

I detected overall 58 species new to some of the studied biogeographical provinces. Moreover, I found one near threatened species, *Pholiotina pygmaeoaffinis*, which had one occurrence in a presently grazed study site, and three in presently ungrazed study sites. I also found one data deficient and eight agaric species which were not evaluated in the latest Red List of Finnish species (von Bonsdorff et al. 2010) The data deficient species, *Psathyrella tenuicula*, was found from one presently ungrazed site, and its latest record before this was from southern Finland in 1879. I also found one agaric species which was new to Finland, *Coprinellus brevisetulosus*. Most frequent species were *Armillaria borealis* and *Collybia sp.*, but also *Amanita muscaria var. muscaria*, *Lactarius tabidus*, *Mycena galericulata*, and *Paxillus involutus* occurred in most of the study sites.

Table 2. The number of all fungi, traditional rural biotope fungi (TRBF), mycorrhizal fungi, and saprotrophic fungal species in the study sites. Present grazing status of the study sites is presented. The data are given as total number of species in the two different inventory types (sample plots (SP), time constrained survey (TCS)) and in the two survey types together (Total).

Study site	Present grazing status	All fungi			TRBF			Mycorrhizal fungi			Saprotrophic fungi		
		SP	TCS	Total	SP	TCS	Total	SP	TSC	Total	SP	TCS	Total
1	Yes	80	79	113	14	17	21	28	34	44	52	44	69
2	Yes	79	89	128	10	15	20	42	53	71	35	35	55
3	Yes	73	59	100	17	11	21	33	35	49	39	23	50
4	Yes	72	71	103	14	14	19	27	30	41	44	40	61
5	No	75	74	103	15	13	19	31	33	44	43	40	58
6	No	87	55	110	13	10	16	38	23	50	46	31	57
7	No	73	71	98	12	15	17	32	36	45	40	34	51
8	No	36	34	58	7	4	9	11	16	23	24	17	33
9	No	31	25	45	3	2	4	12	9	19	18	15	25
10	Yes	42	41	58	10	8	11	7	12	13	34	28	44
11	No	44	51	73	7	8	11	9	21	24	34	29	48
12	Yes	56	48	74	10	8	13	21	24	31	33	22	41

Table 3. The number of all fungi, traditional rural biotope fungi (TRBF), mycorrhizal fungi, and saprotrophic fungal species in the presently grazed and ungrazed study sites. The data are given as total number of species in the two different inventory types (sample plots, time constrained survey (TCS)) and in the two survey types together (total).

Fungal species richness		Present grazing status		Total
		Yes	No	
All fungi	Sample plots	187	159	237
	TCS	195	154	248
	Total	250	203	313
TRBF	Sample plots	33	23	37
	TCS	34	25	42
	Total	39	29	47
Mycorrhizal fungi	Sample plots	75	74	100
	TCS	88	75	113
	Total	107	96	137
Saprotrophic fungi	Sample plots	109	81	133
	TCS	105	77	132
	Total	140	103	171

3.2. Effects of present grazing status and grazing history on fungal species richness

3.2.1. Effect of present grazing status on fungal species richness

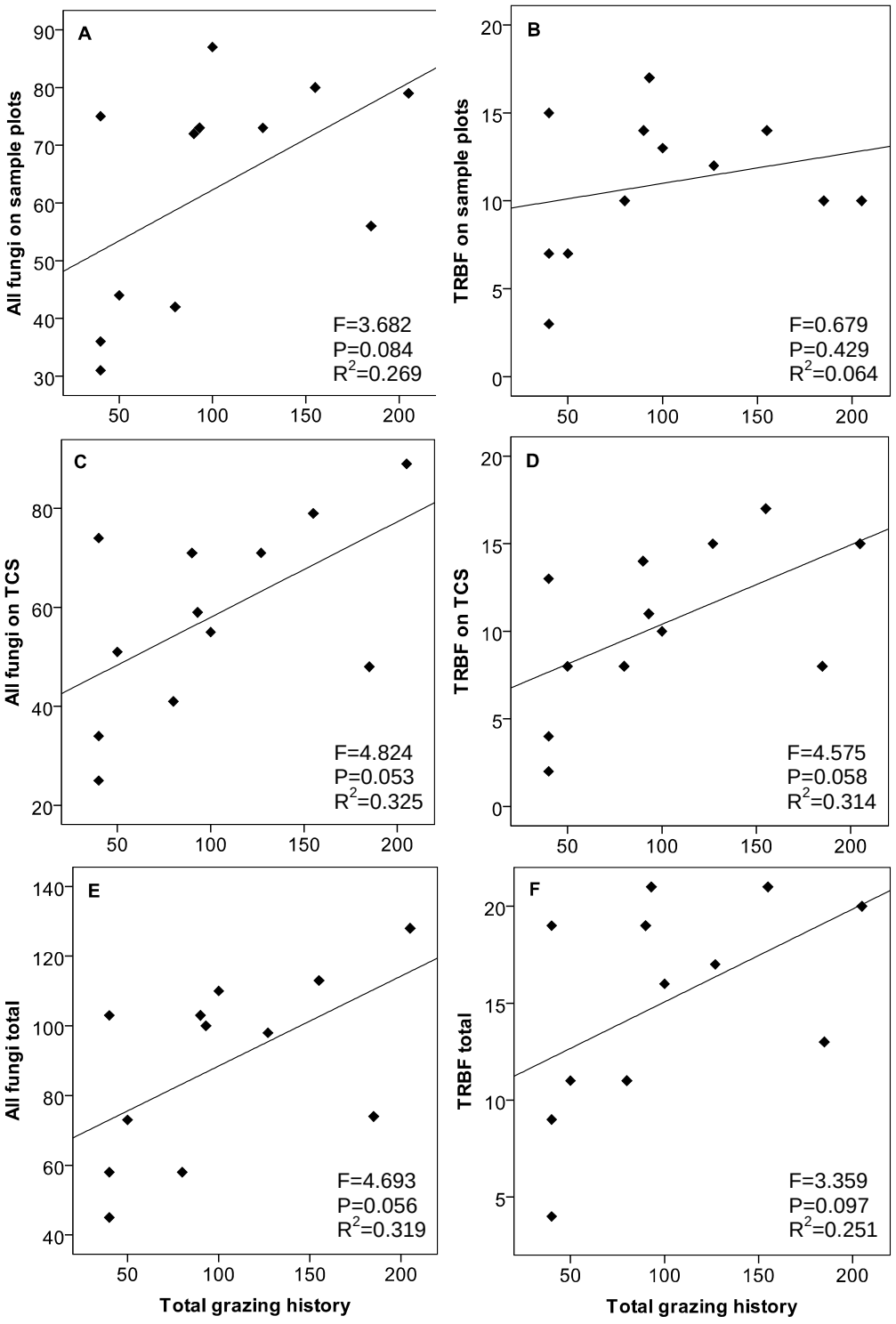
I examined the effect of present grazing status on fungal species richness with one-way ANOVA. The analyses revealed that fungal species richness in the target groups (all fungi, TRBF, mycorrhizal fungi, and saprotrophic fungi) was not affected by present grazing status (Table 4).

Table 4. One-way ANOVA on the fungal species richness (all fungi, traditional rural biotope fungi (TRBF), mycorrhizal fungi, and saprotrophic fungi) between presently grazed and presently ungrazed sites. Fungal species richness is analyzed with sample plots, time constrained survey (TCS) and inventory types together (total). The table includes degrees of freedom of present grazing status (df_1) and of study sites (df_2), the value of the test statistics (F), and the probability for that the observed value of F could be caused by a random variation (P).

Fungal species richness		df_1	df_2	F	P
All fungi	Sample plots	1	10	0.639	0.443
	TCS	1	10	1.367	0.270
	Total	1	10	0.940	0.356
TRBF	Sample plots	1	10	1.837	0.205
	TCS	1	10	1.855	0.203
	Total	1	10	2.729	0.130
Mycorrhizal fungi	Sample plots	1	10	0.321	0.584
	TCS	1	10	1.449	0.256
	Total	1	10	0.559	0.472
Saprotrophic fungi	Sample plots	1	10	0.963	0.350
	TCS	1	10	0.631	0.446
	Total	1	10	1.316	0.278

3.2.2. Effect of total grazing history on fungal species richness

Linear regression analyses revealed that total grazing history tends to explain some of the variation observed in the fungal species richness (all fungi, TRBF, mycorrhizal fungi, and saprotrophic fungi) (Figure 2).


A
All fungi on sample plots
F=3.682
P=0.084
R2=0.269
B
TRBF on sample plots
F=0.679
P=0.429
R2=0.064
C
All fungi on TCS
F=4.824
P=0.053
R2=0.325
D
TRBF on TCS
F=4.575
P=0.058
R2=0.314
E
All fungi total
F=4.693
P=0.056
R2=0.319
F
TRBF total
F=3.359
P=0.097
R2=0.251
Total grazing history
Total grazing history

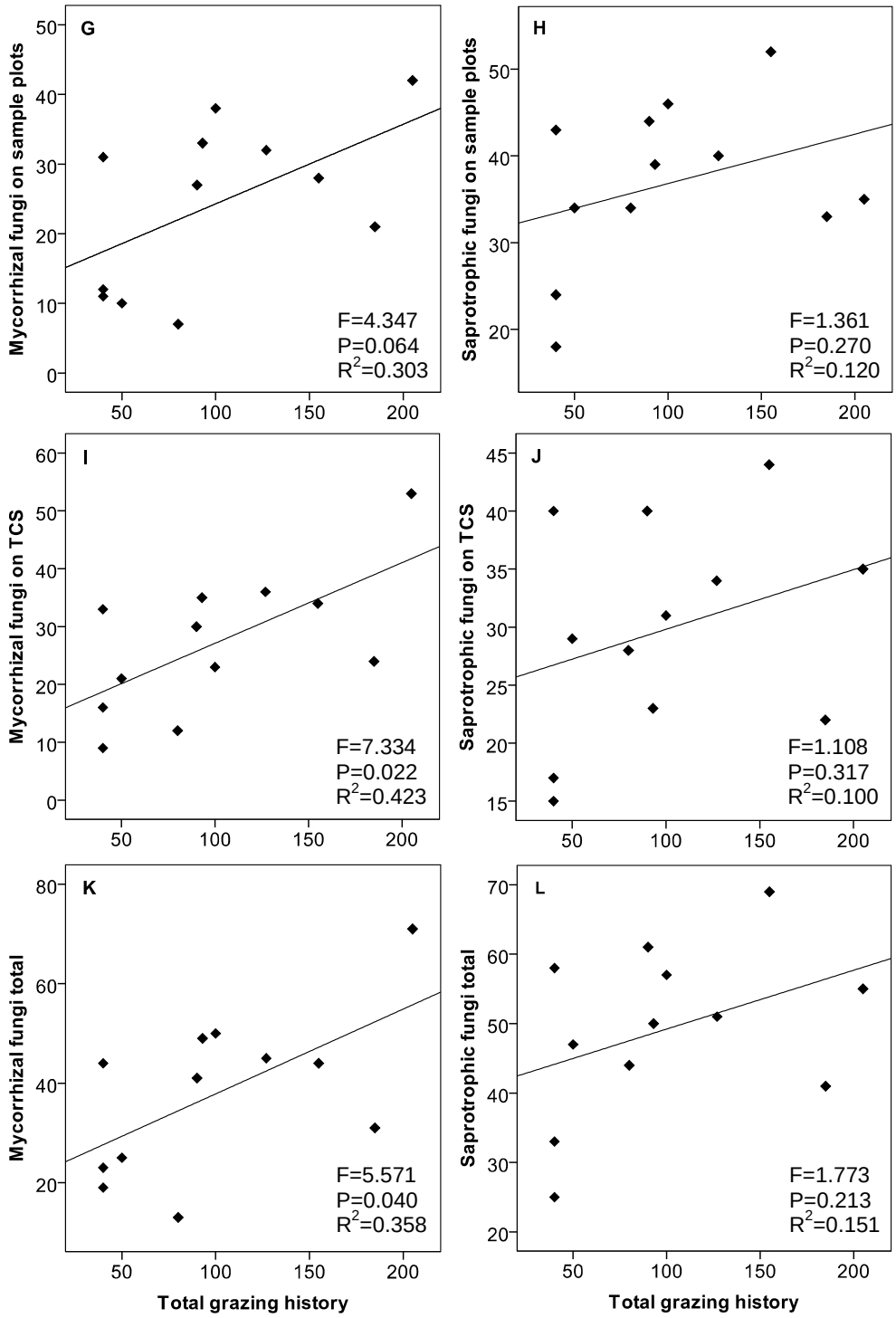


Figure 2. The linear relationships between total grazing history and (A) all fungi on sample plots, (B) traditional rural biotope fungi (TRBF) on sample plots, (C) all fungi on time limited inventory (TCS), (D) TRBF on TCS, (E) all fungi on sample plots and TCS together, (F) TRBF on sample plots and TCS together, (G) mycorrhizal fungi on sample plots, (H) saprotrophic fungi on sample plots, (I) mycorrhizal fungi on TCS, (J) saprotrophic fungi on TCS, (K) mycorrhizal fungi on sample plots and TCS together, and (L) saprotrophic fungi on sample plots and TCS together. The figure includes the value of linear regression analysis test statistics (F), the probability for that the observed value of F could be caused by a random variation (P), and coefficient of determination (R^2). Degrees of freedom with variation of regression were 1 for all tests and degrees of freedom with variation of residual were 10 for all tests.

3.3. Fungal community structure in the study sites

NMS ordination on fungal data which included coprophilous fungi revealed that with three-dimensional ordination result and 28 iterations the final stress was 7.541. Presently grazed sites did not clearly differ from the presently ungrazed sites with species composition (Figure 3A). The difference between presently grazed sites and presently ungrazed sites in terms of fungal species composition was not significant (MRPP: n=12, A=0.016, P=0.124).

NMS ordination with fungal data which did not include coprophilous fungi revealed that with three-dimensional ordination result and 52 iterations the final stress was 7.352. Presently grazed sites did not clearly differ from the presently ungrazed sites in terms of species composition (Figure 3B). The difference between presently grazed sites and presently ungrazed sites in terms of fungal species composition was not significant (MRPP: n=12, A=0.007, P=0.250).

In figures 3A and 3B can be seen that the presently ungrazed study sites with long grazing history are similar with presently grazed sites and all sites with long grazing history are mostly similar with each other.

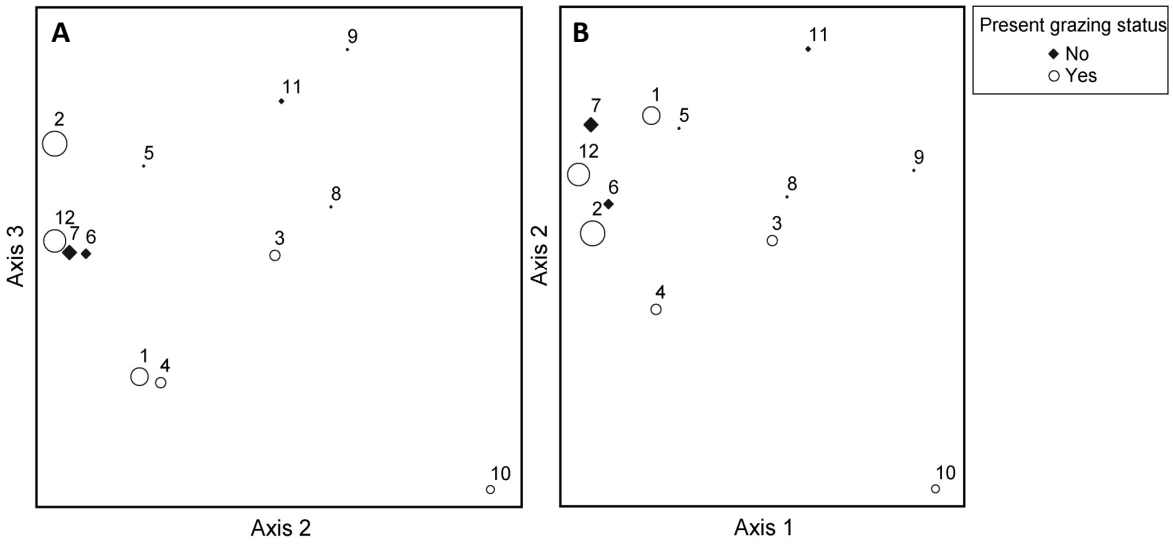


Figure 3. NMS ordination results on presently grazed and ungrazed sites. The symbol size is increasing with total grazing history. A) Position of the study sites on the axes two and three on NMS ordination with coprophilous fungi included. B) Position of the study sites on the axes one and two on NMS ordination with coprophilous fungi not included. Study sites are numbered as in Table 1.

The fungal communities in the study sites differed according to the forest site types (Figure 4). The difference between forest site types was significant when coprophilous fungi were included (MRPP: n=12, A=0.046, P=0.022), and also when they were not included (MRPP: n=12, A=0.052, P=0.015).

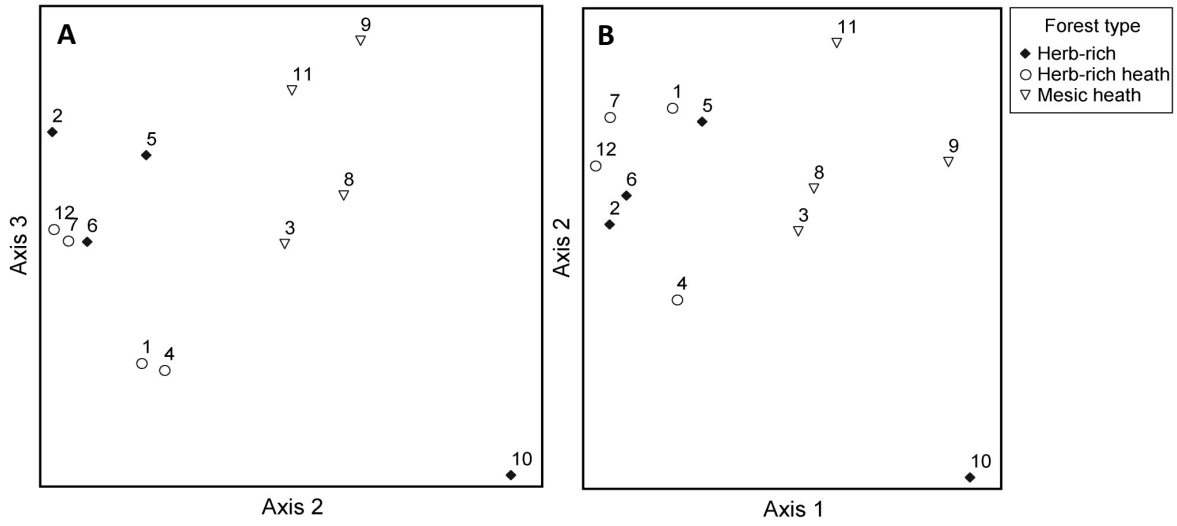


Figure 4. NMS ordination overlaid with forest type. A) Position of the study sites on the axes two and three on NMS ordination with coprophilous fungi included. B) Position of the study sites on the axes one and two on NMS ordination with coprophilous fungi not included. Study sites are numbered as in Table 1.

3.4. Effects of present grazing intensity and bare soil on fungal species richness

Curve regression analysis revealed that present grazing intensity explained variation observed in the fungal species richness in presently grazed sample plots (cubic: df_1=2, df_2=3, F=17.113, P=0.023, R^2=0.919, Figure 5A). However, one must note that the high power is highly dependent on one site with low and one with high grazing intensity, both having very low species richness. Figure 5B revealed that there is considerable variation between study sites in fungal species richness, especially in intermediate grazing intensity.

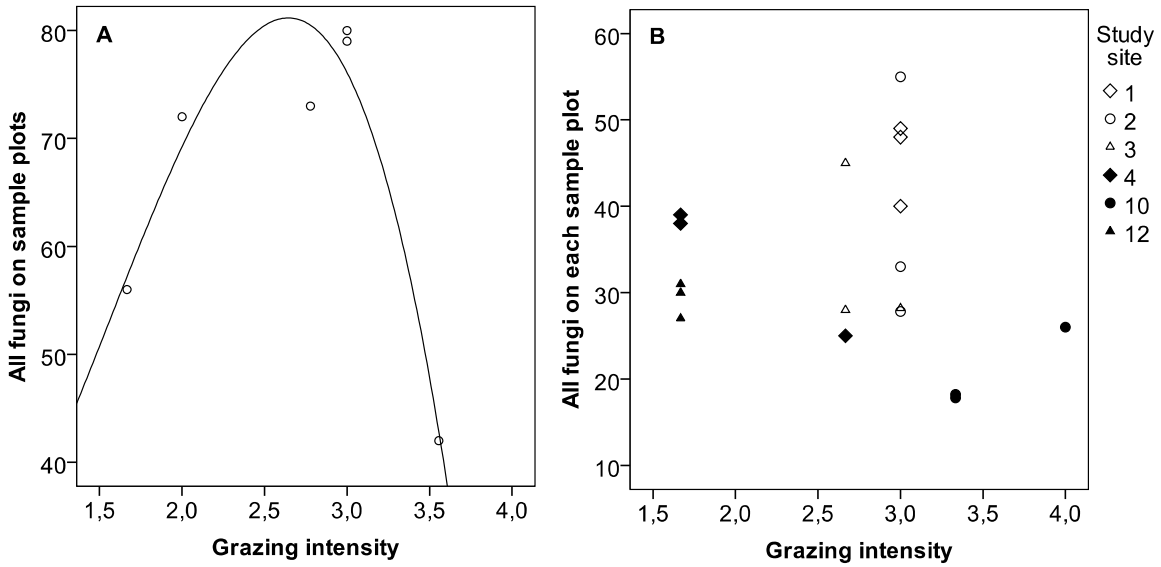


Figure 5. A) The curve (cubic) relationship between species on presently grazed sample plots and grazing intensity. B) The relationship between all fungal species on each sample plot in each presently grazed study site and grazing intensity. Study sites are numbered as in Table 1. Two sample plots of site number 10 have same values.

Instead, linear regression analysis revealed that bare soil does not explain variation observed in the fungal diversity in presently grazed sample plots (df_1=1, df_2=4, F=0.043, P=0.845, R^2=0.011, Figure 6A). Figure 6B revealed that variation in species richness was greatest at intermediate bare soil levels.

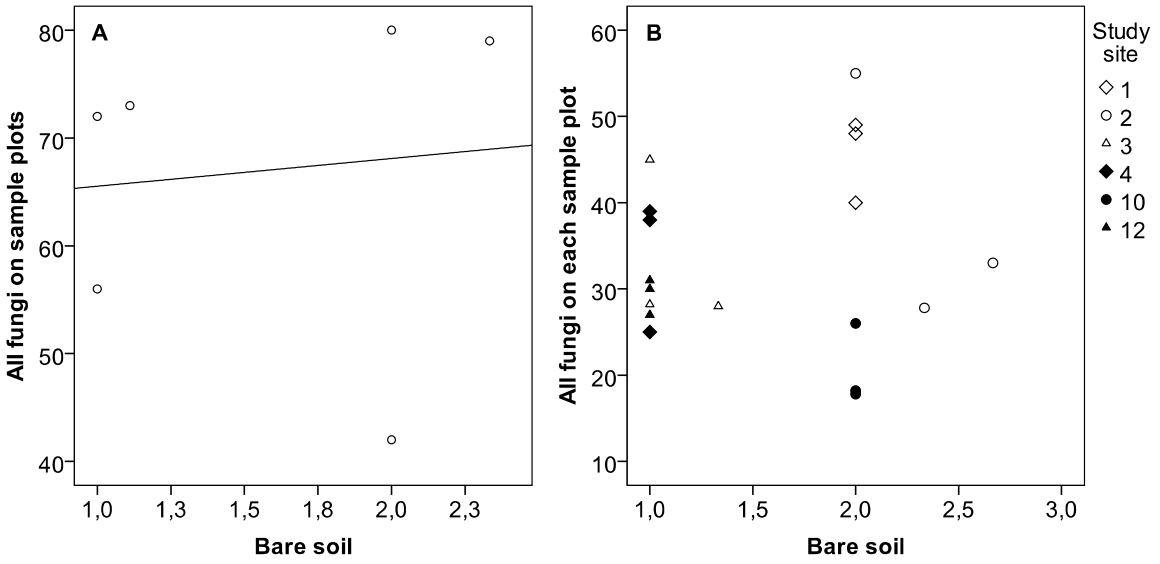


Figure 6. A) The linear relationship between all fungal species in presently grazed sample plots and degree of bare soil. B) The relationship between all fungal species in each sample plots in each presently grazed study site and the degree of bare soil. Study sites are numbered as in Table 1. Two sample plots of site number 10 have same values.

4. DISCUSSION

4.1. Effect of present grazing status and grazing history on fungal species richness

In this study presently grazed study sites did not differ from the presently ungrazed sites considering species richness in any of the studied fungal groups. Even so, fungi species typical to traditional rural biotopes responded strongly to present grazing status. My result does not support the findings with vascular plant species richness on grasslands where presently grazed sites have been noticed to have the greatest species richness (Pykälä 2003). Griffith et al. (2012) also discovered that mowed grasslands had the greatest fungal species richness compared to grasslands that were not mowed. According to my knowledge, the only study focusing on the effects of grazing on fungi was conducted by Trent et al. (1988). They showed that wheat roots colonized by vesicular-arbuscular mycorrhizae were significantly longer in ungrazed than grazed sites but percent of colonization did not differ. Thus, my study is the first evidence of the positive effect of grazing history on fungal species richness.

In my data, there were two study sites that probably affected to the fact that there was no difference between presently grazed and presently ungrazed sites. In one site (site number 12) the study year was the first summer grazed again after a break in the grazing history and so there was not enough time for the vegetation to recover from the ungrazed period. In another site (site number 10), grazing had been too intense and this could have reduced fungal species richness. These sites had low fungal species richness compared to the other presently grazed study sites with equally long total grazing history. It should be noted that I had only 12 study sites with very different grazing history so differences

caused by grazing are difficult to recognize. Thus it may well be that the positive connectivity of vascular plant species richness and grazing in grasslands (Pykälä 2003) is true also for fungi in wood pastures. Although I did not found the connection.

Total grazing history explained some of the variation observed in the fungal species richness. Total grazing history significantly explained variation observed in mycorrhizal fungal species richness observed during time constrained survey and total mycorrhizal fungal species richness. Total grazing history explained as many as 42 % of the mycorrhizal fungal variation in the time constrained survey. Results were near significant in all fungi species in all inventory categories, and in traditional rural biotope fungal species in time constrained surveys and survey types together. In contrast, results were not significant in traditional rural biotope fungi in sample plots and saprotrophic fungi in any inventory categories. Cases with near significance indicate that grazing history has an impact on species richness, but more studies are needed to confirm this. My results support findings with vascular plants where sites with long management history have highest species richness (Cousins & Eriksson 2002, Pykälä 2003). In these studies history variable is categorical where as I considered history continuous. Pykälä (2003) categorized his sample plots to continuously seasonally grazed, restored, and overgrowing. Thus total grazing history could be even higher in restored sites than continuously grazed, but this information is not presented in his study. My results suggest that the length of ungrazed period is not so important to wood pasture fungal species richness than long total grazing history. Therefore, my results are not fully comparable with those obtained by Cousin and Eriksson (2002) and Pykälä (2003).

My results also indicate that mycorrhizal and saprotrophic fungi have different responses to grazing. Mycorrhizal fungi seem to benefit from grazing, but species richness of saprotrophic fungi seem to be indifferent to grazing. Grazing has been shown to decrease litter in soil (Pykälä 2003) which benefits most mycorrhizal fungal species (Arnolds 1991). Grazing also decreases the amount of soil nutrients (Ewald 2000) and Arnolds (1991) has shown that forests with high mycorrhizal fungal diversity have low soil nitrogen and phosphorus content. These findings can explain my results why fungal species richness increases with grazing history and especially why mycorrhizal fungal species richness increases with longer grazing history. Traditional rural biotopes have low nutrient content in the soil because of grazing or mowing (Ewald 2000, Pykälä 2001) and this can be the main reason why many mycorrhizal fungal species occur in wood pastures.

The present grazing status did not significantly affect fungal diversity in any studied target species group and total grazing history did not significantly explain the species richness of traditional rural biotope fungi. This is surprising because with vascular plants it has been shown that grassland specialist species benefit from long managed history and presently grazed grasslands have more species than abandoned ones (Pykälä 2003). Furthermore, habitat loss and fragmentation have been discovered to cause immediate and time-delayed response in vascular plants (Helm et al. 2006, Krauss et al. 2010). Helm et al. (2006) concluded that the response of plant species to habitat fragmentation is slow. Probably, this is the same for fungal response to habitat loss and fragmentation, and therefore the change is not show in my data.

4.2. Effect of present grazing status and grazing history on fungal community structure

NMS-ordinations revealed that study sites with long grazing history have most similar fungal communities. However, present grazing status did not significantly explain community differences. Coprophilous fungal species are an important group in grazed sites but they cannot occur in presently ungrazed sites. Many of those species are specialized for

dung of domestic animals. Therefore, to reveal the difference between presently grazed and ungrazed sites without the impact of dung, I also tested the effect of total grazing history without coprophilous fungal species. However, the results were similar with and without coprophilous fungal species.

Communities of presently grazed sites were mainly similar with each other, but site number 10 showed a clear difference from other communities. This difference is possibly caused by the fact that in the site number 10 there was the highest grazing intensity and sample plots were quite near a fertilized pasture. Nearness of fertilized pasture can cause an increased amount of nutrients in the soil compared to other sites (not measured). It is known that cattle eats in fertilized pastures and goes to wooded areas to get shadow and then defecate there. This transports excess nutrients to wood pastures if they are connected to fertilized pastures.

Two presently ungrazed sites with a long grazing history hosted communities which were very similar with presently grazed sites. This indicates that a long management history has an effect on community structure, even some time after abandonment. This result is somewhat similar with what Pykälä (2003) discovered in vascular plant communities. His study revealed that communities in sites under long management history are similar to each other. One reason for the similarity of ungrazed communities with long grazing history and presently grazed communities is that long disturbance by grazing has been changing vegetation structure substantially in wood pastures compared to original forest (Vainio et al. 2001). Recovery of wood pastures back to forest is slow. Long grazing history has also changed circumstances of soil (Olff & Ritchie 1998, Pykälä 2001), and therefore conditions of soil recover slowly. Thus the community structure of places with long grazing history is similar, even when some time has elapsed from the last grazed year. Maybe one reason for the fact that presently ungrazed sites with a long grazing history have a similar community structure compared with those that have a continuous grazing history is extinction debt. Extinction debt means that due to past fragmentation and habitat loss, species are expected to eventually go extinct, but the extinction has not been realized yet (Tilman et al. 1994). It has been stated that there is a time lag between habitat degradation or fragmentation and extinctions, and this can cause extinction for many species in future (e.g. Hanski 2000). So extinction debt could cause similarity of presently ungrazed sites to grazed sites because there has not been enough time for species to react to changed circumstances and go extinct.

I also studied the effect of forest type on fungal communities with NMS-ordination. In ordination I could see that herb-rich heath and mesic heath forest communities are quite similar to each other, but herb-rich forest communities are apart from the others. MRPP revealed that communities of different forest types differed significantly. The results are the same when coprophilous fungal species are counted and when they are not. Similarity in forest site types can partly explain why ungrazed site 5, which has a short grazing history, has similar community structure with presently grazed sites with long grazing history. For example presently grazed site number 2 has similar community structure with site 5, and they both are herb-rich forests. This result reveals that forest site type affects to communities of wood pastures and probably also to fungal species richness.

4.3. Effects of present grazing intensity and ground erosion on fungal species richness

In this study I discovered that the highest fungal species richness was in sites with an intermediate disturbance regime related to grazing. Results revealed that present grazing intensity significantly explains variation observed in species richness. This result supports findings where the highest vascular plant species richness was in intermediately grazed sites, as predicted by the intermediate disturbance hypothesis (Mwendera et al. 1997). In

contrast, another type of disturbance, i.e. trampling intensity, measured as the area of bare soil in the sample plots, did not explain variation observed in species richness. Nevertheless, there was only one study site with low and one with high grazing intensity, so more studies are needed to confirm this.

Grazing benefits vascular plants because it reduces competition between plants compared to a situation without grazing (Olff & Ritchie 1998, Dullinger et al. 2003). But it is also known that with too intensive grazing, species richness decreases (Milchunas et al.1988, van Wieren 1995) so intermediated grazing is optimal for vascular plant species (van Wieren 1995). Intermediate grazing also has other benefits. It creates and maintains heterogeneity in pastures (Raatikainen et al. 2007). Higher environmental heterogeneity results in more habitats for species (Nauta & Jalink 2001) and therefore species richness can increase. Intermediate disturbance produced by grazing is an important study subject because knowledge of effects on different intensity levels of disturbance could help to plan and conduct optimal management in traditional rural biotopes. The biodiversity effects of grazing are probably different in different biomes and biotopes. I found only two Finnish studies on the effects of intermediate disturbance produced by cattle grazing in traditional rural biotope (Pöyry et al. 2004, Pöyry et al. 2006), but not with fungi. Therefore it is important to conduct further studies on this topic to strengthen the scientific basis of the management procedures.

Griffith et al. (2012) showed that grassland fungal species richness were highest in plots mown to 3 cm height. They also studied plots that were mown at 8 cm and plots that were left uncut. Grazing can affect fungal species somewhat similarly to mowing by removing plant biomass. Intermediate grazing could cause a mixture of different vegetation heights because extensive grazing produces heterogeneity as a mosaic of vegetation (Nauta & Jalink 2001). Moreover, mowing at 3 cm height can be intermediate disturbance to vegetation compared to the fact that grazing also produces bare soil due to trampling. But because grazing also produces bare soil, grazing and mowing studies cannot be fully compared. It would be interesting to compare how grazing and mowing affects fungal diversity in the same study sites and to explore which management type, grazing or mowing, has the greatest effect on fungal species richness. In addition to management type it would also be important to study the effects of different grazing animal species on fungal species richness. It is known that the animal affects vascular plant species richness (Pykälä 2001).

4.4. Confounding factors

Light, nutrients, and temperature stimulate fungal fruit body formation (Boulianne et al. 2000), and grazing increases the amount of light at ground level and the soil temperature (Olff & Ritchie 1998, Pykälä 2001). The differences in species richness may partly reflect different fruit body formation circumstances caused by grazing, instead of actual species richness differences between the sites. So my results have to be interpreted with caution. However, to survive in fragmented landscapes the fungi which are restricted to traditional rural biotopes must be efficient in their dispersal. Thus, the fruit body production is probably a good measure of the overall effects of grazing at least for applied purposes.

Total grazing history is quite a difficult variable to determine perfectly in every site. Land owners' knowledge varied between sites. Mostly owners have accurate information of grazing history, but owners of some sites were unsure of the history. In such cases I tried to make the best possible conclusions to determine grazing history. In spite of this some sites may have lower estimated grazing history duration than what they truly have. Some presently grazed study sites were grazed so that the animals had an access also to fertilized open pastures. This could cause biased results, because nutrients are transferred

from fertilized pastures to wood pastures. However, sites grazed together with fertilized pastures did not have especially long or short grazing history and thus this could not affect the effects of grazing history duration.

Forest site types could cause some error to results because the presently ungrazed sites included more mesic heath forests and fewer herb-rich heath forests than presently grazed sites and the forest type had an effect on the detected community. This is a difficult topic to address, partly because forest type identifications were difficult in some sites with long grazing history. It seems that long-term continuous grazing disturbs the classic forest types and perhaps even causes changes in the forest type.

4.5. Conclusions

My results show that fungal species richness increases with increasing total grazing history. However, presently grazed sites do not have more species than presently ungrazed sites. I also discovered that communities occupying sites with a long grazing history are quite similar with each other, regardless of the present grazing status. This reveals that continuity and duration of grazing are very important factors determining fungal species richness and the community assembly. Because changes in fungal communities take place slowly, long management history is important, even when some years have passed since the last grazed year. This is an important result because this reveals that it is very important to find out total management histories of sites when environmental authorities prioritize management. With right prioritizing, conservation effort can be optimized. I also found that fungal species richness was highest in intermediately grazed sites. Thus it is also important to determine the appropriate grazing intensity for sites because too intense or too light a grazing pressure may reduce species richness.

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APPENDIX 1

List of species and higher taxonomic groups observed on the study. Numbers reveal the amount of study areas where species occurred. Occurrences are separated by grazed and ungrazed sites. Occurrences are given separately in sample plots (SP), time constrained survey (TCS), and inventory types together (ALL). The status of species are reported: near threatened species (NT)(von Bonsdorff et al. 2010), not evaluated (NE), and data deficient (DD)(von Bonsdorff 2012). Agarics and boletes are grouped into traditional rural biotope fungi (TRBF=T), which are species living in environments which are impacted by traditional agriculture. Agarics and boletes are also grouped into mycorrhizal (M) and saprotrophic (S) fungi. These groupings accord with Kytövuori et al. (2005). Nomenclature of agarics and boletoids follows Knudsen & Vesterholt (2008), Gasteromycetes and Pezizomycetes Salo et al. (2006) and Aphylloporales Kotiranta et al. (2009), where the authors of the species can be found. If author of species diverge from the foregoing, author is named after species name.

* Species is included into analyses in genus level

** Species is not included into mycorrhizal/saprotrophic analyses

Species	Grazed			Ungrazed			Status	T	S/M
	SP	TCS	ALL	SP	TCS	ALL			
Agaricus semotus	0	0	0	0	1	1			S
Agaricus sp.	0	1	1	0	0	0			S
Amanita battarrae	0	0	0	1	1	1			M
Amanita citrina f. citrina	0	0	0	0	1	1			M
Amanita crocea	0	2	2	0	0	0			M
Amanita fulva	1	1	2	0	1	1			M
Amanita muscaria var. muscaria	5	6	6	4	5	5			M
Amanita muscaria var. regalis	0	1	1	1	0	1			M
Amanita olivaceogrisea	2	4	4	1	2	2			M
Amanita porphyria	0	1	1	0	0	0			M
Amanita rubescens f. rubescens	1	2	2	0	0	0			M
Amanita virosa	0	0	0	1	2	2			M
Ampulloclitocybe clavipes	0	0	0	0	1	1			S
Armillaria borealis	5	5	6	4	5	5			S
Armillaria lutea	0	0	0	1	0	1			S
Arrhenia acerosa var. acerosa	0	0	0	1	0	1			S
Asterophora lycoperdoides	0	0	0	1	1	1			S
Auriscalpium vulgare	1	1	1	2	3	4			S
Baeospora myosura	1	3	3	1	1	1			S
Bolbitius titubans	1	0	1	0	0	0			S
Boletus edulis coll.	3	5	5	2	3	5			M
Boletus pinophilus	0	0	0	1	0	1			M
Bovista nigrescens	2	1	3	0	0	0			S
Calocera sp.	2	2	4	0	0	0			S
Clavaria sp.	0	1	1	0	0	0			S
Cantharellus cibarius	2	2	2	1	2	3			M
Chalciporus piperatus	4	2	6	2	3	3			M

Species	Grazed			Ungrazed			Status	T	S/M
	SP	TCS	ALL	SP	TCS	ALL			
Clavulina coralloides	1	0	1	1	0	1			S
Clavulinopsis laeticolor	1	0	1	0	0	0			S
Clavulinopsis luteoalba	0	0	0	1	0	1			S
Clitocybe connata	0	1	1	0	0	0			S
Clitocybe fragrans	0	0	0	0	2	2			S
Clitocybe odora var. odora	0	1	1	1	0	1			S
Clitocybe sp.	3	3	4	2	3	3			S
Clitopilus hobsonii	1	0	1	0	0	0			S
Clitopilus prunulus	4	5	6	3	2	4			S
*Collybia cirrata**	0	0	0	1	0	1			S
*Collybia cookei**	2	0	2	0	0	0			S
Collybia sp.	6	6	6	6	5	6			S
*Collybia tuberosa**	3	2	4	3	0	3			S
Conocybe cf. echinata	0	2	2	0	0	0			S
Conocybe cf. rickeniana	0	2	2	0	0	0		T	S
Conocybe juniana var. juniana	4	1	4	2	0	2			S
Conocybe lenticulospora	2	3	3	0	1	1		T	S
Conocybe mesospora	2	0	2	0	0	0		T	S
Conocybe pulchella	1	1	2	0	1	1		T	S
Conocybe sp.	3	0	3	2	1	3			S
Conocybe subalpina	0	1	1	0	0	0			S
Coprinellus brevisetulosus	2	0	2	0	0	0	NE		S
Coprinellus heterosetulosus	1	0	1	0	0	0			S
Coprinellus micaceus	1	2	2	1	1	2			S
Coprinellus sp.	2	1	2	0	0	0			S
Coprinellus xanthothrix	1	1	1	0	0	0		T	S
Coprinopsis atramentarius	1	1	1	0	0	0			S
Coprinopsis echinospora	1	1	1	0	0	0			S
Coprinopsis nivea	1	1	1	0	0	0			S
Coprinopsis sp.	1	0	1	0	0	0			S
Coprinus sp.	3	0	3	1	0	1			S
Cortinarius alboviolaceus	1	0	1	0	0	0			M
Cortinarius anomalus	4	4	5	1	2	2		T	M
Cortinarius argutus	0	1	1	0	0	0		T	M
Cortinarius armillatus	0	0	0	0	1	1			M
Cortinarius caperatus	1	1	1	0	0	0			M
Cortinarius casimiri	4	3	5	3	1	3			M
Cortinarius collinitus	0	1	1	0	0	0			M
Cortinarius decipiens var. decipiens	0	0	0	1	1	1			M
Cortinarius diasemospermus var. leptospermus	2	2	2	2	0	2			M
Cortinarius hemitrichus	0	1	1	0	0	0			M

Species	Grazed			Ungrazed			Status	T	S/M
	SP	TCS	ALL	SP	TCS	ALL			
Cortinarius hinnuleus coll.	0	0	0	1	1	2			M
Cortinarius lucorum	0	1	1	0	0	0		T	M
Cortinarius pholideus	0	1	1	0	1	1			M
Cortinarius porphyropus	0	1	1	0	2	2			M
Cortinarius raphanoides	2	3	4	1	2	2			M
Cortinarius saniosus	1	1	2	1	0	1		T	M
Cortinarius semisanguineus	0	1	1	0	0	0			M
Cortinarius sp.	5	4	5	5	4	6			M
Cortinarius subtortus	0	0	0	0	1	1			M
Cortinarius triumphans	4	6	6	3	3	4			M
Cortinarius trivialis	1	0	1	0	1	1			M
Cortinarius turmalis	0	0	0	1	0	1			M
Cortinarius umbrinolens	2	2	3	1	2	2			M
Craterellus cornucopioides	0	0	0	1	0	1			M
Craterellus sinuosus	0	0	0	1	1	1			M
Crepidotus lundellii	0	1	1	0	0	0			S
Crepidotus versutus	2	0	2	2	1	3			S
Cystoderma carcharias var. carcharias	0	1	1	0	0	0		T	S
Cystoderma sp.	0	0	0	1	0	1			S
Cystolepiota seminuda	0	0	0	1	2	2		T	S
Entoloma sp.	5	4	5	5	4	5			S
Flammula alnicola	0	0	0	0	1	1			S
Flammulaster limulatus var. limulatus	0	1	1	0	0	0			S
Flammulaster rhombosporus	1	1	2	0	0	0			S
Galerina atkinsoniana	3	0	3	3	1	4		T	S
Galerina hypnorum	0	1	1	0	0	0			S
Galerina marginata	2	3	3	5	4	6			S
Galerina mniophila	1	1	2	0	0	0			S
Galerina pumila var. pumila	4	2	4	0	0	0			S
Galerina sp.	1	1	2	3	0	3			S
Galerina vittiformis var. vittiformis f. tetraspora	3	1	4	3	2	3		T	S
Gamundia striatula	2	0	2	0	0	0			S
Gymnopilus penetrans	0	0	0	1	0	1			S
Gymnopus androsaceus	5	3	5	5	2	5		T	S
Gymnopus confluens	1	0	1	0	0	0			S
Gymnopus dryophilus	3	4	4	3	4	5			S
Gymnopus ocior	0	0	0	1	0	1			S
Gymnopus putillus	0	0	0	1	0	1			S
Hebeloma birrus	4	5	5	2	1	2		T	M
Hebeloma mesophaeum	0	0	0	0	1	1			M

Species	Grazed			Ungrazed			Status	T	S/M
	SP	TCS	ALL	SP	TCS	ALL			
Hebeloma sp.	3	2	4	4	4	5			M
Hebeloma theobrominum	2	1	2	0	0	0			M
Helvella macropus	0	1	1	0	0	0			S
Hohenbuehelia fluxilis	1	0	1	0	0	0			S
*Hydnum repandum***	1	1	1	1	0	1			S/M
*Hydnum rufescens***	1	0	1	2	1	3			S/M
Hygrocybe coccinea	0	0	0	0	1	1		T	S
Hygrocybe sp.	1	0	1	0	0	0			S
Hygrophoropsis aurantiaca	1	2	3	0	0	0		T	S
Hygrophoropsis pallida	2	1	2	0	0	0			S
Hygrophorus erubescens	0	0	0	1	0	1			M
Hygrophorus hedrychii	0	0	0	1	1	1			M
Hygrophorus piceae	0	0	0	0	1	1			M
Hygrophorus pustulatus	1	0	1	0	0	0			M
Hypholoma capnoides	1	1	1	1	2	2			S
Hypholoma elongatum	0	1	1	0	0	0			S
Hypholoma fasciculare var. fasciculare	0	1	1	0	0	0			S
Hypholoma lateritium	0	2	2	0	2	2			S
Infundibulicybe gibba	1	0	1	0	0	0		T	S
Inocybe calamistrata	0	1	1	0	0	0			M
Inocybe castanea	2	0	2	1	0	1			M
Inocybe cincinnata var. cincinnata	1	1	2	3	0	3			M
Inocybe curvipes	1	0	1	0	1	1			M
Inocybe flavella	1	0	1	0	0	0			M
Inocybe flocculosa	1	1	2	0	1	1			M
Inocybe geophylla	3	1	3	3	1	4			M
Inocybe lacera var. lacera	1	0	1	0	0	0			M
Inocybe leiocephala	2	1	2	1	0	1			M
Inocybe lilacina	0	1	1	0	0	0			M
Inocybe maculata	0	0	0	1	1	2			M
Inocybe mixtilis	3	1	3	1	0	1			M
Inocybe nitidiuscula	1	1	1	0	0	0			M
Inocybe praetervisa	2	2	2	0	0	0		T	M
Inocybe rimosa	1	1	1	0	0	0		T	M
Inocybe sect. Fibrillosae	1	0	1	0	0	0			M
Inocybe sindonia	0	1	1	0	0	0			M
Inocybe sp1. Vauras	1	0	1	0	0	0			M
Inocybe sp2. Vauras	0	1	1	0	0	0			M
Inocybe sp.	2	0	2	1	0	1			M
Kuehneromyces mutabilis	2	2	4	0	1	1			S
Laccaria bicolor	0	1	1	0	0	0			M
Laccaria laccata	3	6	6	4	2	4			M
Laccaria sp.	1	0	1	1	0	1			M
Laccaria tortilis	1	0	1	0	0	0			M

Species	Grazed			Ungrazed			Status	T	S/M
	SP	TCS	ALL	SP	TCS	ALL			
Lactarius camphoratus	0	0	0	1	1	1			M
Lactarius deterrimus	0	1	1	0	0	0			M
Lactarius fennoscandicus	0	1	1	0	0	0			M
Lactarius flexuosus var. flexuosus	1	2	2	2	2	3			M
Lactarius fuliginosus	0	1	1	0	1	1			M
Lactarius glyciosmus	5	4	5	6	4	6			M
Lactarius lacunarum	1	0	1	1	1	2			M
Lactarius necator	4	3	4	2	1	2			M
Lactarius obscuratus	0	0	0	1	0	1			M
Lactarius spinosulus	1	0	1	1	1	1			M
Lactarius tabidus	4	5	5	5	6	6			M
Lactarius torminosus	3	2	3	2	2	4		T	M
Lactarius trivialis	0	0	0	0	1	1			M
Lactarius uvidus	0	0	0	0	1	1			M
Lactarius vietus	2	2	3	3	3	5			M
Leccinum aurantiacum	0	1	1	0	1	1			M
Leccinum schistophilum	0	0	0	0	1	1			M
Leccinum populinum Korhonen	0	1	1	0	0	0			M
Leccinum scabrum	5	6	6	2	3	3			M
Leccinum sp.	2	0	2	0	0	0			M
Leccinum variicolor	2	3	3	2	4	5			M
Leccinum versipelle	0	2	2	1	1	2			M
Lentinellus flabelliformis	1	0	1	2	0	2	NE		S
Lepiota castanea	0	0	0	0	1	1			S
Lepiota clypeolaria	0	1	1	0	3	3			S
Lepiota felina	0	0	0	1	0	1			S
Lepiota magnispora	0	0	0	0	1	1			S
Lepista nuda	2	1	3	0	0	0			S
Lepista sordida	0	1	1	0	0	0			S
Leucocortinarius bulbiger	1	0	1	0	0	0			M
Lycoperdon perlatum	2	1	2	1	1	2			S
Lycoperdon pyriforme	0	0	0	0	1	1			S
Lycoperdon sp.	0	1	1	0	0	0			S
Lyophyllum rancidum	3	2	3	3	2	3			S
Lyophyllum sp.	0	0	0	1	0	1			S
Lyophyllum tylicolor	0	0	0	1	0	1			S
Macrolepiota procera	0	1	1	0	0	0		T	S
Macrotyphula fistulosa	2	0	2	0	0	0			S
Marasmiellus perforans	1	1	1	1	2	3			S
*Marasmius epiphyllus**	0	1	1	1	0	1			S
*Marasmius setosus**	3	0	3	1	0	1	NE		S
Marasmius sp.	5	2	5	5	4	5			S
Megacollybia platyphylla	1	3	3	1	1	2			S
Mycena acicula	1	0	1	0	0	0			S

Species	Grazed			Ungrazed			Status	T	S/M
	SP	TCS	ALL	SP	TCS	ALL			
Mycena aetites	0	1	1	4	1	4	NE		S
Mycena aurantiomarginata	2	0	2	1	1	2			S
Mycena citrinomarginata	5	1	5	6	5	6			S
Mycena epipterygia coll.	4	5	5	6	5	6			S
Mycena filopes	4	2	4	6	2	6			S
Mycena flavoalba	5	4	5	5	4	5		T	S
Mycena galericulata	6	6	6	5	6	6			S
Mycena galopus	2	4	5	5	5	5			S
Mycena haematopus	2	1	3	2	1	2		T	S
Mycena laevigata	0	0	0	2	1	2			S
Mycena latifolia	2	2	3	2	0	2	NE		S
Mycena leptocephala	6	3	6	6	4	6		T	S
Mycena metata	6	2	6	6	5	6			S
Mycena plumipes	0	0	0	0	1	1		T	S
Mycena polygramma	0	0	0	0	1	1			S
Mycena pterigena	0	0	0	2	0	2			S
Mycena pura	3	3	4	3	4	4		T	S
Mycena rosella	0	0	0	0	3	3			S
Mycena rubromarginata	1	0	1	6	3	6			S
Mycena sanguinolenta	3	0	3	5	0	5			S
Mycena sect. Fragilipes	3	2	4	2	2	3			S
Mycena sp.	5	0	5	6	2	6			S
Mycena speirea	2	0	2	0	1	1			S
Mycena stipata	1	1	2	2	1	3			S
Mycena vulgaris	1	3	3	0	2	2			S
Mycetinis scorodonius	3	2	4	4	4	5		T	S
Myxomphalia maura	0	1	1	0	0	0			S
Naucoria bohemica	1	1	2	0	0	0		T	M
Naucoria cf. scolecina	0	1	1	0	0	0			M
Naucoria escharioides	1	1	2	1	1	2			M
Panaeolus acuminatus	4	1	4	0	0	0			S
Panaeolus alcis	0	0	0	1	0	1			S
Panaeolus olivaceus	2	1	2	0	0	0		T	S
Panaeolus papilionaceus var. papilionaceus	4	4	4	0	0	0		T	S
Parasola leiocephala	0	1	1	0	0	0			S
Parasola misera	1	1	1	0	0	0		T	S
Parasola schroeteri	1	0	1	0	0	0		T	S
*Paxillus involutus***	6	6	6	5	5	6			S/M
Pholiota lenta	0	1	1	2	1	3			S
Pholiota mixta	0	0	0	1	1	2			S
Pholiota tuberculosa	0	1	1	0	0	0			S
Pholiotina brunnea	1	1	1	0	0	0			S
Pholiotina pygmaeoaffinis	1	0	1	2	1	3	NT		S
Pleurotus pulmonarius	0	1	1	0	0	0			S
Pluteus cervinus	0	3	3	5	2	6			S

Species	Grazed			Ungrazed			Status	T	S/M
	SP	TCS	ALL	SP	TCS	ALL			
Pluteus chrysophaeus	1	1	1	0	0	0	NE		S
Pluteus podospileus	0	1	1	0	0	0			S
Polyporus brumalis	2	0	2	1	0	1			S
Polyporus sp.	0	0	0	1	1	1			S
Psathyrella cf. microrrhiza	0	1	1	0	0	0			S
Psathyrella cf. senex	2	2	3	0	0	0			S
Psathyrella cernua	1	0	1	0	0	0			S
Psathyrella corrugis	1	1	1	1	0	1			S
Psathyrella larga	0	1	1	0	0	0	NE		S
Psathyrella lutensis	1	1	2	0	0	0			S
Psathyrella potteri	1	1	2	0	0	0	NE		S
Psathyrella spadicea	1	1	2	1	1	2			S
Psathyrella sp1. Kytövuori	1	1	1	0	0	0			S
Psathyrella sp2. Kytövuori	1	0	1	0	0	0			S
Psathyrella sp3. Kytövuori	0	0	0	1	0	1			S
Psathyrella sp.	2	2	3	0	1	1			S
Psathyrella tenuicula	0	0	0	1	0	1	DD		S
Psilocybe inquilinus	3	1	3	4	3	4			S
Psilocybe semilanceata	0	1	1	0	0	0			S
Psilocybe sp.	1	0	1	0	0	0			S
Rhizomarasmius undatus	0	0	0	2	0	2		T	S
Rhodocollybia butyracea f. asema	3	0	3	2	4	4			S
Rhodocollybia butyracea f. butyracea	1	1	1	1	1	1			S
Rhodocybe nitellina	1	0	1	1	1	1		T	S
Rickenella fibula	1	1	1	0	0	0			S
Rickenella swartzii	2	2	3	1	1	2		T	S
Roridomyces rorida	2	0	2	1	0	1			S
Russula aeruginea	1	4	4	0	2	2			M
Russula aquosa	0	0	0	1	1	2			M
Russula atrorubens	1	0	1	2	0	2			M
Russula aurea	0	0	0	1	1	1		T	M
Russula betularum	3	3	3	3	4	5			M
Russula chloroides coll.	1	2	2	3	4	4		T	M
Russula claroflava	1	3	3	2	2	2		T	M
Russula favrei	1	0	1	0	0	0			M
Russula fennoscandica Ruotsalainen & Vauras ined.	0	1	1	0	0	0			M
Russula foetens	1	2	2	0	2	2			M
Russula globispora	0	0	0	1	0	1		T	M
Russula gracillima	5	4	5	2	4	5			M
Russula grisescens	0	1	1	1	1	2			M
Russula intermedia	3	4	4	5	5	6		T	M
Russula medullata	1	2	3	0	0	0		T	M

Species	Grazed			Ungrazed			Status	T	S/M
	SP	TCS	ALL	SP	TCS	ALL			
Russula nana	0	0	0	2	2	2			M
Russula nauseosa	0	2	2	0	0	0			M
Russula nitida	2	2	3	1	0	1		T	M
Russula olivascens	0	1	1	0	0	0			M
Russula pelargonia	2	2	3	2	1	2			M
Russula puellaris	0	0	0	1	0	1			M
Russula queletii	0	1	1	0	0	0			M
Russula renidens	0	1	1	0	0	0			M
Russula risigallina var. risigallina	0	0	0	1	1	1			M
Russula sanguinea	0	0	0	0	1	1		T	M
Russula sp.	5	2	5	3	0	3			M
Russula velenovskyi	3	2	4	1	1	2			M
Russula versicolor coll.	0	1	1	0	0	0			M
Russula vesca	1	3	3	1	1	1			M
Russula violaceoincarnata	1	2	3	2	3	5		T	M
Russula vitellina	2	3	3	2	1	2			M
Russula xerampelina coll.	0	3	3	1	1	2			M
Sarcomyxa serotina	0	0	0	1	0	1			S
Strobilurus esculentus	3	4	4	3	1	3			S
Stropharia aeruginosa	2	2	3	0	2	2			S
Stropharia cyanea	0	1	1	0	0	0			S
Stropharia hornemannii	1	1	1	0	2	2			S
Stropharia semiglobata	2	4	4	0	0	0		T	S
Suillus luteus	0	2	2	0	1	1			M
Tricholoma fulvum	4	3	4	0	1	1			M
Tricholoma saponaceum var. saponaceum	0	0	0	1	0	1			M
Tricholoma stiparophyllum	1	3	3	3	4	4			M
Tubaria conspersa	3	3	3	2	4	4			S
Tubaria furfuracea	3	3	3	0	2	2			S
Xerocomus badius	0	1	1	0	1	1		T	M
Xerocomus subtomentosus	2	4	4	1	1	2			M
Xeromphalina fraxinophila var. macrocystidiata	1	0	1	3	2	4			S

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