Linking plant community traits to fungal richness and community structures at a landscape scale across Denmark

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Resumé

At forstå de faktorer, der former svampediversitet, er centralt for at forudsige økosystemfunktion og biodiversitetsmønstre. Svampe opdeles i funktionelle grupper med strategier for kulstofoptag og relationer til planter. Det er dog uklart, i hvilken grad plantefællesskabets egenskaber kan forudsige svamperigdom og sammensætning på tværs af habitattyper og abitotiske gradienter. Jeg undersøgte sammenhænge mellem plantesamfund og svampesamfund i terrestriske habitater i Danmark ved hjælp af kvantificerede egenskaber afledt fra plantesamfund, herunder Ellenberg, strukturelle mål og planteartsrigdom. Svampesamfund blev karakteriseret ved DNA-metabarcoding af jordprøver og kvantificeret som relative abundanser. Shannon-diversitet (H') blev testet mod planteegenskaber i GLM-modeller, og svampesamfund blev visualiseret med PCoA og modelleret med dbRDA. Planteegenskaber kunne sikkert forudsige svamperigdom og -sammensætning, især Ellenberg-værdier og planteartsrigdom. De forklarede 31 % af variationen i slægtskomposition og 56 % af variationen i funktionel komposition. Funktionelle forskelle skyldtes især EcM-, AM- og CHEGD-svampe, som reagerede forskelligt på gradienter. 70% af variationen i H' blev forklaret, hvor diversiteten steg med planteartsrigdom, Ellenberg N og trædensitet og faldt med Ellenberg F og L, hvilket indikerer stærke mønstre langs abiotiske og biotiske gradienter. Overordnet viser studiet, at planteegenskaber kan fungere som proxyer for at forudsige svamperigdom og komposition på landskabsniveau, selvom uforklaret variation antyder, at andre faktorer også er vigtige. Disse resultater forbedrer mulighederne for at modellere underjordiske biodiversitetsmønstre og understøtter integration af plante-svampe-interaktioner i naturforvaltning og overvågningsstrategier.

Abstract

Understanding factors shaping fungal diversity is central to predicting ecosystem functioning and biodiversity patterns. Fungi form diverse functional guilds with different carbon acquisition strategies and plant relations. However, the extent to which plant community traits predict fungal richness and composition across large spatial gradients remains unclear. I investigated relationships between plant traits and fungal communities across terrestrial habitats in Denmark using vegetation indicators, including Ellenberg values, structural measures and plant richness. Fungal communities were characterized by DNA metabarcoding of soil samples and quantified in relative abundances. Shannon diversity (H') was tested against plant predictors in GLMs, and communities were visualized via PCoA and modelled with dbRDA. Plant traits strongly predicted fungal richness and composition, particularly Ellenberg values and plant richness. Traits explained 31% of genera composition and 56% of functional composition dissimilarities. Functional differences were especially due to EcM, AM, and CHEGD fungi responding differently to plant gradients. 70% of variation in H' was explained, increasing with plant richness, Ellenberg N, and tree density, and decreasing with Ellenberg F and L, indicating strong abiotic and biotic patterns. Overall, plant traits serve as effective proxies for predicting fungal richness and functional composition at landscape scales, though unexplained variance suggests other factors also shape fungal communities. These findings improve modelling of belowground biodiversity and support integrating plant–fungal interactions into conservation and monitoring frameworks.

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Introduction

Declining biodiversity and political awareness

The biodiversity crisis is a major ecological challenge of the 21st century, driven by human activities such as land and sea overexploitation, climate change, pollution, and invasive species. Species richness, abundance, and distribution are declining globally, with two-thirds of species risking extinction within the coming decades (IPBES, 2019; M.J. Costello et al., 2022). Loss of biodiversity furthermore reduces ecosystem functioning and stability, diminishing essential ecosystem services for humans (Cardinale et al., 2012).

In response, the European Commission launched the *EU Biodiversity Strategy for 2030,* aiming to reverse species loss by improving ecosystem quality, resilience, and connectivity. Targets include protecting 30% of EU land and sea (10% strictly protected) and restoring 20% of degraded areas, prioritizing sites critical for carbon sequestration and groundwater protection (European Parliament, 2025).

To evaluate progress, robust baselines of species diversity, abundance, and distribution are needed, alongside insights into drivers of community composition and turnover. For soil microbes and fungi specifically, such knowledge and baselines lag behind those for plants and animals due to limited attention and restrictions in conventional inventory methods (Cavicchioli et al., 2019; Guerra et al., 2021). For macrofungi, conventional surveys remain a profound inventory method, but they are seasonally restricted, require expert identification, and are influenced by climatic variability (Straatsma et al., 2001; Van der Linde et al., 2012). Consequently, comprehensive baselines for macro- and microfungal communities aggregated and their biogeographic patterns remain poorly established.

Potentials and challenges of eDNA techniques

Environmental DNA (eDNA) refers to genetic material present in environmental samples such as soil, roots, sediment, water, or air. DNA can be extracted, amplified, and sequenced, and metabarcoding assigns sequences to taxa using reference databases. Sequences are clustered into operational taxonomic units (OTUs) based on similarity thresholds, producing taxonomic identifications at varying levels (Taberlet et al., 2018). eDNA enables non-invasive biodiversity assessment (Thomsen & Willerslev, 2015) and represents a major shift in ecological monitoring (Deiner et al., 2017; Willerslev et al., 2003).

For fungal ecology, eDNA detects microscopic taxa that might be dominating ecosystems, but are not detectable by fruiting-body surveys (Tedersoo et al., 2014; Van Nuland et al., 2025). Sampling is less constrained by seasonality because it targets persistent mycelia, allowing year-round studies (Voříšková et al., 2014) and reducing reliance on taxonomic expertise - an expertise that is

declining (Hopkins & Freckleton, 2002; Thomsen & Willerslev, 2015). This approach has facilitated regional inventories (Krah & March-Salas, 2022; Pellissier et al., 2014) with which global aggregated datasets has enables global fungal diversity analyses (Tedersoo et al., 2014; Tedersoo et al., 2022; Van Nuland et al., 2025).

However, eDNA also faces technical and analytical challenges. Contamination, amplification bias, and inhibitors (e.g., humic acids) can distort results, creating false positives and negatives (Coissac et al., 2012; Thomsen & Willerslev, 2015). Clustering thresholds may also misgroup sequences, and incomplete reference databases limit taxonomic resolution (Hibbett et al., 2011; Thomsen & Willerslev, 2015). Furthermore, comparisons with conventional surveys show differing overall richness estimates (Baptista et al., 2015; Frøslev et al., 2019; Rieker et al., 2024). Detection of rare or substrate-specific species is also sometimes lowered compared to conventional inventories (Frøslev et al., 2019) though in other cases, they are simply different rather than lower (Rieker et al., 2024).

Thus, eDNA alone cannot fully capture fungal richness but excels in detecting microfungi and wide fungal diversity estimate, while supporting global databases. Combined with traditional surveys and expanding reference libraries, it offers a powerful tool for comprehensive biodiversity assessment.

Fungal diversity and ecology

The fungal kingdom is among the most species-rich, with ~120,000 described species, representing only 3–8% of the estimated global richness of 2.2–5.1 million species (Blackwell, 2011; Hawksworth & Lücking, 2017). Known Fungi diversify into ~20 phyla, 275 orders, 1,066 families, and 10,210 genera (Põlme et al., 2020). Alongside other microbes, they drive biogeochemical cycling of nutrients and carbon, regulating soil fertility and climate (Bardgett & van der Putten, 2014). They grow as unicellular yeasts or multicellular mycelia composed of hyphae infiltrating substrates. Most fungi produce both sexual and asexual spores. In Ascomycota and Basidiomycota, sexual spores develop in fruiting bodies, the macrofungi targeted by classical surveys (Harley, 1971).

Functionally, fungi are classified by carbon acquisition (saprotrophic vs. biotrophic) or ecological role—parasite, decomposer, predator, or mutualist (Harley, 1971). However, life-stage shifts and context-dependent interactions complicate classification (Põlme et al., 2020; Promputtha et al., 2007). Broadly, functionality is conserved at genus level, enabling eDNA datasets to assign functional traits for community-level ecological analyses (Põlme et al., 2020).

Saprotrophic fungi

Saprotrophs decompose organic matter, utilizing substrates such as wood, litter, and soil (Treseder & Lennon, 2015). In forests, they dominate carbon recycling via hydrolytic degradation of recalcitrant material, facilitating further decomposition of the simplified compounds by other microbes (Hobbie et al., 1999). Decomposition of wood involves fungal succession, driven by niche differentiation (brown and whit rot) and enzymatic capacity (Goodell, 2003; Pointing, 2001). Substrate type, tree species, and wood structure strongly influence colonization by fungi, with richness increasing alongside substrate diversity (Heilmann-Clausen & Christensen, 2004; Tomao et al., 2020).

In grasslands, saprotrophs decompose herbaceous litter above- and belowground. Decaying roots can constitute ~50% of biomass, with root quantity and quality shaping soil fungal communities (Francioli et al., 2021). Aboveground decomposition depends on litter chemistry, water-soluble carbon, and compound diversity (Allison & Vitousek, 2004; Castellano et al., 2015; Hanson et al., 2008). Plant species and tissue type (leaf, stem, twig) further influence fungal composition (Porre et al., 2020).

Biotrophic fungi

Biotrophic fungi live in obligate association with plants as mutualists or parasites, obtaining carbon produced via. photosynthesis from the host. Mutualists enhance host fitness through nutrient exchange and resilience, while parasites exploit hosts with detrimental effects (Smith & Read, 2010). Major mutualistic groups include ectomycorrhizal (EcM), arbuscular mycorrhizal (AM), ericoid mycorrhizal (ErM), and orchid mycorrhizal (OrM) fungi (Smith & Read, 2010). Endophytic fungi occupy an intermediate position, exhibiting both symbiotic and pathogenic traits (Põlme et al., 2020; Promputtha et al., 2007). Less-studied, but distinct, biotrophs include the CHEGD fungi (Clavariaceae, Hygrophoraceae, Entolomataceae, Tricholomataceae and Geoglossaceae) (Halbwachs et al., 2013).

ErM fungi form endomycorrhiza with Ericales, representing ~1.5% of plant species and occurring mainly in heathlands (Brundrett & Tedersoo, 2018; Read & Perez-Moreno, 2003). OrM fungi associate with Orchidaceae, essential for seed germination and adult development (Dearnaley, 2007). Both ErM and OrM also widely exhibit saprotrophic capabilities which complexifies their ecology (Dearnaley, 2007; Põlme et al., 2020). Consequently, in this thesis they will be treated as saprotrophic species.

EcM fungi colonize roots of woody plants of Gymnospermae and Angiospermae, forming a mantle and branched Hartig net for a wide surface for nutrient exchange (Brundrett & Tedersoo, 2018; Read & Perez-Moreno, 2003). Species can be both generalists and specialists and thus, the group exist in a continuum between these, where EcM fungi with high host specificity appear exclusively

with a specific tree family or genus (Mandolini et al., 2025). EcM fungi form association with 2–3% of all plants and only represent 0.5–0.7% of fungi, yet evolved convergently >50 times, spanning 27 Ascomycota and 37 Basidiomycota lineages (Brundrett, 2009; Hawksworth, 2001; Tedersoo et al., 2010). Correspondingly, ecological impact of ectomycorrhizal associations cannot be underestimated as they stabilise forest ecosystems – systems that account for 25% of the world's vegetation (Brundrett & Tedersoo, 2018).

AM fungi colonize plants by forming arbuscules within root cortex cells (Smith & Read, 2010). Though restricted to very few species within Glomeromycota (169–355 species), >72% of all plant species have mycorrhizal associations with AM fungi, underlining their importance (Blackwell, 2011; CICG, 2025). All AM fungi are generalists, strictly asexual, and lack fruiting bodies (Brundrett & Tedersoo, 2018).

Endophytes comprise a wider range of lifestyles, though all species live inside their host for some or all of their lifecycle. They inhabit leaves, roots, or stems, acting as commensals or mutualists that enhance drought tolerance, growth, and herbivore resistance (Currie et al., 2014; Rodriguez et al., 2009). However, many act as latent or facultative pathogens, which can be initiated under stressful conditions, and many switch to saprotrophy upon host death (Ab Razak et al., 2024; Currie et al., 2014; Saikkonen et al., 1998).

CHEGD fungi appear in mesotrophic, acidic grasslands and have similar requirements as plants of semi-natural grassland; decline with enrichment and encroachment (Griffith et al., 2002; Halbwachs et al., 2018). Traditionally viewed as saprotrophs (Vesterholt, 2012), evidence now suggest they have biotrophic interactions with herbs from root hair studies and isotopic signature analysis (Halbwachs et al., 2013; Halbwachs et al., 2018). In this study, CHEGD fungi are treated separately from saprotrophs.

Plant community traits to predict fungal communities

The many intricate and differentiated relationships among fungi and plants underpin their evolutionary ecological connectedness. Given that fungi are heterotrophic organisms that directly acquire carbon via decomposition or via biotic relationships, it is reasonable to assume that plant community traits can be used to predict fungal community composition and turnover. The plant diversity hypothesis states that when plant diversity increases, so does habitat complexity, and this leads to increased diversity belowground (Hooper et al., 2000). Yet, Cameron et al. (2019) find that, at a global scale, the hypothesis is confirmed for tropical and subtropical zones but not for temperate and arctic zones. Though, when isolating soil fungal communities from other microbes, many find the theory to match experimental findings for different fungal groups (Hiiesalu et al., 2014; Peay et al., 2013; Pellissier et al., 2014), in which plant species richness as simplified measures (number of species per site) is positively related to species richness of fungi.

Regarding community composition and turnover in fungal communities, plant community traits have also been found linked. Both Pellissier et al. (2014) and Peay et al. (2013) found a spatial clustering of fungal communities based on habitat type, indicating that similar habitat types shared similar fungal communities. They also both found a correlation between the turnover of plants and turnover of fungi by comparing patterns of distance matrixes, indicating a biotic coupling in turnover. The two studies differ in geography and ecology, with the former conducted in Amazonian rainforests while the latter in Swiss alpine grasslands. This contrast emphasizes that the plant species hypothesis may rely on complex plant–fungus interactions, that are present regardless of habitat type or geographical position.

Of other plant community traits, both plant chemical composition and plant community niches have also successfully been associated with fungal community turnover. Kembel and Mueller (2014) found that leaf N-content were coupled to fungal communities of leaves, and Pellissier et al. (2014) found Leaf N, C and N/C coupled to fungal community structures in soil fungi. Regarding Ellenberg values, strong coupling of the plant niches has also been linked to both fungal alpha and beta diversity. For alpha diversity, taxa have been shown to decrease with Ellenberg L and increase with Ellenberg N (Mulder et al., 2003). Regarding the turnover of fungal community composition, increasing Ellenberg F and decreasing Ellenberg L and R drives composition of deciduous fungal community, whereas decreasing Ellenberg N correlates with alpine grassland communities (Mulder & de Zwart, 2003).

Identifying which plant community traits are most influential requires an integrated multivariate analysis. Additionally, determining whether the traits driving community turnover differ between taxonomic composition and functional composition calls for a comparative approach.

Aims

To provide more fungal ecological insight, this master thesis aims to investigate diversity and composition of fungi across Denmark. The objective is to evaluate the nationwide compositional patterns through various habitat types and to assess the association of fungal communities with plant communities, both at site level (alpha-diversity) and between sites (beta diversity). The following research questions were investigated: 1) How are fungal diversity and community composition structured across habitat types in Denmark? 2) Does the plant community express relatedness to the fungal diversity and community, and if so, which trait variables are most correlated?

Fungal community composition will be analysed as both the taxonomic composition of fungi and as the functional guild composition of fungi. Plant community traits will be quantified into different components within compositional traits, structural traits, Ellenberg traits and leaf chemical traits. Plant community traits will be analysed as individual predictors. Habitat type will be investigated as a categorical value for clustering analysis. The fungal community data consists of an eDNA dataset

of OTUs from soil samples, whereas the plant community trait data is obtained from classical aboveground surveys.

Based on findings by e.g. Mulder and de Zwart (2003), Pellissier et al. (2014) and Peay et al. (2013) I expect that H1) habitat type is a strong predictor of fungal communities, both when quantifying the communities functionally and taxonomically, H2) the fungal diversity within and between sites both express relatedness to plant community traits. Specifically, I expect a positive relation between fungal richness and plant richness and varying relations to Ellenberg indices. H3) functional groups relate differently to plant community traits. For instance, I expect EcM fungi to decrease with light (Ellenberg L), while the CHEGD fungi to increase.

Terminology

In the thesis, the phrases ‘habitat types’ and ‘bio strata’ will be used interchangeably, referring to the exact same thing. Habitat types were defined on a combination of abiotic factors (details in table 2), in which their categorical names do not match scientific defined habitat names. However, the categories can easily be converted to understandable habitats, which will also be emphasised throughout. Furthermore, the phrases ‘ecological groups’, ‘guilds’ and ‘ecological guilds’ all refer to the same ecological classification of fungi based on differences in how they acquire carbon.

Methods

Data used in the project

This thesis is based on the research project BioWide (Biodiversity in Width and Depth) that assessed the biodiversity of Denmark in the period 2014 – 2018. The project was led by Aarhus University in collaboration with The University of Copenhagen, the Natural History Museum of Aarhus and the Natural History Museum of Denmark (more information on Biowide can be found here: https://ecos.au.dk/forskningraadgivning/temasider/biowide). Two datasets from Biowide have been used: The first is an occurrence dataset of fungal eDNA sequences extracted from soil samples at the Biowide field sites. The sequences are clustered into OTUs (operational taxonomic units) and have attached taxonomic information. Data was downloaded from the Global Biodiversity Information Facility (GBIF; Frøslev & Ejrnæs, 2018) at September 1, 2025. The second dataset is a mixed dataset on both abiotic and biotic data gathered at the Biowide field sites. Data was downloaded from the Institute for Ecoscience website (Institut for ecoscience; Ejrnæs, 2019), at September 1, 2025.

Additionally, a third dataset on fungal traits has been used; a curated database that connects ecological traits to fungal genera. This was obtained from the FungalTriats database (Põlme et al., 2020) and downloaded September 3, 2025.

The framework of Biowide

The collection of data in Biowide was done in 2014, 2015 and 2016. A total of 130 field site locations were systematically distributed across all five regions of Denmark. Within each region, sites were grouped into three spatial clusters, resulting in a total of 15 clusters across the study area (Figure 1). Sites spanned through various habitat types (both natural, semi-natural and farmland) that covered gradients of wetness, succession, fertility and degree of cultivation. Moreover, 10 places were included that were believed to be specific biodiversity hotspots (Brunbjerg et al., 2019).

Each of the 130 field sites measured 40m x 40m, and all sites were further sub-divided into four 20m x 20m quadrants. This division was achieved with colour-coded corner flags to delineate each quadrant, together with centrally positioned flags marking both the centre of the entire site and the centre of each subdivision (Figure 2A). Subsequent systematic sub-units were implemented according to the specific data types collected at each site (Figures 2B and 2C) (Brunbjerg et al., 2019).

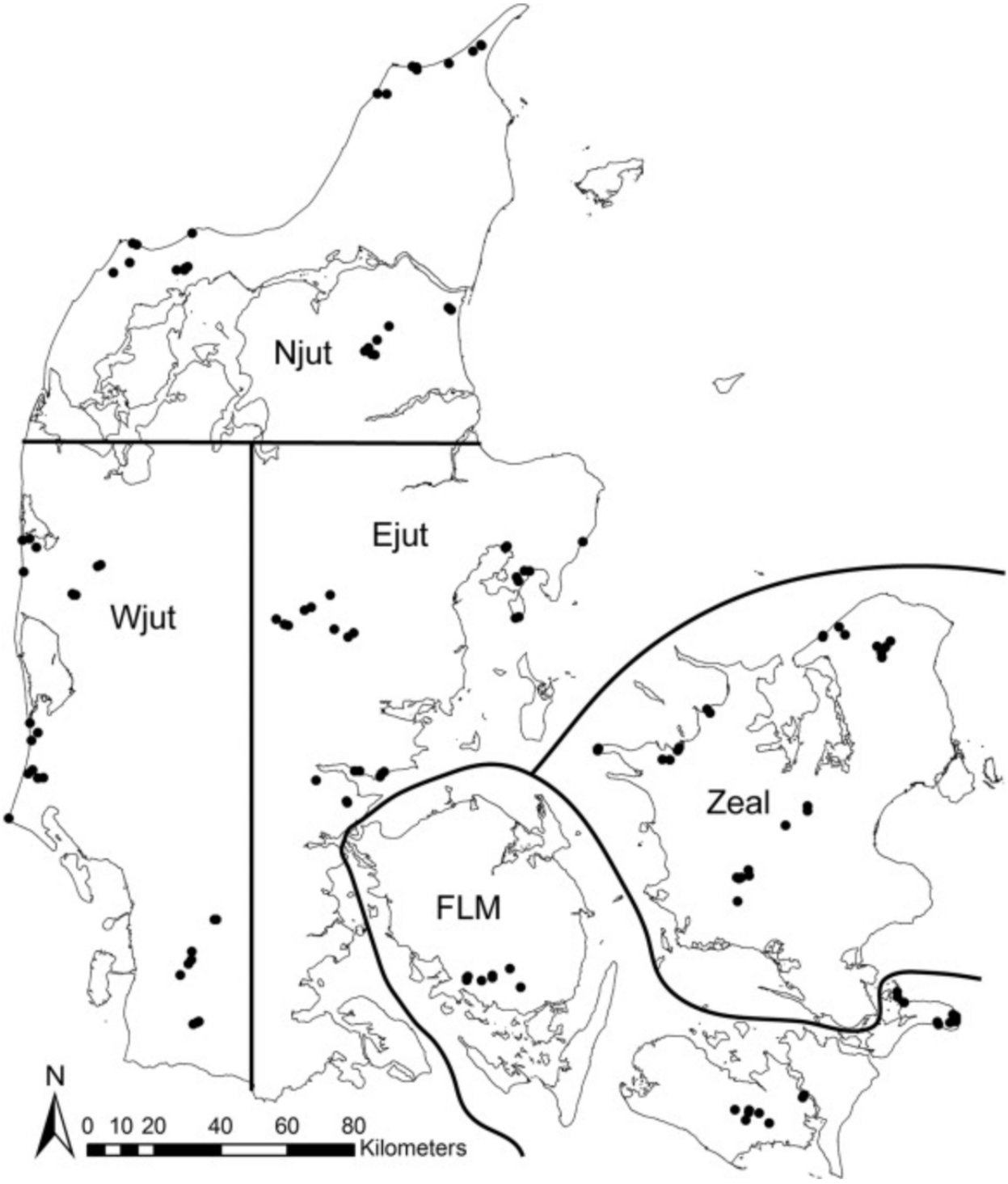

Figure 1: Map of Denmark showing the 130 sample sites and their distribution in 15 clusters within five regions. Njut = Northern Jutland, Ejut = Eastern Jutland, Wjut = Western Jutland, Zeal = Zealand, FML = Funen, Lolland and Møn. Figure is reprinted from (Ejrnæs et al., 2018).

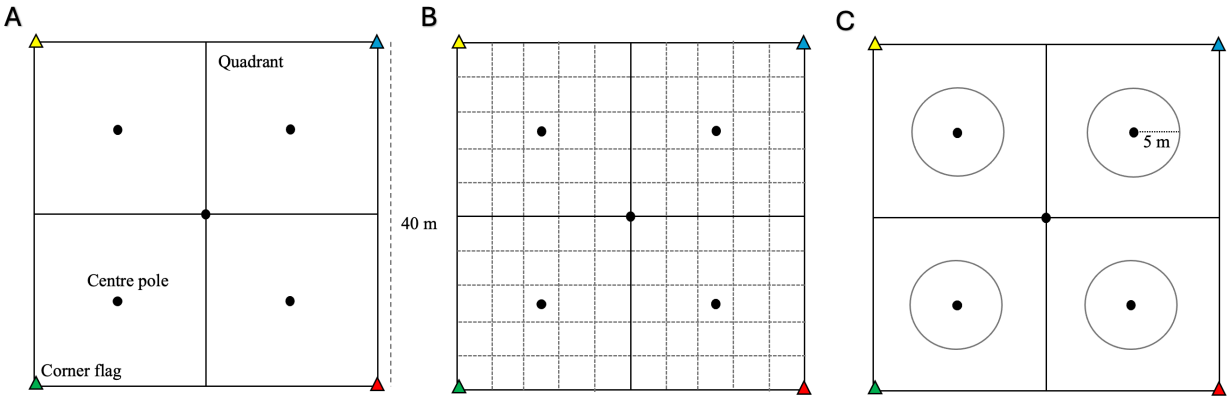

Figure 2: Sampling design of the Biowide project. A) Shows the basic design consisting of a 40m x 40m square further sub-divided into four smaller quadrants. Each division is marked with colour-coded cornerflag, and centres are marked with centre poles. B) Shows grid design for soil sampling (for eDNA extraction). In each of the 81 intersection a soil core was sampled. C) Shows 5m circle design for vascular plant and bryophyte species inventory. Figure is contructed from descriptions of the field inventories in (Brunbjerg et al., 2019).

Gathering of data

eDNA sampling, amplification, sequencing and annotation

To create a fungal sequence list, soil cores were collected, and DNA was extracted, amplified and sequenced. A more thorough and detailed bioinformatic procedure than written in this thesis can be found in Brunbjerg et al. (2019).

For each of the 130 sites, a virtual grid created by 9 horizontal and 9 vertical lines was fitted on top of each site, oriented by the corner flags (Figure 2B). The virtual grid comprised 81 intersections between the lines, and sampling was carried out by taking one soil core at each of these 81 intersections, pooling and mixing them all into one, after which subsamples of the mixture was taken for DNA extraction. Each core was taken in the top 10 cm of the soil using a thistle remover gardening tool with a curved open blade (Wolf-Garten, iW-M 2553000) and aimed at a cores size of ≈ 3-4 cm * 15 cm. The procedure intended to exclude coarse leaf litter, twigs and fresh plant material as thoroughly as possible. The cores were then scraped with clean spoons into a barrel (CurTec 15 litre Wide neck drum, HDPE) and mixed for at least 3 minutes using a drilling machine (HILTI Cordless Combihammer) mounted with a mixing paddle. The sampling, pooling and homogenization of the soil was done within the same 24 hours. After homogenization, 5 subsamples of 5-10 spoonfuls of soil were taken out and frozen for DNA extraction.

DNA extraction was carried out by using the PowerMax Soil DNA Isolation kit (MOBIO, Carlsbad, CA, USA). Afterwards, DNA was amplified from the ITS2 region with relevant primers. PCR products were built into a sequencing librariy using the TruSeq Dna PCR-Free Library Preparation Kit (Illumina). Sequencing was carried out with 250 bp PE runs on MiSeq (Illumina Inc., San Diego, CA, USA) at the Danish national Sequencing Centre.

Lastly, an OTU table was created by clustering sequences with 98,5% similaritiy. This follows the consensus clustering level used to delimit species hypotheses by the UNITE database (Kõljalg et al., 2013) in which the OTUs can be interpreted as separate species. This was achieved by initially filtering errors from the sequence library with DADA2 (Callahan et al., 2016) which identifies the exact amplicon sequences. Subsequently, VSEARCH (Rognes et al., 2016) was used to perform the clustering process followed by post-clustering curating using LULU (Frøslev et al., 2017). Finally, taxonomic assignments of the OTUs was matched against representative sequences in the UNITE database (UNITE, 2019).

Plant community related data

A wide number of variables connected to the plant communities were achieved via diverse inventories. Precise inventory description can be found in Brunbjerg et al. (2019).

Within the four 5-metre circles, the bryophyte cover (%) was estimated, and a site mean cover was afterwards calculated. Vascular plant and moss richness was estimated by registering all species inside the circles. The lists were combined to estimate richness for the total site. Additional species spotted outside the circles were added to the list subsequently, and for bryophytes, inventories on substrates as wood, bark of living trees and soil outside the circles extended the lists. From the full lists of vascular plants, Ellenberg values (N, F, R, L) were identified, and a mean per site was calculated. Furthermore, flower volume was estimated. To estimate the density of deciduous and coniferous trees, woody plants > 3 m height (< 40 cm DBH) were identified and counted inside each 5 m circle, and the density per site was estimated. If no species occurred inside the circles, trees outside were counted per quadrant.

At site levels, the number and richness of tree species > 40 cm DBH was counted. Coarse woody debris (>20 cm diameter, min length 1 m) was counted and the measured in size (diameter x length).

In the quadrants, vegetation height was measured in each corner of the four quadrants, and a mean value for the sites was thereafter calculated. To estimate the plant species leaf content of nitrogen (N), phosphorous (P) and carbon (C), fresh green shoot material was collected from all plants that appeared along a line from the quadrants' corners running into the centre pole. Plant material was afterwards dried, subsamples were analysed for the compounds of N, P and C, and site mean values were calculated (Brunbjerg et al., 2019).

Data analysis

Platform and packages used overall

Handling of data analysis and statistics in this project was conducted in R (version 4.3.3; R Core Team, 2024). The workflow was implemented in RStudio (version 2024.12.1; Posit Software, PBC, 2024) using R Markdown for reproducible reporting. Many base-R functions were used beside a list of packages with other essential functions.

All data manipulation and summarisation were conducted using the tidyverse framework (Wickham et al., 2019); the dplyr-package (version 1.1.4; Wickham et al., 2023) was used to subset, merge and summarise data in the datasets along with the tidyr package (version 1.3.1; Wickham et al., 2024) that was used to pivot data frames. General functions in the language included: mutate(), case_when(), left_join(), select(), group_by() and summarise().

The corrplot-package (version 0.92; Wei & Simko, 2021) was used to create a correlation matrix between all predictors. The vegan package (version 2.7.1; Oksanen et al., 2025) was used for most statistical and ecological analyses along with ordination modelling and for accessing variance inflation factors (VIFs) among predictors. Statistical analysis were supplemented with analyses from the base-R stats package and the car package (version 3.1.3; Fox et al., 2024)

The compositions-package (version 2.0.8; Boogaart et al., 2024) was used to transform abundance and relative abundance matrixes to fit the ecological multivariate analyses, that was conducted via the vegan-package.

The DHARMa package (version 0.4.7; Hartig, 2024) was used to investigate the model fit of error distribution assumptions and residuals from Generalised Linear Models (GLMs). The MuMin package (version 1.47.5; Bartoń, 2023) was used for model selection of GLMs.

The ggplot2 package (version 3.5.2; Wickham et al., 2025) was used for all data visualisation, and the patchwork package (version 1.3.1; Pedersen, 2025) was used to arrange more panels into a single figure.

Initial data handling

Fungal primary and secondary ecological strategies from FungalTraits were merged into the OTU table based on the genus column. Because traits are genus-resolved, only OTUs identified to genus were assigned functions; remaining OTUs were classified as unknown. To streamline subsequent analyses, ecological functions were aggregated into broader guild strategies (Table 1).

Table 1: Ecological strategies assigned the fungal OTUs using the FungalTraits database (right) and subsequently aggregated into higher-level functional categories ("essential strategy") for downstream analyses (left).

Summarised functional guilds	Functionl guilds/strategies from the FungalTraits database
CHEGD fungi	CHEGD
Ectomycorrhizal fungi	Ectomycorrhizal
Arbuscular mycorrhizal fungi	Arbuscular mycorrhizal
Saprotrophic fungi	Litter saprotroph, dung saprotroph, soil saprotroph, wood saprotroph, unspecified saprotroph, nectar/tap/pollen saptrotroph
Endophytes	Foliar endophyte, root endophyte, plant pathogen
Moss associated fungi	Bryophile, moss parasite, moss symbiont
Other fungi	Algal parasite, animal endosymbiont, animal parasite, lichen parasite, epiphyte, lichenized, mycoparasite, protistan parasite, sooty mold, unspecified pathotroph, NAs

To quantify and analyse the fungal OTU data frame, three summarized matrices were generated:

1. *Genus abundance matrix*: Sites (rows) x genera (columns); For each site, the unique OTUs assigned to genus level was aggregated by genus. The OTUs not assigned to genus levels was classified as 'unknown'.
2. *Genus relative abundance matrix*: genus counts were converted to relative abundances by dividing each guild count by the total number of OTUs in the dataset, and zeroes replaced with a pseudo-count ($1e^{-5}$) to facilitate downstream analyses.
3. *Functional guilds relative abundance matrix*: sites (rows) × guilds (columns); counts per guild strategy were converted to relative abundances by dividing each guild count by the total number of OTUs in the dataset, with zeroes replaced by pseudo-counts ($1e^{-5}$).

From the abiotic/biotic dataset (79 variables), the plant community trait variables were extracted to plantvars, along with a categorical bio_stratum (Habitat types quantified by combinations of successional stage, nutrient status, and wetness). To reduce the number of predictors, multivariate and pairwise correlations were assessed. Hence, variance inflation factors (VIFs) were computed with vif.cca() from vegan on genus-level relative abundances, using a VIF ≤ 5 as acceptable (Thompson et al., 2017). Pairwise Pearson correlations were estimated via cor(…, method = "pearson", use = "pairwise.complete.obs") and visualized with corrplot; variables with VIF > 5 and $|r| > 0{,}7$ were removed first (See appendix, table A1 and Figure A1 for details on remaining VIFs and r-values, respectively). The final predictor set (plantvars_final) contained 15 variables (Table 2), all were subsequently z-standardized with scale().

Table 2. Overview of the plant community-derived variables included in the thesis, along with categorical habitat types (bio stratum). Variables were subsetted from a dataset connected to 130 sites and checked multicollinearity (via VIFs) and pairwise correlations. Each variable exhibited a VIF < 5 and had no pairwise correlation above 0,7 or under -0,7.

Variable name	unit	Trait category	Description
Moss cover	%	Structural	The degree of moss cover (%) per site. Mean of four measurements inside 5m-circle
Vegetation height	cm	structural	Estimated vegetation height per site. A mean from 16 measurements in quadrant corners
Volume of dead wood	m^3/HA	Structural	Volume of coarse woody debris per hectare. Estimated from the summarised volume per site
Density of deciduous trees <40dbh	(#/m^2)	Structural	Density of deciduous trees > 3 m (<40DBH) per site. Estimated from four 5m-circles
Density of coniferous trees <40dbh (#/m^2)	(#/m^2)	Structural	Density of coniferous trees > 3 m (<40DBH) per site. Estimated from four 5m-circles
Flower volume	unitless	Structural	Density of flowers per site. Summarised value from all field visits, estimated from four 5-m circles
Moss Richness	#	Compositional	Number of moss/bryophyte species per site. Estimated from four 5m-circles, along with subsequent notations
Vascular plant richness	#	Compositional	Number of vascular plant species per site. Estimated from four 5m-circles, along with subsequent notations
Tree richness > 40DBH	#	Compositional	Number of tree species >40DBH per site
Ellenberg F	unitless	Ellenberg	Mean Ellenberg F-value for the registered plant community in the site
Ellenberg L	unitless	Ellenberg	Mean Ellenberg L-value for the registered plant community in the site
Ellenberg N	unitless	Ellenberg	Mean Ellenberg N-value for the registered plant community in the site
Leaf C-content	%	Chemical	Mean value of C-content (%) in leaves per site. Estimated from four sub-samples of shoot material in each quadrant
Leaf N-content	%	Chemical	Mean value of N-content (%) in leaves per site. Estimated from four sub-samples of shoot material in each quadrant
Leaf P-content	%	Chemical	Mean value of P-content (%) in leaves per site. Estimated from four sub-samples of shoot material in each quadrant
Bio stratum	9 levels	Habitat type	Habitat types quantified by combinations of successional stage, nutrient status, and wetness. 9 different categorical combinations + an agricultural category. • "Early" vs. "Late": Grasslands vs. forests • "Poor" vs. "Rich": Nutrient poor vs. rich conditions • "Wet" vs. "Dry": Moist vs. dry conditions

Diversity within sites

To quantify alpha diversity across the 130 sites, the Shannon–Wiener diversity index (H') was calculated based on the distribution of operational taxonomic units (OTUs) within each genus. The index was computed via vegan using diversity(index = "shannon") that calculate the index by the formula: $H' = -\sum_{i=1}^{S}(p_i \ln(p_i))$, where p_i is the relative abundance of genus i in the local community, and S is the total number of genera observed. The index is a metric that quantifies community diversity by incorporating both the number of taxa present (in this case, genera) and their evenness. Because the formula is logarithmic, rare genera contribute less to the overall index than common genera (Magurran, 2003).

To assess differences in H' among habitat types, the assumptions required for parametric testing were first investigated. The Shapiro–Wilk test was used to evaluate normality of residuals for each habitat type by shapiro_test()**,** and homogeneity of variances was tested using Levene's test by leveneTest() from the car-package. As diagnostics indicated violations, parametric assumptions were not met, and non-parametric procedures were further assessed. I used the Kruskal–Wallis rank-sum test to evaluate global differences among habitat types by kruskal_test(). Futhermore, Dunn's test was performed for pairwise comparisons of the habitats via dunn_test() with Benjamin Hochberg adjusted p-values (p.adjust(method = "BH")). The Shapiro–Wilk test, Kruskal–Wallis rank-sum test and Dunn's test were conducted by Base-R stats-package(). Subsequently, H' to habitat types was visualized in a boxplot.

Drivers of alpha diversity were analysed using a Gaussian generalized linear model (glm(family = gaussian, link = "identity")) from Base-R. Model assumptions and fit were evaluated by the DHARMa package, providing simulation-based diagnostic tools via simulateResiduals(n = 250). Specifically, a QQ plot and residuals vs. fitted values was inspected for distributional deviations, heteroscedasticity, and outliers (results in appendix, figure A2). Model selection was conducted with MuMIn using dredge(m.lim = c(0, 6)) in which the model search was constrained to a maximum of 6 variables with options(na.action = na.fail) to enforce consistent data across candidate models. Models were ranked by AICc, and the best-performing model was identified as the one with the lowest AICc, while competing models were considered if their ΔAICc < 3. The best model was reported with adjusted p-values by the Benjamin-Hochberg method (p.adjust(method = "BH")). For visualization, $H'$was plotted against key predictors with fitted trends and 95% confidence intervals.

Diversity Between Sites

To quantify beta diversity in relative abundance datasets (genera and functional groups), data were transformed using a centered log-ratio (CLR) transformation, followed by calculation of an Aitchison distance matrix. This approach is robust for compositional data and data quantified to

relative measures, as it mitigates compositional bias and enables linear ordination without distortion (Gloor et al., 2017).

Unconstrained beta diversity was visualized using two PCoA plots generated with dist()in vegan**,** based on genera and functional group dissimilarities. Sites were colored by bio-stratum to assess clustering. Drivers of beta diversity were tested using PERMANOVA with marginal effects via adonis2(by = "margin"), which estimates each predictor's unique contribution while controlling for others. P-values were adjusted using the Benjamin–Hochberg method.

To model and visualize variation explained by significant predictors, distance-based redundancy analysis (dbRDA) was performed using capscale(distance = "euclidean"). dbRDA partitions variance into constrained and unconstrained components, enabling visualization of predictor gradients and estimation of explained variance (Borcard et al., 2011). To find the best set of predictor variables, model selection was conducted with ordistep(direction = "forward"), starting from an empty model and using permutation tests and AIC to avoid overfitting and set.seed(1000) for reproducibility. Ordination plots were created in ggplot2()**,** displaying significant predictors from the PERMANOVA tests as vectors and functional groups with distinct symbols. Functional groups were also plotted against key drivers using fitted models.

Finally, post-hoc tests evaluated whether bio-stratum added explanatory power beyond covariates to the dissimilarity matrixes. General associations were tested using adonis2(), followed by conditioned PERMANOVA to account for covariate effects. Because PERMANOVA is sensitive to heterogeneous dispersion, betadisper() was used to investigate potential conflicting dispersion dissimilarities among the bio strata. Mean dispersion per stratum was also calculated.

Results

Overall fungal diversity

Of the 10.490 fungal DNA sequences in the dataset, approximately 94% was assigned to phylum-level, 50% to genus level and 22% was assigned to species level (figure 3). All 50% of the OTUs identified to genus level could be ascribed a functional group from the FungalTraits database. However, 3% belonged to other functionalities than the aggregated groups and were therefore grouped as “other/unknown” along with the unassigned OTUs (details on other functionalities in table 1).

A total of 1038 genera were detected in the dataset. The most abundant genera were also the most species rich ones, as 8 out 10 were shared among the top 10. The most diverse genus was *Cortinarius* with 160 different OTUs detected, though closely followed by *Mortierella* with 155, which was also the far most abundant genus, occurring 1415 times - more than 2,5 times the level of the next most abundant genera *Archaeorhizomyces.* (Appendix, figure A3). The highest proportion of the dataset were saprotrophic fungi consisting of 26%, and the lowest was moss associated fungi of only 0,1% (table 3).

The occurrence frequency of each unique OTU ranged from a presence at a single site to a maximum of 117 sites. Around 46% occured in only one site, 34% occured between two and four sampling sites and 20% occurred in five or more sites (Appendix, figure A4). The taxonomic assignment depth of the OTUs that only occurred at a single site matched the global dataset; half of the sequences were assigned genus-level, whereas the other half were not. This indicates that both rare and more common species were missing in the reference database.

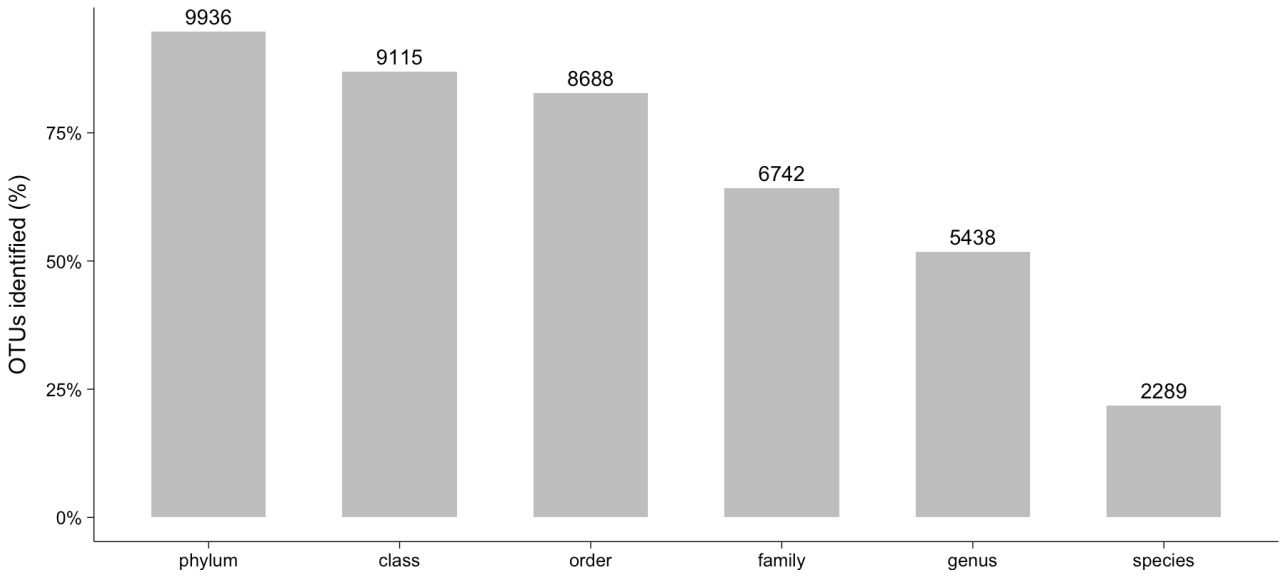

Figure 3: The proportion (%) of fungal OTUs in the dataset that could be assigned different taxonomic levels. Numbers above the bars indicate the count of identified OTUs at that level.

Alpha-diversity

The average relative abundance of EcM fungi in late successional habitats were more than 2 times bigger than within early successional habitats (11-18% and 1-5%, respectively). The opposite pattern appeared for CHEGD fungi, with highest fractions in early successional habitats (1,3-6% and 0-1%, respectively). The fraction of AM fungi was highest in EarlyWetRich (1,28%), which was 5 times higher than the mean of all other habitat types and 20% higher than agricultural sites. The relative abundance of moss associated peaked in the moist early successional habitats with 0,35%, which was 2 times higher than in all other non-agricultural habitat types. The relative fractions of saprotrophs and endophytes varied widely among all habitat types (table 3). Overall, most of the functional groups exhibited a preference for some habitat conditions over other, indicating a non-random distribution.

Table 3: Mean relative fractions (%) of functional groups across the different bio strata. Table is supplemented with the relative fractions of the total dataset. Bold values indicate the highest fraction of the respective functional group among the bio strata.

Bio strata	AM (%)	CHEGD (%)	EcM (%)	Endophytes (%)	Moss associated (%)	Saprotrophs (%)	Other/Unknown (%)
Agricultural	1,06	1,05	0,45	11,8	0,26	33,6	51,9
EarlyDryPoor	0,12	1,43	1,93	10,6	0,07	30,0	**55,9**
EarlyDryRich	0,58	**6,11**	1,01	11,5	0,15	32,6	48,2
EarlyWetPoor	0,10	1,31	5,18	12,6	0,34	28,8	51,7
EarlyWetRich	**1,28**	2,01	5,23	13,0	**0,35**	26,9	51,2
LateDryPoor	0,06	0,27	18,2	8,57	0,09	31,8	41,0
LateDryRich	0,36	0,40	**19,1**	9,21	0,02	**32,8**	38,1
LateWetPoor	0,04	0,24	16,5	11,8	0,17	29,5	41,7
LateWetRich	0,24	0,59	11,3	**15,1**	0,18	29,1	43,5
Total dataset	1,21	2,28	8,66	9,43	0,11	25,9	52,5

The alpha-diversity of fungal genera, measured by Shannon Diversity Index (H'), ranged between 1,973 and 3,922 across all sites, with a mean of 3,158. Across the different biological strata, the highest diversity appeared within LateWetRich (max = 3,89, mean = 3,57), whereas the lowest appeared within EarlyWetPoor (min = 19,7, mean = 2,70). Alfa diversity within the habitat types were overall significantly different from each other ($p < 0,001$), with many pairwise differences that generally tended to separate the early and late succesional habitats as well as nutrient rich and poor habitats (figure 4). Roughly, H' tended to increase from early (mean = 2,91) to late successional habitats (mean = 3,43), though H' of the EarlyDryRich habitats was more similar to H' of the late successional habitats. Furthermore, H' was generally slightly higher in rich conditions (mean = 3,34) compared to poor conditions (mean = 3). Overall, this revealed that the Shannon diversity was different between habitat types, with a tendency to increase with succession and nutrient availability, determined from the habitat categorisations.

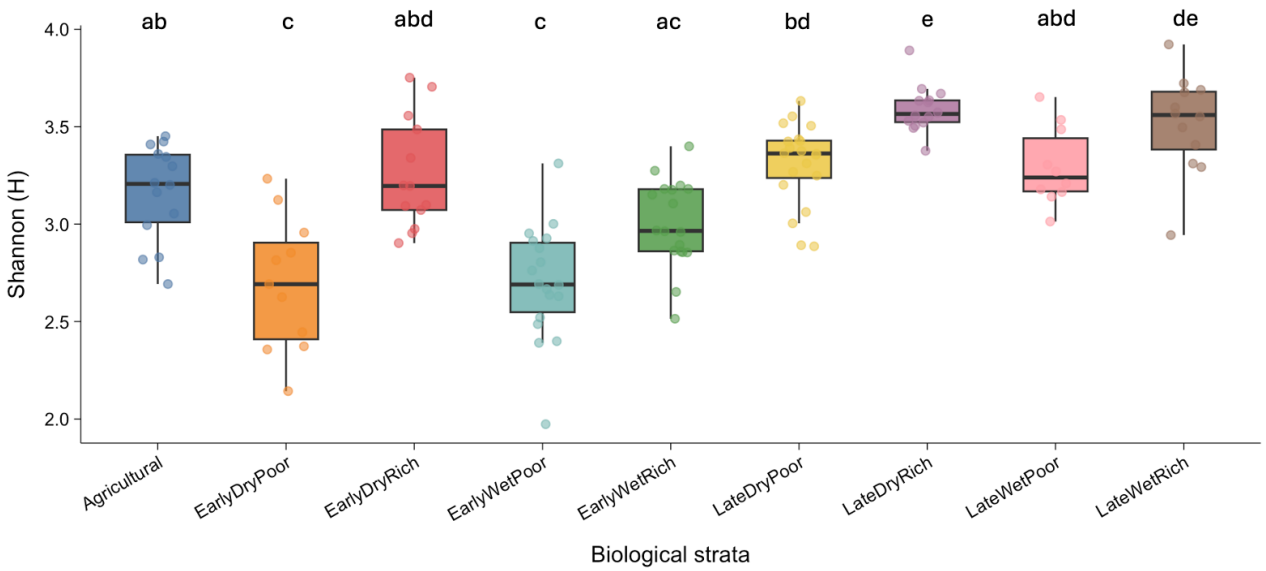

Figure 4: Shannon Diversity Index (H) of fungi across the habitat types, based on the diversity and evenness of OTUs within genera. Boxplots show median and interquartile range for each habitat. Points represent individual sample values within each habitat and are coloured by habitat type. Letters above boxes indicate pairwise significances of adjusted values (Benjamin-Hoch method); groups with shared letters are not significantly different from each other.

A full GLM on alpha-diversity (H') with all continuous variables from the dataset (thereby not including habitat types) explained 71% of the variance. The best-reduced model, evaluated from lowest AICc levels, could still explain 70% variation, while reducing the variables from 15 to the following 6: deciduous tree density, Ellenberg N, Ellenberg F, Ellenberg L, plant richness and moss richness (table 4). All predictors in the reduced model were significantly associated with alpha diversity (all $p < 0{,}05$; table 5), whereas the strongest predictors were Ellenberg N, Ellenberg L and plant richness (all $p < 0{,}001$; visualised in figure 5) The next best model ranked $\Delta AICc = 3{,}65$ and was not considered a better model, hence the set threshold of $\Delta AICc = 3$.

The model selection revealed differentiated relationships between alpha diversity and key plant-derived predictors. Large deciduous trees showed a positive correlation, indicating that denser deciduous forests increase fungal genera diversity and evenness. Ellenberg values exhibited contrasting effects: Ellenberg nutrient values was strongly positively correlated with alpha diversity, while Ellenberg values for light and moisture was negatively correlated. Both plant and moss species richness correlated positively with an increase in alpha diversity indicating that higher local diversity corresponds to higher fungal diversity (table 5).

Overall, the model selection successfully reduced the plant community trait variables to 6 essentials, that could explain the Shannon diversity by 70%. The best model indicated that alfa diversity increases with nutrient availability, structural complexity of deciduous trees, and species richness, while it decreases under conditions of higher light availability and moisture (Table 5).

Table 4: Model table of a full and reduced model on alpha diversity (Shannon Index (H')). The best-reduced model was selected from dredge analysis based on lowest AICc and ΔAICc < 3. The next best model had ΔAICc = 3.65 and was hence not included in the table. Table shows both models' explained variation (R^2), degrees of freedom (df), Log-likelihood, AICc, Delta AICc and Akaike weights.

Model call	R^2	df	Log-likelihood	AICc	Delta AICc	Akaike weight
Full model	0,71	15	21,8652	-5	16,02	1
Reduced model ~ Tree density deciduous + Ellenberg F + Ellenberg F + Ellenberg N + Vascular plant richness + Moss richness	0,70	6	19,113	-21,0	0	0,343

Table 5: Summary of the best-reduced model on alpha diversity (Shannon Diversity Index (H')). Table includes estimated coefficients of each covariate, standard errors, t-values, significance levels (P) and adjusted p-values (P_{adj}).. Bold values indicate statistically significant results ($p \leq 0,05$)

Term	Estimate	Sd Error	t	P	P_{adj}
Intercept	3,15756	0,01883	167,645	**< 0,001**	**< 0,001**
Tree density deciduous	0,06177	0,02335	2,645	**0,009**	**0,011**
Ellenberg F	-0,06698	0.02161	-3,099	**0,002**	**0,003**
Ellenberg L	-0,12270	0,02606	-4,709	**< 0,001**	**< 0,001**
Ellenberg N	0,18179	0,02557	7,110	**< 0,001**	**< 0,001**
Vascular plant richness	0,07540	0,02557	3,487	**0,001**	**0,001**
Moss richness	0,06431	0,02548	2,524	**0,013**	**0,013**

Note: For all variables, df = 1. Adjusted p-values (P_{adj}) followed the Benjamin Hoch method.

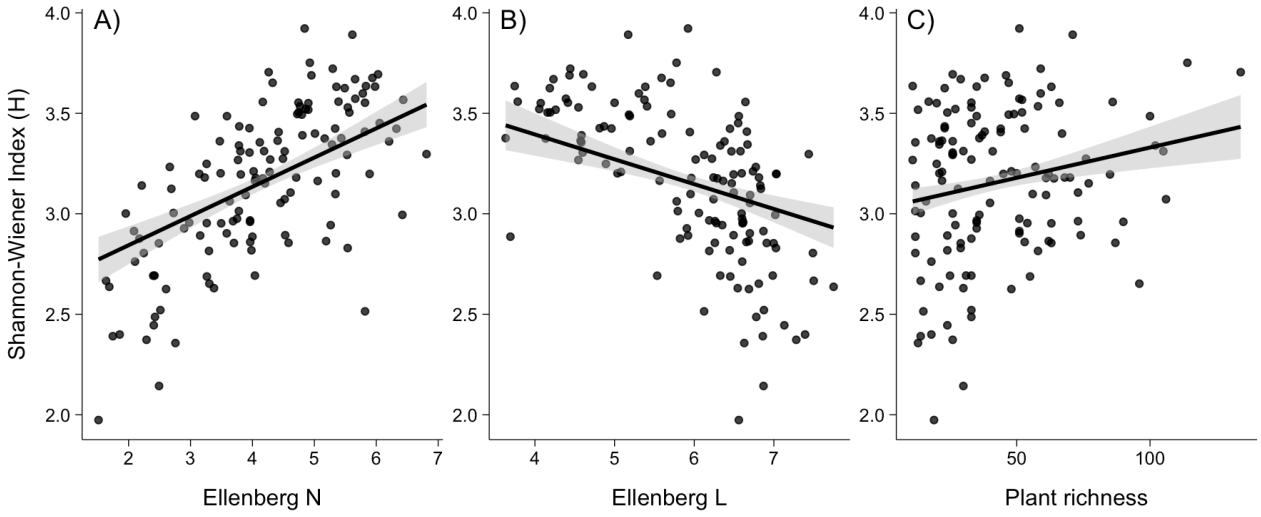

Figure 5: Shannon Diversity Index (H') of fungal genera along three strongest predictors: A) Ellenberg N, B) Ellenberg L, and C) plant species richness. Points represent observed values, while solid lines and shaded areas indicate model-predicted trends and 95% confidence intervals from the best-performing model of alpha diversity.

Beta-diversity

The passive PCoA ordinations revealed that a modest share of the between-site diversity of fungal genera could be explained by the two first ordination axes PCoA1 and PCoA2 (17,8%, figure 6A),

whereas much higher variance was captured for the between-site diversity of functional groups (78,8%, figure 6B). The ordination on genera visually separated communities by habitat types into clusters. Late successional communities appeared in the bottom and right side, and early successional communities in the top and left side. Also, rich nutrient communities clustered in the bottom and left side, whereas nutrient-poor communities clustered in the upper-right side (figure 6A). For the ordination of functional groups however, a clustering appeared more gradual along the PCoA1 with late successional communities to the left and early successional communities to the right (figure 6B). Global Post-hoc PEMANOVA tests revealed a general association of habitat types with both dissimilarity matrixes and a general separation between the biological strata (genera: R^2 = 0,24, P < 0,001; guild: R^2 = 0,5, P <0,001). However, group dispersion via betadisper also revealed a significant uneven dispersion within the habitat types (genera: p = 0.002; functional: < 0,001); a dispersion that ranged between 15 and 20,3 in the genera dissimilarity matrix and between 1,6 and 2,7 in the functional dissimilarity matrix (appendix, table A2).

Overall, the PCoA ordination for especially functional groups dissimilarities captured the variance in the data by the first two axes, whereas the variance captured for genera dissimilarities by the two first axes was lower. Habitat types were significantly associated with both ordinations, and positioning patternsof the habitat types appeared in clusters for the genera dissimilarities, whereas it appeared gradual along the first axis for functional groups dissimilarities. Despite the significant association of habitat types to the ordinations, the groups also exhibited uneven group dispersion.

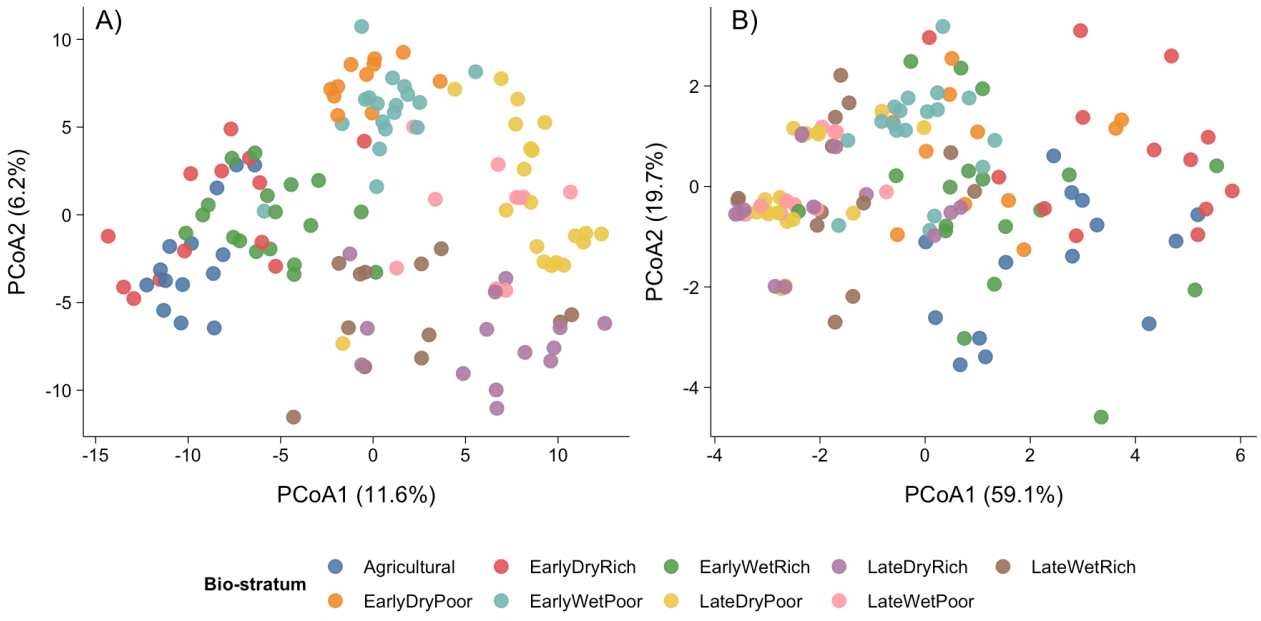

Figure 6: Principal Coordinates Analysis (PCoA) of fungal community composition based on CLR-transformed relative abundances. Figure illustrates dissimilarities in A) genera composition B) functional groups composition. Points represent sites, coloured by habitat types (bio-stratum). Axes indicate the first two PCoA dimensions with explained unconstrained variance.

Drivers of fungal community turnover

PERMANOVA analyses of continuous plant-derived variables revealed that a total 31% of the variance in fungal community composition of genera could be explained by all predictors together (Residual $R^2 = 0{,}686$). For the functional dissimilarities, the explained variance was 56% (Residual $R^2 = 0{,}437$), indicating a stronger overall environmental signal in functional composition. For both matrixes, the predictor that explained most unique marginal variation in fungal turnover was vascular plant richness (genera: $R^2 = 0{,}024$; traits: $R^2 = 0{,}074$). Furthermore, the Ellenberg values L, N and F as well as moss richness exhibited a significant signal with fungal turnover in both matrixes (alle $p < 0{,}05$; table 6). Forest structures (density of deciduous and coniferous trees), vegetation height and leaf phosphorous content were also significant for measuring the turnover of genera composition (table 6).

Overall, the findings indicate that plant community traits are successfully associated with fungal community composition and turnover – most strongly at the level of functional composition and more modestly at the level of genera composition. It indicates that local vascular plant and moss diversity and broad habitat gradients (light, moisture, nutrients) are the plant community traits that shape fungal community turnover for both genera and guild composition, whereas leaf P-content along with structural vegetation and forest attributes also are important variables, but only for genera composition.

Table 6: Results of PERMANOVA showing marginal effects of plant-derived variables on community composition of genera (left) and functional groups (right). Table shows proportion of explained variance (R^2), sum of squares (SumSqs), F-statistics, permutation-based p-values (P) and adjusted p-values (P_{adj}).

	Genera					Functional groups				
Parameters	R^2	Sum Sqs	F	P	P_{adj}	R^2	Sum Sqs	F	P	P_{adj}
Moss cover	0,00738	410	1,2052	0,129	0,169	0,00129	1,72	0,3310	0,813	0,969
Vegetation height	0,00851	472	1,3892	**0,046**	0,087	0,00272	3,62	0,6979	0,539	0,833
Leaf C-content	0,00795	441	1,2984	0,082	0,116	0,00515	6,83	1,3180	0,246	0,465
Leaf N-content	0,00831	461	1,3570	0,069	0,107	0,00678	9,01	1,7371	0,141	0,325
Leaf P-content	0,00910	505	1,4852	**0,029**	0,070	0,00690	9,16	1,7664	0,153	0,325
Density dead wood	0,00836	464	1,3656	0,058	0,099	0,00209	2,77	0,5347	0,664	0,868
Density deciduous trees	0,00905	502	1,4780	**0,033**	0,070	0,00225	2,99	0,5766	0,642	0,868
Density coniferous trees	0,01163	645	1,8986	**0,001**	**0,006**	0,01023	13,58	2,6194	0,063	0,179
Tree richness	0,00714	396	1,1662	0,188	0,228	0,00441	5,86	1,1302	0,316	0,537
Flower volume	0,00488	271	0,7975	0,843	0,843	0,00037	0,50	0,0960	0,976	0,976
Ellenberg F	0,01649	915	2,6919	**0,001**	**0,006**	0,01769	23,49	4,5308	**0,019**	0,065
Ellenberg L	0,01620	899	2,6456	**0,002**	**0,009**	0,04648	61,74	11,9059	**0,001**	**0,006**
Ellenberg N	0,01187	659	1,9383	**0,004**	**0,014**	0,01965	26,10	5,0336	**0,006**	**0,026**
Vascular plant richness	0,02417	1341	3,9466	**0,001**	**0,006**	0,07449	98,93	19,0787	**0,001**	**0,006**
Moss Richness	0,01021	567	1,6679	**0,011**	**0,031**	0,02676	35,54	6,8545	**0,001**	**0,006**
Residuals	0,686	38064				0,437	580,8			

Note: For all variables, df = 1. Adjusted p-values (P_{adj}) have been generated for false discovery rates following the Benjamin Hoch method. Bold values show statistically significant results ($p \leq 0{,}05$) of both P and P_{adj}.

Modelling explained variation by dbRDA models

The optimal reduced beta diversity model, explaining variation among sites based on genera composition, retained 12 of the original 15 variables, thereby only excluding moss coverage, tree species richness, volume of flowers. This lowered the explained variance from 31% to 28%, whereas the unconstrained variation then increased to 72%. For functional composition, the optimal reduced beta diversity model retained only 6 of the original 15 variables, which only decreased explanatory power from 56% to 53% and increased the unexplained variance to 47% (table 7). The model selection for functional groups kept the significant variables from the PERMANOVA test (table 6) along with coniferous tree density and excluded all other variables.

Overall, the model selections included variables that were significantly associated with beta diversity in the PERMANOVA test along with variables that trended toward significance ($0,08 > p > 0,05$; table 6). The exclusion of variables only lowered the explanatory power to an absolute difference of 3% for both dissimilarity models. The explained constrained variation was highest in the functional dbRDA model, though less variables were included than in the dbRDA model of genera.

Table 7: Model summaries of the dbRDA models on fungal community turnover between sites, based on genera composition and functional composition. The table shows full models with all variables from the PERMANOVA and reduced models via model selection from ordistep with forward-selection. The table shows the constrained variance explained by each model (R^2), degrees of freedome (Df), variance, F-statistics, p-values and adjusted p-values.

Model	R^2	Df	Variance	F	P
Genera					
Full model	0,31	15	135,1	3,017	**0,001**
Reduced model	0,28	12	121,86	3,854	**0,001**
~ Coniferous tree density + Deciduous tree density + Ellenberg F + Ellenberg F + Ellenberg N + Vascular plant richness + Moss richness + Vegetation height + Dead wood density + Leaf C-content + Leaf N-content + Leaf P-content					
Functional groups					
Full model	0,56	15	5,794	8,479	**0,001**
Reduced model	0,53	6	5,3647	22,883	**0,001**
~ Coniferous tree density + Ellenberg F + Ellenberg F + Ellenberg N + Vascular plant richness + Moss richness					

Constrained axes of the dbRDA models

In the reduced dbRDA model of genera composition, the first 6 constrained axes were significant ($p < 0,05$). CAP1, CAP2 and CAP3 captured the main environmental gradients by explaining 69% of the total constrained variation. Of the total variation in the data (both constrained and unconstrained), this corresponded to 20% (table 8). The biggest contributions to CAP1 were Ellenberg L, plant richness and moss richness (30%, 19% and 13%, respectively). For CAP2, the biggest contributions were Ellenberg N, leaf N-content and leaf C-content (32%, 16% and 14%,

respectively). For CAP3, the biggest contributions are Ellenberg F, moss richness and vegetation height (58%, 16% and 9%, respectively).

In the reduced dbRDA model of guilds composition, only the first 2 axes were significant (both $p < 0,001$; table 8). CAP1 captured the main environmental gradients itself and explained 82% of the full constrained variation, while adding CAP2 increased the constrained variation to 94%. CAP1 and CAP2 together explained 50% of the total variation in the data. The contribution to CAP1 was mainly from Ellenberg L, plant richness and moss richness (39%, 24% and 19%, respectively). For CAP2, the main contributors were Ellenberg N, moss richness and plant richness (74%, 21% and 4%, respectively).

Overall, most of all constrained variation was captured in the first two or three axes of the dbRDA models. For the functional dbRDA model, CAP1 and CAP2 explained 94% of constrained variation, in which dissimilarities were widely two-dimensionally explained, whereas more dimensions/axes were required to capture the same high amount of the constrained variation for the genera dbRDA model (first three axes = 69%). In both models, CAP1 mainly consisted of contributions from Ellenberg L, plant richness and moss richness, whereas contributions to CAP2 varied between the models, though Ellenberg N was shared.

Table 8: Summaries of the three first canonical axes (CAP1, CAP2, CAP3) of best-performing models (dbRDA) for describing the fungal community structures between sites. The table includes both the model on fungal genera composition and the model on fungal functional groups. The table shows the variance explained by each axis, along with the corresponding F-statistics and p-values.

	Genera			Functional Groups		
Axes	Variance	F	P	Variance	F	P
CAP1	43,284	16,4257	**0,001**	4,4072	112,7941	**0,001**
CAP2	22,868	8,6781	**0,001**	0,6588	16,8605	**0,001**
CAP3	18,191	6,9032	**0,001**	0,1652	4,2268	0,070

Note: For all variables, df = 1. Bold values show statistically significant results ($p < 0,05$). Models were selected on forward-stepwise permutation tests.

Visualising constrained ordination and variance

Visualisations of the fungal dissimilarity matrixes in dbRDA plots, overlayed only with the significant predictors from the PERMANOVA test (table 6), revealed how habitat types and plant community gradients specially distributed and correlated. For genera composition, the clustering of habitat types in the dbRDA ordination's two first axes (figure 6A) appeared like the passive PCoA ordination clustering. For the dbRDA ordination of functional group composition (figure 7), the first axis displayed the habitat types mirrored vertically to the PCoA ordination. However, it became visually clear how late successional communities were affected by increasing Ellenberg F and moss richness, whereas early communities were affected by increasing Ellenberg L and plant richness and how different functional groups associated differently to the ordination (figure 7).

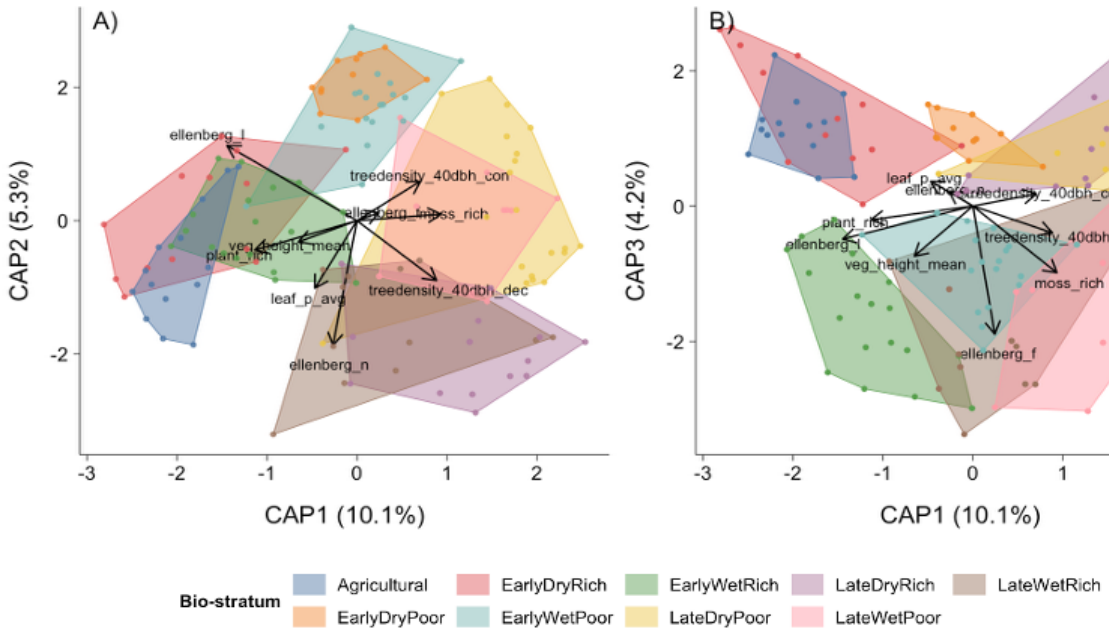

Figure 6: Distance-based redundancy analysis (dbRDA) ordination plots illustrating the beta diversity between sites, based on differences in fungal genera composition. A) illustrates the ordination on CAP1 and CAP2. B) Illustrates the ordination on CAP1 and CAP3. Points represent sampling sites, coloured by habitat types. Polygons outline sites that shares the same habitat type .Black arrows indicate the significant plant-derived variable gradients from the PERMANOVA test (table 6). Axis labels include the percentage of explained variation for each canonical axis.

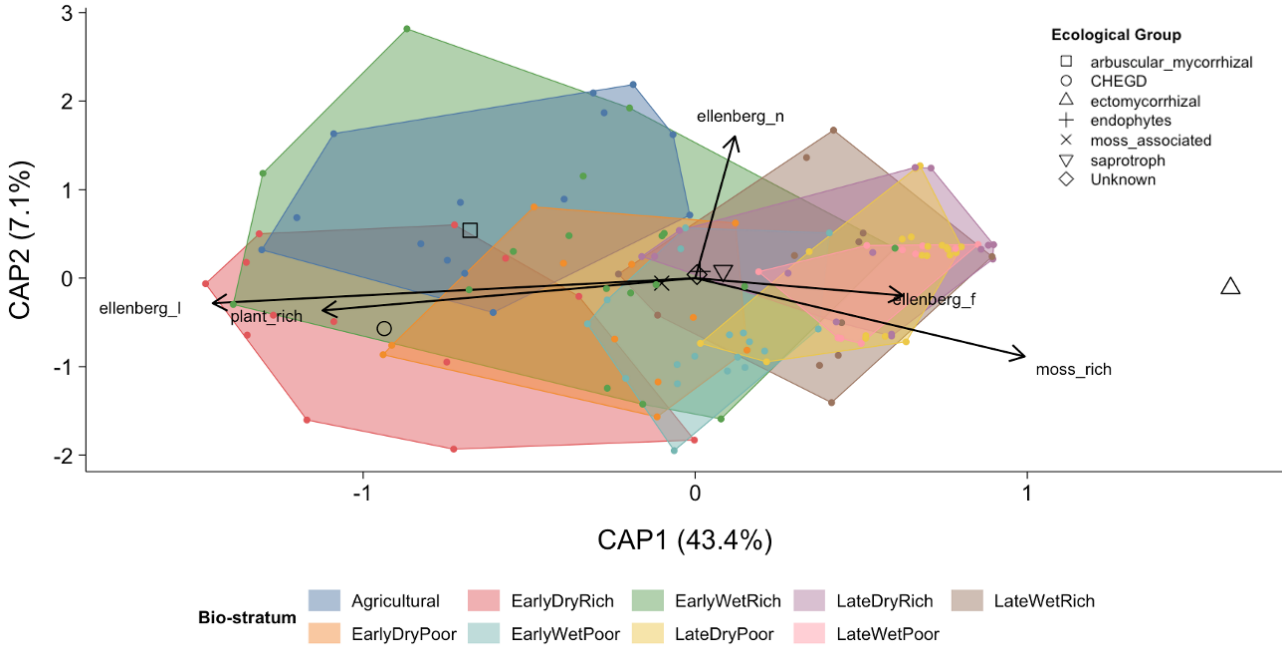

Figure 7: Distance-based redundancy analysis (dbRDA) ordination plot illustrating the beta diversity between sites, based on differences in the composition of fungal functional groups. Points represent sampling sites, coloured by bio-stratum categories. Polygons outline sites that shares the same bio-stratum. Black arrows indicate the significant plant-derived variable gradients from the PERMANOVA test (table 6). Axis labels include the percentage of explained variation for each canonical axis. Symbols represent the functional groups of fungi.

Functional groups association to dbRDA ordination and responses to main gradients

The functional groups that significantly correlated with the functional dbRDA ordination (figure 7) were CHEGD, EcM, AM, moss associated fungi and the unknown group of OTUs (all $p < 0,02$), whereas saprotrophs and endophytes did not. Considering CAP1, The CHEGD and AM fungi followed the gradients of increasing Ellenberg L and plant richness, whereas EcM followed increasing Ellenberg L and moss richness. The group of moss associated, saprotrophs, endophytes and unknowns clustered in the centre of the plot (figure 7).

When depicting the relationship of functional groups along Ellenberg L, the EcM fungi and saptrotrophs abundances generally decreased with light availability, whereas the CHEGD, AM and moss associated increased. Endophytes peaked in middle values. Along Ellenberg N, EcM, AM, saprotrophs and endophytes generally increased with nutrient availability, whereas CHEGD generally decreased. The moss associated peaked within middle values. All groups increased with plant richness besides the ECM fungi (figure 8, figure 9).

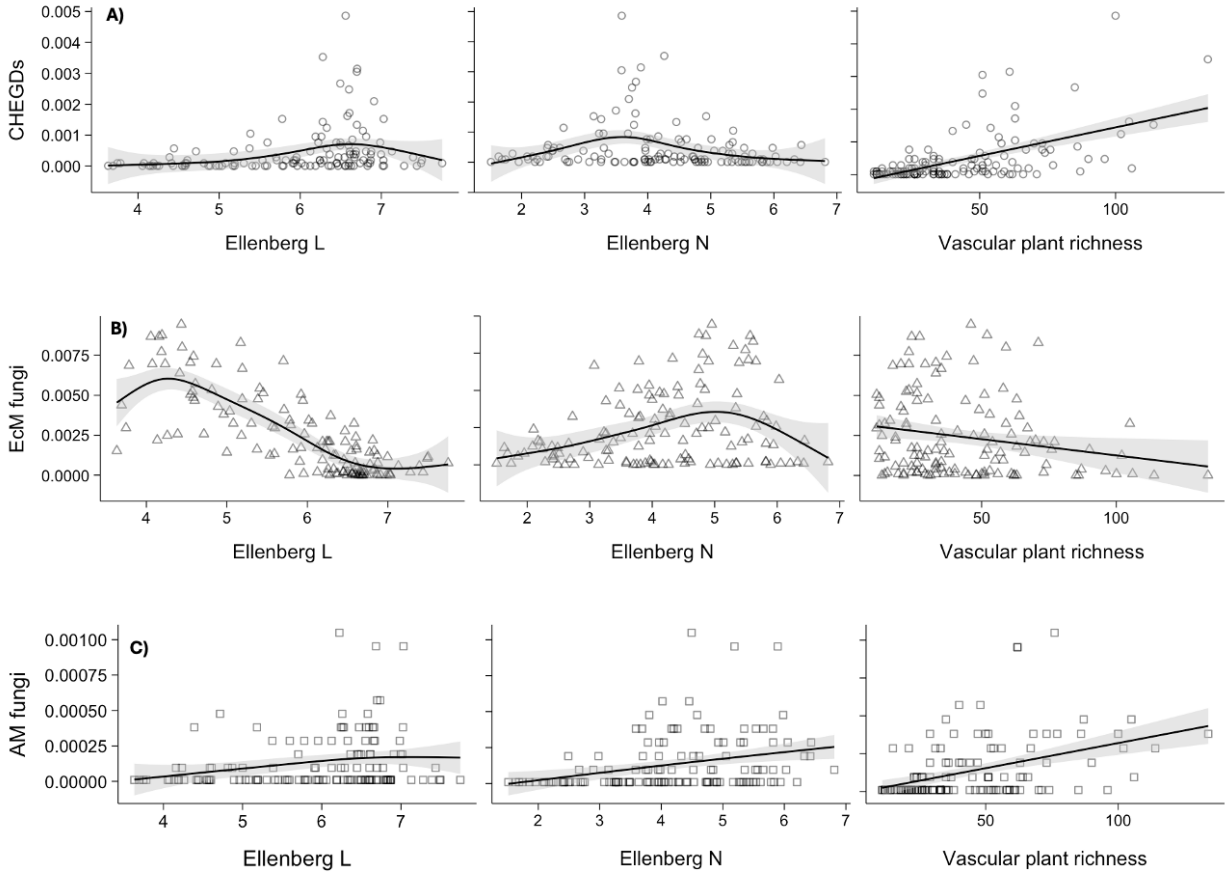

Figure 8: The relative abundance of A) CHEGD, B) EcM fungi and C) AM fungi along the gradients of Ellenberg L (left), Ellenberg N (middle) and vascular plant richness (right). Symbols refer to the functional group from figure x. Fitted tendency curves are chosen on the lowest AIC-level between different modelled fits.

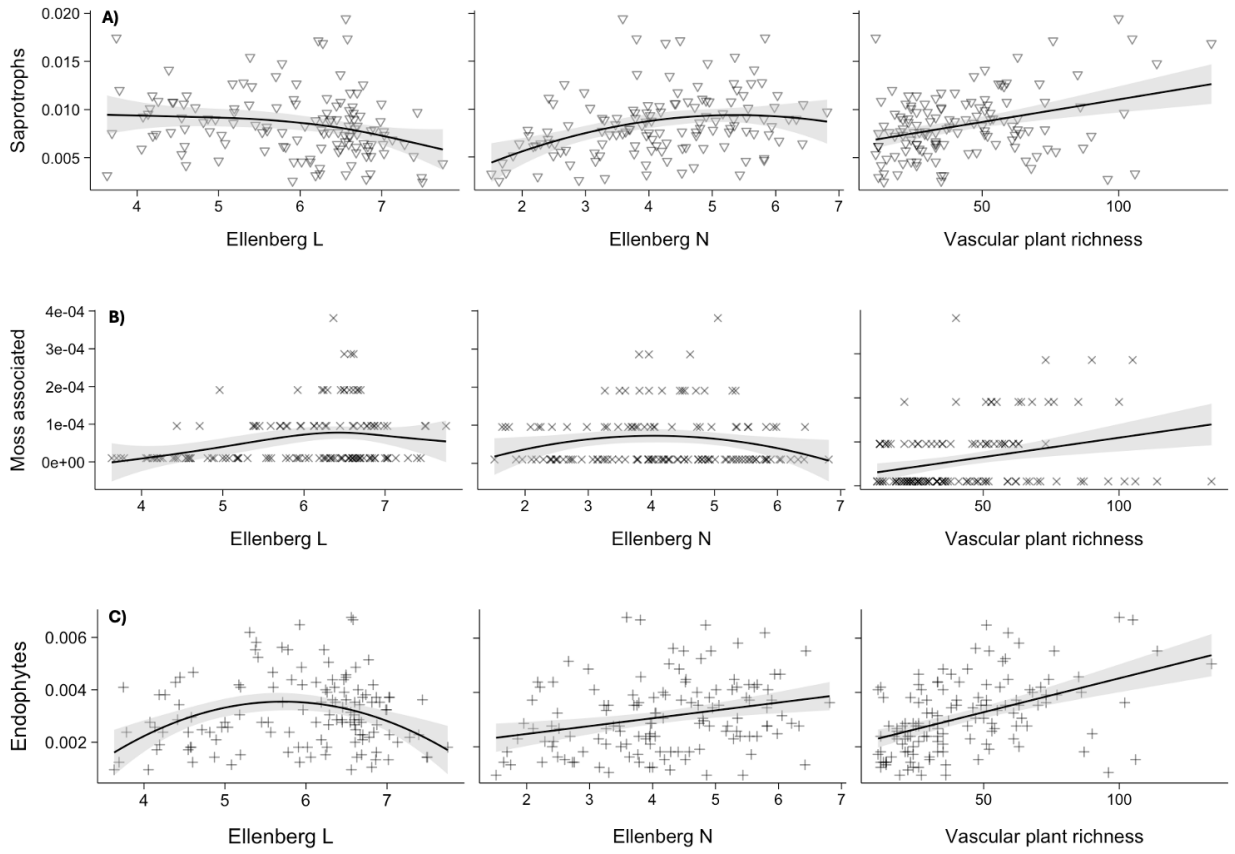

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Figure 9: The relative abundance of A) Saprotrophs, B) Moss associated fungi and C) Endophytes along the gradients of Ellenberg L (left), Ellenberg N (middle) and vascular plant richness (right). Symbols refer to the functional group from figure 7. The fitted regression curves were determined from the best explained relation between functional group and the response.

The added effect of bio strata to dbRDA models

The global PERMANOVA tests showed significant association of habitat on both dissimilarity matrixes (appendix, table A2). However, when conditioning the global PERMANOVA tests by the predictors in the two reduced dbRDA models, bio strata were only still significantly associated with the genera dissimilarity matrix ($R^2 = 0{,}076$, $p < 0{,}001$) but not with the functional dissimilarity matrix ($R^2 = 0{,}039$, $p = 0{,}183$). Thereby, bio strata expressed variance in the turnover on genera, but the variance was already covered in the model variables regarding functional turnover.

Overall, this indicate that the habitat types reflected the variation that the continuous plant community variables in the ordinations covered for functional groups. Hence, the habitat types did not add more meaningful explained variation to the ordination. For the ordination on genera however, the habitat types still explained some variation that was not covered in the continuous variables.

Discussion

Averaged across the whole dataset, of the top 10 most occurring genera, 8 were also the most species rich ones, with *Cortinarious* and *Mortierella* among the top (appendix, figure A3). Such abundant taxa is somewhat consistent with literature. Bahnmann et al. (2018) reported a comparable pattern of abundant genera, including *Cortinarious*, *Mortierella, Tomentella, Mycena, Russula* and *Umbelopsis,* in Central European forests. Furthermore, Lepinay et al. (2024) found five of the families, in which the top 10 genera are nested within, to be the most abundant across Central European grasslands.

H1: habitat type is a strong predictor of fungal diversity and community composition

The differences among alfa diversity and habitat types (figure 4) along with the post-hoc analysis of habitat association with the dissimilarity matrixes, partially confirmed that habitat type is a predictor of fungal community structures.

The alpha diversity was significantly different among several of the bio strata, revealing that diversity and evenness of the genera differ among the habitat types. The late successional habitat types expressed high alpha diversity along with the EarlyDryRich habitat, whereas the EarlyDryPoor, EarlyWetPoor and EarlyWetRich expressed lower (figure 4). High fungal diversity status within grasslands have often historically been linked to high diversity of the CHEGD fungi, acting as indicator species for general high diversity and unfertilised conditions (Griffith et al., 2013). As the biggest fraction of CHEGD also existed within EarlyDryRich (table 3), the link was also present in this study. Regarding the late successional forest habitats, high fungal diversity has widely been linked to structural complexity caused by trees, in where the biodiversity potential increase with e.g disturbance and diversification of tree species, age classes, dead wood decay stages and dead wood structures (Goldmann et al., 2015; Heilmann-Clausen & Christensen, 2003; Tedersoo et al., 2016).

Especially the LateDryRich habitat type expressed high H'. Conversely, the early successional habitats expressed more variation in H', evaluated from bigger interquartile ranges, though they were still significantly different from other habitat types (figure 4). This indicate that diversity and evenness varied from site to site more than it did within the LateDryRich habitats. Such variation could reflect many different things. Firstly, it could reflect that the early successional habitats vary in other abiotic and biotic conditions, as this was not investigated in the thesis. Secondly, it could reflect that the fungal communities are more influenced by stochastic processes than the late successional habitats, leading to uneven dominance of taxa in some of the sites. Thirdly, different management practises could affect alpha diversity greatly in grasslands. Management strategies were not investigated in this thesis, but fungal diversity could be altered trough the coupling with the plant community. Different grazing pressures, species of grazer and grazing seasonality schemes

have proved to affect plant richness and composition in grasslands, with a general positive effect of moderate grazing compared to no grazing (Benthien et al., 2018; Bonavent et al., 2023; Herrero-Jáuregui & Oesterheld, 2018). I this thesis, plant diversity was positively linked to fungal alpha diversity (figure 5) indicating that different management regimes could potentially affect the diversity of fungi in grasslands. However, this would have to be tested formally and is only a hypothesis. Nonetheless, despite greater variations in H' in the early successional habitats than in the late, H' was significantly different between habitat types overall, and many habitat types were pairwise significantly different from each other. Hence habitat was a strong predictor of alpha diversity.

Regarding beta diversity, the habitat types showed a significant association with both beta diversity matrices ($p < 0.001$). However, dispersion tests were also significant in both cases, which consequently affect the interpretation of these results. Therefore, it cannot be ruled out that the observed associations were partly due to differences in dispersion. Dispersion was generally lower in nutrient poor habitat compared to nutrient rich habitats (appendix, table A2). Despite this, visual inspection of the PCoA ordination of genera (Figure 6A) indicated a distinct clustering of at least groups of habitat types, even with uneven dispersion, especially of rich versus poor habitats as well as early versus late habitats. For the PCoA of functional dissimilarities however, the late and early communities clustered in opposite directions, but rather as gradual change instead of distinct change between the habitats. Hence, the hypothesis of habitat association to beta diversity cannot be accepted, especially considering the functional dissimilarity matrix, as the changes in that were more gradual than distinct.

The partial dbRDA models that evaluated the unique variation explained by habitat types, when conditioning the continuous significant variables, revealed the interconnectedness between habitat types and plant community traits; habitats only explained unique variation in dissimilarities of fungal genera composition and not in functional compositions. Thus, the variance within habitat types was coved by the continuous predictors in the dbRDA model on functional community composition. It reflects, that the classification scheme of the habitat types (combining succession, moisture availability and nutrient availability) was successful. As a result, habitat types could mostly be used to visualise habitats, rather than acting as a predictor to avoid strong correlations and circularity with other predictors.

Summarising the hypothesis: habitat type was a strong predictor of alpha diversity but not beta diversity. Habitat types were significantly associated with both dissimilarity matrixes, but visual inspection questioned this; habitat types in the PCoA of genera composition appeared to separate communities by succession and nutrient status but did not separate all habitats distinctly from each other. Visual inspection of habitat types in the functional composition PCoA ordination concluded that the habitat types overlapped greatly along a gradiental appearance. Additionally, the variance explained by the habitat types was covered by the continuous plant community variables in the functional community composition, and the beta dispersion was uneven within habitat types of both

dissimilarity matrixes. Consequently, the hypothesis that habitat type is a strong predictor of fungal community composition and turnover cannot be accepted. However, it was better for the genera dissimilarity matrix, and groups of habitat types could potentially reveal more distinct fungal communities than these nuanced habitat types.

H2: Plant community traits explain fungal richness, community composition and turnover

The hypothesis that both alpha and beta diversity expressed relatedness to plant community traits was highly confirmed. The full model of alpha-diversity explained 71% of the variance, which was only decreased to 70% in the reduced model. For beta diversity, several predictors individually explained a significant proportion of variance in fungal dissimilarities, both when quantifying the fungal community by genera and functional traits. Specifically, all plant predictors in the dataset captured 56% of the functional variance and 31% of the genera variance, which was only reduced to 53% and 28%, respectively, in the models from model selection. However, the unconstrained variance remains unexplained by the plant community traits explored.

The PERMANOVA results of significant drivers on fungal community composition were all included in the best reduced models on beta diversity, while the models also included trending plant community variables. The plant community traits that were shared between the alpha diversity model and the two beta diversity models were Ellenberg F, L and N along with vascular plant and moss richness, indicating the special importance of these traits for understanding fungal communities. It emphasises that fungal alpha and beta diversity responds to the same environmental gradients as plant communities, but also that both alpha and beta diversity is strongly correlated to plant richness. Forest attributes (mainly coniferous and deciduous tree densities) were also included across the models, indicating that forest structures capture unique variance in both diversity and composition when analysed across different successional habitat types. The model on genera community composition furthermore caught relations to leaf chemical traits of both C, N and P, indicating that certain genera, rather than functional groups, change in prevalence by these traits. Pellissier et al. (2014) found that in Swiss grassland ecosystems, nitrogen availability, soil moisture and plant richness also correlated to beta diversity of fungi, though the beta diversity measures were defined differently. Furthermore, their investigation was constricted to grasslands only, in which a successional gradient was not present, which explain why light availability and forest structures were not important for their study. Mulder and de Zwart (2003) found forest fungal communities driven by decreased light, increased moisture and varyingly to nutritional status, which is the same pattern for the late successional communities in the dbRDA model for functional composition (figure 7). Hence, the evaluated important drivers are consistent with other studies.

H' was revealed to decrease with light and moisture and increase with nutritional status, density of deciduous trees, vascular plant richness and moss richness (Table 5). Mulder et al. (2003) also found fungal diversity to increase with nutritional status and decrease with light and moisture,

agreeing to the alpha diversity patterns found within this thesis. The relationship with light could reflect how H' generally increases from grasslands to forests. This interpretation would be consistent with the positive correlation to deciduous tree density and the general high levels of H' in the late successional habitats compared to the early habitats (figure 4). In forests, high fungal diversity has widely been linked to structural complexity caused by trees, with which the biodiversity potential increase with e.g. disturbance and diversification of tree species, age classes, dead wood decay stages and dead wood structures (Goldmann et al., 2015; Heilmann-Clausen & Christensen, 2003; Tedersoo et al., 2016). That the fungal diversity and evenness increase with nutritional status could reflect an increased nutrient availability overall, allowing more fungal species to meet their habitat requirements - the saprotrophic fungi constituted most of the dataset, and as the abundance of saprotrophs increased with nutritional status, this could explain why the general alpha diversity increased with Ellenberg N.

The positive relationship between plant richness and fungal alpha diversity, as consistent with e.g. Pellissier et al. (2014), could reflect that high plant richness increase the potential for specialist associations; high diversity complexifies niches and resources available, accordingly to Waring et al. (2015). This connection was also made by Finck et al. (2025), and Cline et al. (2018) found high fungal diversity linked to both high biomass and high plant diversity in grasslands, from which they hypothesised that high fungal diversity was rather a function of high substrate availability than plant richness itself. The ordination of functional composition (figure 7) supports the hypothesis of community specialisation with increased plant richness, at the position of the CHEGD fungi, that are perceived as specialised fungi (Griffith et al., 2013) followed the direction of plant richness. Thus, the early successional habitat would exhibit more specialised communities than the late communities.

Summarising, both alpha diversity and the two dissimilarity matrixes demonstrated significant associations with the plant community, following abiotic gradients of light, moisture and nutrients and biotic gradients of vascular plant and moss richness along with forest structures. Generally, alpha diversity increased with nutrients and taxa richness, whereas it decreased with light and moisture. Functional community composition was explained mainly by two dimensions with light and plant richness in one direct, moisture and moss richness in the opposite direction, and Ellenberg N directing the second axis. For the genera composition, the variance was more complex than simplified into two dimensions. Plant community traits explained the composition differences in more complex ways.

H3: Functional groups relate differently to plant community traits.

The hypothesis stated that functional groups relate differently to plant community traits were overall confirmed. The dbRDA analysis revealed that the AM, CHEGD, EcM and moss associated fungi were distributed in different directions of the two main axes, away from the centre (figure 7).

This is a direct result of differentiated responses to the plant community traits defining the two main axes (Ellenberg N, L, F and moss and vascular plant richness). Figure 8 and 9 illustrated how the prevalence of the functional groups correlated to the plant community traits Ellenberg N and L and plant richness with differently – with certain optima revealed for some of the groups.

However, no significant association was observed with axes of the functional dbRDA ordination and the guilds of saprotrophs and endophytes. When visualising their abundances to Ellenberg N and L in a scatterplot (figure 9), both guilds expressed high variability in the data and a non-linear response to either Ellenberg N or L. A dbRDA ordination only evaluates linear responses. Therefore, a linear regression of non-linear responses with data that are more spread out than the other guilds, can result in missing signals, which potentially is the explanation in this case.

The expectations to the response of EcM and CHEGD were confirmed; EcM abundances decreased with light, whereas the CHEGD increased, revealing oppositional niches for the two groups. Ellenberg L serves as a proxy shaded conditions that are reflected in plant communities with optima at low Ellenberg L values. Hence, the EcM fungi do not respond to the low light conditions but rather the trees the create the shade (Rosinger et al., 2018), but Ellenberg L were a stronger predictor depicting this association than the measures of tree species, coniferous density and deciduous density. However, the EcM relative abundance of 11-18% in the low-light habitats (table 3) was still lower than reported abundances by Likulunga et al. (2021) where abundance reached 30-50% in beech, douglas-fir and spruce plantations in Europe. Hence, differentiated local conditions and parameters not measured in this thesis could account for that variation.

For the CHEGD, their optimum at Ellenberg L ≈ 6,6 reflect their shared ecological niche with light adapted plant species communities. With their optimum at Ellenberg N ≈ 3,5 and their positive relationship with species richness, the data supports an ecological theory that the CHEGD fungi occur at oligotrophic to mesotrophic grasslands with high vascular plant species diversity (Griffith et al., 2002).

Overall, most functional groups significantly associated with the dissimilarity dbRDA ordination. Especially the EcM, AM and CHEGD fungi revealed distinct patterns according to plant community traits in different directions. All groups increase with plant richness except EcM fungi. All groups increased with Ellenberg N, despite CHEGD and moss associated that revealed optima at intermediate conditions. Furthermore, different relations to Ellenberg L were revealed, and the sub-hypothesis regarding EcM and CHEGD fungi was confirmed; CHEGD fungi increase with light, whereas EcM decrease.

Conclusions

Plant community traits were successfully able to predict the fungal alpha and beta diversity. Alpha diversity showed strong correlation to abiotic Ellenberg conditions N, L and F along with biotic measures of vascular plant richness, moss richness and deciduous tree density. Fungal turnover was most strongly correlated to plant community traits at a functional level. However, for both the level of genera and functional composition, Ellenberg values N, L and F, vascular plant and moss richness along with tree densities were significantly associated. Furthermore, plant chemical traits of C, N and P also drove community turnover significantly, but only for the composition of genera.

I found that the alpha diversity was significantly different between habitat types, in which habitat types can predict fungal diversity. Community compositions were different between habitat types, but the variation within each habitat type varied, in which communities were not conclusively distinct from each other, in which habitat types were not great predictors for community differences, whereas the continuous plant community traits were better at depicting gradiental changes.

Community turnover of functional groups revealed differentiated responses to Ellenberg L, F, N and plant richness. Most notably, CHEGD and AM fungi abundances increased with light and plant richness, whereas EcM fungi exhibited the opposite pattern. AM and EcM fungi exhibited increasing abundances with nutrient status, whereas CHEGD fungi decreased with nutrient status.

Though I found many significant associations between fungal diversity and community composition to plant community traits, variation remained unexplained, which emphasise that plant communities can only partially explain fungal communities. A comparative study that includes other abiotic factors could investigate other intricate drivers' influence on fungal communities and is encouraged.

Future research

The exact relationships of the abundances of each functional group to plant community drivers could be characterised more accurately by modelling each functional group distinctly from each other, as an addition to whole community modelling achieved via dbRDA models. This would allow the detection of non-linear responses of each group of environmental drivers.

The association between plant communities and fungal communities were investigated via quantified methods here. However, further insight could be gained by analysing the relation between a beta diversity matrix of the plants and the beta diversity matrix of the fungi to see, whether the patterns correlate with each other. In addition, investigating the turnover rate of the fungal communities to the plant community traits may reveal whether turnover changes gradually along plant-community gradients or whether it accelerates at particular points. Generalised dissimilarity models could be used to investigate this perspective (Ferrier et al., 2007). All plant

community variables in the thesis were investigated without considering interactions between variables. Hence, interactions among the predictors could potentially add to the analysis.

Finally, to characterise fungal diversity patterns across all of Denmark, alpha and beta diversity models could be used to make spatial predictions on fungal diversity, community composition and community turnover across Denmark. These predictions could be evaluated and verified using observational data from existing databases.

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Appendix

Table A1: Variance inflation factors (VIF) for all candidate variables evaluated prior to data analysis and model fitting. Variables with VIF values that exceeded 5 were excluded in the screening and are not included in the table.

Variable name	VIFs
Moss cover	2,080903
Vegetation height	1,530627
Leaf C-content	1,887112
Leaf N-content	2,734596
Leaf P-content	2,751474
Flower volume	1,641241
Volume of dead wood	1,699779
Density of deciduous trees	1,562861
Density of coniferous trees	1,488682
Tree species	2,469912
Ellenberg F	2,934089
Ellenberg L	3,461898
Ellenberg N	4,576610
Plant richness	1,701945
Moss richness	2,196147

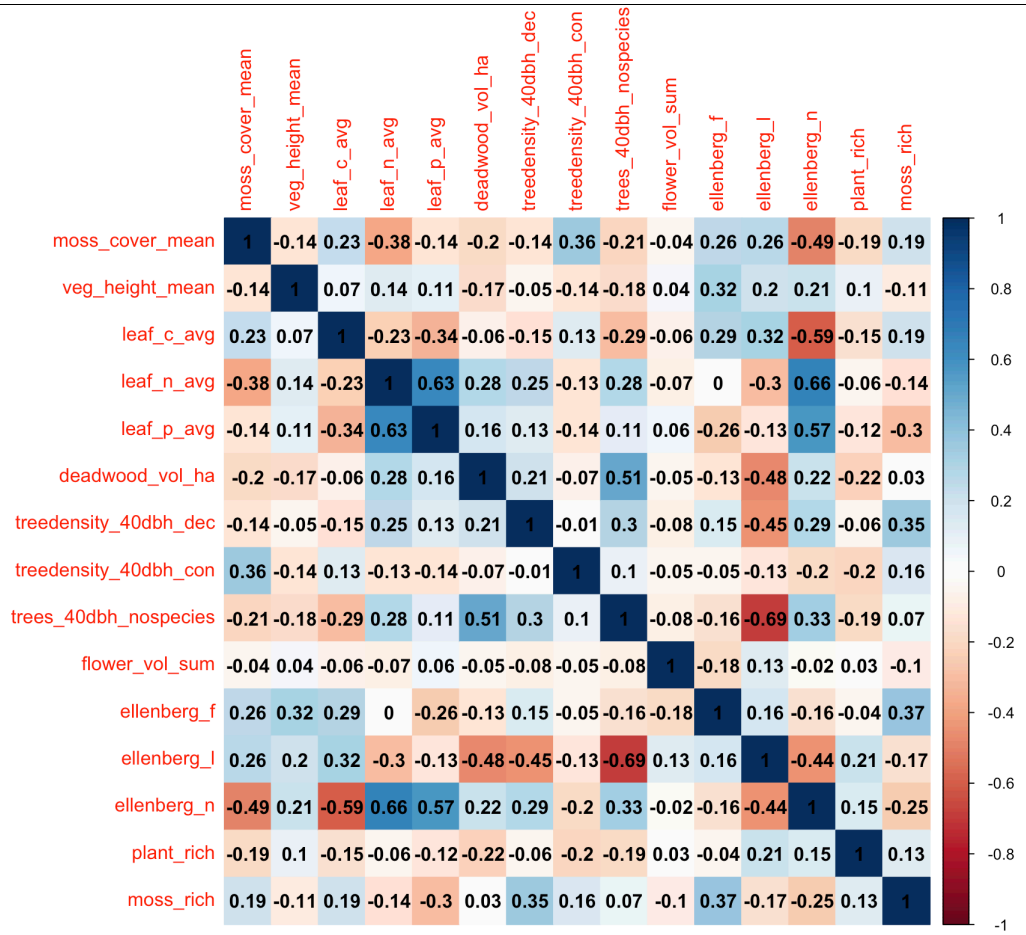

Figure A1: Heatmap showing pairwise Pearson correlations (r) among the selected variables (coefficiencts between 0,69 and -0,69), evaluated prior to data analysis and model fitting. In correlations where r > 0,7 or r < -0,7 one of the variables were removed. Correlation coefficients are shown as numbers on the plot.

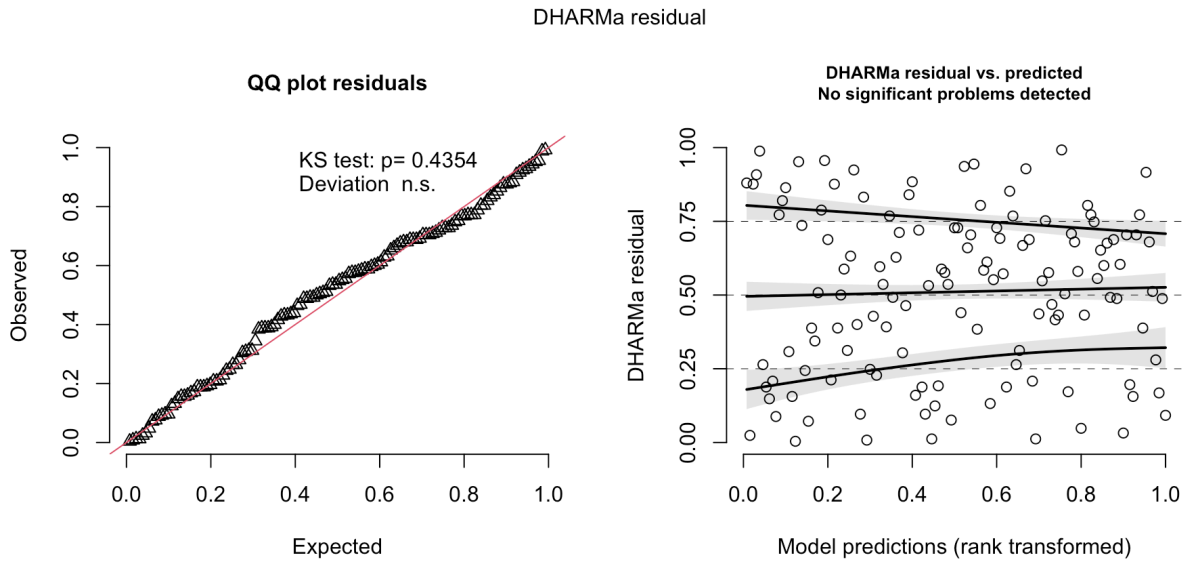

Figure A1: DHARMa QQ plot of residuals and predicted values vs. residuals of the model on alpha-diversity: Shannon ~ treedensity_40dbh_dec + litter_mass +Ellenberg_f + Ellenberg_l + Ellenberg_n + plant_rich + moss_rich

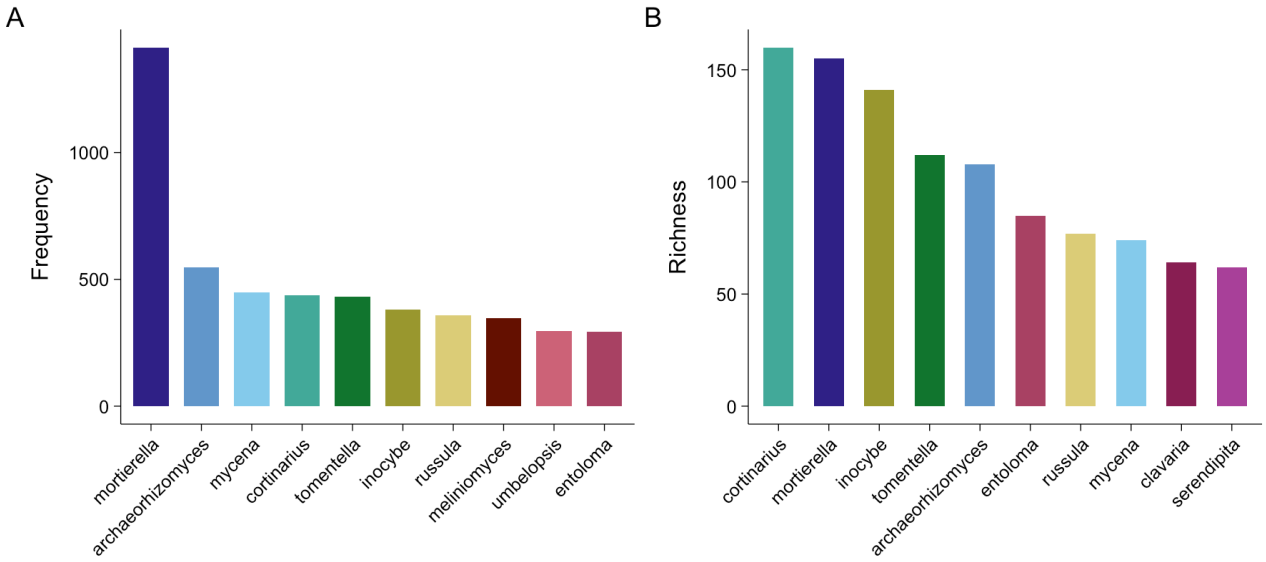

Figure A3: The 10 most frequent fungal genera (A) and 10 most diverse fungal genera (B) across the 130 sampling sites. Panels are sorted by decreasing frequency and richness, respectively. Frequencies in (A) were calculated as the sum of presences of a genus across all sites. Richness in (B) was calculated as the sum of unique OTUs in a genus. Bars are colour-coded by genus with identical colours indicating genera present in both panels.

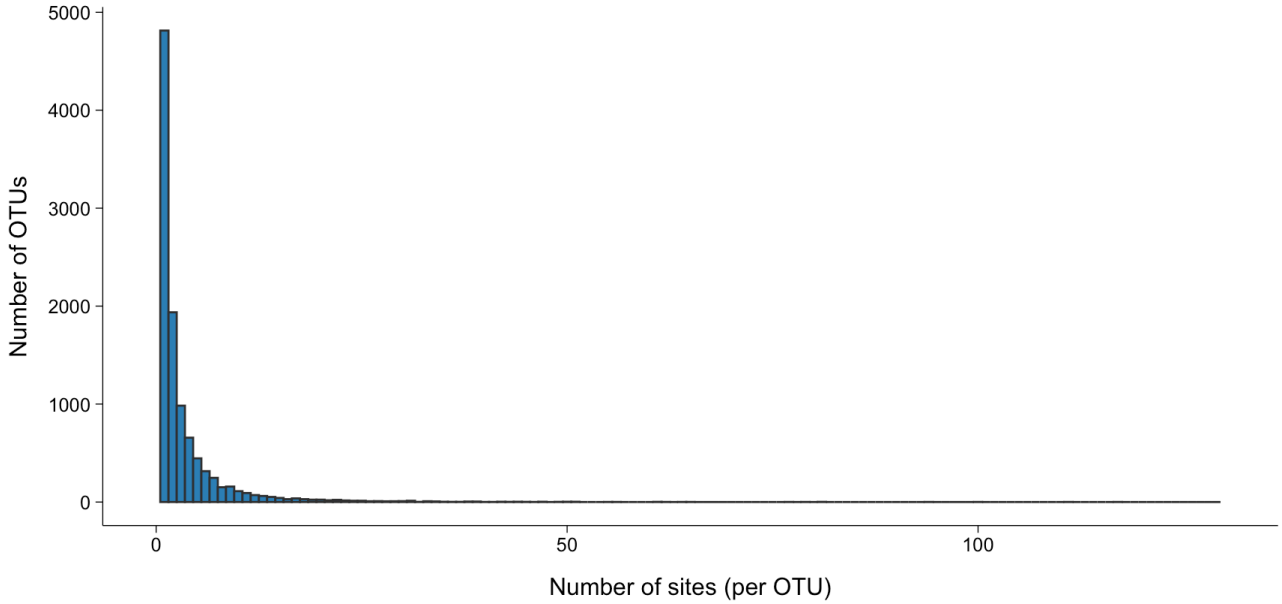

Figure A4: Histogram The number of OTU with repect to the number of times, they appeared in the dataset.

Table A2: Group-wise multivariate dispersion (distance to group centroid) by bio-stratum for two data representations: community composition of ecological functions (left) and community composition of genera. Values were extracted from the betadisper test of bio strata on the distances matrixes. Table includes mean distance values and standard deviation

Bio stratum	Ecofunc (mean ± sd)	Genera (mean ± sd)
Agricultural	2,328 ± 0,624	17,732 ± 1,641
EarlyDryPoor	2,129 ± 0,825	14,997 ± 3,218
EarlyDryRich	2,468 ± 1,038	19,342 ± 2,452
EarlyWetPoor	1,821 ± 0,609	15,670 ± 3,537
EarlyWetRich	2,713 ± 1,307	18,180 ± 2,405
LateDryPoor	1,586 ± 0,880	17,207 ± 2,757
LateDryRich	1,961 ± 0.810	19,624 ± 2,407
LateWetPoor	1,714 ± 0,424	17,085 ± 3,029
LateWetRich	2,246 ± 0,491	20,270 ± 1,641