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Research Paper

The effects of grazing history, soil properties and stand structure on the communities of saprotrophic fungi in wood-pastures

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ABSTRACT

Wood-pastures are threatened anthropogenic biotopes that provide habitat for an extensive group of species. Here we studied the effect of management, grazing intensity, time since abandonment, historical land-use intensity, soil properties and stand conditions on communities of saprotrophic fungi in wood-pastures in Central Finland. We found that the proportion of broadleaved trees and soil pH are the major drivers in the communities of saprotrophic fungi in these boreal wood-pastures. In addition, tree species richness, soil moisture, historical land-use intensity and time since abandonment affected the communities of saprotrophic fungi. Current management or grazing intensity did not have a clear effect on saprotrophic fungal species richness, although dung-inhabiting fungal species richness was highest at intermediate to high grazing intensity. Obviously, there were many more dung-inhabiting fungal species on grazed than on abandoned sites. Our study highlights the conservation value of wood-pastures as hotspots of saprotrophic fungi.

1. Introduction

Traditional agricultural management, such as hay making, slash and burn, and free cattle grazing in forests, have created biodiversity hotspots (Lammi and Ikonen, 2000; Pykälä, 2001; Eriksson, 2021). Wood-pastures have been formed as a result of extensive grazing in forests, forested slash and burn areas or forested semi-natural grasslands. The canopies of these wood-pastures are more open and mosaic-like than natural forests because selective logging and cattle grazing have kept seedlings at low levels. Additionally, some of the trees are removed to promote the growth of grass for the cattle. As a result of these management practices, wood-pastures have a wide range of light conditions, nutrient poor soils interspaced with nutrient rich patches. These semi-open environments provide a suitable habitat for several species from various species groups (Pykälä, 2001; Bergmeier et al., 2010; Garbarino et al., 2011; Chételat et al., 2013; Oldén et al., 2016a, 2016b; Lehtomaa et al., 2018).

The amount of traditional rural biotopes has drastically decreased in Europe as compared to the 1900s (Pliening et al., 2006; Lehtomaa et al., 2018; Eriksson, 2021). In Finland wood-pastures have declined by more than 99% since the 1950s (Schulman et al., 2008). Due to

agricultural intensification, many old meadows and wood-pastures have been abandoned, converted into fields, or managed as commercial forests, and therefore have lost most of their biodiversity value. Considering those that remain, some are grazed together with cultivated grasslands, causing eutrophication in the traditional rural biotope. In Finland, these rural biotopes are classified into 42 types, all of which are threatened. Eight of these biotopes are wood covered (Lehtomaa et al., 2018). In our study, we will use the term wood-pasture to indicate both sparsely and densely wooded pastures.

Several studies have reported factors that affect species richness in traditional rural biotopes. These studies have focused on several species groups, e.g. vascular plants, bryophytes, lichens, other fungi, and insects (Saarinen and Jantunen, 2005; Raatikainen et al., 2007; Paltto et al., 2011; Griffith et al., 2012; Oldén et al., 2016a, 2016b; Komonen and Elo, 2017; Tervonen et al., 2019). These studies have shown that management, long grazing history, habitat heterogeneity, and environmental conditions, such as soil pH and moisture, have an impact on the species richness (Pykälä, 2001, 2003; Cousins and Eriksson, 2002; Vujnovic et al., 2002; Benton et al., 2003; Oldén et al., 2016a, 2016b).

Managed grasslands and wood-pastures have been shown in some studies to have higher plant species richness than the abandoned ones

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(Dullinger et al., 2003; Pykälä, 2003; Oldén et al., 2016a, 2016b). Thus, management itself has a strong impact on species. Mowing or grazing affect vascular plants directly by removing their biomass and breaking soil, which reduces competition between vascular plant species (Olf and Ritchie, 1998; Pykälä, 2001). Because of the reduced plant biomass, soil temperature and light increases and this seems to improve the fruiting conditions for many fungal species (Nitare and Sunhede, 1993; Olf and Ritchie, 1998; Pykälä, 2001). However, in our previous study (Tervonen et al., 2019), we found that ectomycorrhizal fungal species did not have higher species richness on grazed wood-pastures than on abandoned ones. Also, Juutilainen et al. (2016) found that wood-pastures have lower wood-inhabiting fungal species richness than natural forests. Cattle also cause disturbance by trampling, which opens soil patches to new plant species (Olf and Ritchie, 1998; Oldén et al., 2016b). Intermediate grazing pressure has been shown to be best for maintaining the most species rich vascular plant communities (Mwendera et al., 1997; Oldén et al., 2016b).

Older pastures and meadows, exposed to traditional forms of management for extended periods, have been shown to sustain a high plant species richness (Cousins and Eriksson, 2002; Myklestad and Saetersdal, 2003). The continuity of management is crucial for many species. For example, many grassland fungi seem to require management that has continued for decades (Arnolds, 2001). Grazing slowly changes the stand structure because the regeneration of trees is challenged and the old trees eventually die off (Oldén et al., 2016a). During long grazing history in wood-pastures the species that are adapted to forests have most likely decreased due to the decreased amount of dead wood and shade, whereas species that are adapted to open semi-natural grasslands have most likely increased due to increased openness of the sites (Juutilainen et al., 2016; Oldén et al., 2016b). If managed areas are abandoned it is expected that those species that are adapted to half-open conditions decrease whereas forest species increase (Bakker, 1998; Oldén et al., 2016a, 2016b). To summarize, the effects of management and the long continuity of management, create mosaic-like vegetation, which offers many different habitat patches for several species (Olf and Ritchie, 1998; Nauta and Jalink, 2001). Thus, species richness can be very high if habitat heterogeneity is also high (Myklestad and Saetersdal, 2003).

Environmental conditions such as soil moisture and soil pH also affect species richness in traditional rural biotopes. Soil moisture and soil pH are the main drivers in communities of bryophytes, vascular plants and ectomycorrhizal fungi in wood-pastures (Oldén et al., 2016b; Tervonen et al., 2019). Oldén et al. (2016b) found that bryophyte species richness increases with soil moisture and soil pH, and vascular plant species richness response to soil pH was humped. In addition, Rousk et al. (2009) found that fungal species richness peaked at pH 4.5 on arable managed land. In our previous study with ectomycorrhizal fungi, species richness decreased with soil moisture in abandoned wood-pastures, whereas soil pH did not have a significant effect on species richness (Tervonen et al., 2019).

A lot of research has concentrated on vascular plants found in semi-natural grasslands (e.g. Olf and Ritchie, 1998; Myklestad and Saetersdal, 2003; Lindborg and Eriksson, 2004; Pykälä, 2007; Raatikainen et al., 2007), and several studies have focused on grassland fungi (e.g. Arnolds, 2001; Nauta and Jalink, 2001; Öster, 2008). Even though it is well known that fungal communities have a strong impact on natural ecosystems as saprotrophic organisms and mycorrhizal partners (Boddy et al., 2008), only a few studies have focused on fungi in wood-pastures. Sepp et al. (2021) compared communities of open and wooded grasslands with several species groups including ectomycorrhizal and saprotrophic fungal species. Tervonen et al. (2019) and Tedersoo et al. (2006) focused on ectomycorrhizal fungi species and Juutilainen et al. (2016) on wood-inhabiting saprotrophic fungi in wood-pastures. To our knowledge no inclusive ecological studies on saprotrophic agaric communities in wood-pastures have been conducted.

We studied the effect of management, grazing intensity, time since

abandonment, historical land-use intensity, soil properties and stand conditions on species richness and communities of saprotrophic fungi in Boreal wood-pastures. We thus repeated the study of Tervonen et al. (2019), which focused on ectomycorrhizal fungi, with another functional species group. Our study aimed at answering the following questions for saprotrophic fungi: (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) Are there any differences 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? We conducted analyses on all saprotrophic fungi, the species whose main habitat types in Finland are traditional rural biotopes and cultural habitats, and dung-inhabiting species.

2. Materials and methods

2.1. Study sites

Our study was carried out in the province of Central Finland. We studied 36 wood-pastures. They were located on 29 separate farms and on each farm we had one, two or three study pastures. See study site location map in Tervonen et al. (2019).

We compared three different wood-pasture types: broadleaved (birch dominated), coniferous (spruce dominated) 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), 12 sites of each type. Half of the sites of each type were currently grazed, and other half were abandoned wood-pastures. See examples of the study sites from Supplementary Fig. 1.

To reveal the true impact of grazing we selected grazed and abandoned study sites with as similar tree densities (mature trunks/ha) as possible. Because of the small number of potential study sites, we could not control the variation of the forest site types or the type of grazing animal. More information about the study site selection can be found in Oldén et al. (2016b).

2.2. Data collection

At each study site we established three 10 m × 10 m squared study plots which were positioned in the pastures based on the dominant tree species and the mature tree density. All study plots were set at least 17 m apart from each other's boundaries. When selecting suitable study plots we did not pay attention to the ground vegetation and the selection was conducted at a time when there were no fruit bodies of macrofungi present.

The study plots were surveyed carefully for stipitate saprotrophic macrofungi. We counted all fruit bodies from the ground and from the surface of dead wood pieces laying on the ground. We did the survey very carefully by pushing plants aside but we did not turn dead wood pieces around to avoid affecting next survey rounds.

We repeated the survey three times in each of the study sites. Ten of the broadleaved sites were surveyed three times during September–October 2010. Two broadleaved sites and all the coniferous and mixed sites were surveyed twice in August–September 2012 and once in September–October 2013. We identified all fruit bodies to the species level in the field when possible. When this was not possible we collected specimens for microscopic identification (altogether 1700 specimens).

We separated saprotrophic species from ectomycorrhizal fungi based on the ecological information provided in Knudsen and Vesterholt (2012), Kotiranta et al. (2009), and Kytövuori et al. (2005). A few species were reported to use both mycorrhizal and saprotrophic strategy (*Hydnum repandum*, *Hydnum rufescens* coll., etc.) and some species are

further reported to be ectomycorrhizal (*Clavulina cinerea*, *C. coralloides*, *Coltricia perennis*) and they were excluded. We also separated species whose main habitat types are “traditional rural biotopes and cultural habitats” according to FinBIF’s data repository (species.fi), excluding dung-inhabiting fungi species (from now on TRB fungi). In addition, we separated species that mainly live on dung, based on information in Knudsen and Vesterholt (2012), Hausknecht (2009) and Kytövuori et al. (2005). The voucher specimens are stored 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

To estimate the history of land-use intensity for the study sites we created a surrogate for the historical land-use intensity by counting the number of surrounding farms (within 1 km buffer zone around each site) in old cadastral maps drawn in the 1850’s and 1860’s. This surrogate should correlate with the historical grazing intensity and other traditional agricultural activities. We also interviewed the landowners to record the year when the site was abandoned. Time since abandonment varied between 7 and 42 y (calculated from the study year 2012).

To reveal the effect of grazing intensity we placed subplots of sizes 2 m × 2 m inside each corner of each study plot and evaluated the proportion of clipped shoots out of all vascular plant shoots that had been at least 5 cm high in these plots. Thus, there were 12 subplot-scale grazing intensity measures in each study site. These measures were used in the analyses as an average value for the whole study site.

To obtain information about soil moisture and soil pH we collected soil samples from all study plots in June 2013. We collected 16 randomly placed soil samples from each study plot. The litter layer was excluded and the sample was taken with a soil corer (3 cm diameter) to the depth of 5 cm (after which it was usually impossible to core deeper due to large stones and tree roots). The samples from each plot were mixed together and then sieved through a sieve with 4 mm mesh size and frozen before measurements. To measure the soil moisture content, a subsample was placed in a crucible, weighed, dried in an oven (at 105 °C for 12 h), and weighed again. Soil pH was measured three times from a calcium chloride suspension of 1:5 soil CaCl₂ ratio (w/v) after 1 h of shaking, and the median value of the three was used for the plot. We used the average value of the three plots for each study site in the analyses. We also measured the diameter at breast height (130 cm) of each tree that was at least 130 cm high in the study plots. Based on these measures we calculated the basal area of trees separately for broadleaved and coniferous species. We used the basal area data to calculate the proportion of broadleaved trees out of the basal area of all trees for each site. We also calculated the tree species richness in each site.

For more information on the background variables, see Oldén et al., 2016a, 2016b and Tervonen et al. (2019).

2.4. Statistical analyses

We conducted all statistical analyses on site-level data and built separate models for all sites, grazed sites and abandoned sites. Because there was no cattle dung on abandoned study sites, we conducted all analyses without dung-inhabiting species to reveal if there are any differences in saprotrophic fungal communities caused by grazers. We also performed analyses separately for dung-inhabiting species in grazed sites. All statistical analyses were performed with R version 4.0.4 (R Core Team, 2021).

All analyses were performed on species-level data but in some genera we were not able to identify all specimens and observations to species level, thus these observations were pooled and the genus was analyzed as one “species”. If only a few specimens in a genus were unidentified, those observations were dropped from the analyses.

We calculated correlations between the continuous explanatory variables separately for all sites, grazed sites and abandoned sites

(Supplementary Table 1). As the correlations were not extremely strong, all explanatory variables (historical land-use intensity, soil moisture, soil pH, tree species richness, grazing intensity, time since abandonment, proportion of broadleaved trees) were included in the statistical models. Proportion of broadleaved trees and tree species richness were not used in the same analyses.

We used Moran’s test 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 study sites. The test revealed that soil moisture (Moran I = 0.221, p = 0.045) and historical land-use intensity (Moran I = 0.328, p = 0.007) were spatially autocorrelated within 2nn level. Time since abandonment was nearly significant within 4nn level (Moran I = 0.114, p = 0.079). The observed autocorrelation is probably due to our sampling setup as we had two study sites in five farms and three study sites in one farm, thus 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 (Supplementary Table 2).

We used Generalized Linear Models (GLM, McCullagh and Nelder, 1983) to analyze the effect of management situation (grazed or abandoned), historical land-use intensity, grazing intensity, time since abandonment, and stand conditions on species richness. The response variable was the species richness of saprotrophic fungi (excluding dung-inhabiting fungi), explanatory discrete variable was the 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 built separate models for all sites, grazed sites and abandoned sites because some variables are relevant only for all, grazed or abandoned sites. For all sites and for abandoned sites we used negative binomial GLM due to overdispersion. For grazed sites, a Poisson GLM was applied. We included both linear and quadratic terms for soil pH, soil moisture, grazing intensity and time since abandonment in the models. In addition, we conducted Poisson GLM for TRB fungi in all sites, grazed sites and abandoned sites, and for dung-inhabiting fungal species in grazed sites. When building these models, we used the same continuous variables as for saprotrophic fungi species (see above).

We used unstandardized data in all analyses. To avoid multicollinearity issues we centered variables which had quadratic terms before model fitting. We also first included the inventory time period (ITP, either 2010 or 2012 + 2013) as a random effect in our models. However, as model fits revealed that species richness did not vary within ITP, we dropped the term from our final model. Based on our study questions, our main interest was to study the effect of management, grazing intensity (on grazed sites), time since abandonment (on abandoned sites) and historical land-use intensity on species richness. These variables were therefore always included in the models. Variable selection was conducted by adding explanatory continuous variables (soil pH, soil moisture, tree species richness, linear or quadratic) to model one by one (by varying the order in which they were added in the model), and keeping the variable in the model if the effect was found significant. We then chose the best model based on Akaike’s Information Criterion values. To evaluate the variance explained by the covariates, we calculated the pseudo-R² values for each of the models (McFadden, 1974). The analyses were performed with the functions glm (for grazed sites) and glm.nb (for all sites and abandoned sites) from the R packages stats and MASS (Venables and Ripley, 2002), respectively.

We used Bioenv-analysis (Clarke and Ainsworth, 1993) to find the best subset of environmental variables (management situation, historical land-use intensity, grazing intensity, time since abandonment, soil pH, soil moisture, the proportion of broadleaved trees) having maximum correlation with community dissimilarities. To visualize the effects of environmental variables on saprotrophic fungal species (excluding dung-inhabiting fungi) we used Nonmetric Multidimensional Scaling (NMDS, Clarke and Ainsworth, 1993). Our data are based on the observed fruit bodies, thus survey year and survey times affect observed

species. Because of this, we used Chao's dissimilarity index in Bioenv-analysis, which takes into account the number of unseen species (Chao et al., 2005; Oksanen et al., 2015). Due to the categorical variables we used Gower distance for calculating distances between the environmental variables. We used functions bioenv and metaMDS from the R package vegan by Oksanen et al. (2015). For NMDS we chose a three-dimensional result. We overlaid the ordination results with the environmental factors whose location shows the average location of sites in that category, and with vectors related to environmental covariates. The lengths of the vectors show the correlation between site locations and continuous environmental covariates.

3. Results

We found 230 saprotrophic fungal species out of which 172 species were found from grazed sites and 159 from abandoned sites. Excluding dung-inhabiting species, we found 208 species, 153 from grazed sites and 155 from abandoned sites. Thus 22 dung-inhabiting species were found altogether, 19 on grazed sites and four in abandoned sites. Considering TRB fungi we observed 45 species, 28 in grazed sites and 31 in abandoned sites. We recorded altogether 63 952 fruit bodies, and 63 359 of them were identified to species level and were therefore included in the analyses, 26 297 in grazed and 37 062 in abandoned sites. On average, grazed sites hosted 33.9 species and abandoned sites 37.2 species without dung-inhabiting species.

The most frequent species were *Collybia* spp. (2905 fruit bodies on 36 sites), *Gymnopus androsaceus* (3771 fruit bodies on 34 sites), *Entoloma* spp. (465 fruit bodies on 33 sites), and *Mycena metata* (488 fruit bodies on 32 sites). In addition, *Marasmiellus perforans* (28 787 fruit bodies on 23 sites) and *Mycena vulgaris* (5412 fruit bodies on 19 sites) were the most abundant species. Most frequent dung-inhabiting species were *Deconica crobula* (262 fruit bodies on 22 sites), *Panaeolus papilionaceus* (97 fruit bodies on 11 sites), and *Conocybe juniana* (38 fruit bodies on 11 sites). We found one near threatened species, *Pholiotina pygmaeoffinis*, nine data deficient (DD) species, and three not evaluated (NE) species. We also found one Hodophilus species, probably *Hodophilus subfoetens*, for which the red list status is not yet evaluated. *Hodophilus foetens* is listed as vulnerable (VU) in Finland, but in 2017 it was separated as four species (Adamčík et al., 2017). In addition, we identified four species which were not included in the previous evaluation of threatened species in Finland. Also two *Psathyrella* species, one *Coprinellus* species and one *Riparitipes* species could not be identified to species level by specialists, thus they might be new species to Finland. The nomenclature follows the information provided by Finnish Biodiversity Information Facility (species.fi). See the whole species list in the Supplementary material.

The results based on GLM analyses are shown in Table 1 and Fig. 1. Tree species richness had a significant positive effect on species richness of saprotrophic fungi (excluding dung-inhabiting species) among all sites, grazed sites and abandoned (Table 1, Fig. 1D). Soil moisture had a significant effect on species richness among grazed sites and abandoned sites (Fig. 1C). In addition, historical land-use intensity had a significant negative effect on species richness on abandoned sites and near significant negative effect on all sites (Fig. 1B). Time since abandonment also had a significant positive effect on species richness on abandoned sites (Fig. 1F). Management did not have a significant effect on species richness on all sites and grazing intensity did not have a significant effect on species richness on grazed sites. The goodness of fit of the models (pseudo R²) was 0.307 for all sites, 0.547 for grazed sites and 0.618 for abandoned sites.

Among TRB fungi (excluding dung-inhabiting species) soil pH had significant positive effect on species richness among all sites and abandoned sites (Table 2, Fig. 2C). Tree species richness had significant positive effect among grazed sites and time since abandonment had a significant positive effect among abandoned sites (Fig. 2E and G). In addition, soil moisture had a near significant negative effect among

Table 1

Estimated regression coefficients and their 95% confidence intervals based on the negative binomial GLM for saprotrophic fungi species (excluding dung-inhabiting species) in all sites and abandoned sites and based on the Poisson GLM for saprotrophic fungi species in grazed sites. Management is a dichotomous variable (grazed or abandoned). The continuous variables were historical land-use intensity (the number of farms surrounding the site within 1 km in the 1850s–60s), tree species richness, grazing intensity, time since abandonment, and soil moisture. Variables marked with + were always kept in the models irrespective of their significance.

	RR	95% CI	P
All sites			
Baseline count	25.992	19.329–34.948	<2e-16 ***
+Management: Grazed	1.013	0.845–1.215	0.890
+Number of farms	0.963	0.924–1.005	0.085
Tree species richness	1.081	1.035–1.130	0.0005 ***
Grazed sites			
Baseline count	15.807	9.791–25.326	<2e-16 ***
+Number of farms	1.009	0.964–1.055	0.696
+Grazing intensity	1.000	0.996–1.003	0.864
Tree species richness	1.094	1.053–1.136	2.81e-06 ***
Soil moisture	1.010	1.002–1.019	0.018 *
Abandoned sites			
Baseline count	44.402	26.892–73.318	<2e-16 ***
+Number of farms	0.944	0.899–0.991	0.022 *
+Time since abandonment	1.011	1.001–1.021	0.032 *
Tree species richness	1.071	1.006–1.139	0.030 *
Soil moisture	0.979	0.968–0.990	0.0001 ***

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

abandoned sites (Fig. 2D). Management, historical land-use intensity or grazing intensity did not have significant effects on species richness. The goodness of fit of the models (pseudo R²) was 0.440 for all sites, 0.315 for grazed sites and 0.689 for abandoned sites.

Among dung-inhabiting fungi grazing intensity had significant linear and humped effects on species richness among grazed sites (Table 3, Fig. 3C). In addition, soil pH had a significant humped effect on species richness of dung-inhabiting fungi (Fig. 3B). Historical land-use intensity did not have a significant effect on dung-inhabiting fungi species richness. The goodness of fit of the model (pseudo R²) was 0.434.

The Bioenv-analysis (Supplementary Table 3) and the NMDS ordination plots (Fig. 4), showed that the community structure of saprotrophic fungi (excluding dung-inhabiting species) was mainly explained by the proportion of broadleaved trees. For all sites and for grazed sites the best subset of variables explaining the community structure included the proportion of broadleaved trees and soil pH (Supplementary Table 3, Fig. 4A, B, 4D, and 4E). Among abandoned sites one variable, the proportion of the broadleaved trees, explained community structure best (Supplementary Table 3, Fig. 4C and F). Management did not affect community composition significantly, but the sites are somewhat divided over management situation on axis 3 in the NMDS ordination (Fig. 4D). Although historical land-use intensity did not have an effect on community structure in all sites (Table 3, Fig. 4A), it seemed to have some effect on community structure in grazed sites (Fig. 4B). In addition, grazing intensity or time since abandonment did not have much effect on community composition. Furthermore, Fig. 4 indicates that those sites that are birch (biggest circles) or spruce dominated (smallest circles) have clearly different communities. The final stress values for the three-dimensional NMDS ordinations were 0.162 for all sites, 0.131 for grazed sites, and 0.093 for abandoned sites.

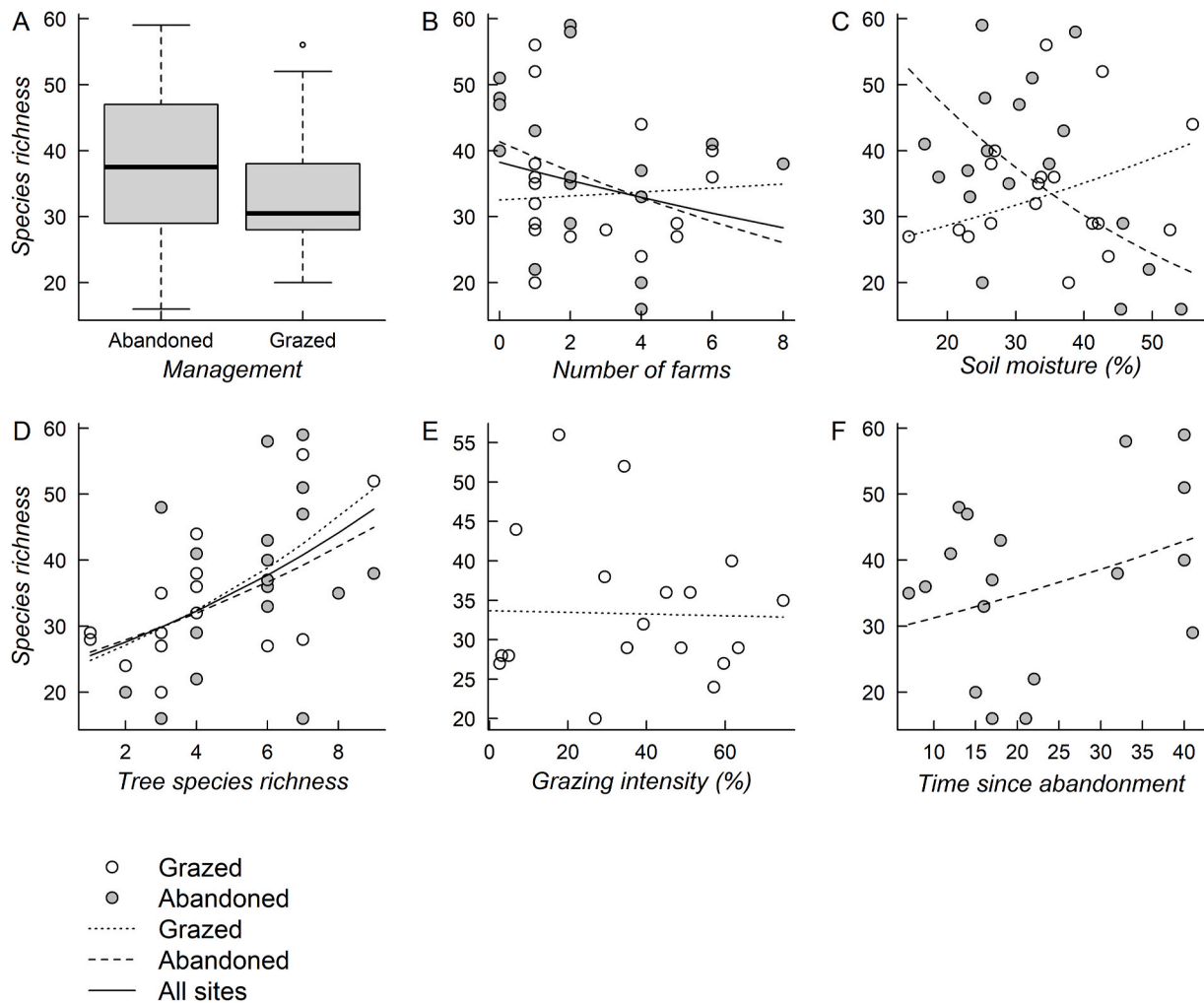


Fig. 1. Responses of saprotrophic fungi species (excluding dung-inhabiting species) richness to (A) management, (B) the number of farms surrounding the site within 1 km in the 1850s–60s (historical land-use intensity, (C) soil moisture (% content from the ground), (D) tree species richness, (E) grazing intensity (% of clipped shoots) for grazed sites, and (F) time since abandonment (years) for abandoned sites. The dots are the observed values of species richness plotted against each covariate. The curves are predicted regression curves obtained from the (full) negative binomial model (all sites and abandoned sites) or (full) Poisson model (grazed sites) and they represent the effect of each covariate on species richness. When computing predicted curves, we used the mean values as values for other covariates.

4. Discussion

4.1. Management affected mostly dung-inhabiting fungi

Our study indicated that the grazed sites did not have higher saprotrophic fungal species richness (excluding dung-inhabiting species) than the abandoned sites. Limiting the analysis to TRB fungi (excluding dung-inhabiting species) did not change this result. However, the species richness of dung-inhabiting fungi was notably higher on currently grazed sites.

Moreover, saprotrophic fungal communities did not differ according to the management situation (excluding dung-inhabiting species). Our findings are thus similar to observations in the same habitats with ectomycorrhizal fungi (Tervonen et al., 2019). In addition, Juutilainen et al. (2016) showed that for saprotrophic wood-inhabiting fungi grazed wood-pastures have lower species richness than natural forests. Probably the reason why grazed wood-pastures have lower saprotrophic fungi species richness than natural forests is that there may be a lower amount of coarse and fine woody debris (Juutilainen et al., 2016). Especially bushes, tree seedlings and some mature trees are taken off from grazed sites by grazers or landowners. This creates a more open canopy than what is typical for abandoned sites. In addition, reduced vegetation by grazers can also create somewhat drier and warmer

microclimate, which may discourage saprotrophic fungal growth (Juutilainen et al., 2016). One reason why the species richness did not differ in our study, may be species turnover: some fungal species prefer light and warm conditions (Nitare and Sunhede, 1993; Olf and Ritchie, 1998; Pykälä, 2001), and others prefer more closed canopy. However, this should cause notable changes in community composition.

Grazing intensity did not have significant effects on the species richness of all saprotrophic fungi or TRB fungi and it did not have a clear effect on the community assembly of saprotrophic fungi. However, when analyses were limited to dung-inhabiting fungi, grazing intensity had a clear positive and humped effect on species richness. Thus, dung-inhabiting fungi species richness is highest in moderate to high intensity grazed sites. The reason why species richness peaks in moderate grazing intensity may be that when grazing intensity is too low, the available resource (dung) is scarce and may not be present in our study plot. On the other hand, if grazing intensity is too high, dung piles may be trampled before fungi species can inhabit it. Very heavy grazing intensity may also reduce dung-inhabiting species via drier microclimate in the absence of protective vegetation, resulting in dung patches to dry out quickly. It is surprising that grazing intensity did not have a strong effect on TRB fungal species richness, because many of these species are common in constantly disturbed habitats like open grasslands and other anthropogenic habitats.

Table 2

Estimated regression coefficients and their 95% confidence intervals based on the Poisson GLM for saprotrophic traditional rural biotope fungi species (excluding dung-inhabiting species) in all sites, grazed sites and abandoned sites. Management is a dichotomous variable (grazed or abandoned). The continuous variables were historical land-use intensity (the number of farms surrounding the site within 1 km in the 1850s–60s), soil pH, tree species richness, grazing intensity, time since abandonment, and soil moisture. Variables marked with + were always kept in the models irrespective of their significance.

	RR	95% CI	P
All sites			
Baseline count	0.291	0.063–1.311	0.109
+Management: Grazed	0.888	0.623–1.258	0.506
+Number of farms	0.955	0.880–1.033	0.260
Soil pH	1.869	1.223–2.831	0.003 **
Tree species richness	1.082	0.984–1.188	0.102
Grazed sites			
Baseline count	35.671	32.130–39.451	0.114
+Number of farms	0.984	0.900–1.074	0.791
+Grazing intensity	0.982	0.898–1.074	0.202
Tree species richness	1.177	1.089–1.1272	0.028 *
Abandoned sites			
Baseline count	0.223	0.017–2.686	0.243
+Number of farms	0.977	0.875–1.082	0.669
+Time since abandonment	1.019	1.001–1.038	0.042 *
Soil pH	2.354	1.357–4.066	0.002 **
Soil moisture	0.978	0.952–1.003	0.099 .

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

Time since abandonment did have a clear positive effect on species richness of saprotrophic or TRB fungi (both excluding dung-inhabiting species). When more time has passed, more saprotrophic fungal species occur in abandoned wood-pastures. Probably the explanation for our result is that these long abandoned sites are closer to natural forests and have more coarse and fine woody debris than those sites that have been abandoned only a few years ago. However, this cannot be the reason with TRB fungi. The most likely explanation is that the time since abandonment is still too short and those species are still surviving even though their habitat has been changed unfavorably. This phenomenon is known as extinction debt (Kuussaari et al., 2009). Overall, the agricultural and forest practices in Finland intensified since the 1950's and as a result, most wood-pastures, abandoned or not, were transformed into more intensive land uses (Kontula and Raunio, 2018). Studying wood-pastures that have been abandoned for over 100 years is difficult as the sites are scarce and difficult to identify.

Another potential reason may be that our data includes two broad-leaved wood-pastures that have been abandoned for a long time (about 40 years) and apparently just by coincidence have especially rich fungal communities (for example see Tervonen et al., 2015). Time since abandonment had only a weak effect on community composition. This is surprising, because species richness is affected by time since abandonment so one would expect that it has also an effect on communities, especially if the reason for higher species richness is more natural sites.

Species of fungi, other than dung-inhabiting fungi, did not react to management clearly. One reason for this might be that our study design could not observe all the within-site variation of the communities. Wood-pastures are patchy habitats, promoting high within-site community turnover (see Oldén and Halme, 2016). Our study design might not have captured all of this variation.

4.2. Historical land-use intensity affected species richness

Historical land-use intensity (historical number of farms surrounding the site within 1 km) had a negative effect on saprotrophic fungal species richness (excluding dung-inhabiting species) in all studied sites (nearly

significant) and in abandoned sites. Within TRB fungi (excluding dung-inhabiting species) or dung-inhabiting species historical land-use intensity did not seem to have a strong effect. Our result is a bit surprising because we expected that when there were more farms historically, several different types of traditional rural biotopes might have been present in the landscape, thus affecting present-day species richness positively. In addition, we do know that semi-natural grasslands host high species richness of saprotrophic fungi (Griffith and Roderick, 2008; Griffith et al., 2012). However, in a past study, we observed similar results with ectomycorrhizal fungi (Tervonen et al., 2019). Notice, however, that several studies have shown that historical landscape connectivity and land-use have a strong positive effect on vascular plant species richness on semi-natural grasslands (Cousins and Eriksson, 2002; Lindborg and Eriksson, 2004; Helm et al., 2006). One reason for our finding with saprotrophic fungi could be that saprotrophic fungal species react to forest habitat loss and fragmentation more sensitively than vascular plants, and fungal species do not benefit as much from disturbance as vascular plants. Thus, historical land-use intensity could have decreased the number of forest fungi species that are sensitive to disturbance and increased light, which decreases the number of those saprotrophic fungal species. It is also possible that in landscapes where there have been many farms historically, there has not been as much woody debris as in the landscapes with few farms. Thus, the dispersal of saprotrophic fungal species could have been historically more difficult, affecting present-day species richness negatively.

4.3. Soil pH has clear implications for community structure

Soil pH was one of the main drivers for the composition of saprotrophic fungal communities (excluding dung-inhabiting species). In all sites and grazed sites, the effect was stronger than in the abandoned sites. In addition, the response of dung-inhabiting fungi species richness to soil pH was positive and humped, whereas for saprotrophic fungal species richness (excluding dung-inhabiting fungi), soil pH did not seem to have an effect. This result is similar to that observed in our ectomycorrhizal fungal study on the same sites (Tervonen et al., 2019). With TRB fungi soil pH affected species richness positively in all sites and abandoned sites. In previous studies with vascular plants and bryophytes species richness increased with soil pH, and also its impact on community composition has been noticed to be considerable (Roem and Berendse, 2000; Oldén et al., 2016a, 2016b).

Interestingly, species richness peaked at intermediate soil pH level with dung-inhabiting fungi. Our result (peaking at pH 4.0) was similar to Rousk et al. (2009) where species richness peaked at pH 4.5. However, our data with dung-inhabiting fungi is quite small, thus just coincidence can affect our result strongly. Only one site with high soil pH did not have any dung-inhabiting fungi species. That specific site was heavily trampled, which probably affects visible dung-inhabiting fungi species.

4.4. Soil moisture has a clear effect on species richness but not on communities

Soil moisture had significant, but opposite effects on species richness among grazed and abandoned sites. When soil moisture increased, saprotrophic fungal species richness increased in grazed sites and decreased in abandoned sites (excluding dung-inhabiting species). The result for the abandoned sites is similar to our findings with ectomycorrhizal fungi (Tervonen et al., 2019). However, soil moisture did not have as clear an effect on the composition of saprotrophic fungi communities as it had on ectomycorrhizal fungi communities (Tervonen et al., 2019). In addition, in our previous study with bryophytes the effect of soil moisture on species richness was positive whereas with vascular plants there was no effect (Oldén et al., 2016b), thus it is clear that different species groups respond to soil moisture differently in wood-pastures.

It is interesting that saprotrophic fungal species in differently

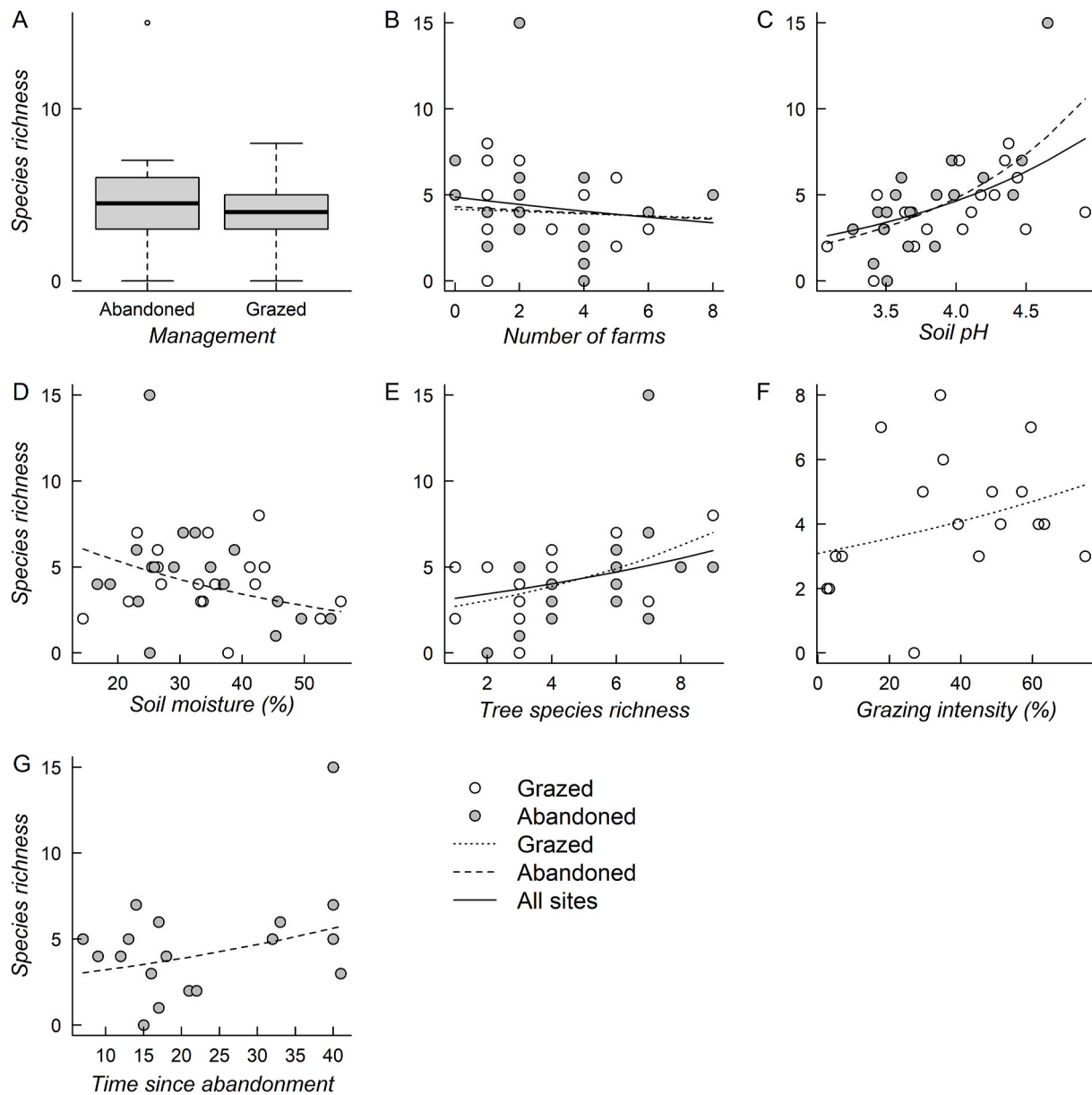


Fig. 2. Responses of saprotrophic traditional rural biotope fungi species (excluding dung-inhabiting species) richness to (A) management, (B) the number of farms surrounding the site within 1 km in the 1850s–60s (historical land-use intensity, (C) soil pH, (D) soil moisture (% content from the ground), (E) tree species richness, (F) grazing intensity (% of clipped shoots) for grazed sites, and (G) time since abandonment (years) for abandoned sites. The dots are the observed values of species richness plotted against each covariate. The curves are predicted regression curves obtained from the (full) Poisson models and they represent the effect of each covariate on species richness. When computing predicted curves, we used the mean values as values for other covariates.

Table 3

Estimated regression coefficients and their 95% confidence intervals based on the Poisson GLM for dung-inhabiting fungi species in grazed sites. The continuous variables were historical land-use intensity (the number of farms surrounding the site within 1 km in the 1850s–60s), grazing intensity, and soil pH. Variables marked with + were always kept in the models irrespective of their significance.

	RR	95% CI	P
Grazed sites			
Baseline count	5.880	3.090–10.623	1.62e-08 ***
+Number of farms	1.063	0.936–1.207	0.344
+Grazing intensity	1.005	0.992–1.019	0.481
Grazing intensity ²	0.999	0.998–0.9998	0.016 *
Soil pH	0.796	0.385–1.640	0.532
Soil pH ²	0.156	0.022–0.784	0.040 *

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

managed sites differ in their response to increasing soil moisture. One reason might be the difference in microclimate. In grazed sites, there is less vascular plant biomass than in abandoned sites, and the canopy is more open. This could affect microclimate so that it is drier in grazed sites. If the soil is naturally moist, this can be beneficial for the saprotrophic fungi fruiting on those sites. On the other hand, the abandoned sites have naturally moister microclimate and if the soil is too moist, it is no longer beneficial for fungal fruiting. This speculation is supported by [McHugh and Schwartz \(2016\)](#) study, where they found that water treatment decreased fungal diversity.

4.5. Tree species have remarkable effects on fungal species richness and communities

Saprotrophic fungal species richness increased with tree species

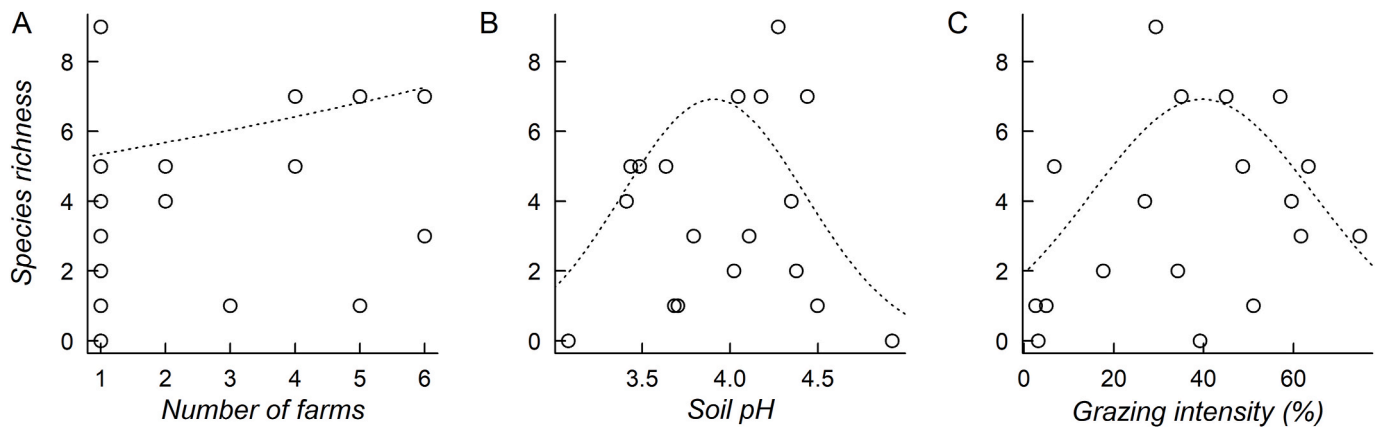


Fig. 3. Responses of dung-inhabiting saprotrophic fungi species richness to (A) the number of farms surrounding the site within 1 km in the 1850s–60s (historical land-use intensity), (B) soil pH, and (C) grazing intensity (% of clipped shoots) for grazed sites. The dots are the observed values of species richness plotted against the covariates. The curves are predicted regression curves obtained from the (full) Poisson model and they represent the effect of each covariate on species richness. When computing predicted curves, we used the mean values as values for other covariates.

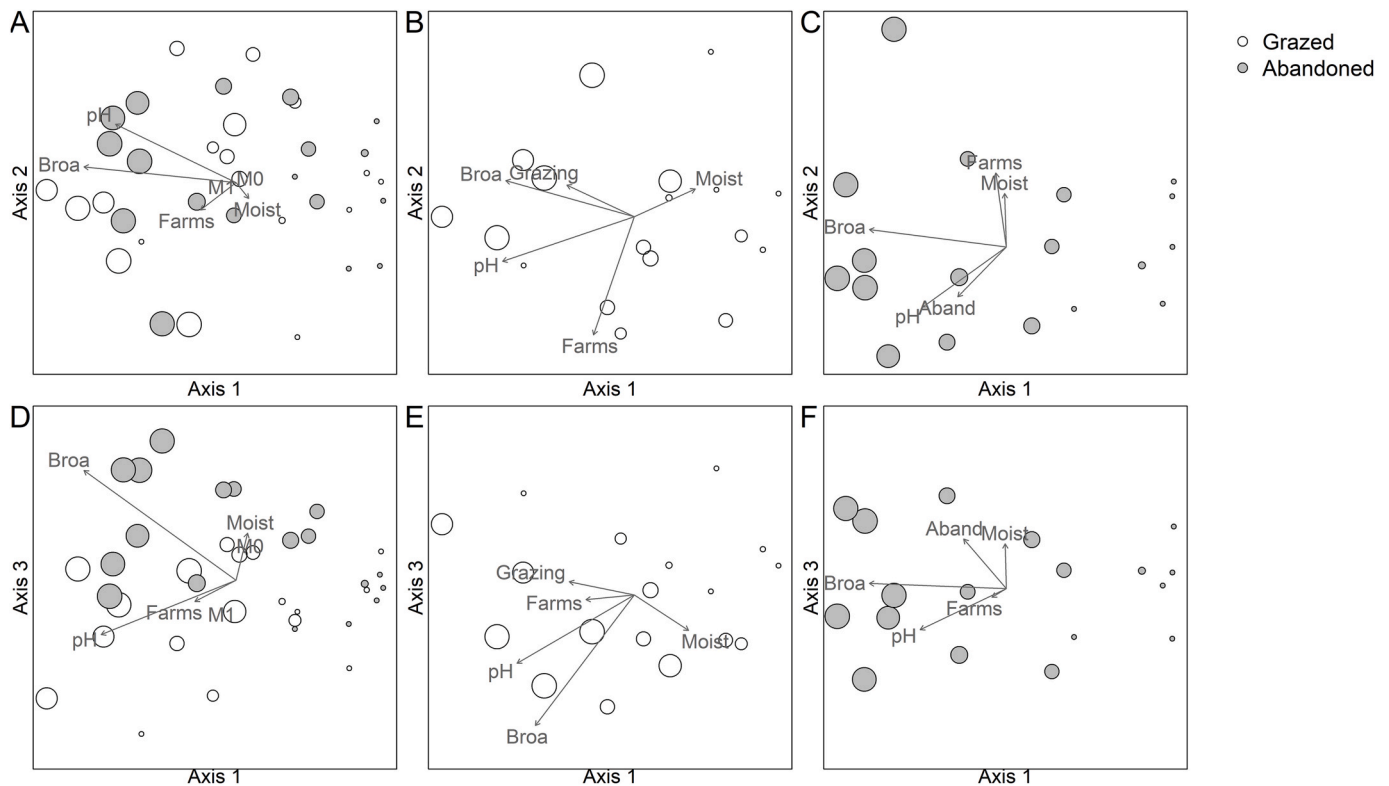


Fig. 4. Ordination plots for the community structure of saprotrophic fungi species (excluding dung-inhabiting species) based on nonmetric multidimensional scaling (NMDS) among (A) all sites, (B) grazed sites, and (C) abandoned sites with axes 1 and 2, and (D) all sites, (E) grazed sites, and (F) abandoned sites with axes 1 and 3. Analyses were done using Chao's dissimilarity index. For the dichotomous variable 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 (Moist), soil pH, the proportion of broadleaved trees (Broa), grazing intensity (Grazing) on grazed sites, and time since abandonment (Aband) on abandoned sites. Symbol size represents the proportion of broadleaved trees.

richness. Also, the species richness of TRB fungi in grazed sites increased with tree species richness (both excluding dung-inhabiting species). Our result is expected, because higher tree species diversity also diversifies the woody debris and provides more diverse resources for various species to inhabit them. Many saprotrophic fungal species prefer specific decayed tree species (Purahong et al., 2018). In our previous study with ectomycorrhizal fungi, we did not find tree species richness to affect ectomycorrhizal fungal species richness significantly (Tervonen et al., 2019). Thus, saprotrophic fungal species probably benefit more from

high species richness of tree species than ectomycorrhizal fungal species. The proportion of broadleaved trees was the main driver in saprotrophic fungal communities. It is thus clear that dominant tree species has an effect on community structure. This result also supports our finding with ectomycorrhizal fungal species where the proportion of broadleaved trees was the main driver in communities (Tervonen et al., 2019). We found that especially those sites that are birch or spruce dominated had clearly different communities. The effect was clearest in abandoned sites where also sites with mixed deciduous and coniferous trees were

separated in the ordination analyses. The reason for this clear effect is probably the fact that the dominating tree species dominates also the woody debris that saprotrophic fungi can inhabit. Another explanation could also be the different soil pH in wood-pastures that have different dominant tree species. We noticed that in our data the proportion of broadleaved trees correlated with soil pH quite strongly. Those sites that have higher soil pH (max 4.9) were birch dominated sites and those in the lower end were spruce dominated sites. Our observation is the same as in Hansson et al. (2011), with birch dominated areas having higher pH soils, thus tree species strongly affect soil composition and hence the fungal species.

5. Conclusions

Different species groups react differently to continuous management and these specific reactions should be taken into account when planning the management or conservation of wood-pastures. In our study, saprotrophic fungal species richness increased with time since abandonment. The increasing species richness is probably due to increasing woody debris. Therefore, woody debris should be retained in grazed wood-pastures during the management. In addition, our study revealed that the present tree species composition and soil properties have a strong effect on saprotrophic fungal species richness and communities, and thus stand conditions should be noted in planning. The most remarkable effect of grazing on saprotrophic fungi species living on wood-pastures is dung insertion. It creates valuable habitat for dung-inhabiting species. However, other saprotrophic fungal species in our study did not have a clear response to the management. We recommend that besides fungi, some other species groups (e.g. vascular plants) should also be used as a source of information when planning wood-pasture management. More detailed research is still needed to understand better the full role of grazing to saprotrophic fungi communities.

Declaration of competing interest

Authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.funeco.2022.101163>.

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