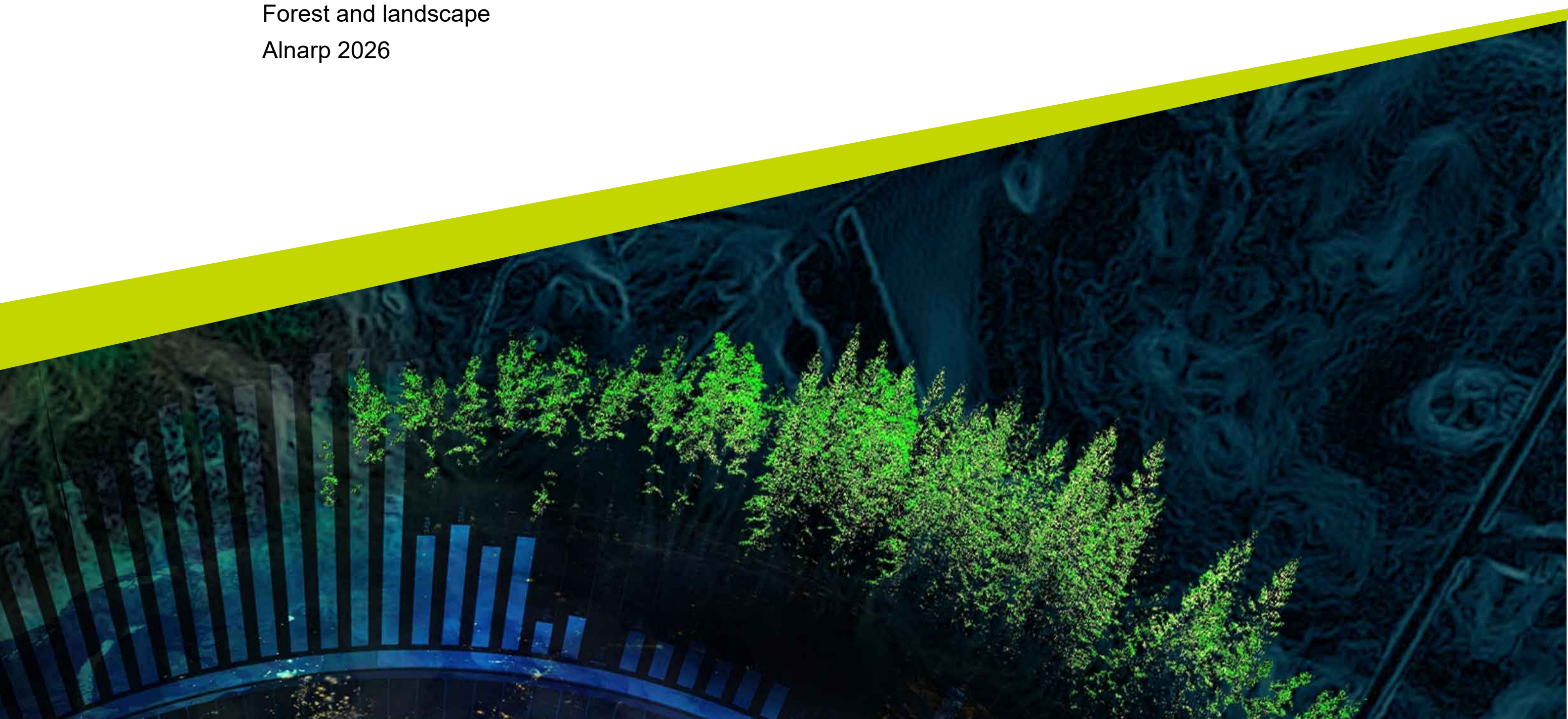
Ecological niches of edible Boletaceae and *Suillus* in Swedish forests

Thom van Lent

Degree project/Independent project • 15 credits
Swedish University of Agricultural Sciences,
Southern Swedish Forest Research Centre
Forest and landscape
Alnarp 2026



Ecological niches of edible Boletaceae and Suillus in Swedish forests

Thom van Lent

Supervisor:	**Per-Ola Hedwall, SLU, Southern Swedish Forest Research Centre**
Assistant supervisor:	Björn Lindahl, SLU, Department of Soil and Environment; Soil biology
Examiner:	Patrick Sherwood, SLU Alnarp, Southern Swedish Forest Research Centre
Credits:	15
Level:	G2E
Course title:	Independent project in Forestry science
Course code:	EX1012
Programme/education:	Forest and landscape BSc
Course coordinating dept:	Southern Swedish Forest Research Centre
Place of publication:	Alnarp
Year of publication:	2026
Copyright:	All featured images are used with permission from the copyright owner.
Keywords:	Boletaceae, *Suillus*, ectomycorrhizal fungi, DNA metabarcoding, ecological niches, Swedish forests, tree species composition

Swedish University of Agricultural Sciences
Faculty of Forest Science
Southern Swedish Forest Research Centre

Abstract

It is essential for biodiversity conservation and sustainable foraging to understand the ecological niches of edible ectomycorrhizal fungi. This study investigates, with the use of soil DNA metabarcoding data from the Swedish Forest Soil Inventory, how forest characteristics and soil properties influence the occurrence of species within the Boletaceae family and *Suillus* genus. The effects of the variables: stand age, tree species composition, soil pH, nitrogen availability (N:C ratio) and nitrogen deposition on fungal presence were analysed.

Generalized additive models (GAMs) were used to investigate the relationships between these variables and fungal occurrence across multiple taxonomic levels (family, genus, and species). In this study, it was found that tree species composition was the strongest predictor of fungal presence. The species within the genus *Suillus* were negatively associated with spruce, birch and other trees, supporting claims from previous literature stating that species within the genus *Suillus* are prone to choose pine as their host trees. In contrast, species within Boletaceae, such as *Boletus edulis* and genus *Leccinum* showed positive associations with spruce and birch. Boletaceae and *Leccinum* were more common in younger stands, while *Suillus* occurred more frequently in older stands.

Higher soil pH values were generally negatively associated with fungal occurrence, indicating a preference for acidic conditions. The N:C ratio showed a positive association with several taxa, suggesting the importance of a nutrient rich soil. Nitrogen deposition however, showed no significant effect on any of the fungal taxa. Spatial distribution patterns at larger taxonomic scales showed no strong geographic clustering, although several species exhibited a more restricted distribution.

This study demonstrates the effect of forest composition and soil properties on the occurrence of Boletaceae and *Suillus* species in Sweden. The findings of this study contribute to a better understanding of their preferred habitats and can therefore aid in forest management and conservation strategies, as well as improve the knowledge for recreational mushroom foraging.

Keywords: Boletaceae, *Suillus*, ectomycorrhizal fungi, DNA metabarcoding, ecological niches, Swedish forests, tree species composition

Table of contents

1. Introduction

Picking mushrooms has been part of Swedish culture for more than a hundred years. It started in the 1830s, when a few academic mycologists started campaigns trying to inform people about edible mushrooms. This was met with great resistance, since most people did not see mushrooms as food. In the 20th century, the urban middle class, followed by the working class, started accepting it as a viable food source, although many limited themselves by only eating the chanterelle (*Cantharellus cibarius Fr.*) (Svanberg & Lindh, 2019). With increasing interest, mushroom picking is now, in the 21st century, integrated in the Swedish culture and has become a thriving pastime activity (Svanberg & Lindh, 2019). Mushroom picking not only adds recreational value to a forest, but fungi also offer many health benefits when consumed (Konsue et al., 2025).

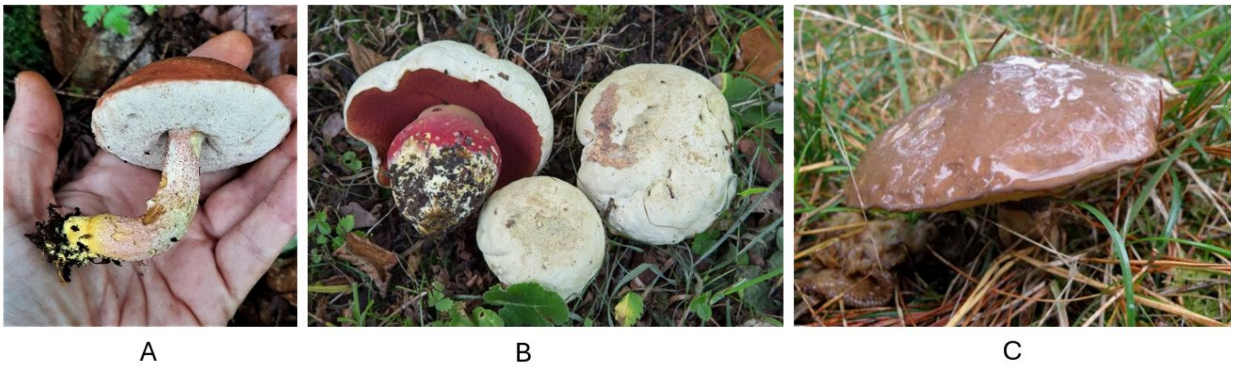
While foraging is often seen as something that damages natural ecosystems, evidence suggests that mushroom picking has an opposite effect. Foraging food from the forests increases the nature relatedness of people (Schunko & Brandner, 2021), which results in a higher urge to protect nature and improve biodiversity to battle climate change (Ágoston et al., 2024). Additionally, foraging mushrooms, if done correctly, shows no reduction in species richness of the fungi, or future yields of the fruit bodies. Although forest floor trampling does reduce fruit body numbers, it appears to do no underground damage to the soil mycelia (Egli et al., 2005). Although direct evidence is limited, wild mushroom foraging may have a substitution effect by reducing demand for cultivated or other agricultural food products such as meat, which are typically associated with higher environmental impacts (Procházka et al., 2023).

There is no peer reviewed scientific paper published that tells how many edible mushrooms are present in Sweden. However, research has been conducted with 100 participants, in which they were collectively able to mention 136 edible mushroom species, of which 91 represented scientific species that were not synonyms (Svanberg & Lindh, 2019). While participants varied considerably in their knowledge of edible mushrooms, the *Boletus edulis*, a member of the Boletaceae family was known by most participants and is one of the most picked mushrooms in Sweden (Svanberg & Lindh, 2019). Another, less known, mushroom family classified in the order of Boletales that are present in Swedish forests, are the Suillaceae. In the family Suillaceae, there is a genus called *Suillus*. All *Suillus* species occurring in Sweden are considered edible (Judžentienė & Šarlauskas, 2025), which makes them popular for foraging.

This project focuses not only on the edible species of the Boletaceae family, since they are one of the most popular for gathering in Sweden (Svanberg et al., 2025), but also members of the genus *Suillus* from the family Suillaceae, since they are present in high abundances in the Northern hemisphere (Lofgren et al., 2024), resulting in a high occurrence in Swedish forests. Species within the Boletaceae and Suillaceae families can be distinguished by their tubular hymenophore, which appears as spongy pores on the underside of the cap instead of gills (Ayala-Vásquez et al., 2023) (Figure 1A), and they have fruit bodies with a strong flavour. None of the species present in Sweden in the family Boletaceae and genus *Suillus* are deadly according to the Giftinformationcentralen (Giftiga Svampar, n.d.), although some species from Boletaceae are considered to be poisonous, such as the bitter bolete (*Tylopilus felleus*), the Satan's bolete (*Rubroboletus satanas*) (Figure 1B), and other red-pored boletes within the family Boletaceae, such as *R. legaliae*, and *R. rhodoxanthus* . These are known to cause gastrointestinal symptoms, including nausea and vomiting (Andersson et al., 2016) and are excluded in this research. The species that are in the genus *Suillus* are all edible, although there are some species that can cause possible stomach issues if they are prepared inadequately. This is the case for the species *Suillus luteus* (Slippery Jack) (Figure 1C), which can cause issues when consumed if the slimy cap is not removed (Prager & Goos, 1984), but the species will be included in the research, since it is often picked.

Figure 1

A) Tubular hymenophore, B) Satan's Bolete (Rubroboletus satanas) and C) Slippery Jack (Suillus luteus)



Note. A) Tubular hymenophore, which appears as spongy pores on the underside of the cap, used to distinguish the Boletaceae family and *Suillus*. From “All about boletes: An introduction to bolete foraging and identification” by Mushroom Appreciation (2025), https://www.mushroom-appreciation.com/all-about-boletes.html. Copyright (2025, October 2) Jenny.
B) Satan's Bolete, which is known to be a poisonous mushroom from the family Boletaceae. From “Artfakta: djävulssopp (*Rubroboletus satanas*)” by SLU Artdatabanken (2026), https://artfakta.se/taxa/161. Copyright n.d. Michael Krikorev.
C) Slippery Jack (*Suillus luteus*), which can cause stomach issues if not prepared right. From “Suillus luteus, Slippery Jack mushroom” by First Nature (n.d.), https://www.first-nature.com/fungi/suillus-luteus.php

Species of the genus *Suillus* mainly occur in temperate and boreal forests of the Northern Hemisphere (Judžentienė & Šarlauskas, 2025). Similarly, many species within the family Boletaceae are widely distributed across Europe, Asia, and North America, while some species have also been introduced to regions such as South Africa and New Zealand through non-native tree plantations. Their distribution is correlated with a cool-temperate to subtropical climate. They are strongly associated with forests since they are dependent on ectomycorrhizal relationships with trees (Hall et al., 1998), in which they receive carbon from the roots and exchange nutrients, such as phosphorus and nitrogen, to the tree (Niedzielski et al., 2024). Because of this relationship, they can occur in dense forest stands, but can also thrive in more open landscapes, close to isolated trees.

The Boletaceae family shows a broad range of host trees, since they can grow in association with *Quercus* (oak), *Fagus* (beech), *Betula* (birch), *Picea* (spruce), and *Pinus* (pine), but are influenced by the maturity of the trees. In mature stands, they grow in higher abundance, although they can also be found in younger stands (Hall et al., 1998). Other characteristics of species in the Boletaceae family, is that they can be found on all sorts of soil, but they are mostly found in nutrient rich soils with high Fe and C:N ratio (Hall et al., 1998). The soil pH likely plays a role in their abundance, but the mechanism is unclear and more research is needed in this area (Niedzielski et al., 2024).

Since the Boletaceae family and the genus *Suillus* have not been successfully cultivated on a commercial scale, because of their dependence on the ectomycorrhizal relationships with trees, they remain exclusively available through foraging (Hall et al., 1998). This highlights the importance of understanding their habitat requirements to support their conservation, as these species depend entirely on natural habitats.

Within the Boletaceae family the genera *Leccinum*, *Xerocomus* and *Xerocomellus* are ecologically important ectomycorrhizal taxa, on which a focus will be placed in this study. Species of *Leccinum* are mostly found with specific host trees such as *Betula* (birch), *Populus* (poplar), and *Salix* (willow) (Budau et al., 2026), showing a tendency to occur in broadleaf stands, while species within *Xerocomus* and *Xerocomellus* show broader host tree preferences occurring in broadleaf stands and coniferous stands (Wu et al., 2016) (Nuhn et al., 2013).

Species within the genus *Suillus* are commonly associated with *Pinus* (pine) species, particularly *Pinus sylvestris* (Scots pine), which act as their primary host trees (Liao et al., 2016). Some species are found mostly in nutrient poor peatlands, but also in moist sites dominated by pine. An example of a species that occurs in these types of moist landscape is *Suillus flavidus*, but wetlands being one of the most threatened ecosystems endangers their existence (Stasińska, 2025). Other species included in this study are *Suillus variegatus* and *Suillus bovinus*. *S. variegatus* is mostly dominant in mature stands, while *S. bovinus* is more characteristic for younger stands (Dahlberg, 1997). It is possible for *S. bovinus* to be part of a tripartite interaction with a tree and mycoparasitic fungi (Gomphidius roseus), showing a complexity of ecological networks for this species (Olsson et al., 2000).

Although previous research has been done, it is still important to get more accurate data on the Boletaceae family and *Suillus* genus and their favoured habitats, to improve our understanding of where these mushrooms thrive and which environmental conditions and forest characteristics are most suitable for their growth. This knowledge will not only benefit recreational users that like to forage these mushrooms, but can also help with identifying and maintaining optimal habitats. This is essential for conserving and protecting these mushrooms, by adapting forest management for biodiversity reasons, particularly because Boletaceae and *Suillus* cannot yet be cultivated.

To increase the amount of data available and accuracy about the influence of forest characteristics on the presence of various species in the Boletaceae family and *Suillus* genus, DNA sequence data from the Swedish Forest Soil Inventory will be used. Statistical modelling will be done of ecological niches with respect to forestry and soil fertility. DNA obtained from soil samples allows for the detection of species without any visible fruiting bodies, making it an increasingly important tool for studying fungi. Compared to traditional survey methods based on above-ground observations, DNA sequences can reveal a much higher diversity of fungi (Peay et al., 2016). Especially for the Boletaceae family, it is of importance since their fruiting is variable, due to a high dependence on environmental conditions. Furthermore, soils act as reservoirs of fungal diversity, which increases the likelihood of detecting Boletaceae species in soil samples compared to above-ground observations. Tree roots contribute greatly to fungal diversity (Fjelde et al., 2025), which is relevant since Boletaceae and *Suillus* form ectomycorrhizal relationships with trees and are often found in the soil around these roots. This makes the combination of soil DNA data and forest characteristics especially useful for studying their distribution.

This study addresses the following research question: how do forest characteristics and soil properties influence the presence of Boletaceae and *Suillus* species in Swedish forests, as detected through soil DNA sequencing? It is hypothesized that the presence of Boletaceae and *Suillus* species is strongly influenced by tree species composition and soil properties, with higher occurrence in mature forests and nutrient-rich soils. To test this, a range of environmental variables was analysed, including stand age, tree species composition, soil pH, nitrogen availability (N:C ratio), and nitrogen deposition.

2. Methods

2.1 Samples

The 2277 samples used in this research were gathered between 2014 and 2021 by the Swedish Forest Soil Inventory (Lindahl et al., 2026). They were gathered from locations systematically distributed across Sweden, with a higher density in the south, since there is a larger variety in forest stands there. Access to the dataset was provided through collaboration with researchers affiliated with the Swedish Forest Soil Inventory and the Swedish University of Agricultural Sciences (SLU).

The measurements used in this analysis include N:C ratio, pH, stand age, square-root stand age, tree species composition (spruce, birch and other trees) and nitrogen deposition. These forest- and soil characteristics were selected because of their ecological relevance, availability and based on previous literature on ecological niches of ectomycorrhizal fungi. The N:C ratio and pH were measured directly on the soil samples. These samples were from the organic topsoil layer, with the use of a corer at multiple smaller subplots within each circular plot, with a 20 meter radius. After removal of fresh litter the soil cores from each plot were combined into a composite sample. The concentration of carbon and nitrogen was determined using an elemental analyser, with the nitrogen availability being expressed as the N:C ratio, while the pH was measured in a soil–water slurry using a pH electrode (Lindahl et al., 2026).

All tree data was gathered by the Swedish National Forest Inventory. The stand age was calculated with the use of increment boring of selected trees (Lindahl et al., 2026). Stand age was included in both square-root transformed and non-transformed forms, to allow for non-linear dependencies. Tree species composition was measured in plots with a 20 m radius (Fridman et al., 2014) and was expressed as proportional stand dominance values ranging from 0 to 1. The dominant tree species in the sampled stands were mainly *Picea abies* (Norway spruce) and *Pinus sylvestris* (Scots pine), often mixed with *Betula* (birch) species and other broadleaf trees. The spruce category consisted exclusively of *P. abies*. The pine category was dominated by *P. sylvestris*, but also included a small proportion of *Pinus contorta* (lodgepole pine). Because tree species other than spruce, pine, and birch occurred at relatively low frequencies, they were grouped into the category “other trees” for statistical analyses. Although less abundantly around 5% of the stands included in the data were broadleaf dominant.

Nitrogen deposition data was gathered by the Sveriges meteorologiska och hydrologiska institut (SMHI).

2.2 DNA sequencing to detect fungal species in the Boletaceae family and Suillus genus

The DNA sequence data used in this study originated from soil samples collected through the Swedish Forest Soil Inventory and were generated previously as part of the study by Lindahl et al. (2026). DNA was extracted from organic soil material and the fungal ITS2 region (Lindhal et al., 2026), a commonly used barcode marker for fungal identification, was amplified using the general fungal primers gITS7 and ITS4 (Ihrmark et al., 2012). These primers target a broad range of fungal taxa and are not specific to Boletaceae or Suillus species. Amplicon sequencing was performed using the PacBio platform as described by Lindahl et al. (2026). Sequence reads were filtered and clustered using the SCATA pipeline (Ihrmark et al., 2012), after which operational taxonomic units were assigned to species hypotheses using the UNITE reference database (Abarenkov et al., 2023). For this study, the processed sequence dataset was used to determine the presence or absence of the family Boletaceae and the genus Suillus in each soil sample.

2.3 Statistical analysis

2.3.1 Data preparation

The analysis in this study included the variables stand age, square-root stand age, tree species composition (spruce, birch and other trees), soil pH, N:C ratio, and nitrogen deposition.

These variables were recorded for each sample site and linked to fungal occurrence data using unique sample identifiers. From the complete fungal dataset, records belonging to the order Boletales were selected. Only edible species belonging to the family Boletaceae and the genus *Suillus* were retained for further analysis. In Excel, multiple filtered datasets were created to enable analyses at different taxonomic levels: family, genus, and species. At species level the presence of *B. edulis*, *S. variegatus, S. bovinus, S. luteus* and *S. flavidus* were compared with the forest characteristics. While the genus *Leccinum, Xerocomus* and *Xerocomellus* were grouped because of lower occurrence and compared. To find broader preferences of these mushrooms the entire family Boletaceae was grouped, same as the genus *Suillus*.

2.3.2 R

The statistical analysis was performed in R (version 4.5.1). The packages readxl (Wickham et al., 2019), dplyr (Wickham et al., 2023), mgcv (Wood, 2017), corrplot (Wei et al., 2021) and DHARMa (Hartig, 2016) were used. The data with the occurrence of certain fungal species and forest characteristics were prepared in excel as stated above, and in R they were combined using unique sample codes. To analyse the fungal occurrence, a binary response variable was created. When a fungus was present, it was stated as 1 and when the fungus was absent, it was stated as 0. This was done per taxonomic level individually, since the excel data was split between either a family, genus or species, to get results on different scales.

To increase the relevance and accuracy of the analysis of fungal occurrence, some variables were removed. These variables were temperature sum, since it was not relevant for this analysis and days until freezing, because previous analyses by Lindahl et al. (2026) showed that these variables had little influence on fungal occurrence patterns. The most common tree species in the stands, pine, was excluded from the analysis to make analysis of the species composition possible. Otherwise, tree species composition would always result in perfect multicollinearity. Pine was chosen as the reference category, because association with *Suillus* and pine was in literature already well established, and it was the most dominant tree species in the dataset. Therefore, a high proportion of spruce, birch, and other trees indicated a relatively lower proportion of pine within the stand. When negative associations are found for all investigated species this may indicate a positive association with pine. Square-root transformed stand age was included to account for the hypothesis that ecological changes occur more rapidly during the early stages of forest development than in mature forests (Máliš et al., 2023). This transformation places greater emphasis on variation among younger stands while reducing the influence of differences between older stands.

Ending up with one data set in R including the occurrence of the fungi species linked to the forest characteristics of the samples. These variables included longitude and latitude, pH, N:C ratio, stand age, square-root transformed stand age, tree species composition, nitrogen deposition, and the square-root transformed total number of DNA sequences per sample. The latter was included to account for variation in sequencing depth among samples, thereby reducing differences in detection probability and improving the precision of the model estimates. Tree species composition included spruce, birch and other trees (excluding pine as stated above). These variables were standardized using z-transformation (subtracting the mean and dividing by the standard deviation), which improved the comparability of the effects.

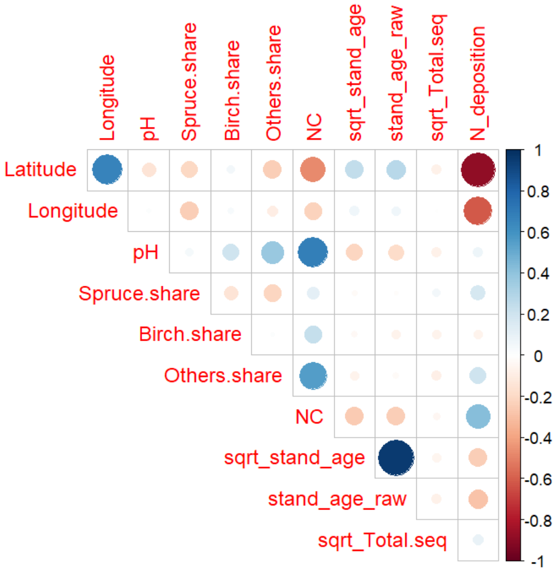
The relationship between the forest characteristics and presence of fungi in the family Boletaceae or genus *Suillus* was analysed using Generalized Additive

Models (GAM), with a binomial error distribution and logit link function. This model type was chosen, because of their ability to analyse non-linear relationships and to account for the spatial autocorrelation. This spatial autocorrelation was accounted for in the models using a two-dimensional smooth term of longitude and latitude. For each taxonomic level (family, genus or selected species), two models were created, one including raw stand age and one including square-root stand age. These were not included together since they were strongly correlated. In both models, the other forest characteristics were included, and all smoothing parameters were estimated with the use of restricted maximum likelihood (REML). Providing a stable estimation of model parameters and smoothness selection.

The model was evaluated with a combination of statistical, diagnostic and structural criteria. A Pearson correlation matrix was used to check for multicollinearity among explanatory variables (Figure 2). When a correlation coefficient exceeded 0.7 it was considered a strong correlation and split in different models if it influenced the results (Dormann et al., 2013), which was the case for square-root stand age and stand age (0.96). Another strong correlation was found between nitrogen deposition and latitude (0.89). Both variables were retained in the model, because latitude was required to account for spatial autocorrelation, while nitrogen deposition represented a separate environmental variable with potential ecological effects on ectomycorrhizal fungi. Nitrogen deposition seemed to be of ecological relevance in the model since nitrogen availability is, according to literature, often reported to influence ectomycorrhizal communities heavily (Lilleskov & Bruns, 2001). However, due to the strong correlation, interpretation of their individual effects should be done with caution.

Figure 2

Correlation matrix of the variables included in the generalized additive models. Circle size and colour intensity indicate the strength of the correlation between variables, with blue representing positive correlations and red representing negative correlations. Strong correlations were observed between stand age and square-root stand age, and between latitude and nitrogen deposition. Variables with correlation coefficients above 0.7 were considered strongly correlated and were evaluated carefully before inclusion or separation in the models.



Akaike's Information Criterion (AIC) was used to compare the models, and performance if some forest characteristics were left out, which was indicated by a lower AIC. The model with all the variables included except square-root stand age was selected for the results, since the AIC showed a difference smaller than 2, which meant the model was considered equally plausible to other possible models (Burnham & Anderson, 2002). The model with regular stand age was used for statistical analysis of the forest characteristics, while the model with square-root stand age was only used for the effect of square-root stand age on the presence of fungi. The gam.check function was used to inspect residual patterns and evaluate the smooth terms. These residual patterns were evaluated closer using the DHARMa package, which made it possible to test for dispersion, uniformity and outliers to identify deviations from model assumptions. To check for overlapping in information by some predictors the concurvity function was used.

The R codes used for these models were created with the help of AI, literature and experts.

2.3.3 Spatial visualization

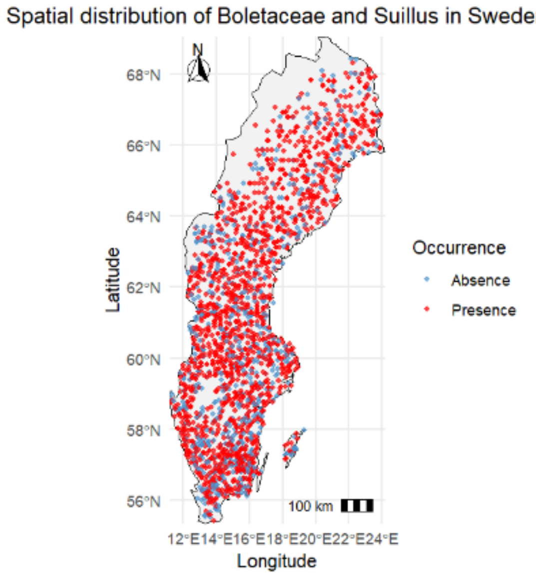
R was used for the visualization of the spatial distribution of the studied fungi. The packages used to create these maps included ggplot2 (Wickham et al., 2024), sf (Pebesma & Bivand, 2023), rnaturalearth (Massicotte et al., 2026) and ggspatial (Wickham et al.,2024). The occurrence data was merged with the forest characteristics dataset using the unique sample identifiers and made into presence-absence values. The geographical coordinates needed for plotting the sample locations on the map were drawn from the longitude and latitude data received from the Swedish Forest Soil Inventory. When a species was present this would be indicated as a red spot, whilst absence was either left out of the map or shown as a light blue spot. For every taxonomic group researched in this paper a map was made.

3. Results

3.1 Spatial distribution

Figure 3

Spatial distribution of the family Boletaceae and genus Suillus across Sweden based on soil DNA samples from the Swedish Forest Soil Inventory. Red dots indicate samples where these species were detected and blue spots indicating absence, showing visually no clear signs of clustering. The spatial distribution of samples shows a higher sampling intensity in southern Sweden compared to northern Sweden.



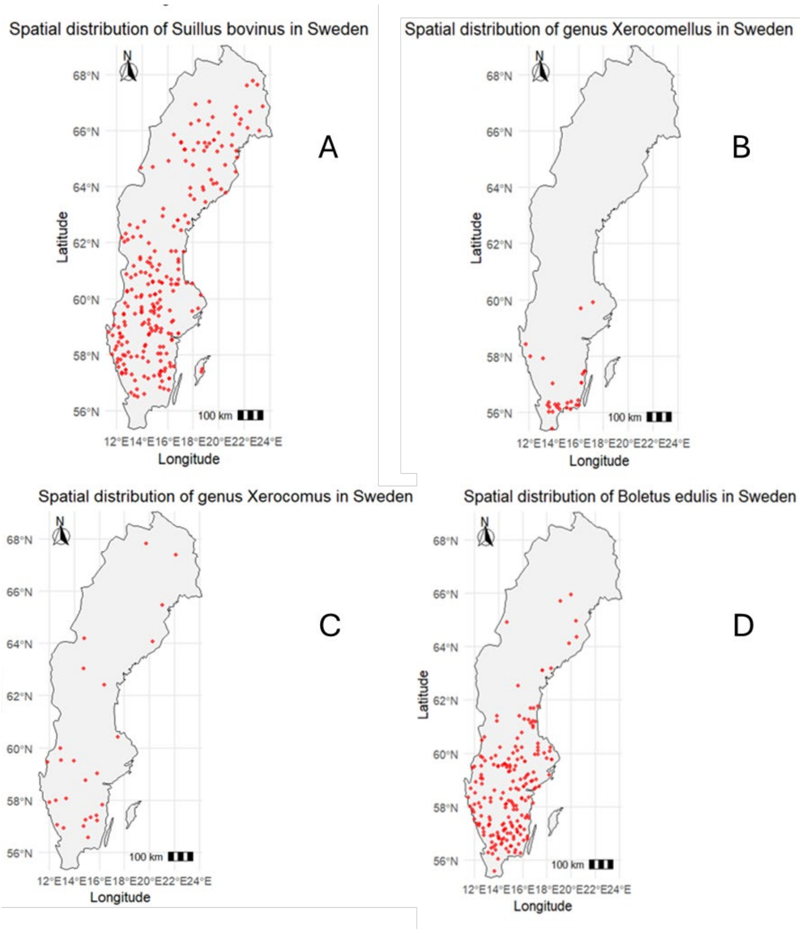
In Figure 3 the spatial distribution of Boletaceae and *Suillus* is represented across Sweden. Both groups were widely distributed throughout the study area, with no clear large-scale clustering. This suggests that these fungal communities are not restricted to specific regions and occurrence is unlikely to be explained by geographic locations alone. Therefore, environmental and stand-related variables likely influence their occurrence. However, some specific species showed a more restricted scattering, in the genus *Suillus* (Figure A1); *S. flavidus, S. luteus* and *S. bovinus*. *S. bovinus* (Figure 4A) showed a higher density of occurrence in southern Sweden, while *S. luteus* (Figure A2) and *S. flavidus* (Figure A3) were distributed more evenly, but found in fewer places. *S. variegatus* (Figure A4) appeared to be very common in Sweden, since it was found in more than 44% of the samples.

Although the Boletaceae family as a whole was relatively evenly distributed (Figure A5), with a higher density in the south, genera and species within this family appeared to be more specific in their geographic preference. The genus *Xerocomellus* was only recorded in southern Sweden (Figure 4B), while the genus *Xerocomus* was also sporadically found further north in Sweden (Figure 4C).

Similarly, *B. edulis* (Figure 4D) and the genus *Leccinum* (Figure A6) showed a higher density in the south of Sweden with fewer occurrences northwards.

Figure 4

Spatial distribution of S. bovinus (A), Xerocomellus (B), Xerocomus (C), and B. edulis (D) across Sweden based on soil DNA samples from the Swedish Forest Soil Inventory. Red dots indicate locations where each taxon was detected. Xerocomellus (found in 28 samples) was primarily restricted to southern Sweden, whereas Xerocomus (found in 26 samples) and B. edulis (found in 194 samples) showed broader but still southern dominant distribution. S. bovinus (found in 238 samples) was more widely distributed, with a higher density of detection in southern Sweden.

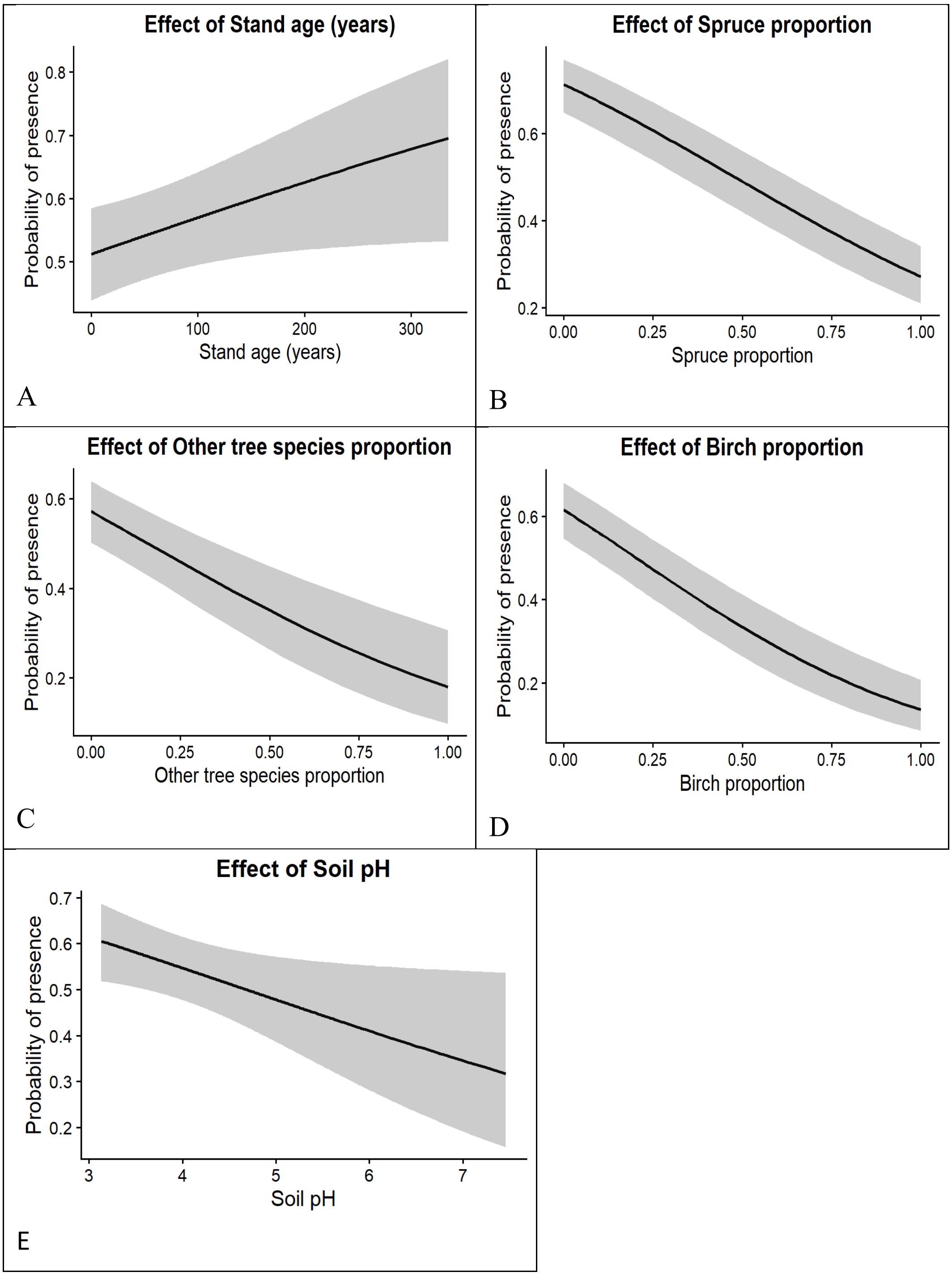


3.2 The genus *Suillus*

Suillus occurrence was positively related with both stand age (*β* (estimate) = 0.114*, p* = 0.0387) (Figure 5A*)* and square-root transformed stand age (*β* = 0.131, *p* = 0.0142). Tree species composition showed strong association with *Suillus* presence, with negative correlations with spruce share (*β* = -0.720*, p* < 0.001) (Figure 5B), other tree species share (*β* = -0.348, *p* < 0.001) (Figure 5C) and birch share (*β* = -0.501*, p* < 0.001) (Figure 5D). A significant negative relationship was found between *Suillus* occurrence and pH (*β* = -0.163, *p* = 0.0314) (Figure 5E). No significant effects were found for nitrogen deposition and N:C ratio (Table B1). The model explained 18.8% of the deviance in *Suillus* occurrence and had an adjusted R^2 of 0.235. Among the significant predictors, spruce share showed the strongest negative association, whereas the effects of stand age and pH were comparatively small (Table B1).

Figure 5

Effect plots of stand age (A), spruce share (B), others share (C), birch share (D) and pH (E) on genus Suillus occurrence.



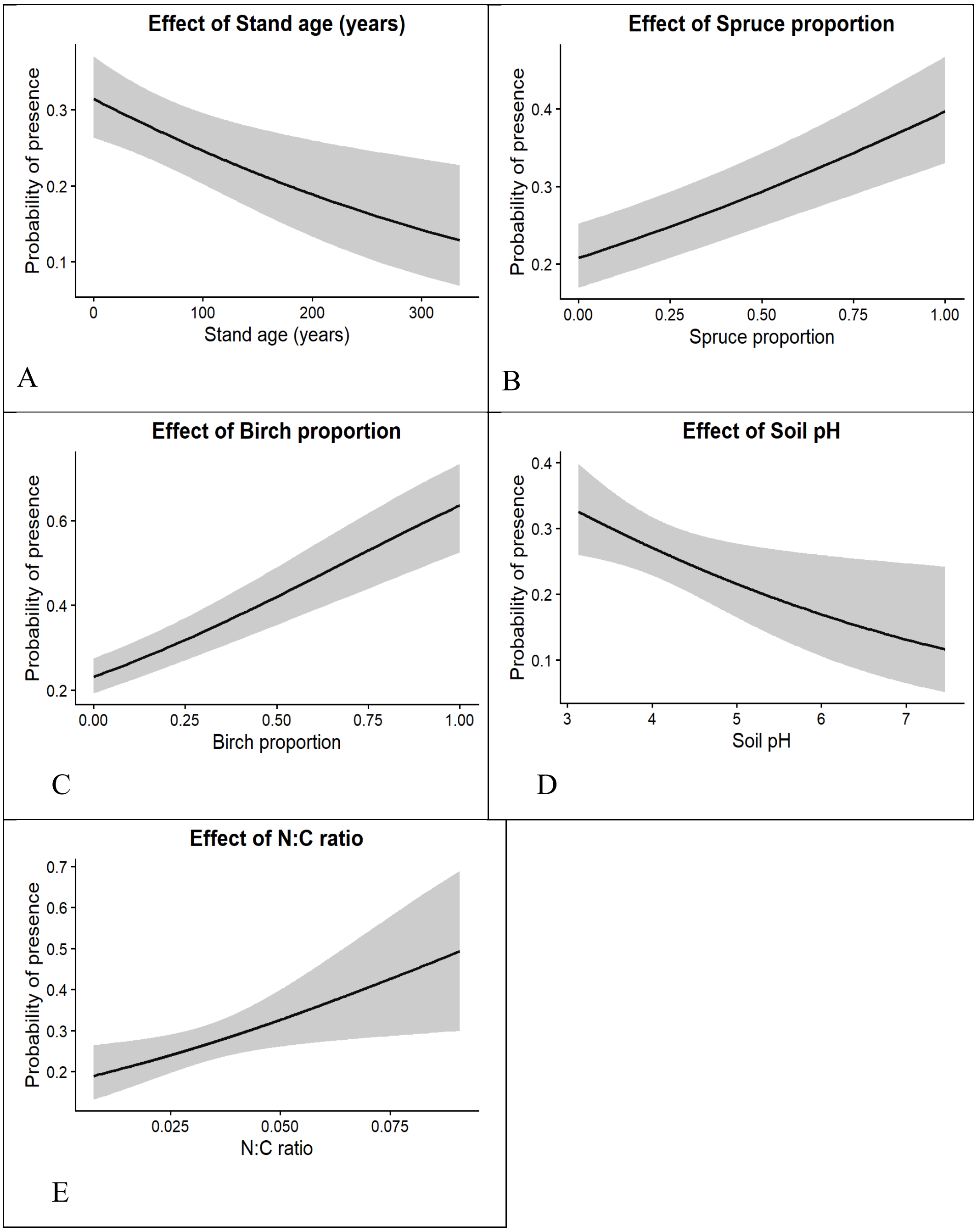
Note. The shaded area represents the 95% confidence interval.

3.3 The Boletaceae family

Stand age had a negative and significant association with Boletaceae occurrence *($\beta = -0.166$, $p = 0.0038$)* (Figure 6A). Spruce share *($\beta = 0.348$, $p < 0.001$)* (Figure 6B) and birch share *($\beta = 0.381$, $p < 0.001$)* were significantly positively correlated (Figure 6C). There was a negative correlation between occurrence and pH *($\beta = -0.177$, $p = 0.0188$)* (Figure 6D) and a positive association with N:C ratio *($\beta = 0.216$, $p = 0.0161$)* (Figure 6E). No significant relationship was found with the occurrence of Boletaceae and other tree species, square root stand age and nitrogen deposition (Table B2). The model explained 8.7% of the deviance in Boletaceae occurrence and had an adjusted R^2 of 0.095. Among the significant predictors, tree species composition had the strongest influence on Boletaceae occurrence, with positive associations for birch share ($\beta = 0.381$) and spruce share ($\beta = 0.348$). The effects of stand age, soil pH, and N:C ratio were comparatively weaker (Table B2).

Figure 6

Effect plots of stand age (A), spruce share (B), birch share (C), pH (D) and N:C ratio (E) on Boletaceae occurrence



Note. The shaded area represents the 95% confidence interval.

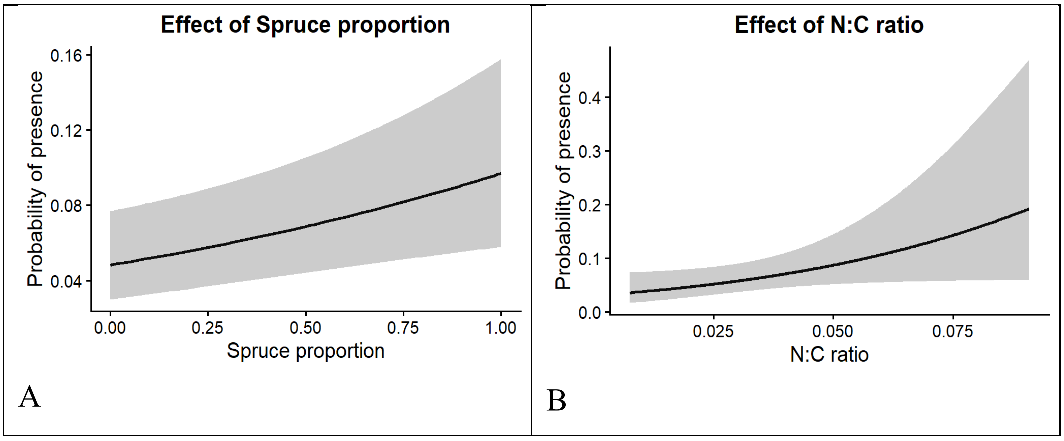
3.4 *Boletus edulis*

A positive relationship was found with the occurrence of *B. edulis* and spruce share ($\beta = 0.284$, $p = 0.0027$) (Figure 7A) and N:C ratio ($\beta = 0.282$, $p = 0.0474$)

(Figure 7B). No variables other than spruce share and the N:C ratio were significantly associated with *B. edulis* occurrence (Table B3). The model explained 16% of the deviance in *B. edulis* occurrence and had an adjusted R^2 of 0.081.

Figure 7

Effect plots of spruce share (A) and N:C ratio (B) on B. edulis occurrence



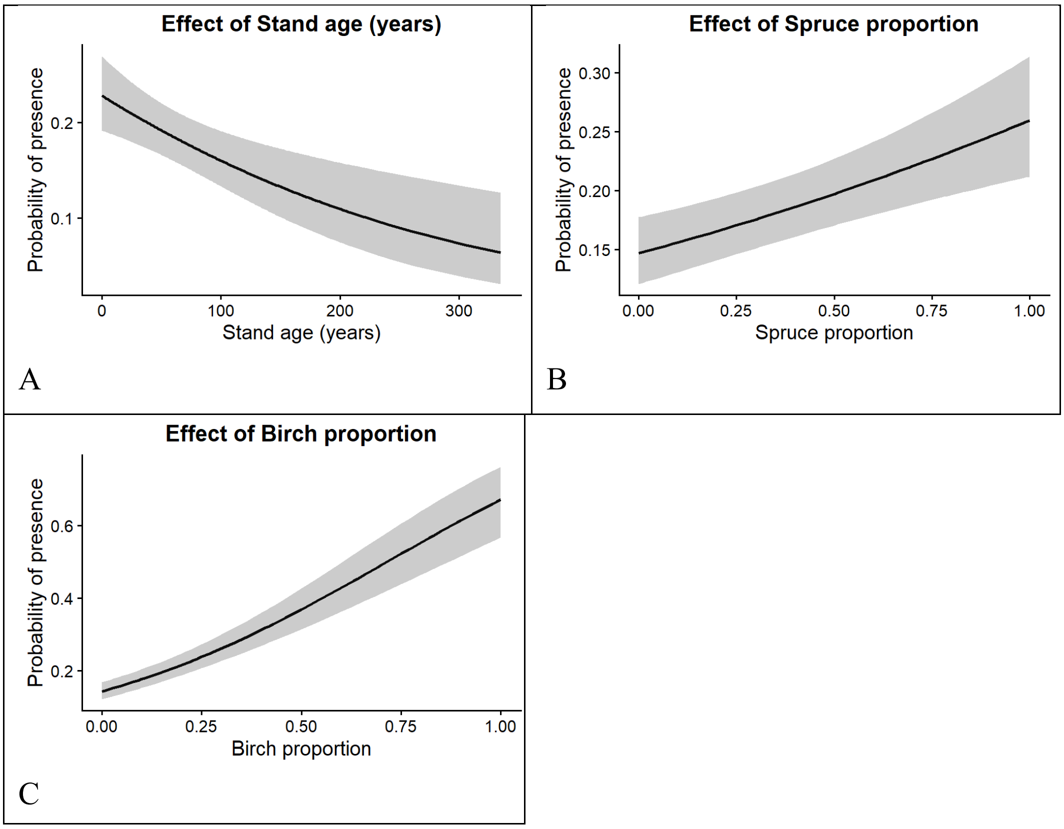
Note. The shaded area represents the 95% confidence interval.

3.5 The genus *Leccinum*

Both stand age ($\beta = -0.214$, $p < 0.001$) (Figure 8A) and square-root stand age ($\beta = -0.162$, $p = 0.0072$) had a significant negative relation with *Leccinum* occurrence. Spruce ($\beta = 0.269$, $p < 0.001$) (Figure 8B) and birch ($\beta = 0.541$, $p < 0.001$) (Figure 8C) showed a positive association with *Leccinum* occurrence, while no significant effects were found for other tree species, soil pH, nitrogen deposition and N:C ratio (Table B4). The model explained 8.1% of the deviance in *Leccinum* occurrence and had an adjusted R^2 of 0.076. Birch share showed the strongest positive association with Leccinum occurrence, whereas the effects of spruce share and stand age were comparatively smaller (Table B4).

Figure 8

Effect plots of stand age (A), spruce share (B) and birch share (C) on genus Leccinum occurrence



Effect of Stand age (years)

Effect of Spruce proportion

Effect of Birch proportion

Note. The shaded area represents the 95% confidence interval.

3.6 The genus *Xerocomus*

No significant associations were found between *Xerocomus* occurrence and the tested variables (Table 1) (Table B5). The model explained 10.6% of the deviance in *Xerocomus* occurrence and had an adjusted R^2 of 0.011.

Table 1

Results from R showing estimates and p-values of genus Xerocomus. No significant associations were found between the variables and Xerocomus occurrence.

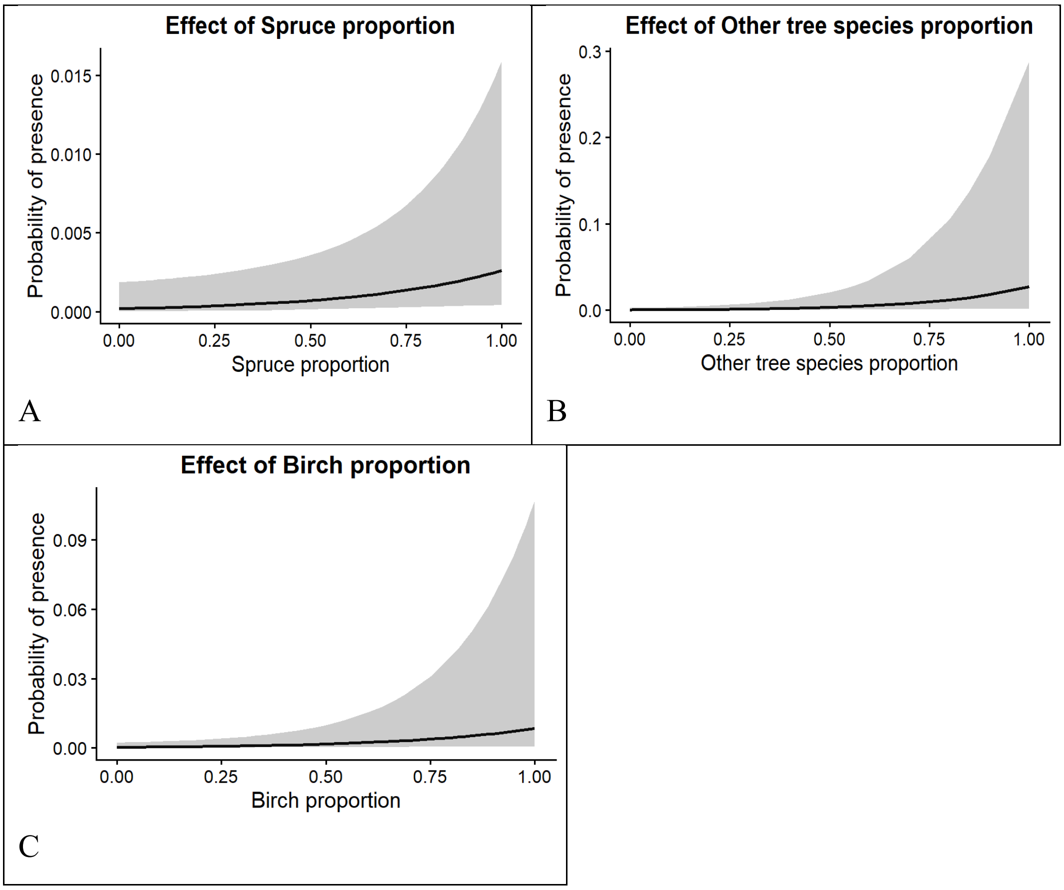
***Xerocomus* variables**	**Estimate**	**P value**
stand_age_raw	-0.4141	0.158
sqrt_Total.seq	0.3022	0.106
Spruce.share	0.1127	0.641
Others.share	-0.5338	0.128
Birch.share	0.1927	0.266
pH	0.393	0.103
N_deposition	0.2016	0.641
NC	0.3522	0.226
sqrt_stand_age	-0.3462	0.133

3.7 The genus *Xerocomellus*

Spruce ($\beta = 0.989$, $p = 0.0423$) (Figure 9A), other tree species ($\beta = 0.811$, $p = 0.0021$) (Figure 9B) and birch ($\beta = 0.689$, $p = 0.0332$) (Figure 9C), were significantly positively correlated with occurrence of the genus *Xerocomellus*. No significant effect was found for stand age, square-root transformed stand age, soil pH, nitrogen deposition and N:C ratio (Table B6). The model explained 35.2% of the deviance in *Xerocomellus* occurrence and had an adjusted R^2 of 0.146. Tree species composition strongly influenced Xerocomellus occurrence, with spruce share showing the strongest positive association, followed by other tree species share and birch share (Table B6).

Figure 9

Effect plots of spruce share (A), others share (B) and birch share (C) on genus Xerocomellus occurrence



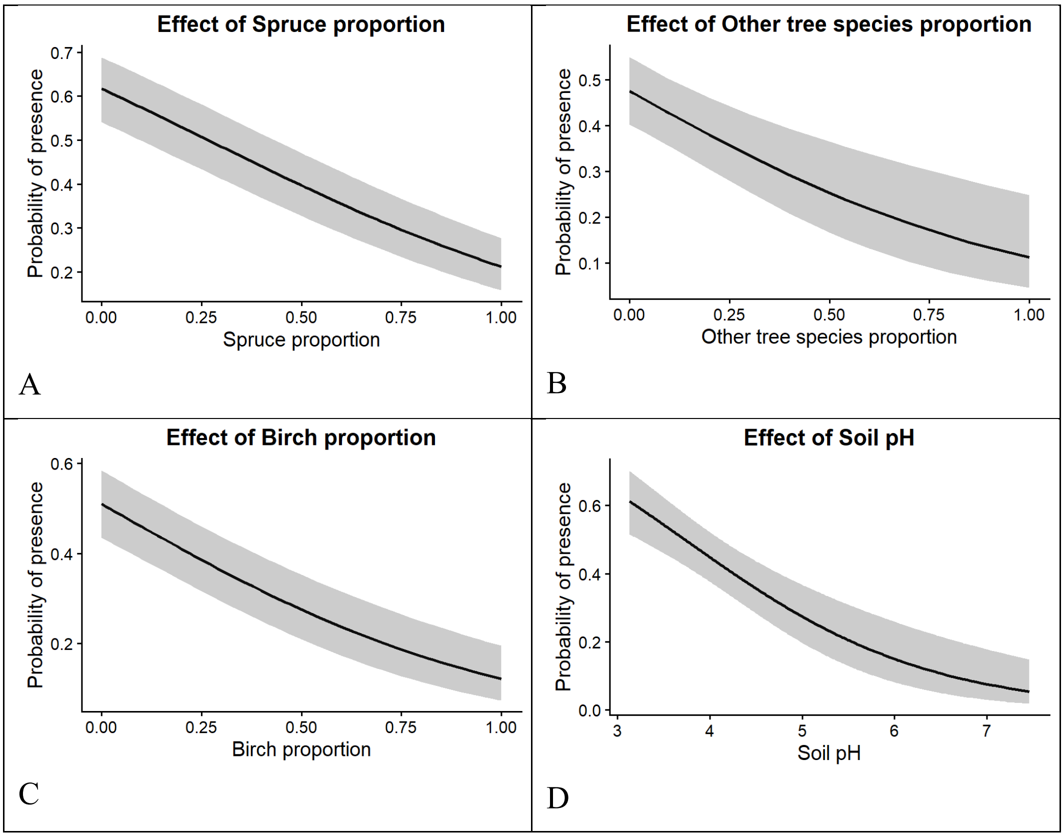
Note. The shaded area represents the 95% confidence interval.

3.8 *Suillus variegatus*

The occurrence of *S. variegatus* was positively associated with square-root transformed stand age ($\beta = 0.133$, $p = 0.0193$). Spruce ($\beta = -0.679$, $p < 0.001$) (Figure 10A), other tree species ($\beta = -0.378$, $p < 0.001$) (Figure 10B) and birch ($\beta = -0.435$, $p < 0.001$) (Figure 10C) all showed, together with soil pH ($\beta = -0.451$, $p < 0.001$) (Figure 10D), a significant negative correlation with the occurrence of this species. Stand age, nitrogen deposition and N:C ratio had no significant correlation with the occurrence of *S. variegatus* (Table B7). The model explained 24.5% of the deviance in *S. variegatus* occurrence and had an adjusted R^2 of 0.299.

Figure 10

Effect plots of spruce share (A), others share (B), birch share (C) and pH (D) on S. variegatus occurrence



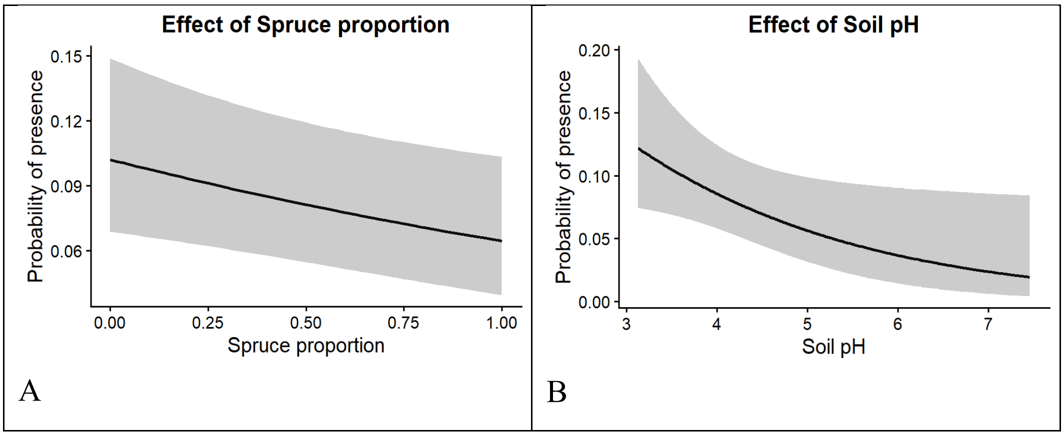
Note. The shaded area represents the 95% confidence interval.

3.9 *Suillus bovinus*

Spruce ($\beta = -0.190$, $p = 0.0216$) (Figure 11A) showed a negative association, together with soil pH ($\beta = -0.265$, $p = 0.0371$) (Figure 11B), with the occurrence of *S. bovinus*. For stand age, square-root stand age, other tree species, birch, nitrogen deposition and N:C ratio, no significant relation was found (Table B8). The model explained 6.5% of the deviance in *S. bovinus* occurrence and had an adjusted R^2 of 0.041.

Figure 11

Effect plots of spruce share (A) and pH (B) on S. bovinus occurrence



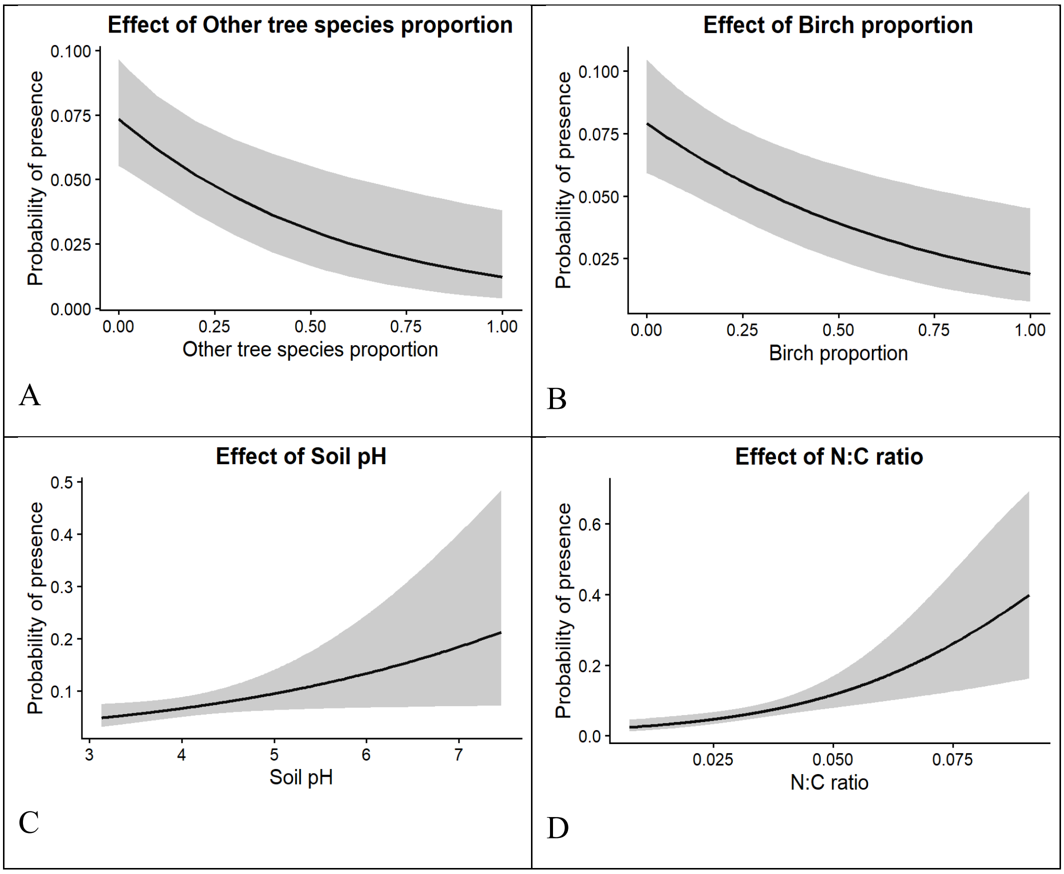
Note. The shaded area represents the 95% confidence interval.

3.10 *Suillus luteus*

Whilst spruce showed no significant effect on *S. luteus* occurrence, other tree species (β = -0.358, p = 0.0016) (Figure 12A) and birch (β = -0.322, p = 0.0014) (Figure 12B) did show a negative correlation. Soil pH (β = 0.226, p = 0.0364) (Figure 12C) and N:C ratio (β = 0.498, p < 0.001) (Figure 12D) showed a positive association with the occurrence of *S. luteus*. The other variables had no significant effect, including stand age, square-root stand age and nitrogen deposition (Table B9). The model explained 5.9% of the deviance in *S. luteus* occurrence and had an adjusted R^2 of 0.024.

Figure 12

Effect plots of others share (A) and birch share (B), pH (C) and N:C ratio (D) on S. luteus occurrence



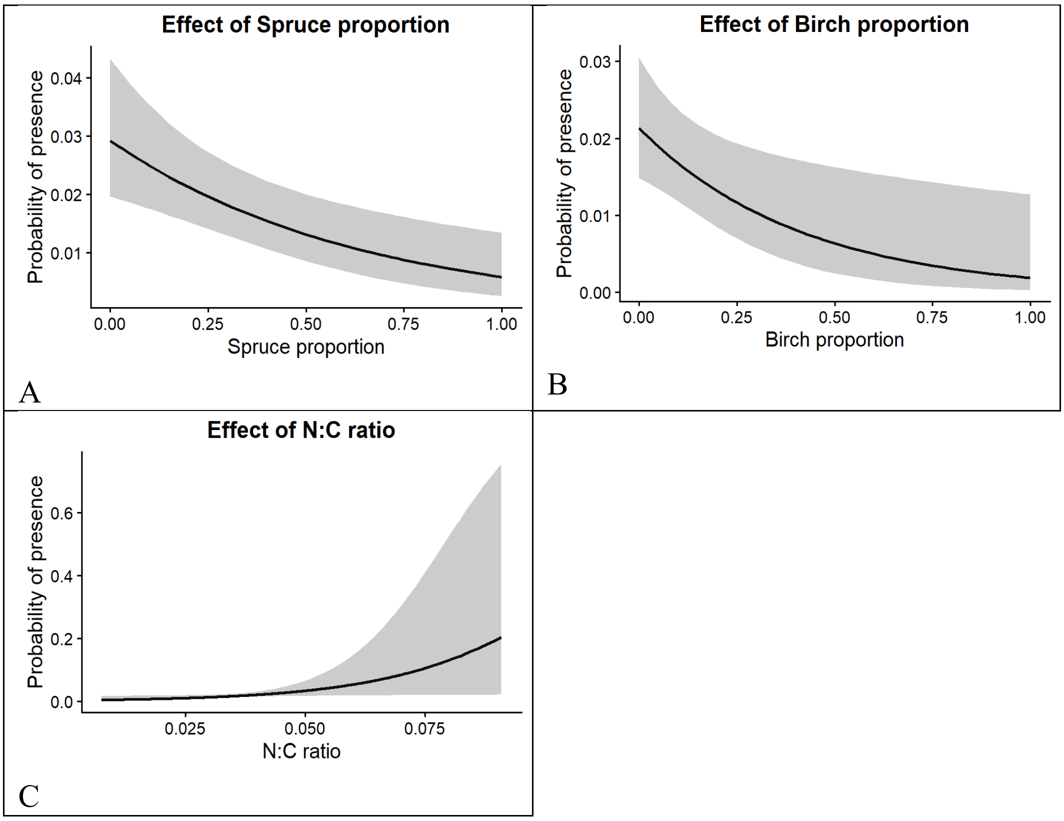
Note. The shaded area represents the 95% confidence interval.

3.11 *Suillus flavidus*

The occurrence of *S. flavidus* was negatively influenced by spruce (β = -0.619, *p* = 0.00136) (Figure 13A) and birch (β = -0.529, *p* = 0.0175) (Figure 13B), whilst the N:C ratio (β = 0.619, *p* = 0.0345) (Figure 13C) showed a positive relation. Stand age, square-root stand age, other tree species, soil pH and nitrogen deposition had no significant effect (Table B10). The model explained 6.1% of the deviance in *S. flavidus* occurrence and had an adjusted R^2 of 0.015.

Figure 13

Effect plots of spruce share (A), birch share (B) and N:C ratio (C) on S. flavidus occurrence



Note. The shaded area represents the 95% confidence interval.

3.12 Summary results

Table 2

Summary of significant relationships found in this study between variables and the occurrence of the Boletaceae family, genus Suillus and species within these groups in Swedish forests. Positive (+) and negative (-) symbols indicate significant positive or negative associations, identified by generalized additive models. Empty cells indicate no significant relationship ($p < 0.05$). The environmental variables include: stand age, square-root stand age, tree species composition (spruce, other trees and birch), soil pH, nitrogen deposition (N dep.), and nitrogen availability (N:C ratio).

Taxon / Variable	**Stand age**	**Sqrt. Stand age**	**Spruce**	**Other trees**	**Birch**	**pH**	**N dep.**	**N:C**
Suillus (genus)	+	+	-	-	-	-		
Boletaceae (family)	-		+		+	-		+
Boletus edulis			+					+
Leccinum	-	-	+		+			
Xerocomus								
Xerocomellus			+	+	+			
Suillus variegatus		+	-	-	-	-		
Suillus bovinus			-			-		
Suillus luteus				-	-	+		+
Suillus flavidus			-		-			+

4. Discussion

This study demonstrates that forest characteristics and soil properties have a significant influence on the presence of different species in the family Boletaceae and genus *Suillus*. Although no strong large-scale spatial clustering was observed for most taxa, environmental and stand-level variables are themselves spatially structured across Sweden. This suggests that the occurrence patterns of these ectomycorrhizal fungi are likely influenced by ecological gradients linked to both forest characteristics and geographic variation.

The hypothesis of this study, implying a significant association between forest composition and soil properties and the occurrence of Boletaceae and *Suillus* was partly supported by the results. Forest composition showed a clear association with the occurrence of members in this fungal community, as reflected by tree species composition and stand age. The same was found for soil properties indicated by the variables pH and N:C ratio. However, this was not the case for nitrogen deposition which contrasts with the hypothesis. A higher occurrence in mature stands was not found for all species, this is possibly the case for the genus *Suillus* but not for the Boletaceae family. Nutrient rich soils did seem to be a clear indication for higher occurrence of these species as positive associations were often found with N:C ratio.

Tree species composition appeared to be the strongest and most consistent predictor of fungal occurrence in the studied taxa. This was shown in previous literature, highlighting tree species composition as a primary indicator for the presence of different ectomycorrhizal fungal taxa (Rosinger et al., 2018), although it differed greatly between species which tree host they preferred. *B. edulis* showed a positive relation with spruce together with Boletaceae, *Leccinum* and *Xerocomellus*, which also showed a positive association with birch. However, all the species in the genus *Suillus* showed a negative association with these tree species. This indicates a broader host range for species of the Boletaceae family, which was also found in previous literature (Hall et al., 1998), compared to the more specialised host associations found in *Suillus* species. In current literature, *Suillus* is commonly associated with pine, as many species form specialized ectomycorrhizal relationships with this tree species (Liao et al., 2016). The negative association with spruce, other trees and birch found in this study for the genus *Suillus* as a whole and *S. variegatus* supports these findings. Pine was excluded from the statistical analysis in R, due to the strong negative correlation with spruce and used as reference. However, a negative effect of spruce, birch and other trees can thus be interpreted as a positive association with pine.

Significant effects of stand age were dominantly found in larger fungal communities. *Suillus* had a positive association with stand age and occurrence. This positive association means a higher occurrence in older stands, which was also suggested in previous literature, where *Suillus* occurred more frequently in mature stands (Rineau et al., 2015). Some *Suillus* species have, however, been frequently found in younger forests after disturbances (Visser, 1995). Boletaceae and *Leccinum* species showed negative relationships with stand age. The presence of Boletaceae in younger stands was previously found in a study of Hall et al. (1998). While in this study the Boletaceae family and *Leccinum* genus were more frequently found in younger stands, suggesting a possible preference for younger forests. The variation of occurrence for these species reflects the differences in colonization strategies and indicates a difference in ecological niches for these fungi of the Boletes order.

Higher soil pH was generally negatively correlated with fungal occurrence, suggesting a preference for acidic soils for this fungal community. Acidic soils are typically found in boreal forests in Sweden, demonstrating that these ectomycorrhizal fungi are adapted to low pH environments. *S. luteus* showed a positive relationship with pH, suggesting that some species may tolerate or prefer less acidic conditions. *S. luteus* was found in previous literature to grow best in soil with pH of 5 (Barros et al., 2006). While most soil samples in this study were acidic, pH values around 5 represented the less acidic conditions within the sampled soils.

Nitrogen availability is often reported to influence ectomycorrhizal communities heavily (Lilleskov & Bruns, 2001). However, in contrast to these expectations, nitrogen deposition did not show a significant effect on the occurrence of any of the studied taxa. A possible explanation for this result could be the strong correlation between latitude and nitrogen deposition, which were both included in the model, decreasing the accuracy of the results, since the effects of both could not be interpreted by the model. Nonetheless, the N:C ratio was positively correlated with many taxa, including Boletaceae, *B. edulis*, *S. luteus* and *S. flavidus*, suggesting that nutrient richness in the soil may play a role in the spatial distribution of these fungi.

No significant relationships were found for the occurrence of genus *Xerocomus*. This either indicates a broader ecological tolerance or could be the result of limited findings of these fungi. This genus was only found in 26 of the total 2277 samples, which may have been too few to find indicators for their presence. *B. edulis* showed a limited number of significant predictors, suggesting that its occurrence may be influenced by a broader ecological tolerance or by environmental variables not included in this study. The results of the genus *Suillus* should be interpreted with caution, since *S. variegatus* was found considerably more often in the samples than the other *Suillus* species included in this study. The results are likely to represent *S. variegatus*, rather than being fully representative of the genus as a whole.

Although several variables showed significant associations with fungal occurrence, the explanatory power of many models remained low. Several species had less than 10% proportion of deviance explained, suggesting that important variables were not included in the analyses. Factors such as soil moisture, soil texture, light availability and environmental variables could possibly explain the spatial distribution of these fungi more accurately. Therefore, the identified relationships should be interpreted as important associations rather than a complete explanation of the ecological niches of these fungi.

4.1 Forest management implications

The findings of this study suggest that forest management practices may indirectly affect Boletaceae and *Suillus* species in Swedish forests. Tree species composition appeared to be associated with their occurrence the most, with Boletaceae showing a broad host range and for some *Suillus* species a greater importance for pine dominated stands. Maintaining a variation of tree species, including some pine dominant patches within a stand could contribute to maintaining suitable habitat for these species.

Stand age also influenced their fungal occurrence patterns, with *Suillus* occurring more in older forests and Boletaceae and *Leccinum* appearing more frequently in younger stands. Different forest age classes in a stand may help sustain different ecological niches and support these fungal species.

Soil properties may play a role in maintaining suitable habitats, as several taxa showed positive associations with nutrient availability (N:C ratio), while many fungal species appeared to prefer acidic soil conditions. Although soil characteristics were not directly linked to specific forest management practices in this study, management influencing soil conditions may indirectly contribute to supporting these fungal communities.

Forest management strategies supporting these fungi could contribute to a stable habitat and occurrence of these mushrooms, while also maintaining recreational ecosystem services, including mushroom foraging opportunities in Swedish forests.

4.2 Limitations

4.2.1 DNA metabarcoding

For gathering the soil data, DNA metabarcoding based on ITS sequences was used, which is a widely used approach and makes large-scale assessment of fungal communities possible. Since this method relies on random sampling of environmental DNA, it reduces the probability of detecting rare species and even an extremely common one in Swedish forests called the Golden Chanterelle (*Cantharellus cibarius*) (Lindahl et al., 2026). This indicates that this method show some limitations, since mushrooms from the Boletes order could have been missed or could have been found in random samples of habitats where they are commonly not present. Another limitation of DNA metabarcoding is that it cannot distinguish between dead and living organisms, showing only the presence and not whether the fungal community is actually alive in this sample (Rossmann et al., 2021). The samples that were gathered in the forests were sent by regular mail to the lab, taking some samples up to 47 days, because of the remoteness of some sampling areas. The effect of transportation of soil samples used for the analysis of DNA metabarcoding has not been researched excessively, but some studies indicates that it affects the accuracy of fungal analyses (Clasen et al., 2020). In Lindahl et al. (2026), ”time until frozen” was included in statistical analyses, but had little influence. Suggesting that storage has stronger effects on relative abundance of different taxa than on presence-absence.

4.2.2 The genus Leccinum

The accuracy of the results of the genus *Leccinum* is limited by the used dataset in this study. The samples used in this paper were mostly conifer dominated, with few broadleaf dominated stands. This represents Sweden accurately, although it might result in less accurate results for the genus *Leccinum*. *Leccinum* occur mainly in broadleaf stands, as they are typically associated with broadleaf host trees and have a high host driven specialisation (Budau et al., 2026). Since there is little data included on their normal preferred habitat, the results should be interpreted with caution.

4.2.3 Xerocomus and Xerocomellus

Among the species in the genus *Xerocomus* and *Xerocomellus* there have been a lot of changes in taxonomy. First, all the species were in the genus *Xerocomus*, but many of these species were later placed in different genera, since Xerocomus was found to be polyphyletic. The species used in this study were identified according to the current taxonomic framework as outlined by Jaroslav Šutara, while we looked at *Xerocomus ferrugineus, Xerocomus subtomentosus* and *Xerocomellus pruinatus* (Šutara, 2008).

4.2.4 Data Processing and Statistical Analysis

With the usage of both R and Excel there are several methodological considerations. Excel was used for filtering the data of the entire order Boletes on taxonomic level, to sort it into different analytical levels (family, genus and species). This resulted in a clearer overview of the fungal data and allowed sub setting of relevant taxa such as the Boletaceae and *Suillus*.

The data of the fungal occurrence was made into a binary presence-absence variable, which was in line with the focus of the research on distribution patterns instead of abundance. This binary approach results in a loss of ecological detail, such as relative abundance and detection intensity between samples. However, it reduced the noise associated with sequencing depth and detection variability in soil DNA datasets.

The samples that are used in this paper from the Swedish Forest Soil Inventory are sampled throughout Sweden, with a higher intensity in the South. The reason for the higher intensity of sampling in the south is a greater diversity in the forests compared to northern Sweden. This results in an overrepresentation of southern Sweden in the dataset, which should be considered when interpreting the results. Because some samples were collected in close proximity to each other, it was important to use Generalized Additive Models (GAM). By making use of the smoother for longitude and latitude the spatial autocorrelation was partly accounted for, ignoring spatial structure would otherwise lead to inaccurate results. The GAM also accounts for the ecological relationships between fungal occurrence and forest characteristics, which are often non-linear.

Since the forest characteristics are measured on different scales it could result in the models making certain characteristics more important. The z-standardization of the variables accounted for this scale difference and made it easier to compare the results and aided in the accuracy of the models.

To identify strongly correlated variables, a correlation matrix was used, with a limit of 0.7. This limit was chosen with the use of a paper from J. de Winter reviewing multicollinearity in statistical analysis, in which the limit is stated by different researchers from >0.7 (Dormann et al., 2013) up to 0.9 (Mason & Perreault, 1991) (De Winter, 2025). This value was chosen because it was the lowest value, resulting in the most reliable results. When characteristics were correlated above this threshold, they were separated into different models, which was the case for stand age and square-root stand age. By separating these variables, instability in parameter estimation was prevented and allowed comparison of alternative ecological hypotheses of linear versus non-linear stand age effect. Accounting for the hypothesis of larger changes in young forests compared to older forests. While latitude and nitrogen deposition were also correlated above the 0.7 threshold, both variables were retained in the model because latitude was needed to account for spatial autocorrelation, while nitrogen deposition represented a separate environmental variable with potential ecological effects on ectomycorrhizal fungi. Overall, strong correlations were addressed by separating variables into different models, some remaining weaker correlations between forest characteristics remained in the models such as stand age, pH and

N:C ratio (Lindahl et al., 2026), making it more difficult to interpret their individual effects on the occurrence of fungi. This means the results should be interpreted with some caution, as some variables overlap and explain the same patterns in the data.

The models per taxonomic selection were chosen with the use of Akaike's Information Criterion (AIC), which gave an objective way to compare models and see the contribution of individual forest characteristics. While AIC is often used in statistical analysis, it does not account for the most ecologically significant model, creating the risk that the chosen model is not the most ecologically meaningful. To prevent this risk, the model excluding square-root stand age, but including all the other variables, was used for the results, since the AIC did not differ greatly between the other models. The models were evaluated with the use of DHARMa and GAM-specific checks. This made assessment of residual patterns, dispersion, uniformity and outliers possible, increasing the chances of reliable results. The concurvity check improved this reliability, but despite these efforts, some limitations remain. Not all environmental variables were calculated and accounted for in these samples, while these could be correlated with the forest characteristics that were included in this paper. With future inclusion of other environmental variables, it may improve the model performance and increase the accuracy of the results. Increasing our understanding of the effects of forest characteristics on fungal presence.

In conclusion, despite these caveats, this study suggests that forest characteristics such as tree species composition, stand age and soil properties are associated with Boletaceae and *Suillus* occurrence in Swedish forests. While some expected effects, such as nitrogen deposition, were not found, this may be related to correlations between environmental variables and methodological limitations. The relatively low proportion of deviance explained by several models suggests that additional environmental variables may influence fungal occurrence. Future research including more environmental variables and samples could help to further clarify these relationships between environmental variables and improve our understanding of preferred habitats of ectomycorrhizal communities.

Nevertheless, the findings of this study contribute to a better understanding of the ecological niches of Boletaceae and Suillus, with potential future use for forest management and recreational foraging. The results suggest that tree species composition, stand age and soil properties may play an important role in maintaining ectomycorrhizal fungal communities in Swedish forests. Maintaining variation in forest composition and stand structure could therefore contribute to the conservation of different fungal taxa.

References

Abarenkov, K., Nilsson, R. H., Larsson, K., Taylor, A. F. S., May, T. W., Frøslev, T. G., Pawlowska, J., Lindahl, B., Põldmaa, K., Truong, C., Vu, D., Hosoya, T., Niskanen, T., Piirmann, T., Ivanov, F., Zirk, A., Peterson, M., Cheeke, T. E., Ishigami, Y., . . . Kõljalg, U. (2023). The UNITE database for molecular identification and taxonomic communication of fungi and other eukaryotes: sequences, taxa and classifications reconsidered. *Nucleic Acids Research*, 52(D1), D791–D797. https://doi.org/10.1093/nar/gkad1039

Ágoston, C., Buvár, Á., Dúll, A., Szabó, Z. Á., & Varga, A. (2024). Complex pathways from nature relatedness and knowledge to pro-environmental behavior through eco-emotions. *Journal of Cleaner Production*, 468, 143037. https://doi.org/10.1016/j.jclepro.2024.143037

Andersson, M., Knutsson, T., & Krikorev, M. (2016). Djävulssopp, falsk djävulssopp och deras djävulskt lika dubbelgångare. *SLU Publication Database (SLUpub)*. https://publications.slu.se/?file=publ/show&id=80761

Ayala-Vásquez, O., Martínez-Reyes, M., Pérez-Moreno, J., Martínez-González, C. R., Pinzón, J. P., De La Fuente, J. I., Castro-Rivera, R., García-Jiménez, J., Balbuena-Carrasco, S., Ramírez-Carbajal, E., & Yu, F. (2023). Five new species of Aureoboletus and chalciporus (Boletaceae, boletales) and their ethnomycological aspects. *Journal of Fungi*, 9(10), 1041. https://doi.org/10.3390/jof9101041

Barros, L., Baptista, P., & Ferreira, I. C. (2006). Influence of the culture medium and pH on the growth of saprobic and ectomycorrhizal mushroom mycelia. *Biblioteca Digital Do IPB (Instituto Politecnico de Braganca).* http://hdl.handle.net/10198/824

Budau, R., Vicas, S. I., Bei, M. F., Dejeu, D. A., Dinca, L., & Chira, D. (2026). The genus Leccinum: Global advances in taxonomy, ecology, nutritional value, and environmental significance. *Journal of Fungi*, 12(1), 70. https://doi.org/10.3390/jof12010070

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). Springer. https://doi.org/10.1007/b97636

Clasen, L. A., Detheridge, A. P., Scullion, J., & Griffith, G. W. (2020). Soil stabilisation for DNA metabarcoding of plants and fungi. Implications for sampling at remote locations or via third-parties. *Metabarcoding and Metagenomics, 4*. https://doi.org/10.3897/mbmg.4.58365

Cory, N., Nilsson, P., Fridman, J., & Kempe, G. (2013). *Skogsdata 2013. SLU:S Publikationsdatabas (SLUpub).* https://publications.slu.se/?file=publ/show&id=51713&lang=se

Dahlberg, A. (1997). Population ecology of *Suillus variegatus* in old Swedish Scots pine forests. *Mycological Research, 101*(1), 47–54. https://doi.org/10.1017/s0953756296002110

De Winter, J. (2025). *Multicollinearity in Statistical Modeling: A review*. ResearchGate. https://www.researchgate.net/publication/395360487_Multicollinearity_in_Statistical_Modeling_A_Review

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2012). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36(1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Edgar, R. C. (2010). Search and clustering orders of magnitude faster than BLAST. *Bioinformatics, 26*(19), 2460–2461. https://doi.org/10.1093/bioinformatics/btq461

Egli, S., Peter, M., Buser, C., Stahel, W., & Ayer, F. (2005). Mushroom picking does not impair future harvests – results of a long-term study in Switzerland. *Biological Conservation, 129*(2), 271–276. https://doi.org/10.1016/j.biocon.2005.10.042

First Nature. (n.d.). *Suillus luteus (Slippery Jack mushroom).* Retrieved June 4, 2026, from https://www.first-nature.com/fungi/suillus-luteus.php

Fjelde, M., Kauserud, H., Halvorsen, R., Nilsen, C., Konestabo, H., Skrede, I., & Maurice, S. (2025). *Ecosystem sequencing of the boreal forest mycobiome reveals high substrate specificity*. Research Square. https://doi.org/10.21203/rs.3.rs-7774568/v1

Fridman, J., Holm, S., Nilsson, M., Nilsson, P., Ringvall, A., & Ståhl, G. (2014). Adapting National Forest Inventories to changing requirements – the case of the Swedish National Forest Inventory at the turn of the 20th century. *Silva Fennica, 48*(3). https://doi.org/10.14214/sf.1095

Giftinformationscentralen. (n.d.). *Giftiga svampar*. Retrieved June 4, 2026, from https://giftinformation.se/svampregister/

Hall, I. R., Lyon, A. J. E., Wang, Y., & Sinclair, L. (1998). Ectomycorrhizal fungi with edible fruiting bodies 2.Boletus edulis. *Economic Botany, 52*(1), 44–56. https://doi.org/10.1007/bf02861294

Hartig, F. (2022). *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models* (R package version 0.4.6) [Computer software]. https://doi.org/10.32614/cran.package.dharma

Ihrmark, K., Bödeker, I. T., Cruz-Martinez, K., Friberg, H., Kubartova, A., Schenck, J., Strid, Y., Stenlid, J., Brandström-Durling, M., Clemmensen, K. E., & Lindahl, B. D. (2012). New primers to amplify the fungal ITS2 region - evaluation by 454-sequencing of artificial and natural communities. *FEMS Microbiology Ecology, 82*(3), 666–677. https://doi.org/10.1111/j.1574-6941.2012.01437.x

Jenny. (2025, October 2). *All about boletes: An introduction to bolete foraging and identification* - Mushroom appreciation. Mushroom Appreciation. https://www.mushroom-appreciation.com/all-about-boletes.html

Judžentienė, A., & Šarlauskas, J. (2025). Comparative Research of Antioxidant, Antimicrobial, Antiprotozoal and Cytotoxic Activities of Edible Suillus sp. Fruiting Body Extracts. *Foods, 14*(7), 1130. https://doi.org/10.3390/foods14071130

Kõljalg, U., Nilsson, R. H., Abarenkov, K., Tedersoo, L., Taylor, A. F. S., Bahram, M., Bates, S. T., Bruns, T. D., Bengtsson-Palme, J., Callaghan, T. M., Douglas, B., Drenkhan, T., Eberhardt, U., Dueñas, M., Grebenc, T., Griffith, G. W., Hartmann, M., Kirk, P. M., Kohout, P., Larsson, K. (2013). Towards a unified paradigm for sequence-based identification of fungi. *Molecular Ecology, 22*(21), 5271–5277. https://doi.org/10.1111/mec.12481

Konsue, N., Ketnawa, S., & Qin, S. (2025). Indigenous Wild Edible Mushrooms: Unveiling the chemical compositions and health impacts. *Foods, 14*(13), 2331. https://doi.org/10.3390/foods14132331

Kumar, A., Devi, R., Dhalaria, R., Tapwal, A., Verma, R., Rashid, S., Elossaily, G. M., Khan, K. A., Chen, K., & Verma, T. (2024). Nutritional, Nutraceutical, and Medicinal Potential of Cantharellus cibarius Fr.: A Comprehensive Review. *Food Science & Nutrition, 13*(1), e4641. https://doi.org/10.1002/fsn3.4641

Liao, H., Chen, Y., & Vilgalys, R. (2016). Metatranscriptomic Study of Common and Host-Specific Patterns of Gene Expression between Pines and Their Symbiotic Ectomycorrhizal Fungi in the Genus Suillus. *PLoS Genetics, 12*(10), e1006348. https://doi.org/10.1371/journal.pgen.1006348

Lilleskov, E. A., & Bruns, T. D. (2001). Nitrogen and ectomycorrhizal fungal communities: What we know, what we need to know. *The New Phytologist*, 149(2), 156–158. https://www.jstor.org/stable/3186167

Lindahl, B. D., Clemmensen, K. E., Stendahl, J., & Dahlberg, A. (2026). Long-term effects of clear-cutting forestry on ectomycorrhizal fungi in boreal forest. *New Phytologist*. https://doi.org/10.1111/nph.71165

Lofgren, L., Nguyen, N. H., Kennedy, P. G., Pérez-Pazos, E., Fletcher, J., Liao, H., Wang, H., Zhang, K., Ruytinx, J., Smith, A. H., Ke, Y., Van T Cotter, H., Engwall, E., Hameed, K. M., Vilgalys, R., & Branco, S. (2024). Suillus: an emerging model for the study of ectomycorrhizal ecology and evolution. *New Phytologist*, 242(4), 1448–1475. https://doi.org/10.1111/nph.19700

Máliš, F., Ujházy, K., Hederová, L., Ujházyová, M., Csölleová, L., Coomes, D. A., & Zellweger, F. (2023). Microclimate variation and recovery time in managed and old-growth temperate forests. *Agricultural and Forest Meteorology, 342*, 109722. https://doi.org/10.1016/j.agrformet.2023.109722

Mason, C. H., & Perreault, W. D. (1991). Collinearity, power, and interpretation of multiple regression analysis. *Journal of Marketing Research, 28*(3), 268–280. https://doi.org/10.1177/002224379102800302

Massicotte, P., & South, A. (2026). *rnaturalearth: World map data from Natural Earth* (R package version 1.2.0.9000) [Computer software]. https://docs.ropensci.org/rnaturalearth/

Mielke, L. A. (2022). *Mycorrhizal guild functions and conservational values in boreal forests* [Doctoral dissertation, Swedish University of Agricultural Sciences]. *Acta Universitatis Agriculturae Sueciae*. https://doi.org/10.54612/a.75ms1inoet

Niedzielski, P., Siwulski, M., Szostek, M., Budka, A., Budzyńska, S., Krzesłowska, M., Kalač, P., & Mleczek, M. (2024). Mineral composition variation in Boletales mushrooms—indication of soil properties and taxonomic influence. *Environmental Science and Pollution Research, 31*(28), 41137–41154. https://doi.org/10.1007/s11356-024-33916-4

Nuhn, M. E., Binder, M., Taylor, A. F., Halling, R. E., & Hibbett, D. S. (2013). Phylogenetic overview of the Boletineae. *Fungal Biology, 117*(7–8), 479–511. https://doi.org/10.1016/j.funbio.2013.04.008

Odin, H., Eriksson, B., & Perttu, K. (1983). *Temperature climate maps for Swedish forestry.* https://agris.fao.org/search/en/providers/122495/records/64712745804410faf61efbae

Olsson, P. A., Münzenberger, B., Mahmood, S., & Erland, S. (2000). Molecular and anatomical evidence for a three-way association between *Pinus sylvestris* and the ectomycorrhizal fungi *Suillus bovinus* and *Gomphidius roseus*. *Mycological Research, 104*(11), 1372–1378. https://doi.org/10.1017/s0953756200002823

Patocka, J. (2018). Bolesatine, a toxic protein from the mushroom *rubroboletus satanas*. *Military Medical Science Letters, 87*(1), 14-20. https://mmsl.cz/pdfs/mms/2018/01/03.pdf

Peay, K. G., Kennedy, P. G., & Talbot, J. M. (2016). Dimensions of biodiversity in the Earth mycobiome. *Nature Reviews Microbiology, 14*(7), 434–447. https://doi.org/10.1038/nrmicro.2016.59

Pebesma, E., & Bivand, R. (2023). *Spatial data science: With applications in R*. CRC Press. https://doi.org/10.1201/9780429459016

Pickles, B. J., Genney, D. R., Potts, J. M., Lennon, J. J., Anderson, I. C., & Alexander, I. J. (2010). Spatial and temporal ecology of Scots pine ectomycorrhizas. *New Phytologist*, 186(3), 755–768. https://doi.org/10.1111/j.1469-8137.2010.03204.x

Prager, M. H., & Goos, R. D. (1984). A case of mushroom poisoning from *Suillus luteus*. *Mycopathologia, 85*(3), 175–176. https://doi.org/10.1007/bf00440949

Procházka, P., Soukupová, J., Mullen, K. J., Tomšík, K., & Čábelková, I. (2023). Wild Mushrooms as a Source of Protein: A Case Study from Central Europe, Especially the Czech Republic. *Foods, 12*(5), 934. https://doi.org/10.3390/foods12050934

Rineau, F., Stas, J., Nguyen, N. H., Kuyper, T. W., Carleer, R., Vangronsveld, J., Colpaert, J. V., & Kennedy, P. G. (2015). Ectomycorrhizal fungal protein degradation ability predicted by soil organic nitrogen availability. *Applied and*

Environmental Microbiology, 82(5), 1391–1400. https://doi.org/10.1128/aem.03191-15

Rosinger, C., Sandén, H., Matthews, B., Mayer, M., & Godbold, D. L. (2018). Patterns in ectomycorrhizal diversity, community composition, and exploration types in European beech, pine, and spruce forests. *Forests, 9*(8), 445. https://doi.org/10.3390/f9080445

Rossmann, S., Lysøe, E., Skogen, M., Talgø, V., & Brurberg, M. B. (2021). DNA metabarcoding reveals broad presence of plant pathogenic oomycetes in soil from internationally traded plants. *Frontiers in Microbiology, 12*, 637068. https://doi.org/10.3389/fmicb.2021.637068

Schunko, C., & Brandner, A. (2021). Urban nature at the fingertips: Investigating wild food foraging to enable nature interactions of urban dwellers. *AMBIO, 51*(5), 1168–1178. https://doi.org/10.1007/s13280-021-01648-1

SLU Artdatabanken (2026). *Artfakta: djävulssopp (Rubroboletus satanas).* https://artfakta.se/taxa/161

Stasińska, M. (2025). Suillus flavidus, a Peatland-Associated Mycorrhizal Fungus in Poland: Ecology, Distribution, Conservation Threats, and Sustainability Considerations. *Sustainability, 17*(18), 8244. https://doi.org/10.3390/su17188244

Šutara, J. (2008). Xerocomus s. l. in the light of the present state of knowledge. *Czech Mycology*, 60(1), 29–62. https://doi.org/10.33585/cmy.60104

Svanberg, I., & Lindh, H. (2019). Mushroom hunting and consumption in twenty-first century post-industrial Sweden. *Journal of Ethnobiology and Ethnomedicine*, *15*(1), 42. https://doi.org/10.1186/s13002-019-0318-z

Svanberg, I., Løvaas, M., & Ståhlberg, S. (2025). How funnel chanterelle (Craterellus tubaeformis) became an urban forager favorite in Scandinavia. *Journal of Ethnobiology and Ethnomedicine, 21*(1), 37. https://doi.org/10.1186/s13002-025-00789-x

Visser, S. (1995). Ectomycorrhizal fungal succession in jack pine stands following wildfire. *New Phytologist*, *129*(3), 389–401. https://doi.org/10.1111/j.1469-8137.1995.tb04309.x

Wei, T., & Simko, V. (2021). *corrplot: Visualization of a correlation matrix* (R package version 0.92) [Computer software]. https://www.scirp.org/reference/referencespapers?referenceid=3377798

Wickham, H., & Bryan, J. (2023). *readxl: Read Excel files* (R package version 1.4.3) [Computer software]. https://www.scirp.org/reference/referencespapers?referenceid=2761680

Wickham, H., Chang, W., Henry, L., Pedersen, T. L., Takahashi, K., Wilke, C., Woo, K., Yutani, H., Dunnington, D., & van den Brand, T. (2024). *ggplot2: Create elegant data visualisations using the grammar of graphics* (R package version 3.5.1) [Computer software]. https://www.scirp.org/reference/referencespapers?referenceid=3937583

Wickham, H., François, R., Henry, L., Müller, K., & Vaughan, D. (2023). *dplyr: A grammar of data manipulation* (R package version 1.1.4) [Computer software]. https://www.scirp.org/reference/referencespapers?referenceid=3610085

Wood, S. N. (2017). *Generalized additive models: An introduction with R* (2nd ed.). CRC Press. https://doi.org/10.1201/9781315370279

Wu, G., Li, Y., Zhu, X., Zhao, K., Han, L., Cui, Y., Li, F., Xu, J., & Yang, Z. L. (2016). One hundred noteworthy boletes from China. *Fungal Diversity*, *81*(1), 25–188. https://doi.org/10.1007/s13225-016-0375-8

Appendix A

Figure A1

Spatial distribution of the genus Suillus across Sweden based on soil DNA samples from the Swedish Forest Soil Inventory. Red dots indicate samples where Suillus was detected, showing visually no clear signs of clustering. Genus Suillus was found in 1220 of the 2277 samples.

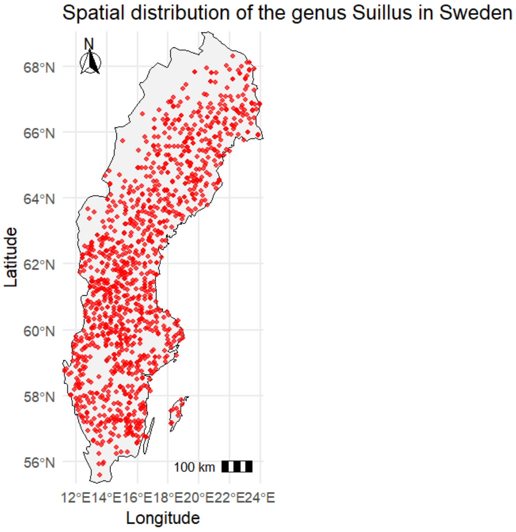


Figure A2

Spatial distribution of S. luteus across Sweden based on soil DNA samples from the Swedish Forest Soil Inventory. Red dots indicate samples where S. luteus was detected, showing visually no clear signs of clustering. S.luteus was found in 164 of the 2277 samples.

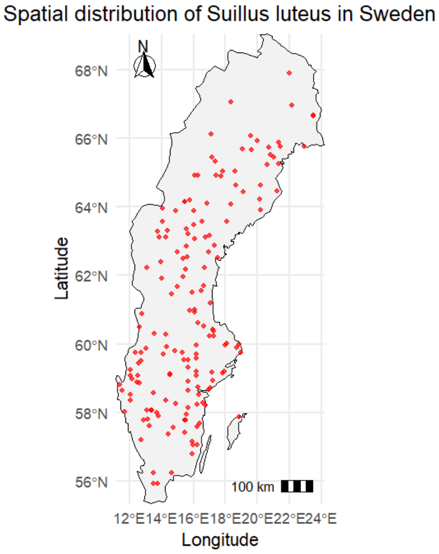


Figure A3

Spatial distribution of S. flavidus across Sweden based on soil DNA samples from the Swedish Forest Soil Inventory. Red dots indicate samples where S. flavidus was detected, showing visually no clear signs of clustering. S. flavidus was found in 50 of the 2277 samples.

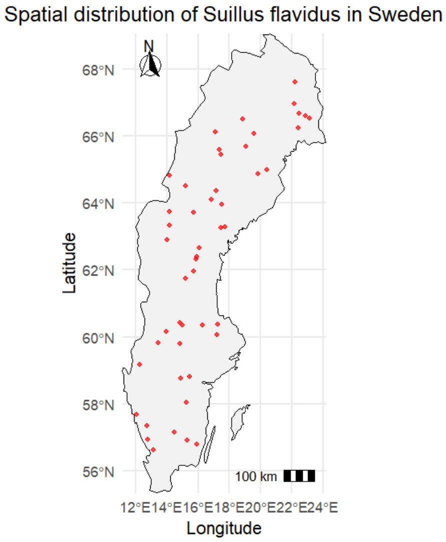


Figure A4

Spatial distribution of S. variegatus across Sweden based on soil DNA samples from the Swedish Forest Soil Inventory. Red dots indicate samples where S. variegatus was detected, showing visually no clear signs of clustering. S. variegatus was found in 1013 of the 2277 samples.

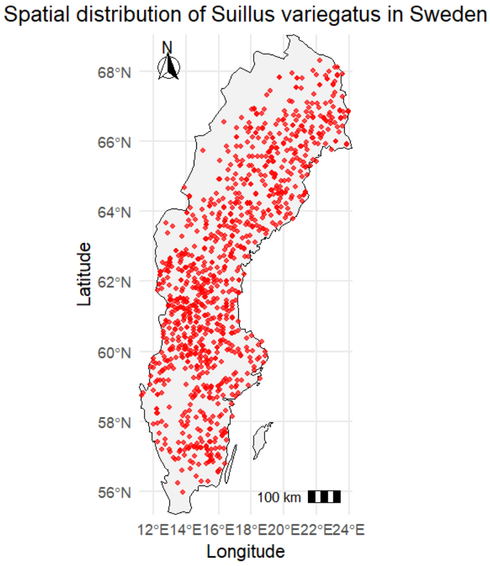


Figure A5

Spatial distribution of the family Boletaceae across Sweden based on soil DNA samples from the Swedish Forest Soil Inventory. Red dots indicate samples where Boletaceae was detected, showing visually no clear signs of clustering. The family Boletaceae was found in 706 of the 2277 samples.

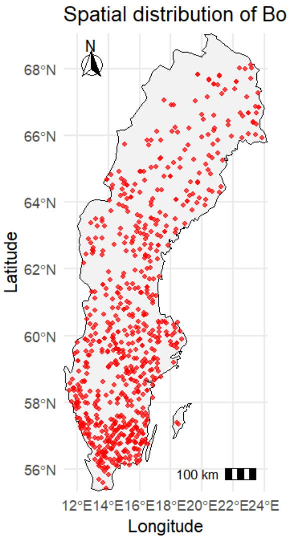
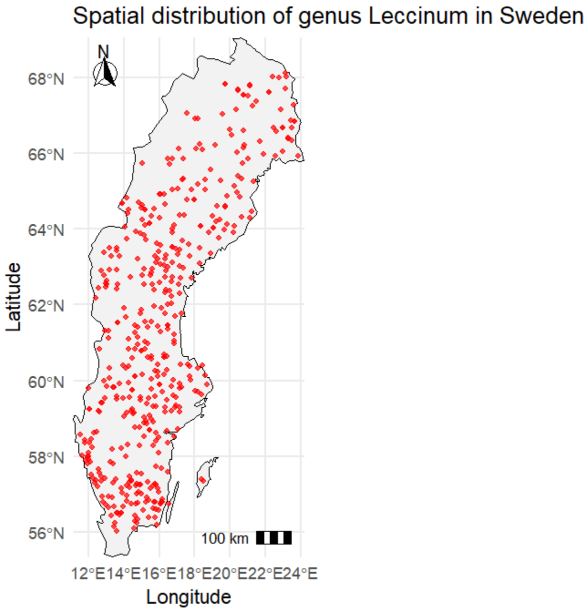


Figure A6

Spatial distribution of the genus Leccinum across Sweden based on soil DNA samples from the Swedish Forest Soil Inventory. Red dots indicate samples where Leccinum was detected, showing visually no clear signs of clustering. Genus Leccinum was found in 454 of the 2277 samples.



Appendix B

Table B1

Results of the generalized additive model (GAM) for occurrence of the genus Suillus, showing estimated coefficients, standard errors, z-values, p-values and significance of the explanatory variables. Significant relationships (p < 0.05) are indicated with "X".

***Suillus* genus variables**	**Estimate**	**Std. Error**	**Z value**	**P value**	**Significance**
(Intercept)	0.182	0.04841	3.758	<0.001	X
stand_age_raw	0.114	0.05508	2.067	0.039	X
sqrt_Total.seq	0.381	0.05154	7.400	<0.001	X
Spruce.share	-0.720	0.0563	-12.791	<0.001	X
Others.share	-0.348	0.06748	-5.164	<0.001	X
Birch.share	-0.501	0.0542	-9.251	<0.001	X
pH	-0.163	0.07582	-2.152	0.031	X
N_deposition	0.035	0.14797	0.238	0.812	
NC	0.112	0.09317	1.210	0.226	
sqrt_stand_age	0.131	0.05342	2.453	0.0142	X

Table B2

Results of the generalized additive model (GAM) for occurrence of the Boletaceae family, showing estimated coefficients, standard errors, z-values, p-values and significance of the explanatory variables. Significant relationships (p < 0.05) are indicated with "X".

Boletaceae family variables	**Estimate**	**Std.Error**	**z value**	**P value**	**Significance**
(Intercept)	-0.89435	0.04942	-18.097	<0.001	X
stand_age_raw	-0.16562	0.05715	-2.898	0.004	X
sqrt_Total.seq	0.3257	0.04907	6.637	<0.001	X
Spruce.share	0.34802	0.05632	6.179	<0.001	X
Others.share	0.07748	0.06265	1.237	0.21619	
Birch.share	0.3807	0.0507	7.509	<0.001	X
pH	-0.17678	0.07523	-2.350	0.019	X
N_deposition	0.14257	0.12567	1.134	0.257	
NC	0.21551	0.08951	2.408	0.016	X
sqrt_stand_age	-0.08836	0.05306	-1.665	0.096	

Table B3

Results of the generalized additive model (GAM) for occurrence of B. edulis, showing estimated coefficients, standard errors, z-values, p-values and significance of the explanatory variables. Significant relationships ($p < 0.05$) are indicated with "X".

Boletus edulis **variables**	**Estimate**	**Std.Error**	**z value**	**P value**	**Significance**
(Intercept)	-3.077001	0.143224	-21.484	<0.001	X
stand_age_raw	-0.167365	0.11408	-1.467	0.142	
sqrt_Total.seq	0.338632	0.078179	4.332	<0.001	X
Spruce.share	0.283724	0.09467	2.997	0.003	X
Others.share	0.001245	0.097771	0.013	0.989	
Birch.share	-0.042843	0.098092	-0.437	0.662	
pH	-0.234942	0.12804	-1.835	0.067	
N_deposition	0.300548	0.215051	1.398	0.162	
NC	0.28155	0.141998	1.983	0.047	X
sqrt_stand_age	-0.085728	0.093942	-0.913	0.361	

Table B4

Results of the generalized additive model (GAM) for occurrence of the genus Leccinum, showing estimated coefficients, standard errors, z-values, p-values and significance of the explanatory variables. Significant relationships ($p < 0.05$) are indicated with "X".

Leccinum **genus variables**	**Estimate**	**Std.Error**	**z value**	**P value**	**Significance**
(Intercept)	-1.52127	0.05826	-26.111	<0.001	X
stand_age_raw	-0.21388	0.06466	-3.308	<0.001	X
sqrt_Total.seq	0.2853	0.05454	5.231	<0.001	X
Spruce.share	0.26948	0.06583	4.094	<0.001	X
Others.share	0.0445	0.08001	0.556	0.578	
Birch.share	0.54109	0.05367	10.083	<0.001	X
pH	-0.06371	0.08501	-0.75	0.454	
N_deposition	0.13348	0.12991	1.027	0.304	
NC	0.11688	0.10089	1.158	0.247	
sqrt_stand_age	-0.16197	0.0603	-2.686	0.00723	X

Table B5

Results of the generalized additive model (GAM) for occurrence of the genus Xerocomus, showing estimated coefficients, standard errors, z-values, p-values and significance of the explanatory variables. Significant relationships ($p < 0.05$) are indicated with "X", although no significant relationships were found.

***Xerocomus* genus variables**	**Estimate**	**Std.Error**	**z value**	**P value**
(Intercept)	-4.9575	0.2813	-17.621	<0.001
stand_age_raw	-0.4141	0.2934	-1.412	0.158
sqrt_Total.seq	0.3022	0.1867	1.619	0.106
Spruce.share	0.1127	0.242	0.466	0.641
Others.share	-0.5338	0.351	-1.521	0.128
Birch.share	0.1927	0.1732	1.113	0.266
pH	0.393	0.2409	1.631	0.103
N_deposition	0.2016	0.4322	0.466	0.641
NC	0.3522	0.2906	1.212	0.226
sqrt_stand_age	-0.3462	0.2306	-1.502	0.133

Table B6

Results of the generalized additive model (GAM) for occurrence of the genus Xerocomellus, showing estimated coefficients, standard errors, z-values, p-values and significance of the explanatory variables. Significant relationships ($p < 0.05$) are indicated with "X".

***Xerocomellus* genus variables**	**Estimate**	**Std. Error**	**z value**	**P value**	**Significance**
(Intercept)	-7.572223	0.88135	-8.592	<0.001	X
stand_age_raw	0.522679	0.29752	1.757	0.078	
sqrt_Total.seq	0.353816	0.21660	1.633	0.102	
Spruce.share	0.988742	0.48680	2.031	0.042	X
Others.share	0.810896	0.26409	3.071	0.002	X
Birch.share	0.689421	0.32372	2.130	0.033	X
pH	-0.088236	0.25310	-0.349	0.727	
N_deposition	-0.119152	0.51111	-0.233	0.816	
NC	-0.004917	0.33664	-0.015	0.988	
sqrt_stand_age	0.481671	0.25345	1.900	0.057	

Table B7

Results of the generalized additive model (GAM) for occurrence of S. variegatus, showing estimated coefficients, standard errors, z-values, p-values and significance of the explanatory variables. Significant relationships (p < 0.05) are indicated with "X".

***Suillus variegatus* variables**	**Estimate**	**Std. Error**	**z value**	**P value**	**Significance**
(Intercept)	-0.3534	0.05278	-6.695	<0.001	X
stand_age_raw	0.09794	0.0569	1.721	0.085	
sqrt_Total.seq	0.35953	0.05277	6.813	<0.001	X
Spruce.share	-0.67873	0.05816	-11.669	<0.001	X
Others.share	-0.37793	0.09323	-4.054	<0.001	X
Birch.share	-0.43482	0.05875	-7.402	<0.001	X
pH	-0.45093	0.09235	-4.883	<0.001	X
N_deposition	-0.10544	0.16689	-0.632	0.527	
NC	0.04832	0.1084	0.446	0.655	
sqrt_stand_age	0.13283	0.05678	2.340	0.019	X

Table B8

Results of the generalized additive model (GAM) for occurrence of S. bovinus, showing estimated coefficients, standard errors, z-values, p-values and significance of the explanatory variables. Significant relationships (p < 0.05) are indicated with "X".

***Suillus bovinus* variables**	**Estimate**	**Std. Error**	**z value**	**P value**	**Significance**
(Intercept)	-2.305	0.078	-29.745	<0.001	X
stand_age_raw	0.009	0.08102	0.107	0.914	
sqrt_Total.seq	0.311	0.06734	4.623	<0.001	X
Spruce.share	-0.189	0.0825	-2.298	0.021	X
Others.share	-0.097	0.10259	-0.952	0.341	
Birch.share	-0.168	0.08865	-1.892	0.058	
pH	-0.265	0.12721	-2.084	0.0371	X
N_deposition	0.296	0.21047	1.407	0.159	
NC	0.260	0.14211	1.835	0.066	
sqrt_stand_age	0.004	0.07873	0.048	0.961	

Table B9

Results of the generalized additive model (GAM) for occurrence of S. luteus, showing estimated coefficients, standard errors, z-values, p-values and significance of the explanatory variables. Significant relationships (p < 0.05) are indicated with "X".

Suillus luteus **variables**	**Estimate**	**Std. Error**	**z value**	**P value**	**Significance**
(Intercept)	-2.73405	0.09285	-29.446	<0.001	X
stand_age_raw	-0.06352	0.09405	-0.675	0.499	
sqrt_Total.seq	0.33016	0.07845	4.208	<0.001	X
Spruce.share	-0.17258	0.09338	-1.848	0.064	
Others.share	-0.35759	0.11302	-3.164	0.002	X
Birch.share	-0.32228	0.10086	-3.195	0.001	X
pH	0.22599	0.10802	2.092	0.036	X
N_deposition	0.08264	0.2036	0.406	0.684	
NC	0.49845	0.13841	3.601	<0.001	X
sqrt_stand_age	-0.01391	0.08816	-0.158	0.874	

Table B10

Results of the generalized additive model (GAM) for occurrence of S. flavidus, showing estimated coefficients, standard errors, z-values, p-values and significance of the explanatory variables. Significant relationships (p < 0.05) are indicated with "X".

Suillus flavidus **variables**	**Estimate**	**Std. Error**	**z value**	**P value**	**Significance**
(Intercept)	-412.499	0.18747	-22.004	<0.001	X
stand_age_raw	-0.055	0.1489	-0.373	0.709	
sqrt_Total.seq	0.16285	0.14083	1.156	0.247	
Spruce.share	-0.61942	0.19336	-3.203	0.001	X
Others.share	-0.30491	0.22163	-1.376	0.168	
Birch.share	-0.52924	0.22268	-2.377	0.017	X
pH	-0.26184	0.25682	-1.020	0.307	
N_deposition	-0.23407	0.3491	-0.67	0.502	
NC	0.61891	0.29273	2.114	0.035	X
sqrt_stand_age	-0.04154	0.14919	-0.278	0.780	

Publishing and archiving

☒ YES, I, Thom van Lent, have read and agree to the agreement for publication and the personal data processing that takes place in connection with this

☐ NO, I/we do not give my/our permission to publish the full text of this work. However, the work will be uploaded for archiving and the metadata and summary will be visible and searchable.