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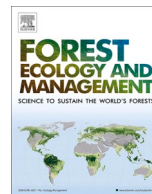
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Standing at the crossroads: Path analysis highlights potential levers to preserve fungal richness when shifting tree species for forest adaptation

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ABSTRACT

Tree species risk living outside their ecological niche due to climate change. Assisted tree migration is proposed as an adaptive strategy, but its impact on forest biodiversity remains unclear. This study examines soil fungal diversity responses to tree species substitution (that is to say clear-cut of a stand and plantation of a different tree species) and its underlying mechanisms. Three substitution treatments were tested across 69 stands in Northern France: (1) from mature *Fagus sylvatica* to young *Quercus petraea*, (2) from mature *Pinus sylvestris* to young *P. nigra* subsp. *Laricio*, and (3) from mature *P. sylvestris* to young *Q. rubra*. Holorganic and organo-mineral horizons were sampled to assess Ascomycota and Basidiomycota species richness with eDNA metabarcoding. Tree species identity was translated into trait values along the plant economic spectrum. Structural Equation Models (SEM) were used to separate the effects of tree traits, stand age, basal area and tree diversity on fungal diversity across four pathways: (1) stand structure, (2) edaphic humidity, (3) plant understorey (cover of dominant plant species and species richness), and (4) humipedon using variables describing the horizonation process of the holorganic horizon. After 25 years, Ascomycota and Basidiomycota richness did not respond to substitution treatments. SEM analyses showed that Basidiomycota richness in the organo-mineral horizon correlated positively with acquisitive tree species. Ascomycota richness was negatively linked to dominant understorey cover, following canopy openness and humipedon horizonation. In the organo-mineral horizon, Ascomycota richness increased with root nitrogen and wood density, spontaneous tree diversity and was favoured by reduced basal area related to stand rejuvenation. Forest management that promotes spontaneous tree diversity and reduces basal area could enhance Ascomycota richness in both horizons, mitigating the impacts of tree rejuvenation and species change.

1. Introduction

Climate is one of the major factors shaping tree ecological niches (Hutchinson, 1965; Booth et al., 1988). With climate change, tree species face the risk of locally losing their suitable climatic niches. Some tree species may neither have the genetic adaptive potential nor the dispersal ability to migrate as swiftly as climate changes (Davis and Shaw, 2001), with a strong risk of forest decline as evidenced in *Picea rubens* plantations (Cook and Johnson, 1989). To help forests adapt, assisted migration — where non-native tree species or varieties are planted — is an increasingly common adaptive forestry practice (Spittlehouse, 2005; Jandl et al., 2019). However, the risks related to assisted migration such as maladaptation, spread of invasive species and local biodiversity loss remain understudied (Xu and Prescott, 2024).

The response of native fungal communities to the introduction of tree species adapted to climate change is particularly important. Fungi encompass diverse trophic guilds (saprotrophs, pathogens and mutualists) sustaining forest ecosystem functioning. Saprotrophic and ectomycorrhizal fungi (EMF) are vital for nitrogen (N) and phosphorus (P) availability for plant growth, and strongly contribute to shape humus forms (Ponge, 2003; Trap et al., 2011a; Tedersoo and Bahram, 2019; Zanella et al., 2022).

Few studies have assessed the impact of tree species substitution on soil fungal community richness, and most of them compare fungal communities in adjacent stands of different tree species without accounting for the potential legacy effects of the pre-substitution tree species (Lofgren et al., 2018). The legacy effect concept refers to the persistent and long-term impacts of a species on abiotic or biotic

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ecosystem properties even after the species removal or inactivity. Legacy can influence the distribution and occurrence of other species (Cuddington, 2011). To disentangle the mechanisms underlying the effects of tree species substitution on soil fungal communities, soil fungal richness should be investigated both in stands similar to the pre-substitution state and in stands following the introduction of new tree species. Moreover, tree substitution research often focuses on the replacement of mature, native broadleaved stands by exotic conifer plantations (Buée et al., 2011; Purahong et al., 2014; Nakayama et al., 2019; Trentini et al., 2020; Mundra et al., 2022). These studies generally conclude that fungal richness is higher in native broadleaf stands compared to exotic conifer plantations. However, such a loss of fungal richness may be reversible. When a conifer plantation is substituted by a plantation of young native trees, fungal richness can increase (Heine et al., 2019, 2021). Studies focusing on less intense substitution, i.e. conifer with other conifers or broadleaf with different broadleaf tree species are less common. For example, no difference in richness was found among stands of different broadleaved species (including young beech) nor among plantations of different conifer species (Buée et al., 2011), excepting for rhizosphere soil fungal richness (Sawada et al., 2021). Conversely, a decrease in fungal richness has been reported when native deciduous forests have been converted to poplar plantation (Vitali et al., 2016). One of the possible mechanisms underlying the lack of consensus about the effect of tree species substitution on soil fungal richness may be the interaction between effects of the rejuvenation by plantation and of the introduced tree species (Buée et al., 2011; Kubartová et al., 2009). Fungal richness can increase after clear-cutting due to the persistence of fungal propagules in soil and the reduced EMF richness being offset by increases in saprotroph and pathogen richness (Varenus et al., 2017; Parladé et al., 2019; Tomao et al., 2020; Rähn et al., 2023). However, the rejuvenation effect is often overlooked as most substitution studies lack a young, rejuvenated stand of the pre-substitution tree species as a control. Such a control is crucial to disentangle the effect of stand rejuvenation from tree-specific effects: the substituted species (legacy effect) and the newly introduced species (substitution effect).

The mechanisms by which the identity of a tree species can influence soil fungal communities may be multiple. Responses can vary with fungal groups, Ascomycota or Basidiomycota richness being favoured independently either by the substituted tree species or by the substitution species, respectively (Mundra et al., 2022). Tree species in a stand may influence fungal communities by serving as their trophic resource, then modification of tree species can influence this trophic source and lead to bottom-up forcing (Ripple et al., 2016) of trees on fungus. Tree-fungi narrowed interactions as mycorrhiza symbiosis, tree-pathogen interaction and endophyte symbiosis often result in fungi host preference or specificity (Zhou and Hyde, 2001). Arguably, this is particularly important for some fungal pathogens, which tend to have a narrow host range, often limited to a few plant species or cultivars (Li et al., 2020). EMF typically have broad host ranges, extending to the family or genus level, with a few counter-examples including family specificity to Pinaceae in the *Suillus* genus (Lofgren et al., 2018). Some EMF can associate preferentially with a specific tree species when various potential tree species are occurring, a phenomenon named fungal preference (Newton, 1991). Saprotrophic fungi may exhibit a preference for specific substrates, a preference thought to be influenced by factors such as nitrogen and tannin content in leaves, as well as the stage of decay (Tokumasu et al., 1994; Frankland, 1998). This preference affects the fungi's association with their host, a phenomenon known as host recurrence, where the fungi's occurrence is dependent on these substrate preferences (Zhou and Hyde, 2001).

Beyond trophic interactions, trees also modify the abiotic environment of soil fungal communities (Jones et al., 1994; Ellison, 2019). Trees create a microclimate under their canopy by retaining atmospheric and soil humidity, but also by solar radiation and rain interception (De Frenne et al., 2019). Amongst trees, individuals express phenotypes,

described by biological characteristics (traits) named effect traits when affecting ecosystem functioning (Violle et al., 2007). For instance, tree leachates, atmospheric contaminant interception, tree mineral nutrition and root exudates are known to modify soil chemical parameters (Riha et al., 1986; Ranger and Nys, 1994; Meessenburg et al., 2009; Joly et al., 2016). Also, specific tree architecture and leaf traits lead to specific light interception that can influence composition and structure of understorey plant communities (Valladares et al., 2016; Balandier et al., 2022). Other effect traits describing litter and wood decomposability are associated with plant mineral nutrition processes or soil organic C dynamics (Aerts, 1999; Freschet et al., 2012). Consequently, by impacting these forest biotic and abiotic compartments (e.g. soil, understorey vegetation, microclimate), change in tree canopy composition may also impact soil fungal richness (Hiiesalu et al., 2017; Li et al., 2019; Lang et al., 2023).

The main objective of this study was to assess the response of soil fungal OTUs richness to tree species substitutions with consideration to several potential confounding effects such as tree species identity, legacy effect and stand rejuvenation. We aimed to understand whether fungal richness responses were directly influenced by forest management practices or indirectly mediated by understorey vegetation. Specifically, we hypothesised that: (i) tree substitution in a context of assisted migration impacts fungal richness in humipedon (i.e. holorganic and organo-mineral horizons), this effect being more important when precedent and current tree species were not both deciduous or both conifers; (ii) the effect of tree substitution on fungal richness can be attributed to both the changes in tree species identity and stand rejuvenation; (iii) these effects on fungal richness can be indirect resulting from changes in humipedon, microclimate and understorey plant communities and (iv) tree species traits explain direct and indirect impacts of tree substitution on fungal richness. To investigate these hypotheses, 69 forest plots were selected from three substitution scenarios in Normandy: (1) from mature *Fagus sylvatica* to young *Quercus petraea*, (2) from mature *Pinus sylvestris* to young *Pinus nigra* subsp. *laricio* and (3) from mature *P. sylvestris* to young *Quercus rubra*, along with young *P. sylvestris* and *F. sylvatica* stands as controls of rejuvenation effect. Fungal communities in holorganic and organo-mineral (OM) horizons of humipedon were investigated by metabarcoding and description of understorey flora, humipedon characteristics and canopy openness were done. The effects of tree species substitution were dissected into four pathways using path analysis: humipedon, canopy openness, understorey plant diversity and stand structure.

2. Materials and methods

2.1. Description of study sites

Our study was carried out in five temperate forests managed by the French National Forestry Office (ONF) in northwestern France along the Seine river (Fig. 1). *Fagus sylvatica* L., 1753 and *Pinus sylvestris* L., 1753 are amongst regionally typical dominant species in forest managed for timber production. The first one is native from the studied area whereas the second is not native but intensely planted for timber production since the beginning of the 19th century (Carlisle and Brown, 1968). From 1990s to 2010s, the ONF experimented their substitution with planted *Quercus petraea* (Matt.) Liebl., 1784 (a native species extensively used for timber production in the considered region) and with planted, European non-native species *P. nigra* subsp. *laricio* Palib. ex Maire, 1928 and the non-European species *Q. rubra* L., 1753. Plantation of these two species has been documented in the area since the beginning of the 20th century. All plantations in this study were 15–35 years old, samplings were conducted in 2020.

Within these forests, all stands chosen for the sampling design displayed similar soil types, all developed on acidic parental material from ancient alluvial deposits of the Seine River and varying from sandy to sandy-loamy texture and with a moderate to high stoniness (Brêthes,

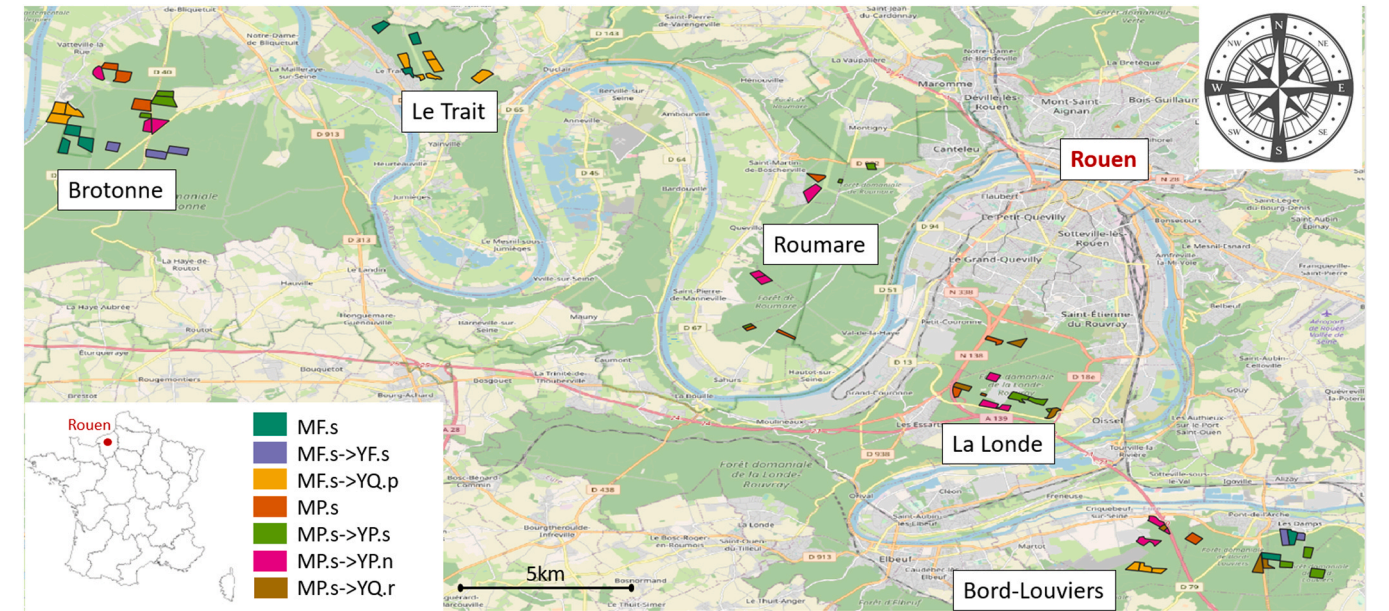


Fig. 1. Map of the studied area indicating the investigated forest stands in the five public forests massif. The Brotonne and Bord-Louviers massif include all treatments. Roumare and La Londe massif include pine substitution treatments. Finally Le Trait massif only include MF.s and MF.s->YQ.p treatments. treatments (MP.s: Mature *P. sylvestris*, MP.s->YP.s: *P. sylvestris* plantation after mature *P. sylvestris*, MP.s->YP.n: *P. nigra* subsp. *laricio* plantation after mature *P. sylvestris*, MP.s->YQ.r: *Q. rubra* plantation after mature *P. sylvestris*, MF.s->YQ.p: *Q. petraea* plantation after *F. sylvatica*, MF.s: Mature *F. sylvatica*, MF.s->YF.s: *F. sylvatica* plantation after mature *F. sylvatica*).

1984). These soil types are particularly prone to increased water deficit under climate change. Eight stand treatments including mature vs. planted stands were studied to disentangle rejuvenation from tree substitution effects. Each treatment was repeated 6–12 times among the studied forest (Table 1).

The sampling design for the substitution over *F. sylvatica* involved mature stands of *F. sylvatica* (9 stands - MF.s), plantations of young *F. sylvatica* (6 stands - MF.s->YF.s) and plantations of young *Q. petraea* (12 stands - MF.s->YQ.p), both after clear-cutting of the precedent *F. sylvatica* mature stand. The sampling design for the substitution over *P. sylvestris* involved mature stands of *P. sylvestris* (12 stands - MP.s), plantations of young *P. sylvestris* (12 stands - MP.s->YP.s), plantations of young *P. nigra* subsp. *laricio* (12 stands - MP.s->YP.n) and plantations of *Q. rubra* (6 stands - MP.s->YQ.r) both after clear-cutting of the precedent *P. sylvestris* mature stand.

In each stand, five circular plots (diameter: 10 m) were defined along

two 40-metres transects crossing on the central plot. These plots were used for DNA sampling, humipeden description and vegetation survey.

2.2. Sequencing of humipeden fungal communities

Environmental metabarcoding was used to describe fungal richness in holorganic horizons (L, F, H) and 0–15 cm organo-mineral horizons (thereafter referred to as “OM horizon”). For each stand, holorganic material and organo-mineral material were separately sampled on a 20 × 20 cm area within the five plots, at more than 2 m away from mature tree, away from dead wood, understorey patch or logging road when possible. They were then pooled as one composite holorganic sample and one composite organo-mineral sample for each stand leading to 69 holorganic samples and 69 OM samples. Tools used for field sampling were washed with soap, then rinsed with 70 % ethanol and allowed to air-dry between each stand to avoid contamination between samples. All samples were stored at 4°C before being processed in the laboratory where the fresh composite samples were homogenised on a 2 mm mesh.

For each sample, total eDNA was extracted with DNeasy® PowerSoil Pro kit (Qiagen) from 250 mg of material, then eDNA concentration was standardised at 10 ng/μl. Molecular barcode locus for fungi ITS2 was amplified, following procedures by Yu et al. (2022), in triplicate PCR using primers ITS3/ITS4 (White et al., 1990) complemented with Miseq adaptors (ITS3-adapted: CTTTCCTACACGACGCTC TTCCGATCTG-CATCGATGAAGAACGCAGC, ITS4-adapted: GGAGTTCAGACGTGTGCTCTTCCGATCTTC CTCCGCTATTGATATGC) then the three amplicons per sample were pooled for sequencing. Amplicon libraries were finalised at the GeT-Biopuces Platform (INSA/TBI Genotoul_Toulouse). The PCR1 were made by adding the sequences of the half Illumina adaptors P5 and P7. The purification was carried out on magnetic beads, followed by quality control of PCR1. The quantity of PCR products was evaluated by nanodrop measure (for all the samples) and the quality on a DNA12000 labchip (Bioanalyzer Agilent only for 12 samples). The PCR2 (addition of the missing half-adapters and indexing) was done with an in-house protocol involving addition by PCR of barcoded (only on the P7) Illumina adaptors to the PCR1. After the PCR1, the same purification

Table 1
Summary of the forest stands used in this study. MP.s: Mature *P. sylvestris*, MP.s->YP.s: young *P. sylvestris* plantation after mature *P. sylvestris*, MP.s->YP.n: young *P. nigra* subsp. *laricio* plantation after mature *P. sylvestris*, MP.s->YQ.r: young *Q. rubra* plantation after mature *P. sylvestris*, MF.s->YQ.p: young *Q. petraea* plantation after *F. sylvatica*, MF.s: Mature *F. sylvatica*, MF.s->YF.s: young *F. sylvatica* plantation after mature *F. sylvatica*.

Treatment	Substituted tree species	Current tree species	Age (years)	Number of replicates
MF.s	-	<i>F. sylvatica</i> , mature	60–150	9
MF.s->YF.s	<i>F. sylvatica</i>	<i>F. sylvatica</i> , young	22–45	6
MF.s->YQ.p	<i>F. sylvatica</i>	<i>Q. petraea</i> , young	19–30	12
MP.s	-	<i>P. sylvestris</i> , mature	68–126	12
MP.s->YP.s	<i>P. sylvestris</i>	<i>P. sylvestris</i> , young	20–33	12
MP.s->YP.n	<i>P. sylvestris</i>	<i>P. nigra</i> subsp. <i>Laricio</i> , young	15–36	12
MP.s->YQ.r	<i>P. sylvestris</i>	<i>Q. rubra</i> , young	23–36	6

and quality control were done and an equimolar pool was made with the four barcoded libraries. The two pools were sequenced in 2×250 bp on a Miseq Illumina device using Miseq Reagent Kit v3 (600-cycle) according to Illumina recommendations producing ca. 25 Mbp of 250 bp, paired-end reads. The demultiplexed fastq files and fastQC were available on the NG6 interface (Mariette et al., 2012).

2.3. Bioinformatic analyses of sequencing data

Bioinformatic analyses were carried out on Linux using the pipeline PIPITS (Gweon et al., 2015). Raw sequences were first dereplicated for calculation efficiency and ITS sequences were extracted with ITSx.

Then, sequences shorter than 100 bp and singletons (unique sequences appearing only once across the dataset) were removed and remaining sequences were subject to chimera detection using the function *pipit_process*. Sequences were then grouped in OTUs using the 97 % similarity default threshold considering the level of intraspecific variation associated with locus ITS2 (Schoch et al., 2012). The assignment was done at the levels of Kingdom, Phylum, Class, Order, Family, Genus and Species using the naive Bayesian RDP classifier (Wang et al., 2007; Abarenkov et al., 2010). The RDP classifier examines the presence or absence of 4-nucleotides words of into target 8-nucleotides words within reference sequences, in this study the fungi-specialised UNITE molecular database UNITE_retrained_27.10.2022 (Kõljalg et al., 2005). All RDP searches were repeated 100 times and a bootstrap threshold of 0.80 was used to balance the number of sequences successfully classified and the reliability of classification.

2.4. Field description of humipedons

Humipedons of the five plots per stand were characterised in a $20\text{ cm} \times 20\text{ cm}$ square using 18 variables visible to the naked eye for holorganic and OM horizons following the methods of Association française pour l'étude du sol (AFES) et al. (2009) and Brêthes et al. (2007); Supplementary material 1). Within plots, sampling points were located away from vehicle tracks, harvesting residues, and tree trunks since they are likely to affect humipedon characteristics, soil biota and humus systems (Aubert et al., 2018).

2.5. Vegetation inventory

In order to assess the effects of vegetation on fungal richness, the vegetation of each stand was described in Spring 2022 following the method by Braun-Blanquet (1932) that emphasises the percent of recovery of each species in a stratum. On each stand, description on the five plots (near 400 m^2 in total) accounted for spatial variability as recommended by Canullo et al. (2020). The following strata were used: ground moss layer, herbaceous layer (all herbs and forbs and woody plants lower than 50 cm), shrubs layer (0.5–2 m and woody plants) and tree layer (woody plants > 2 m). Plants were identified in situ using Rameau et al. (2018), Möhl and Eggenberg (2008), De Foucault et al. (2014) and Hugonnot et al. (2017).

Tree diameter at breast height (DBH) was measured with a Vernier calliper. Canopy basal area and the non-dominant trees basal area were distinguished by graphically classifying DBH in descending (or inverse J distribution), unimodal and bimodal distribution (Rouvinen and Kuuluvainen, 2005) that assess stand vertical heterogeneity. A PCA was then carried on the following variables from the non-dominant stand trees layer in order to deal with multicollinearity: number of stems, tree basal area, tree richness and tree Shannon index. The main axis accounting for 75 % of total PCA inertia and opposing dense and diverse non-dominant stand trees tree layers to scarce and poorly diverse ones was kept (Supplementary material 2).

The understorey was defined as plants lower than two metres including woody ones (De Lombaerde et al., 2021). In order to assess the soil humidity, Julve's edaphic humidity value was retrieved from the

database baseflor (Julve, 1998) for understorey plants. In order to not bias the result with stand target tree species values, they were removed from the dataset. Community mean indicator values for soil humidity were then calculated considering only Presence-Absence of species according to Diekmann (1995).

To reduce the number of variables used for path analysis, the understorey response was summarised in dominant understorey plant species cover and plant specific richness. Some social plant species can dominate both vertically and horizontally the understorey and should represent a great part of its aerial biomass in studied stands. Such dominant understorey plants can modify soil microclimate (Kovács et al., 2017), decrease plant richness by exclusive competition (Decocq et al., 2004) and modify fungal richness (Laperrière et al., 2019). To assess their effect in studied stands, dominant understorey species were defined as follows: they can cover more than 30 % of a plot, are not liana or seedlings and can grow above 0.5 m. Those plants were *Vaccinium myrtillus* L., 1753, *Rubus* sp. and *Pteridium aquilinum* (L.) Kuhn, 1879. They were grouped as dominant understorey plants and their cover sums calculated by plot. The mean cover of those species in each stand was then calculated.

2.6. Canopy openness

In order to estimate the light reaching understorey vegetation, canopy openness was measured using hemispherical photographs taken using a circular fisheye (Sigma 8 mm F3.5 EX-DG) associated with a camera (Canon eos70d). On each stand, a photograph was taken at the centre of each of the 5 plots, the camera's bottom oriented to the north. Photographs were analysed and canopy openness (Diffuse non-interceptance) calculated with R software v4.3.2 (R Core Team, 2021) using the hemisphR package (Chianucci and Macek, 2023). To obtain a unique value for each stand, the mean of the 5 plots was computed.

2.7. Tree species functional traits characterisation

The aim was to separate tree identity effect on fungal richness from tree effect through biotic and abiotic parameters linked to tree characteristics. Consequently, 12 traits from TRY database (Kattge et al., 2011) were selected and related to: i) the species leaf ecologic spectrum: specific leaf area, photosynthesis rate per leaf dry mass, leaf N content per leaf dry mass, leaf P content per leaf dry mass and leaf lifespan (Wright et al., 2004); ii) the species wood economic spectrum: Stem nitrogen content per stem dry mass, Stem specific density and Embolism vulnerability (Chave et al., 2009); iii) the root economic spectrum: specific fine root length and fine root N per fine root dry mass (Liese et al., 2017); and iv) the growth strategies i.e. fast vs slow: life expectancy and seed mass (Reich, 2014). Because of a lack of values for *P. nigra* subsp. *Laricio*, values for *Pinus nigra* and other subspecies were used. The selected traits values were summarised in Supplementary material 3.

In order to use the main components as continuous variables in further analysis, a PCA was done and the two first axes were kept: PCA-Tretraits1 and PCA-Tretraits2. A functional substitution distance (absolute difference in PCA-Tretraits1 between the pre-substitution tree species and the species used for young stands) was also computed.

2.8. Statistical analyses

All statistical analyses were done using R v4.3.2 (R Core Team, 2021). As Ascomycota and Basidiomycota dominate forest humipedon communities (Adamo et al., 2020) and ITS2 region resolution power and amplification is limited for fungal phyla (Schoch et al., 2012) only the influence of substitution on those two phyla was investigated. Differences in OTUs mean taxonomic richness of Ascomycota and Basidiomycota between treatments were tested with a permutational analysis of

variance (PERMANOVA) because of heteroscedasticity using the RVAIdeMemoire package (Hervé, 2023). In order to reduce collinearity and focus on the variables explaining the greater part of humipedon variability, a PCA was done on the humipedon dataset. Humipedons were also classified as humus forms using the *Association française pour l'étude du sol* (AFES) et al. (2009) humipedon classification. A Structural Equation Model (Fig. 2) was then designed using the piecewiseSEM package (Lefcheck, 2016). The SEM was structured using variables that could directly influence fungal richness (Supplementary 4). All initial model paths were designed based on hypotheses drawn from literature (Supplementary material 5). Variables that could mediate the tree main species effect on fungal OTUs richness (Age, Tree canopy basal area, Tree canopy Shannon) were also considered. Moreover, the tree main species effect was decomposed into two functional identity axes derived from the aforementioned PCA. The substitution intensity distance (Dist1 substitution) defined as the distance between the PCA-Treetraits1 values of current tree species and substituted species was also added. Indirect effects were considered through the change of tree layer characteristics (tree basal area of the canopy, thick and diverse second tree layer),

humipedon, dominant understorey plant coverage, understorey layer richness and edaphic humidity.

Tests of directional separation (d-separation) were done in order to test SEM model goodness-of-fit through checking that no missing links exist among unconnected variables. It statistically mimics experimental manipulations: testing the linkage between two unconnected variables while statistically controlling for all other predictors of these unconnected variables, i.e. conditional independence claim (Shipley, 2009). Testing the d-separation of each possible link between unconnected variables allows us to identify potential missing links. We used the Shipley's d-sep test (Fisher's C statistics and associated P-value) of the selected SEM model by combining the probabilities of each conditional independence claim. Then the resulting Fisher's C statistics was compared to a Chi2 distribution (Shipley, 2009). Shipley's d-sep test focuses on the adequation of model topology with data. The X^2_{ML} (Shipley and Douma, 2020) was also used to consider model topology as well as the nature of the relation (ex linear or nonlinear). It consists of a comparison between the observed and model-fitted covariance matrix. A stepwise backward selection from the initial SEM model was done

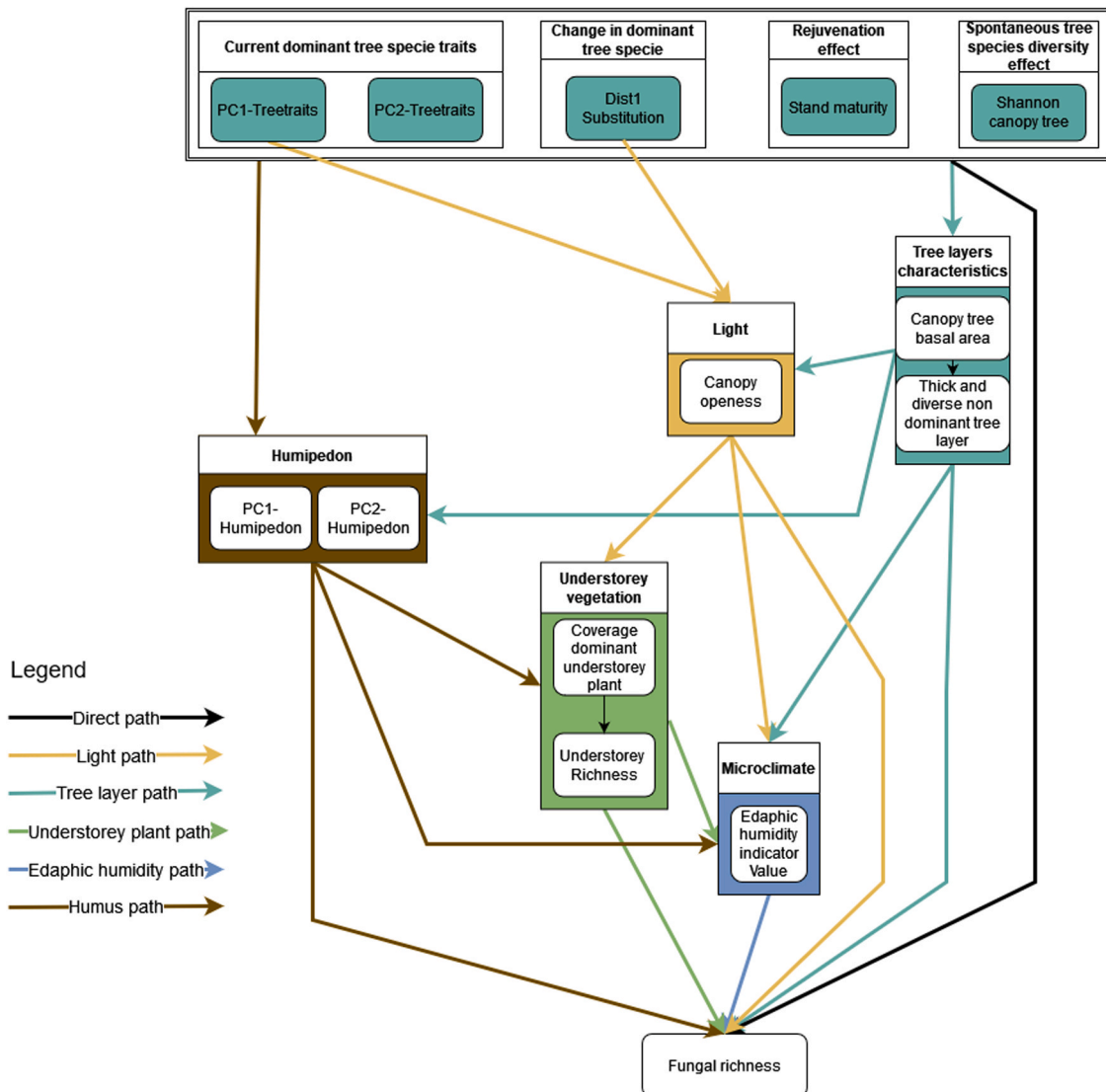


Fig. 2. Metamodel before model selection. For all variables, a direct effect on fungal richness was considered. External variables are in the first layer and are directly managed by foresters. Correlated errors between external explanatory variables (not shown) were included. Tree layers characteristics were considered as partially dependent on external variables along with management. Light, humipedon, understorey vegetation and microclimate variables were considered as dependent from external variables and tree layers characteristics variables and then referred to as indirect effect or path. Note that a relationship linked to an external rectangle prevails for all the variables in the rectangle.

using information-theoretic methods adapted to SEM (AIC) to choose the most parsimonious SEM model (Shipley and Douma, 2020). Model estimates were standardised by standard deviation. Links were considered as significant for a p -value ≤ 0.05 .

3. Results

3.1. Illumina dataset results

Out of 10,838,299 initial reads, 6,689,904 sequences (62 % of the initial sequences) were retained after filtering and removal of chimera. They were grouped into 12,748 OTUs at a 97 % similarity level. After taxonomic assignment, 9033 OTUs (71 %) were identified as fungi, including 5755 Ascomycota OTUs and 2089 Basidiomycota OTUs. The rarefaction curves for both phyla exceeded the inflexion point without reaching a plateau, indicating that while sequencing depth was sufficient to screen the overall fungal community, not all rare OTUs were sampled. Rare OTUs, defined as those present in only one or two samples, represented 1219 Ascomycota OTUs (21 % of Ascomycota OTUs, 4 % of Ascomycota reads) and 519 Basidiomycota OTUs (25 % of Basidiomycota OTUs, 4 % of Basidiomycota reads).

3.2. Ascomycota and Basidiomycota richness were not different among treatments

PERMANOVA on Ascomycota and Basidiomycota richness in holorganic horizons was not significantly associated (p -value = 0.29 and 0.09, resp.) with the substitution tree species if considered as a categorical treatment (Fig. 3). Similar results were observed for Ascomycota and Basidiomycota in the organo-mineral horizon (p -value = 0.21 and

0.12, resp.).

3.3. PCA on tree species life traits

The two first PCA axes (referred to as PC1-Tretraits and PC2-Tretraits) explained 55 % and 22 % of tree functional traits variance, respectively (Fig. 4). The five variables that contributed the most to axis PC1-Tretraits were mean specific SLA, mean leaf N content, mean photosynthetic leaf capacity per mass, mean leaf P content and mean stem N content. These traits related to the acquisitive versus conservative plant strategies gradient (Wright et al., 2004) lead to interpreting PC1-Tretraits as an acquisitive versus conservative trait gradient, defined latter as the plant economic spectrum (Reich, 2014). Axis PC2-Tretraits discriminated species with dense wood, long lifespan and nitrogen-rich fine roots (positive values) from those with low values of those variables (negative values). With low values along both axes, *P. sylvestris* could be considered as a leaf-conservative and light-wood species, whereas *P. nigra* had low values for PC1-Tretraits but high values for PC2-Tretraits, suggesting it could be considered as a leaf conservative species with a high life expectancy. *Q. petraea* displayed high values for PC2-Tretraits and moderate values for PC1-Tretraits, characterising it as hardwood species with an intermediate position in the plant economic spectrum. Finally, *Q. rubra* and *F. sylvatica* displayed high values on axis PC1-Tretraits but moderate values on PC2-Tretraits, classifying them as leaf-acquisitive species.

3.4. PCA on humipedon characteristics

The two first axes of the PCA (referred to as PC1-humipedon and PC2-humipedon) explained 13 % and 11 % of humipedon forms

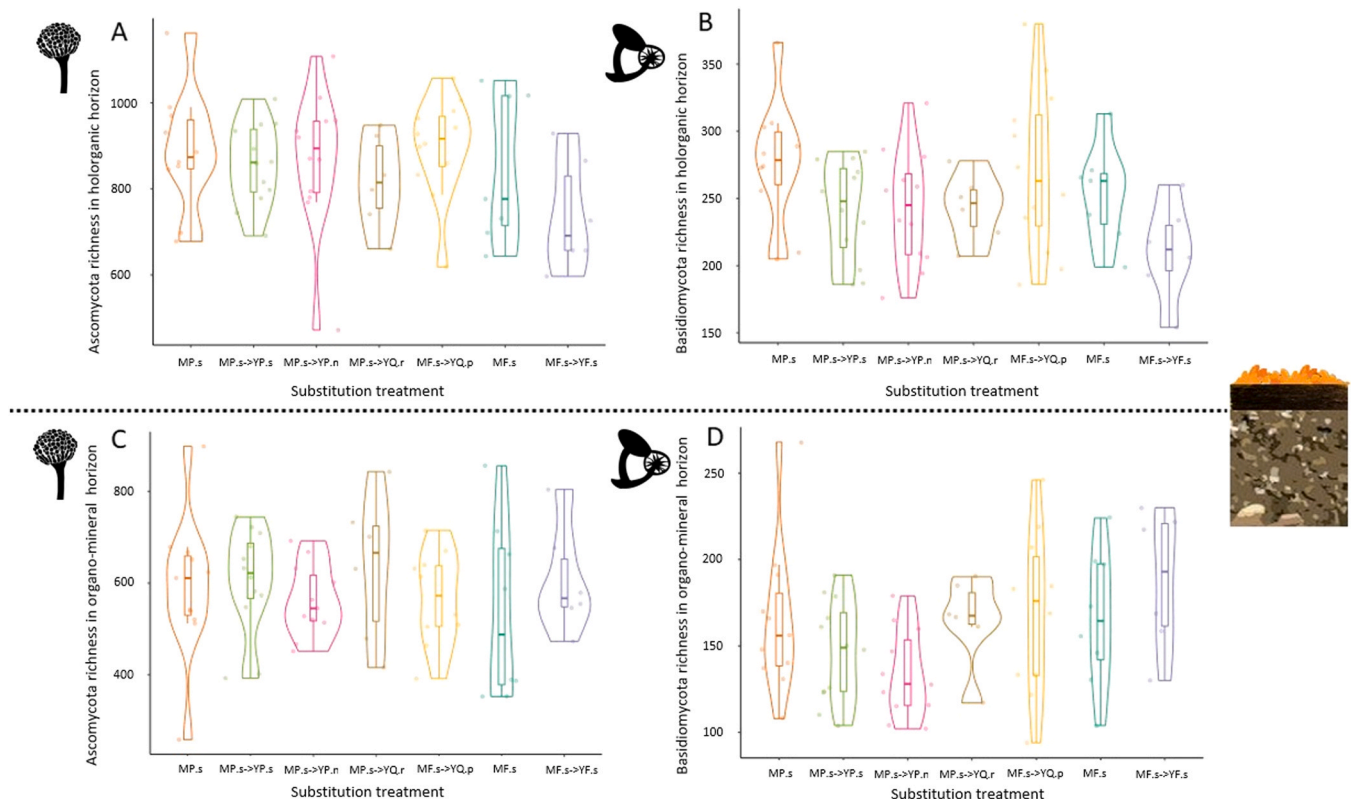


Fig. 3. Violin plots displaying OTU fungal richness for Ascomycota and Basidiomycota in the two categories of humipedon horizons by substitution treatments (MP.s: Mature *P. sylvestris*, MP.s->YP.s: *P. sylvestris* plantation after mature *P. sylvestris*, MP.s->YP.n: *P. nigra* subsp. *laricio* plantation after mature *P. sylvestris*, MP.s->YQ.r: *Q. rubra* plantation after mature *P. sylvestris*, MF.s->YQ.p: *Q. petraea* plantation after *F. sylvatica*, MF.s: Mature *F. sylvatica*, MF.s->YF.s: *F. sylvatica* plantation after mature *F. sylvatica*). A) Ascomycota OTU richness in holorganic horizon (N = 65), B) Basidiomycota OTU richness in holorganic horizon (N = 65), C) Ascomycota OTU richness in OM horizon (N = 64), D) Basidiomycota OTU richness in OM horizon in each substitution treatment (N = 64).

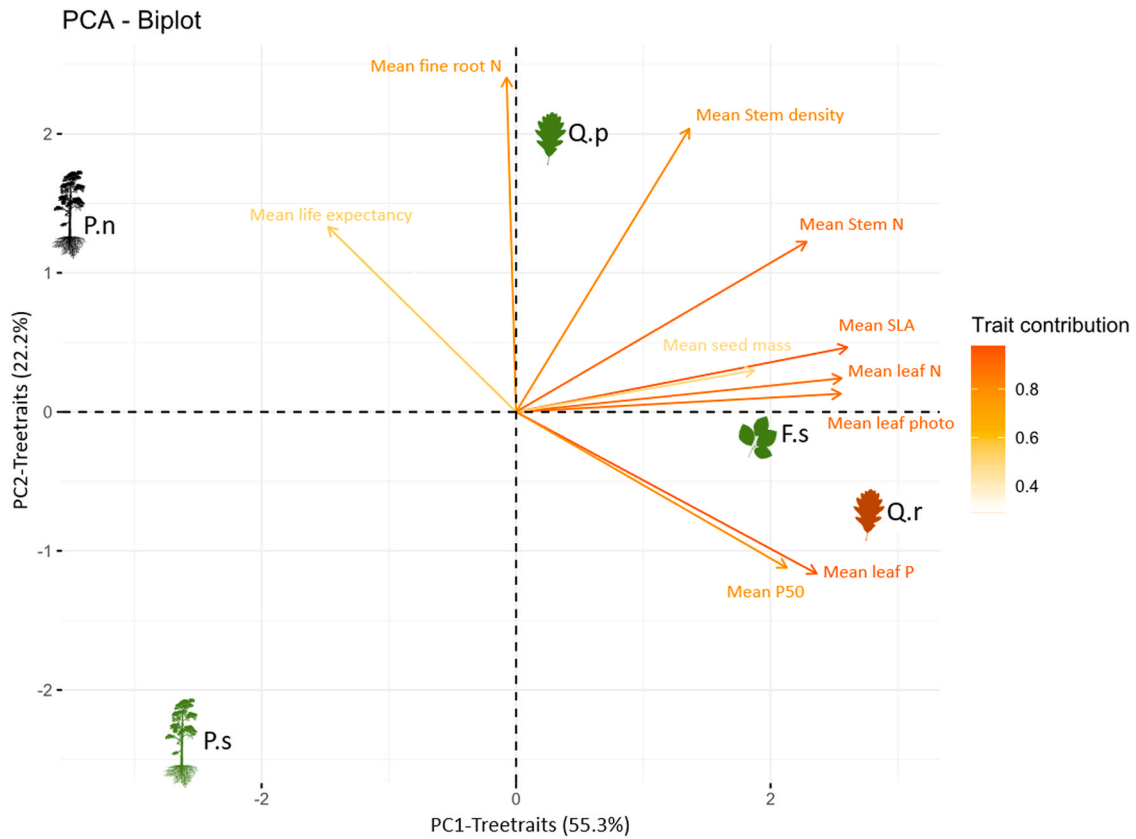


Fig. 4. Two-dimensional PCA biplot of tree species (P.n: *Pinus nigra*, Q.p: *Quercus petraea*, F.s: *Fagus sylvatica*, Q.r: *Quercus rubra*, P.s: *Pinus sylvestris*) coordinates in relation with traits contribution (Mean SLA: Specific leaf area, petiole excluded; Mean leaf photo: Photosynthesis rate per leaf dry mass; Mean leaf N: Leaf N content per leaf dry mass; Mean leaf P: Leaf P content per leaf dry mass; Mean stem N: Stem nitrogen content per stem dry mass; Mean stem density: Stem specific density; Mean P50: embolism vulnerability; Mean fine root N: Fine root N per fine root dry mass). Arrow ends indicate trait coordinates and tree species abbreviation indicate tree species coordinates. All traits were included in the analysis but only those contributing the most to the two first component axes were displayed. Arrow colours are proportional to the contribution of traits to plan.

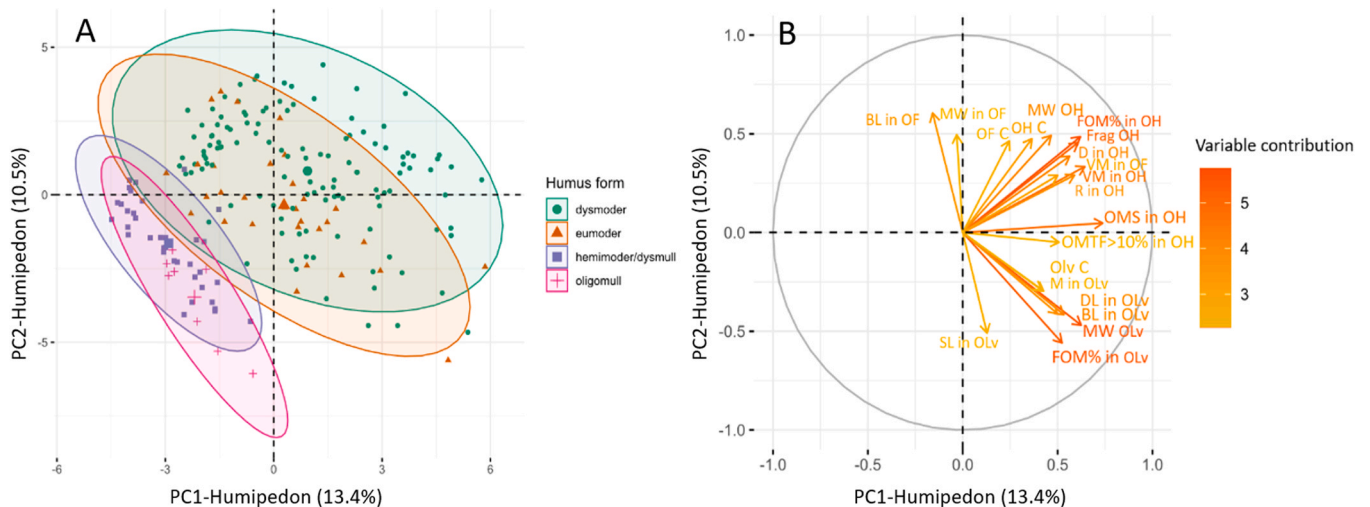


Fig. 5. A) Two-dimensional PCA plot of stand plots coordinates in relation to the 18 variables used for humipedon characterisation. Ellipse and colours indicated the humus form classification ([Association française pour l'étude du sol \(AFES\) et al., 2009](#)). N = 196 humipedon plots in 68 stands. B) Two-dimensional PCA plot of variable coordinates for the 15 humipedon variables that contributed the most to PC1-humipedon et PC2-humipedon. Arrow and variable name colours are proportional to variable contribution to the analysis. Arrowhead indicates the variable coordinates. Horizons: OLv: Old organic litter horizon, OF: Fragmented organic horizon, OH: Humic organic horizon. Variables: BL: Presence of brown leaves, C: Cohesion intensity of the horizon, D: Presence of soil fauna faecal pellet in the horizon, DL: Presence of discoloured leaves in the horizon, FOM %: Fine organic matter percentage, Frag: Presence of fragmented material in the horizon, M: Mycelium abundance in the horizon, MW: Maximal width of the horizon, OMS: Organic matter structure intensity of the horizon, OMTF: Transformation of the organic matter by fauna > 10 %, R: Roots abundance in the horizon, SL: Presence of skeletonised leaves in the horizon, VM: Presence of vegetal material in the horizon.

variance, respectively (Fig. 5). Axis PC1-humipedon mainly increased with organic matter structure complexification in OH (massive or fibrous OH), the amount of dead plant material in OH, the width of OLv horizon, the percent of fine organic matter and root abundance in OH. Axis one significantly separated dysmoder and eumoder humus forms (according to Association française pour l'étude du sol (AFES) et al. (2009) classification) from hemimoder/dysmull and oligomull based on a pairwise mood median test (Bartlett's K-squared = 50.107, p -value = 0.001; Mood test, p -value = 1.10×10^{-13}). Neither the variance nor the mean PC1-humipedon were significantly different between substitution treatments (Bartlett's K-squared = 8.027, p -value = 0.06; permutation analysis of variance p -value = 0.10). Thus PC1-humipedon can be interpreted as opposing mull to moder humus forms and indicating the horizonation process of the hologranic horizon.

3.5. Structural equation model on Ascomycota and Basidiomycota richness

Despite the high number of variables studied, the R^2 values of the fungal richness of all the fitted models were low: 0.07 for Ascomycota in hologranic horizons, 0.23 for Ascomycota in OM horizon and 0.09 for Basidiomycota for the same horizons. Soil fungal richness responded differently in the two soil horizons and for the two fungi phyla.

A stable model explaining the origin of variation in Ascomycota richness in hologranic ($\chi^2 = 17.12$, $p = 0.50$, $df = 17$ and Fisher's C = 30.3, $p = 0.65$, $df = 34$, AIC = 1355; Fig. 6) and in OM horizons ($\chi^2 =$

35.93, $p = 0.20$, $df = 29$ and Fisher's C = 58.7, $p = 0.45$, $df = 58$, AIC = 1144; Fig. 7). Ascomycota richness in the hologranic horizon was indirectly decreased in stands harboring leaf acquisitive dominant tree species (-0.08, Fig. 6). This result indicated that tree substitution weakly impacted Ascomycota richness in the hologranic horizon because of change in tree species leaf traits, but not notably by rejuvenation nor substitution distance effect. This result was mainly associated with an increase in canopy closure (-0.53, canopy openness) and a direct negative effect of acquisitive tree traits (-0.28) causing a decrease in dominant understorey plant cover that in return increased edaphic humidity. Edaphic humidity was the proximal factor decreasing Ascomycota richness in the hologranic horizon (-0.26). Increasing dominant understorey cover increased Ascomycota richness in hologranic horizons through edaphic humidity reduction (+ 0.16). Consequently, leaf acquisitive traits decreased understorey plant cover partially due to canopy openness reduction increasing edaphic humidity and decreasing hologranic Ascomycota richness.

For Ascomycota richness in OM horizon, substitution by *Q. petraea* and *P. nigra* subsp *Laricio* had a strong negative direct effect on OTU richness through the wood density, life expectancy and rich root N axis (-0.28, PC2-Treetraits) (Fig. 7). Increased canopy tree diversity directly increased Ascomycota OTU richness in this horizon (+ 0.32). Stand maturity also indirectly increased Ascomycota richness in the OM horizon (-0.13). Acquisitive tree species indirectly increased Ascomycota richness in OM horizons (+ 0.05). Substitution of two species with different leaf traits strategies weakly decreased Ascomycota richness in

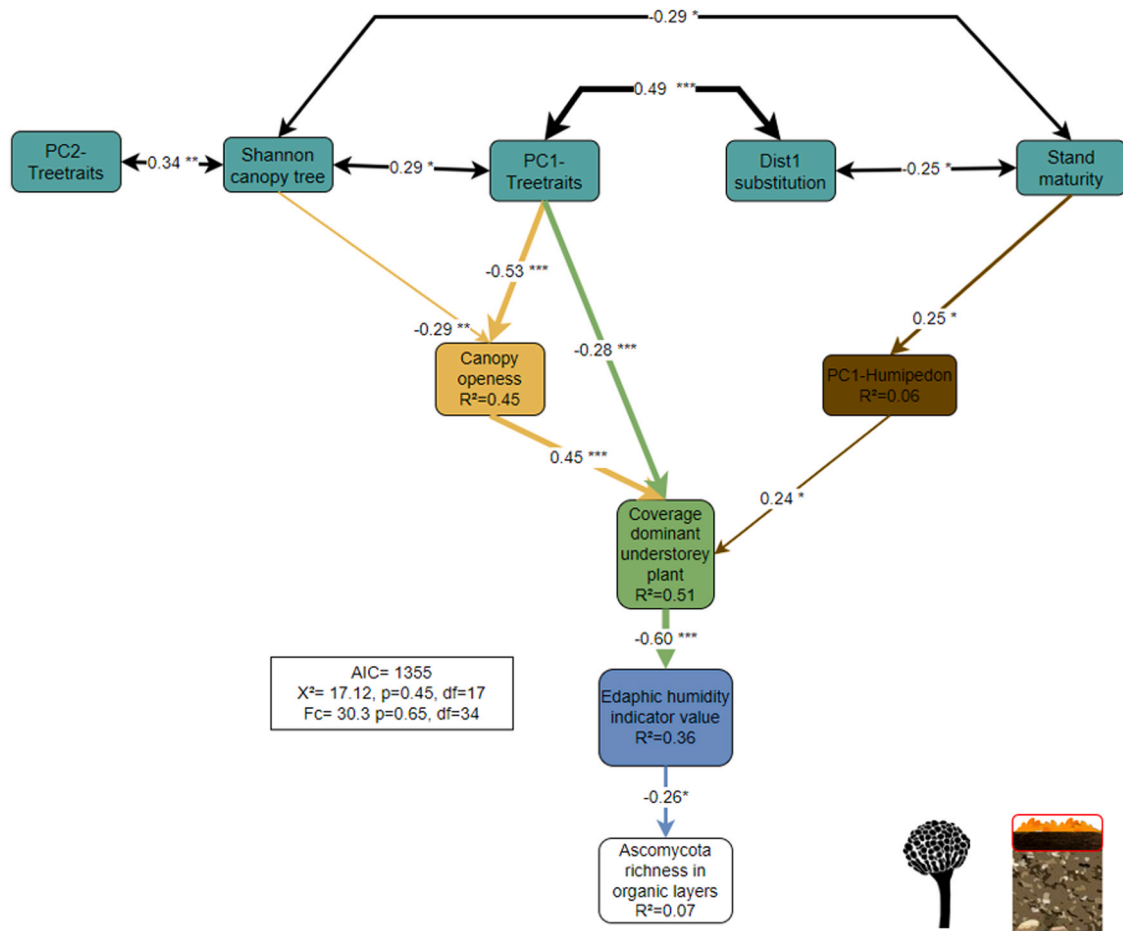


Fig. 6. SEM unravelling the effect of substitution variables on Ascomycota richness in hologranic horizons. Humipedon, vegetation, light and humidity variables are displayed respectively in brown, green, yellow and blue. Double head black arrow describes correlated errors. The model is composed of 5 linear submodels. Arrows are linking predictors and variables to be explained. Arrow widths are proportional to the path coefficient of the corresponding predictor. R^2 : coefficient of determination of the linear submodel explaining the variable. Significance thresholds: * < 0.05, ** < 0.05, *** < 0.005. N = 65.

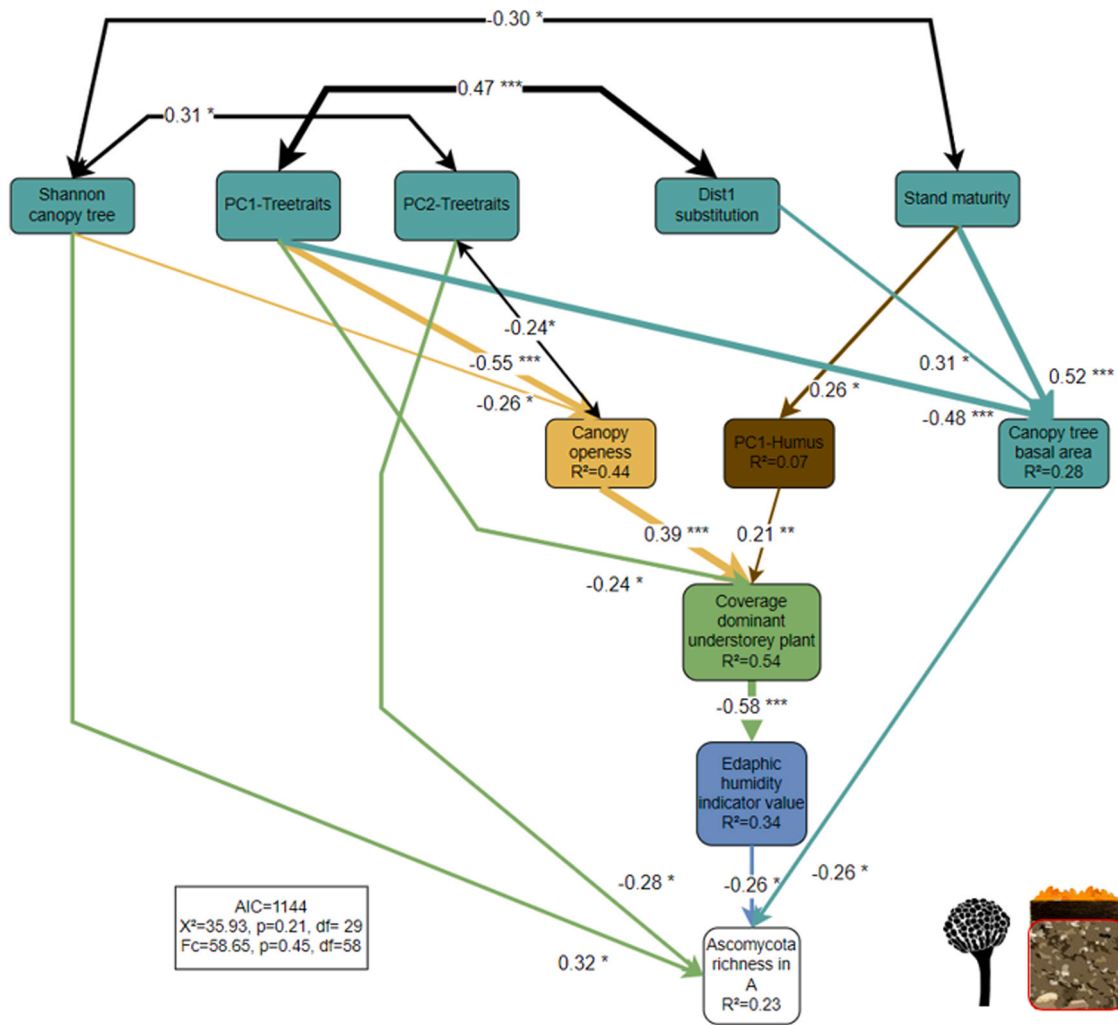


Fig. 7. SEM unravelling the effect of substitution variables on Ascomycota richness in the OM horizon. Humipedon, vegetation, light and humidity variables are displayed respectively in brown, green, yellow and blue. Double head black arrow describes correlated errors. The model is composed of 6 linear submodels. Arrows are linking predictors and variables to be explained. Arrow widths are proportional to the path coefficient of the corresponding predictor. R^2 : coefficient of determination of the linear submodel explaining the variable. Significance thresholds: $^* < 0.05$, $^{**} < 0.05$, $^{***} < 0.005$. $N = 65$.

the OM horizon through an increase in tree basal area (-0.08). Thus, tree substitution affected Ascomycota OTU richness in the OM horizon primarily due to direct changes in tree wood/root traits, and to a lesser extent, via indirect effects related to rejuvenation, tree leaf traits and substitution distance.

The negative effects of stand age and substitution trait distance were linked to a significant increase in tree basal area ($+ 0.52$ and $+ 0.31$ respectively). The weak and positive impact of traits aggregated in PC1-Treetraits influenced Ascomycota richness in OM horizons by being associated mainly with a reduction in tree basal area ($+ 0.12$). However, this positive effect was partially offset by weaker influences, such as a decrease in understorey dominant plant cover through decreased canopy openness (-0.05) and unidentified effect (-0.03) similar to what was observed in the holorganic horizon. Both tree basal area and edaphic humidity were key proximal variables, each having a negative impact on Ascomycota OTU richness in the OM horizon (-0.26 each). Consequently, the rejuvenation effect and the potential legacy effect were mediated by changes in tree basal area.

For holorganic Basidiomycota richness, the model selection process led to removing all interactions. A unique linear model was obtained for Basidiomycota richness in OM horizon ($AIC = 647.89$; Fig. 8). Basidiomycota richness in OM horizon was directly and strongly increased only by the leaf acquisitive value of the substitution species ($+ 0.31$).

4. Discussion

4.1. Tree substitution effect

The current study highlighted that the effects of tree species substitution on the OTU richness of Ascomycota and Basidiomycota varied across soil horizons and could not be directly attributed to the substitution treatments. In particular, substituting one deciduous species (here, *F. sylvatica*) for another (here, *Q. petraea* for climate adaptation) did not impact Ascomycota nor Basidiomycota richness 15–36 years after plantation, contrasting with the findings of Kubartová et al. (2009) who showed a positive rejuvenation effect on fungal richness in the OL horizon but not in the OF horizon. This discrepancy might result from the aggregated sampling of the entire holorganic layer in the present study, potentially masking subhorizon-specific responses and emphasizing the need for more detailed investigations of holorganic horizons. Differences in stand structure could also explain these discrepancies as our study examined mature, even-aged beech forests, while Kubartová et al. (2009) focused on mixed beech-oak coppices.

To our knowledge, our study is the first exploring the effects of resinous-to-resinous species substitution (here, from *P. sylvestris* to *P. nigra* subsp. *Laricio* for climate adaptation) on soil fungal communities. The main results show that substituting *Pinus* species does not reduce

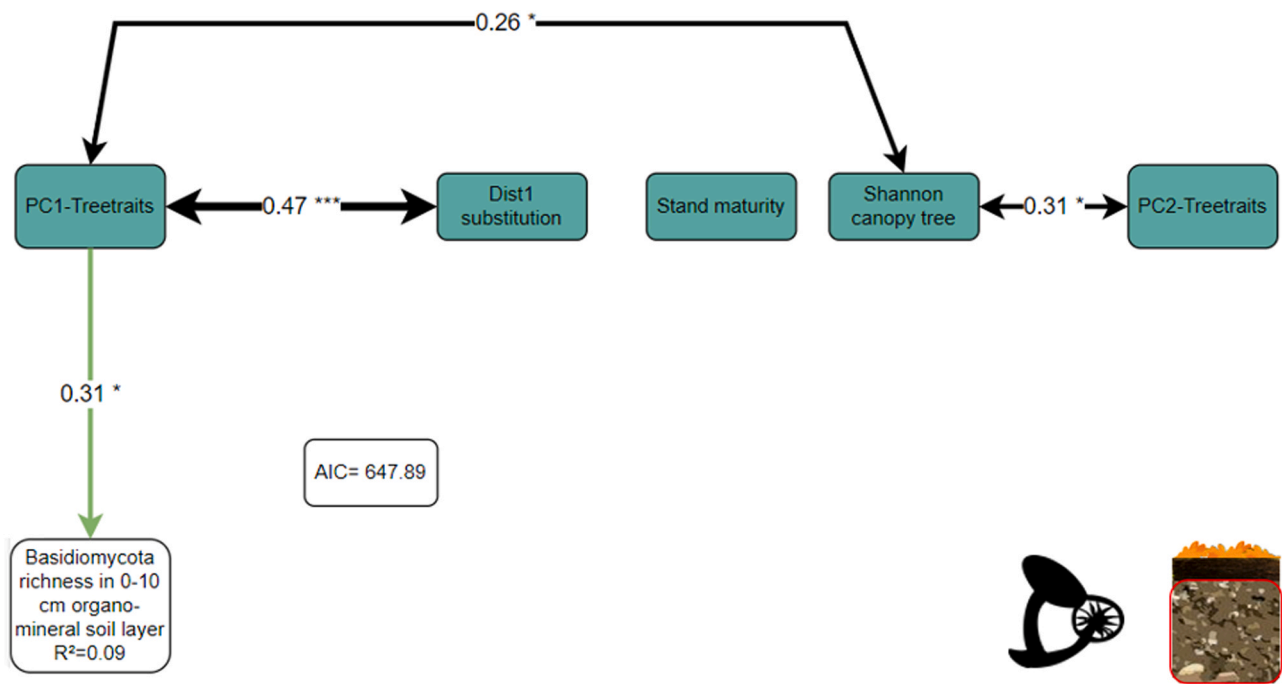


Fig. 8. Structural equation model unravelling the effect of substitution variable on Basidiomycota richness in 0–10 cm OM horizon. Double head black arrow describes correlated errors. The model is composed of 1 linear submodel. Arrows are linking predictors and variables to be explained. Arrow widths are proportional to the path coefficient of the corresponding predictor. R^2 : coefficient of determination of the linear submodel explaining the variable. Significance thresholds: * < 0.05, ** < 0.05, *** < 0.005. $N = 64$.

soil Ascomycota and Basidiomycota richness 15–36 years after plantation. The evolutionary proximity or the low functional dissimilarity between the two conifer species may explain this lack of response. Lastly, the current study did not reveal any significant difference in fungal richness between mature pine stands, rejuvenated pine stands and American red oak (*Q. rubra*) planted over mature pine stands. However, significant differences in the composition of Ascomycota and Basidiomycota communities in the two soil layers were observed between treatments. Even if they are not the scope of this paper, these differences are important to assess, as they have implications not only for fungal conservation but also potentially for ecosystem functions. Indeed, fungal community composition has been shown to be more closely associated with ecosystem functions than fungal richness (Runnel et al., 2025), although it is more challenging to incorporate into models such as structural equation models (SEM). For these reasons, the observed differences in fungal community composition will be explored in greater depth in a forthcoming paper. Although substitution treatments did not directly affect fungal richness, examining the results focusing on i) gradients of studied tree traits and ii) rejuvenation effects suggests that substitution impacts fungal richness directly and indirectly through environmental modifications.

4.1.1. Tree life traits as direct drivers of soil fungal richness

Ascomycota and Basidiomycota responded differently to tree traits. In the OM horizon, Ascomycota richness decreased directly because of an increase in wood density, N concentration in root and tree life expectancy, those three variables correlating with each other. Contrastingly, Basidiomycota richness in this horizon increased toward the acquisitive pole of the plant economic spectrum.

Increasing tree lifespan (ranging from 432 ± 260 to 601 ± 190 years), N root content (12.43 ± 3.94 to 15.80 mg/g) and wood density (0.54 ± 0.07 to 0.71 ± 0.08) decreases the Ascomycota richness in the 0–10 cm OM horizon. This corresponds to *P. sylvestris* and *Q. rubra* being more favourable for fungal richness than *Q. petraea* and *P. nigra* subsp. *Laricio*. As in current study, fine root N and stem density are often found to not be correlated with the plant economic spectrum (Chave et al.,

2009; Marañón et al., 2020; Carmona et al., 2021). Macrofungal richness increases with wood density (Schmit, 2005; Purahong et al., 2018b). However, metabarcoding added hindsight into microfungi biodiversity, including most Ascomycota biodiversity. Many Ascomycota are soft rot agents and cannot decompose dense wood effectively (Zanella et al., 2018), potentially explaining the negative correlation between Ascomycota richness and wood density. The nitrogen (N) content of tree fine roots have been found to correlate with N uptake by roots before (Luke McCormack et al., 2012). It is also partially linked to the amount of N rich fungal tissues in roots, indirectly representing tree mycorrhizal capacity or fungi tissue N storage in roots (Weemstra et al., 2016) and is also linked to an important metabolic trait: root respiration (Burton et al., 2002; Reich et al., 2008). Ascomycota, which are more often saprotrophic or pathogenic fungi than ectomycorrhizal, may be negatively affected by tree ectomycorrhizal root colonisation potential.

Ascomycota richness in the OM horizon was influenced by tree leaf traits through an indirect pathway involving stand basal area, canopy openness and dominant understory cover. The basal area of the acquisitive species (broadleaved) was lower than that of conservative species (conifers); broadleaved trees being able for a given tree diameter to support larger crown, closing the canopy and increasing inter-tree competition (Urgoiti et al., 2023). Forestry techniques adjusted to tree species may also explain observed differences (Lanier et al., 1994). More acquisitive tree species (*Q. rubra* and *F. sylvatica*) directly favoured Basidiomycota richness in OM horizon compared to more conservative species (*P. sylvestris* or *P. nigra*). This effect is likely linked to trade-off between traits enhancing light utilisation (SLA, leaf N, leaf photosynthesis, leaf P) and those that protect leaves against stress (e.g. P50, low SLA; Reich, 2014; Walker et al., 2014; Greenwood et al., 2017). Teng et al. (2021) found a positive correlation between leaf P, leaf N and EMF, saprotroph and pathogen richness. In contrast, leaf C showed a negative correlation in their study. This may be explained by acquisitive species producing and distributing more photosynthates to fungal partners (including ECM fungi that are mainly Basidiomycota) or to the presence of root traits favourable to fungi richness as many root traits (though not root nitrogen content) are part of the plant economic spectrum with leaf

traits (Marañón et al., 2020).

Edaphic humidity reduction seemed to increase Ascomycota richness both in OM organo-mineral and holorganic horizons. Negative paths through dominant understorey plants impact Ascomycota richness in the organic horizon mitigating the positive path from basal area. Acquisitive tree species by having higher leaf area and probably different architecture bring shade to the dominant understorey plants, decreasing their cover. No direct effect of foliar tree traits on fungal richness through humipedon modification was observed in current study. This is surprising because soils parameters linked to humipedon (N potential mineralisation, nutriment availability, C/N) are expected to modify fungal richness during substitution (Buée et al., 2011; Heine et al., 2019, 2021; Mundra et al., 2022). Even if they could have been impacted, decomposition processes do not lead to different humus form when changing tree species in the context of the present study (forest stands developed on sandy acidic soil). Our results highlighted the negative correlation of a dense dominant plant cover with edaphic humidity. As edaphic humidity was assessed using indicator values from plant communities without ponderation by species abundance, it is difficult to assign this humidity reduction to dominant understorey plant development. Nevertheless, social plant species are known to greatly contribute to understorey evapo-transpiration (eg. *Rubus* sect. *fruticosi* and *Pteridium aquilinum* transpiration range from 0.75 to 2.25 and 0.25 to 0.50 mm/day/leaf.m² respectively), reducing edaphic humidity (Gobin et al., 2015). Present results are in contradiction with the fact that edaphic humidity reduction effects on fungal richness are generally negative (Buée et al., 2011, Li et al., 2019). However, the different fungal guilds could react differently, mycoparasites being for example favored by drought (Leclerc et al., 2023) whereas ECM fungi richness can be insensitive to moderate drought (Richard et al., 2011). Increased evapotranspiration of dominant understorey plants may have caused hydric stress, weakening tree fine roots (Fotelli et al., 2001) and providing resources for stress-tolerant saprotrophic fungi. Lower soil moisture could also boost bacterial necromass, which is consumed by some fungi (Bottner, 1985; Griffiths et al., 2003). Then increase in total fungal richness with reduced edaphic humidity could have been caused by response of a particular fungal guild or taxa.

Overall, the beneficial effect of acquisitive tree species on OM Basidiomycota richness is 3-fold more important than the negative effect on Ascomycota in OM horizon. Planting leaf acquisitive tree species seems to be a promising approach for enhancing Ascomycota and Basidiomycota richness in soils at intermediate forest stage.

4.1.2. Rejuvenation and legacy: two effects interacting with substitution?

Forest tree former effect on soil fungal richness has been rarely investigated so far, while precedent crop effect is commonly studied in agriculture (Meriles et al., 2009; Venter et al., 2016; Orrù et al., 2021). According to our results, the former tree species appears to have no impact on fungal richness at intermediate forest stage, as substitution distance did not directly affect the soil fungal richness. However, as substitution distance was experimentally confounded with *P. sylvestris* substitution by *Q. rubra*, other studies are needed. If validated, it would have significant silvicultural implications, suggesting that after 20 years, the fungal OTUs richness remains unaffected, even when planting a functionally distinct tree species.

Rejuvenation increased soil Ascomycota richness (but not for Basidiomycota) through a decrease in tree basal area independently from canopy openness. This corroborates a study focusing on wood Ascomycota sporocarp richness in thinning experiments (Norden et al., 2008). Reduced tree basal area is known to be linked with an increase in soil horizontal heterogeneity as abiotic variables vary spatially (Helbach et al., 2022). Ascomycota are known to be more stress-tolerant than Basidiomycota (Sterkenburg et al., 2015; Maisnam et al., 2023) and to be favoured in mineral rich young stands compared to olds ones (Allison et al., 2010).

4.2. Forestry levers to favour fungal richness when substituting tree species

Results highlight that tree basal area, canopy cover, spontaneous tree diversity and dominant understorey plant cover are key factors impacting fungal richness.

4.2.1. Tree basal area and canopy cover management

In the current study, tree basal area varied widely, ranging from 14 to 65 m²/ha. Reduction in the canopy tree basal area had a moderate positive effect on total Ascomycota richness in the OM horizon. Increasing canopy openness had a minor positive effect on total Ascomycota richness in both horizons because of dominant understorey plant proliferation. However, opening canopy could also decrease soil humidity according to SEM results making it less advisable in drought-prone soils. Canopy openness can favor edaphic humidity if associated with tree thinning (Elkin et al., 2015) but it seems that increase in dominant understorey due to canopy opening can buffer microclimate between canopy and soil (Heilmann-Clausen, 2001; Decocq et al., 2004; Kovács et al., 2017). Positive, negative and no effect of thinning on fungal richness have been reported (Müller et al., 2007; Castaño et al., 2018; Collado et al., 2021; Qiang et al., 2023). Canopy openness may decrease fungal richness by increasing microclimate fluctuations and sunlight exposure (Heilmann-Clausen, 2001; Santos-Silva et al., 2011; Baral et al., 2015, but see Lindhe et al., 2004) though this effect may also depend on understorey conditions.

A special attention could be drawn to the basal areas of stands dominated by acquisitive trees, such as *Q. rubra* and *F. sylvatica*. Our results suggest that moderately reducing the basal area in stands of acquisitive species (without a long-term canopy opening) could favour Ascomycota richness in OM horizon. The impact of *Q. rubra* on forest biodiversity is debated, with some studies characterizing it as an invasive species having negative impact on EMF sporocarp richness and lower understorey plant diversity (Trocha et al., 2012; Stanek and Stefanowicz, 2019) and others considering the negative effects for example on plant communities richness being mediated by the silvicultural practices associated to this tree species (Chmura, 2020). The present study could indicate that if not too densely managed, *Q. rubra* may support a greater total fungal richness than other tree species at intermediate forest stage, likely due to its acquisitive tree status. More analyses are however needed to invest if this increase in richness concern all fungal guilds, only particular ones and was none at the detriment of some guild.

4.2.2. Management of spontaneous plant communities

Tree species diversity is often advocated as increasing biodiversity and resilience (Seidl et al., 2011). In the present study, even if stands were always dominated by a management-fixed tree species, three co-dominant species could reach 49 % of tree cover, and total tree species richness could reach as much as nine species in young stands. Spontaneous tree species diversity directly and moderately increased Ascomycota richness in OM horizon probably by increasing underground spatial and trophic heterogeneity and hosting their specific fungal partners. Surprisingly, non-dominant trees in stands had neither direct nor indirect effect on total Ascomycota and Basidiomycota richness whereas denser non-dominant tree stratum influence on light availability and microclimate for understorey vegetation were expected. This result aligns with studies showing no increase in soil fungal richness with stand vertical structure (Sabatini et al., 2016; Penone et al., 2019; Lang et al., 2023).

The study areas had sandy-loamy soils with high stoniness, and edaphic humidity levels ranged from perixerophiles communities to mesohydric understorey plant communities. As previously discussed, the cover of dominant understorey plant species had a weak positive effect on total Ascomycota richness in both soil horizons correlating with a decrease in bio-indicated edaphic humidity. Effect of dominant

understorey plants on fungal richness varies, with some studies finding positive correlations and others negative, depending on the species involved (Fernandez et al., 2022; Laperriere et al., 2019; Mundra et al., 2022). The question of forest understorey management would become of paramount importance because climate change could favour understorey development in the future as expected for *Pteridium aquilinum* (Pakeman and Marrs, 1996). Water stress risk is becoming an important limiting growth factor for trees with climate change in temperate Europe (David et al., 2016) and dominant understorey plant proliferation can reduce tree growth in water limited stations (Bon et al., 2023). Understorey shrub suppression in water limited soil can increase edaphic humidity (Prévosto et al., 2020; Biryol, 2024). Understorey removal modifies fungal communities reducing (Fanin et al., 2018) or not affecting (Deng et al., 2023) fungal richness, but always impacting fungal community composition (Fanin et al., 2018; Deng et al., 2023). Foresters would have to choose between favouring Ascomycota richness or soil moisture in perixerophile to mesohydric station.

4.3. Contrasting fungal richness sensitivity to management depending on phylum

Ascomycota richness was more strongly influenced by forest management than Basidiomycota richness. Ascomycota richness increased with the cover of dominant understorey plants and the associated reduction in soil moisture, but it decreased with tree basal area. It also decreased with an increase in root N, wood density and tree lifespan. The responses differed notably between holorganic and OM horizons. In contrast, Basidiomycota richness in the OM horizon was only and directly affected by the identity of the acquisitive dominant tree identity. Few studies have examined how Ascomycota and Basidiomycota richness respond differently to management or environmental factors. Mundra et al. (2022) found higher Ascomycota richness in native birch stands compared to Norway spruce, while the opposite was true for Basidiomycota. The two fungal phyla responded differently to variables like decaying wood properties, nitrogen enrichment, and dominant tree species (Nordén et al., 2004; Morrison et al., 2016; Purahong et al., 2018a, 2018b). Such dissimilarities are often attributed to differences in substrate colonisation strategies, degradation capability and nutritional requirements. Ascomycota are considered as early decomposers of leaves and fine wood, often preferring fine wood substrate over coarser one. Unlike Basidiomycota, Ascomycota typically lack the enzymatic ability to degrade lignified substrates, which limits their access to recalcitrant nitrogen from organic matter (Voříšková et al., 2014; Purahong et al., 2018a). This might explain why Ascomycota richness tends to be highest in a N rich environment. However, this generalisation should be tempered, as some Ascomycota species can efficiently degrade wood, especially under water stress conditions (Boddy et al., 1989). Ascomycota could also be favoured in ecosystems that experience cycles of drying and rewetting due to their ability to degrade easily available C sources after rewetting (Liu et al., 2019; Jaeger et al., 2023) explaining the observed correlation between Ascomycota richness and soil moisture.

5. Conclusion

Direct and indirect effects of substitution-related parameters were tested on Ascomycota and Basidiomycota OTU richness, with the assumption that forestry practices could impact the fungal richness bequeathed by the former state of forest stand. The primary influence of tree substitution on fungal richness after 15–36 years was dependent on the traits of the substitution tree species and the rejuvenation of the stand. The substituted tree species did not seem to impact the soil fungal richness of the young stands. The impact of tree substitution on Ascomycota richness was mainly indirect, driven by environmental changes, while the effect on Basidiomycota richness was more direct. Acquisitive tree species supported richer fungal communities compared to

conservative ones. Acquisitive tree species should be planted to favour fungal richness in humipedon with the hypothesis that richer fungal communities will allow better ecosystem resilience to climate change. This clearly contrasts with climate change adaptation forestry recommendations promoting plantation of more drought-tolerant species, i.e. probably more conservative species as *Sorbus torminalis*, *Quercus cerris*, *Sequoia sempervirens*, *Pinus pinea* or *Calocedrus decurrens*. Structural equation model analyses identified potential levers for foresters to enhance fungal richness during substitution such as reducing tree basal area or promoting spontaneous tree diversity. The models also emphasised the link between fungal diversity and both dominant understorey plant cover and soil moisture. Further research is needed to better understand the mechanism behind the dominant understorey plant cover, soil moisture and Ascomycota richness in OM horizons. Impact of tree species substitution on fungal community composition will be assessed in a forthcoming paper.

CRedit authorship contribution statement

Vincenot Lucie: Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition, Data curation, Conceptualization. **Buquet Sylvaine:** Writing – review & editing, Investigation. **Aubert Michaël:** Writing – review & editing, Validation, Supervision, Investigation, Conceptualization. **Ribémont Robinson:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Colin Yannick:** Writing – review & editing, Validation. **Moulin Vincent:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Henneron Ludovic:** Writing – review & editing, Validation, Methodology.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2025.122772](https://doi.org/10.1016/j.foreco.2025.122772).

Data availability

Data will be made available on request.

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