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Temporal variation of macrofungal communities in forest stands afforested on former agricultural land

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Abstract Our study aimed to assess inter-annual (2016–2020) temporal variability in macromycete species richness, diversity, abundance, and community composition for saprotrophic (SAP) and ectomycorrhizal (ECM) fungi in Norway spruce-dominated stands of different ages (21, 31 and 51 years; a proxy for succession) afforested on former agricultural land (locality Vrchdobroč, central Slovakia). We observed significant inter-annual variability in macromycete species richness, diversity, and abundance, depending on ecotrophic fungal groups. Year had a greater influence than fungal group on all characteristics except species richness, where both factors had similar importance. Stand age affected only macromycete abundance, with differences between ecotrophic groups. The models explained more variability in species richness and abundance than in diversity. Inter-annual variability in fungal community composition exceeded the variability attributable to stand age, with ECM macromycete communities exhibiting greater inter-annual variability than SAP macromycete communities. No direct interaction effects between stand age and sampling year were detected, suggesting that macromycete communities may be shaped by processes operating at broader spatial or temporal scales than those captured by the study plots (416.16 m^2) and sampling period. Consequently, in short-term studies, high inter-annual variability in macromycete species richness, diversity, abundance, and community composition could obscure the influence of other factors of interest.

Keywords: afforested agricultural land, macromycetes, *Picea abies*, temporal variability.

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Introduction

A few decades ago, many former pastures in central Europe were reforested after being abandoned or left to a natural succession process (Gere et al. 2022). During the long decades of absence of management on such lands, changes have occurred in the physical, chemical and biological properties of the soils. Therefore, it is necessary to know the effect of trees on soil properties after subsequent afforestation, which is important for planning the composition of future forests. In the former Czechoslovakia, the most commonly used species for afforestation of abandoned agricultural areas was Norway spruce - *Picea abies* L. Karst. (Štefančík & Kamenský 2009; Gere et al. 2022). Spruce forest ecosystems in Slovakia create a specific environment for the occurrence of a large number of fungal species that grow either only in such ecosystems or in environments where spruce is more or less represented (Mihál 2023).

Knowledge of spatiotemporal patterns in species distributions is the basis for understanding the ecological and evolutionary processes that shape communities (Bahram et al. 2014). This is undoubtedly also true for macromycete communities, which play an irreplaceable role in ecological processes in forest ecosystems (Gryndler et al. 2004; Hofmeister et al. 2014; Ujházy et al. 2018). In our case, this mainly concerns two important ecotrophic groups of macromycetes – ectomycorrhizal and terrestrial saprotrophic fungi.

Ectomycorrhizal fungi (hereafter ECM) are of great importance in forest ecosystems, especially as symbionts of forest trees. It is well known that the symbiotic relationship between ECM fungi and woody plants has positive effects on the health of woody plants, on the biochemical activity of forest trees and on the overall stability of forests (e.g., Mihál 2005; Ujházy et al. 2018). Mycorrhizal fungi also play an irreplaceable role in the maintenance and survival of stands affected by disturbance events, resulting in stand opening, lightening and increased solar radiation at ground layer. Power and Ashmore (1996) showed that beech roots infected with mycorrhizae were much more resistant to soil desiccation than non-mycorrhizal roots. A special biota is represented by spruce stands planted on former non-forest land, where the process of successive colonization of such stands by macromycetes is very complex, but undoubtedly very interesting for mycological research (cf. Kałucka 2009; Pešková et al. 2009; Luptáková & Mihál 2018, 2020). The structure of macromycete communities in artificially planted forests could be compared to changes in the structure of fungal communities in forests after sudden habitat disturbances, e. g. after human logging. This usually results in a reduction in macromycete species diversity, as reported by Salerni et al. (2020).

Terrestrial saprotrophic (humicolous) fungi (hereafter SAP) are one of the most important groups of ecotrophic fungi. Their abundance in forests, species diversity and fruiting body biomass dynamics are indicators of the quality of humification and other biological processes in the soil. Most of the mycological works deal with the evaluation of the role of SAP fungi in decomposition processes in forest litter and soil. For example, Lagana et al. (2002) studied the population biology of SAP fungi in mixed stands. Wiklund et al. (1995) investigated the succession and the production of SAP fungi in coniferous forests. Vašutová (2004) studied macromycete communities in different types of cultivated stands in the Czech Republic, and the research also included the dynamics of macromycete communities in spruce plantations of different ages, which were very similar to the design of the spruce plantations we studied. In Slovakia, the fructification and succession of fruiting bodies of SAP fungi has been studied, for example, by several authors (Luptáková et al. 2018; Mihál & Luptáková 2016; Ujházy et al.2018).

Species diversity dynamics, fruiting body abundance, biomass production and successional relationships of spruce-associated fungi or environments formed by spruce differ depending on the amount and intensity of climatic and environmental conditions such as precipitation, temperature, soil moisture, drought effects, phytocoenosis composition, geological substrate (Kałucka 2009; Pešková et al. 2015), stand age (Arnolds et al. 2004; Bonet et al. 2004; Pešková et al. 2009; Mihál & Luptáková 2016), woody plant composition of stands (Buée et al. 2011; Štefančík & Kamenský 2009; Tóth et al. 2016), and effects of immissions (Brunner 2001; Tesař & Dobrovolný 2011).

Various disturbances in the forest environment change the overall structure of woody plants and the microclimate of the affected forest, which is also reflected in the structure of mycocoenoses. Buée et al. (2011) investigated the effect of woody plant composition on the species richness of epigeic fungi. Wu et al. (2013) found that the age of the forest stand, the elevation of the study plots and soil organic carbon were the most important factors shaping the composition of the fungal community in their study of the relationships (plants – fungi – age of the forest stand). Rudolph et al. (2018) found that the effect of climatic conditions on fungal species richness varied by taxonomic and ecological group, with temporal patterns of occurrence of Basidiomycota and mycorrhizal fungi strongly associated with temperature and humidity, while other fungal groups were only weakly associated with abiotic conditions. These cultivated stands form biotopes in which the presence of ectomycorrhizae was previously not expected due to the nature of the agricultural land and the absence of trees.

The aim of the present study aimed to characterise the structure of ECM and SAP mycofloral communities in forest stands dominated by Norway spruce, afforested on former agricultural land, in response to succession and inter-annual variability. Different stand ages serve as a proxy for succession, while multiple years of sampling represent inter-annual variability.

Material and methods

Study site

The study of the mycoflora of spruce monocultures planted on former non-forest soils was carried out in the locality of the Vrchdobroč forest complex in central Slovakia, in the western part of the Slovenské Rudohorie mountains, in the Veporské vrchy hills, in the headwaters of the Ipeľ river. The village of Vrchdobroč is situated at an altitude of 740–917 m. The geological substrate is granodiorite crystalline, the predominant soil type is brown forest soil (cambisol), sandy loam. The skeletal content of the soil is 20–50%. The average annual temperature in the vegetation period from 2016 to 2018 was 14.32°C; the average precipitation in the vegetation period from 2016 to 2018 was 492 mm (according to the Slovak Hydrometeorological Institute – Weather Station Detvianska Huta; SHMÚ 2019).

The locality of Vrchdobroč is a former agricultural area that was used as pastureland for two centuries. In 1960, an area of 26,000 ha was designated as important for water management, particularly for flood protection. Between 1960 and 1985, afforestation efforts covered more than 5,166 ha, increasing forest cover from 29% to 49%. Conifers were the primary species used for afforestation. A detailed description of the study area and site can be found in Luptáková & Mihál (2020), while the characteristics of the individual mycological study plots are presented in Table 1.

Methods of research

The study was carried out from 2016 to 2020. A total of nine plots, each measuring 416.16 m², were established – three plots in each of the three stand age classes (21, 31, and 51 years as of 2016). The average spruce proportion (based on the total number of all trees in a plot) in the plots was 87.9% (SD = 18.0) (Table 1).

The macromycetes species composition and the abundance of fruiting bodies were monthly (June to October) recorded. Five surveys per year were conducted in the plots to obtain more accurate and thus reliable estimates (e. g. Halme & Kotiaho 2012). Species abundance in each plot was aggregated annually, and our study was based on yearly abundance data per plot. Controversial or unidentified species observed in the field were later determined in the laboratory according to the identification literature of various authors (see Luptáková & Mihál 2020 for a specific list of literature sources). Comparative material from the first author's herbarium collection was also used for species identification. The fungal species not previously

Table 1 Basic characteristics of the studied plots in forest stands at Vrchdobroč Hill (Central Slovakia). Spruce – proportion of spruce based on the total number of all trees in a plot, Age – stand age (in 2016), Exp – exposure. Other tree species at plots: Plot A1: *Larix decidua* 26.8%, *Populus tremula* 0.6%, plot A2: *Larix decidua* 44.7%, B2: *Populus tremula* 0.9%, plot B3: *Larix decidua* 0.9%, plot C2: *Abies alba* 3.3%, plot C3: *Abies alba* 32.0%, *Fagus sylvatica* 2.0%.

Plot No.	Altitude (m)	Location	Spruce (%)	Age (yr)	Exp.	pH (H_2O)	Slope (°)	Humus (%)	Ca (g/kg)	C (%)	N (%)	K (g/kg)	P (mg/kg)	Al (g/kg)
A1	870	48°32′00′′N 19°34′44′′E	72.6	21	SW	4.36	30	7.48	3.23	4.34	0.27	2.24	760	19.2
A2	890	48°32′02′′N 19°34′46′′E	55.3	21	SW	4.41	30	4.53	3.14	2.63	0.19	2.39	771	20.5
A3	830	48°31′52′′N 19°33′45′′E	100	21	E	4.27	15	9.41	2.60	5.46	0.35	1.69	781	19.5
B1	850	48°31′58′′N 19°34′31′′E	100	31	E	4.23	15	7.50	2.07	4.35	0.31	1.68	654	20.3
B2	820	48°31′46′′N 19°34′06′′E	99.1	31	SW	4.19	30	6.34	1.74	3.68	0.23	1.52	630	19.6
B3	830	48°31′48′′N 19°34′09′′E	99.1	31	SW	4.18	30	8.02	2.18	4.65	0.30	1.91	709	21.2
C1	820	48°31′42′′N 19°34′16′′E	100	51	S	4.80	30	9.45	3.63	5.48	0.45	1.69	921	19.7
C2	800	48°31′33′′N 19°34′05′′E	96.7	51	E	4.42	20	9.46	3.08	5.78	0.39	1.8	739	22.8
C3	825	48°31′38′′N 19°33′50′′E	66.0	51	S	4.10	20	4.12	4.40	2.74	0.16	2.39	918	18.4

recorded at the Vrchdobroč site (Luptáková & Mihál 2020) were herbarised and stored in the herbarium collections of the Institute of Forest Ecology of the Slovak Academy of Sciences in Zvolen. The scientific nomenclature and abbreviations of the identified macromycetes were largely taken from the database of Cooper and Kirk (2024), and the mycorrhizal status of the macromycetes from the database of Kuo (2024) and Tedersoo & Smith (2013).

The value of the mycorrhizal percentage (is very important parametes for evaluation of the forest stands health status, similart to the mycohrrhizal potential value, which is the ratio of ECM species to terrestrial SAP species of macromycetes. Therefore we determined the mycorrhizal percentage values, i.e. the percentage of ECM macromycetes, calculated as the ratio of the abundance of ECM species to the abundance of all identified macromycetes species (according to Gulden et al. 1992; Gáper & Mihál 2008).

Data analysis

Statistical analyses were performed using R 4.3.1 (R Core Team 2023) statistical software in RStudio (RStudio Team 2023).

For each plot, the diversity of saprotrophic (SAP) and ectomycorrhizal (ECM) macromycete groups was characterised by three forms of Hill's diversity – species richness, Hill-Shannon diversity and Hill-Simpson diversity (Hill 1973; Roswell et al. 2021). These indices were calculated separately for each fungal group based on annual species abundance data. Traditional diversity indices, such as the Shannon and Simpson indices, have different units and do not scale intuitively with species gain and loss. The Hill method of measuring diversity solves this problem by using the same general equation, but the three forms of Hill diversity differ only in how they scale rarity: While species richness emphasises rare species (and therefore remains very sensitive to rare species), Hill-Shannon diversity emphasises neither rare nor common species, and Hill-Simpson diversity emphasises common species (Roswell et al. 2021). We calculated sample Hill diversities [i. e. so-called Hill numbers of order q = 0 (species richness), 1 (Hill-Shannon diversity – traditional Shannon entropy index) and 2 (Hill-Simpson diversity)] using the renyi function in the vegan package (Oksanen et al. 2022), using annual species abundance data.

We applied generalized linear mixed models (GLMM) with a Poisson error distribution for species richness and a negative binomial distribution with quadratic parameterization (without zero-inflation) for abundance data. Additionally, we used linear mixed models (LMM) with Gaussian error distribution for Hill–Shannon and Hill–Simpson diversities as response variables. Stand age (21, 31, and 51 years) and years of sampling (2016–2020) were treated as ordinal explanatory variables (fixed effects), while fungal group (SAP or ECM) was included as a categorical explanatory variable (fixed effect). Plot identity was used as a random effect factor (random intercepts) to account for the non-independence of the observations. Full models were fitted. The lme4 (Bates et al. 2015) and glmmTMB (Brooks et al. 2017) packages were used to fit the models. The diagnostics (uniformity and dispersion tests, outliers) on the models using the simulate residuals function from the DHARMa package (Hartig 2022) was performed. The Anova function of the car package (Fox & Weisberg 2019) to compute type III analysis of variance tables for the objects of the models was utilized. Significant overall tests were followed by post-hoc tests (pairwise comparisons based on estimated marginal means with Tukey's adjustments) computed using the emmeans function from the emmeans package (Lenth 2023). The pseudo-R^2 for the models analysed was calculated using the function r.squared GLMM (the delta method was used to derive the variance at the observation level) from the MuMln package (Bartoń 2022). The marginal R^2, which represents the variance explained by the fixed factors, and the conditional R^2, which represents the variance explained by the entire model including the random effect, are also presented in the paper. The package ggplot2 3.3.2 (Wickham 2016) was used for plotting.

To explain the structure of macromycete communities in response to the explanatory variables – stand age and year – we performed an ordination analysis separately for the two fungal groups using the package vegan (Oksanen et al. 2022). To assess whether the community composition data were homogeneous or heterogeneous, and thus to decide whether to use linear or unimodal ordination, we first used detrended correspondence analysis (DCA; the decorana function from the vegan package). Subsequently, we performed the constrained unimodal ordination method – canonical correspondence analysis (CCA; functions cca, RsquareAdj and Anova.cca), as it is recommended for heterogeneous data and can be used for homogeneous data (Lepš and Šmilauer 2003). We used year as an ordinal variable, which allowed us to model non-linear relationships (Duncan & Kefford 2021). We partitioned the variation in macromycete community structure by stand age, year and their interaction using partial CCAs.

In addition, we performed an indicator species analysis using the R package indicspecies 1.7.12 (De Cáceres and Legendre 2009) to identify SAP and ECM macromycete species particularly associated with year of sampling or stand age. The indicator value indices (the argument func = "IndVal.g" in the multipatt function) were used to inspect the predictive values of the species significantly associated with the plot groups, indicating (A) the probability that the surveyed plot belongs to the target plot group if the species is found (species specificity or positive predictive value) and (B) the probability of finding the species in plots belonging to the plot group for the species (species fidelity or sensitivity).

Results

In total, we recorded 61 ECM and 49 SAP macromycete species were recorded during the period 2016–2020. In total, ECM macromycete species produced a total of 17,330 fruiting bodies and SAP macromycete species produced 19,583 fruiting bodies. The production values of fresh biomass of fruiting bodies were 5,049.4 kg ha^{-1} for ECM macromycetes and 2,060.6 kg ha^{-1} for SAP macromycetes, respectively.

The order of the first 20 most abundant ECM and SAP species found in this study is shown in Table 2. An interesting finding from the present research was the occurrence of rare and seldom occurring species of macromycetes namely *Lactarius spinosulus* (known in Slovakia only from 5 localities), *Stropharia albonitens* (known only from 4 localities) and *Clitopilus cystidiatus* (a relative of the species *Clitopilus prunulus* overlooked by mycologists, distinguished by the presence of cystids in the hymenium).

Significant temporal (inter-annual) variability in species richness, diversity and abundance of macrofungi, influenced by the ecotrophic fungal group was observed (Table 3). Stand age affected only the macromycete abundance, with contrasting patterns between fungal groups – SAP fungi were less abundant than ECM fungi in 50-year-old stands, whereas the opposite pattern was observed in younger stands (Table 3, Figure 1). The models accounted for more variability in species richness and abundance than in diversity. Across all characteristics except species richness, the effect of year contributed more to explained variability than the fungal group, whereas for species richness, both factors had similar importance (Table 3).

ECM macromycete communities exhibited greater heterogeneity (first DCA axis length = 4.38 SD units) compared to SAP communities (DCA axis length = 2.71 SD units). Macromycete species composition was influenced by both stand age and sampling year, with year accounting for more variation than stand age (CCA; Table 4). These factors

Table 2 The ranking of the first 20 most abundant ectomycorrhizal (ECM) and saprotrophic (SAP) macromycetes species. (Ab - total number of fruiting bodies for the entire research period).

ECM	Ab	SAP	Ab
Ramaria formosa (Pers.) Quél.	4,865	*Rhodocollybia butyracea* (Bull.) Lennox	3,959
Hygrophorus pustulatus (Pers.) Fr.	1,692	*Mycena cinerella* (P. Karst.) P. Karst.	3,899
Lactarius aurantiacus (Pers.) Gray	1,596	*M. pura* (Pers.) P. Kumm.	2,946
L. rufus (Scop.) Fr.	1,136	*M. citrinomarginata* Gillet	1,929
Clitopilus prunulus (Scop.) P. Kumm.	856	*Ampulloclitocybe clavipes* (Pers.) Redhead, Lutzoni, Monclavo & Vilgalys	924
Paxillus involutus (Batsch) Fr.	799	*Lycoperdon umbrinum* Pers.	759
Laccaria laccata agg.	578	*Mycena vulgaris* (Pers.) P. Kumm.	596
Clavulina rugosa (Bull.) J. Schröt.	563	*M. aurantiomar*ginata (Fr.) Quél.	587
Cortinarius brunneus (Pers.) Fr.	492	*M. rosella* (Fr.) Kumm.	553
Clavulina corraloides (L.) J. Schröt.	453	*Clitocybe dicolor* (Pers.) Murrill	444
Inocybe lacera (Fr.) P. Kumm.	421	*Mycena atropapillata* Kühner & Maire	312
Leccinum aurantiacum (Bull.) Gray	307	*Peziza badia* Pers.	280
Amanita rubescens Pers	283	*Paralepista flaccida* (Sowerby) Vizzini	252
A. excelsa (Fr.) Bertill.	217	*Lycoperdon perlatum* Pers.	239
A. muscaria (L.) Lam.	175	*Otidea leporina* (Batsch) Fuckel	156
Hebeloma mesophaeum (Pers.) Quél.	150	*Gymnopus androsaceus* (L.) Della Magg. & Trassin	138
Imleria badia (Fr.) Vizzini	128	*G. confluens* (Pers.) Antonín, Halling & Noordel.	115
Suillus grevillei (Klotzsch) Singer	119	*Marasmius rotula* (Scop.) Fr.	86
Laccaria bicolor (Maire) P.D.Orton	111	*Mycena alcalina* agg.	65
Gomphidius glutinosus (Schaeff.) Fr.	57	*Spathularia flavida* Pers.	65
Total	**14,998**	**Total**	**18,304**

Table 3 Analysis of variance tests for the generalized linear mixed models and linear mixed models examining the effects of stand age (21, 31 and 51), sampling year (2016–2020), fungal group (saprotrophic and ectomycorrhizal fungi) and the interaction between plot type and previous land cover on macromycetes species richness, diversity and abundance (n = 45).

Model term (d.f.)		**Response variable**			
		Species richness	**Hill-Shannon diversity**	**Hill-Simpson diversity**	**Abundance**
Intercept (1)	χ^2	3384.423	318.527	225.344	2608.628
	P	< 0.001	< 0.001	**< 0.001**	**< 0.001**
Stand age (2)	χ^2	3.663	3.045	1.915	1.099
	P	0.160	0.218	0.384	0.577
Year (4)	χ^2	23.002	13.812	14.654	66.140
	P	**< 0.001**	**0.008**	**0.005**	**< 0.001**
Fungal group (1)	χ^2	25.718	7.842	3.902	0.073
	P	**< 0.001**	**0.005**	**0.048**	0.788
Stand age × Year (8)	χ^2	5.279	4.986	5.624	3.873
	P	0.727	0.759	0.689	0.868
Stand age × Fungal group (2)	χ^2	3.595	1.885	1.487	6.712
	P	0.166	0.390	0.476	**0.035**
Year × Fungal group (4)	χ^2	11.206	19.623	15.721	11.314
	P	**0.024**	**< 0.001**	**0.003**	**0.023**
Stand age × Year × Fungal group (8)	χ^2	3.085	3.414	5.251	3.454
	P	0.929	0.906	0.730	0.903
	R^2_m	0.56	0.35	0.30	0.63
	R^2_c	0.58	0.39	0.35	0.70
	Error structure	P	G	G	NB2

Note: d.f. = degrees of freedom; R^2_m = marginal pseudo-R^2; R^2_c = conditional pseudo-R^2; P = significance values ($P < 0.05$ are in bold); Error structure: P = Poisson, G = Gaussian, NB2 = negative binomial with quadratic parametrization.

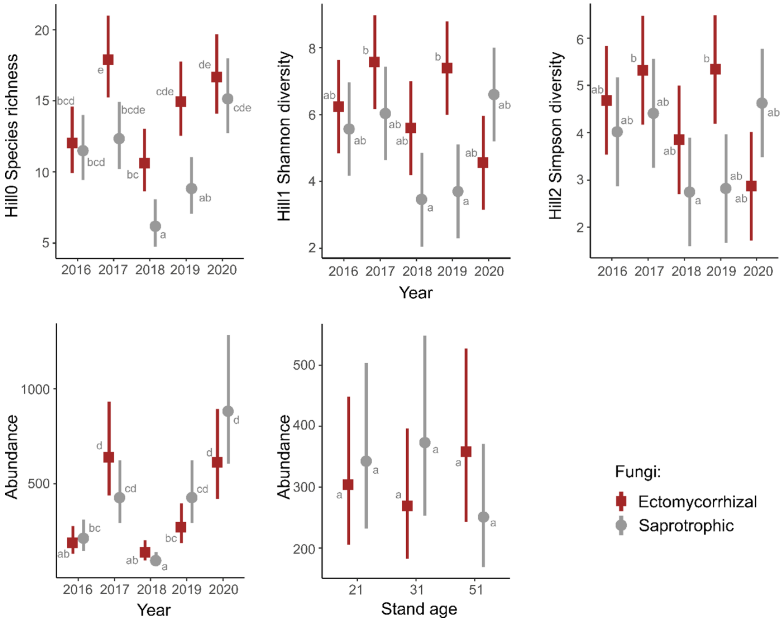

Figure 1 Significant differences in macromycete species richness, diversity and abundance for saprotrophic and ectomycorrhizal fungi sampled in Norway spruce-dominated forest stands sampled in 2016–2020 GLMM-based estimates (dots) are shown with their 95% confidence intervals (error bars). The same grouping letter indicates statistically non-significant differences between levels of explanatory variables – years and/or fungal group (Tukey's pairwise contrast, α = 5%)

explained a greater proportion of variation in ECM macromycete composition than in SAP composition. The joint proportions of variation in species composition explained by stand age and year were negative, suggesting that species composition was better explained by their combined effect than by either variable alone. However, the net interaction between stand age and sampling year were not statistically significant. This suggests that macromycete communities may be shaped by processes operating at a broader spatial or temporal scales than those captured by the study plots and sampling period. Indicator species analysis confirmed inter-annual shifts in the composition of ECM and SAP macromycete communities (Table 5). Comparable proportions of ECM (12/61) and SAP (9/49) species (approximately 19% of species) were significantly ($P < 0.05$) associated with particular years. On the other hand, the proportion of SAP species significantly associated with specific stand ages was lower (5/49, 10.2% species) compared to the proportion of ECM species (12/61, 19.7%).

The dynamics of mycorrhizal percentages in individual years and in individual stands are shown in Table 6. The highest values of mycorrhizal percentage were recorded mainly in the youngest stands (21 years) and in the middle-aged stands (31 years), while the lowest values were recorded in the oldest stands (51 years), which, compared to the younger stands, had greater crown light permeability, lower soil moisture values and a thicker layer of needle litter, which was more suitable for the occurrence of SAP macromycetes. These values ranged from 31.25% to 48.84%, highlighting the varying relationship between ECM and SAP fungal species in response to the changing climatic and ecological conditions across different years and stand types. In general, the higher the values of mycorrhizal percentage, the higher the representation of ECM fungi in the forest stand, which contributes to the improvement of the vitality and health of the forest stand. Average values of 37.69% to 41.76% for individual stands can be considered quite favourable in our case.

Table 4 Partitioning of variation in the composition of macromycetes communities sampled between 2016 and 2020 in forest stands of different ages dominated by Norway spruce on the Vrchdobroč Hill, using canonical correspondence analysis.

Fungal groups	**Explanatory variable(s)**	**Conditions**	**R$^2_{adj}$**	**F**	**d.f.**	**P**
Saprotrophic	Stand age	-	0.038	1.859	2, 42	0.002
	Year	-	0.100	2.144	4, 40	**0.001**
	Stand age + Year	-	0.141	2.178	6, 38	**0.001**
	Stand age + Year + (Stand age: Year) *	-	0.164	1.607	14, 30	**0.001**
	Stand age	Year	0.045	2.026	2, 38	**0.001**
	Year	Stand age	0.103	2.229	4, 38	**0.001**
	Stand age: Year	Stand age + Year	0.025	1.133	8, 30	0.145
Ectomycorrhizal	Stand age	-	0.045	2.038	2, 42	**0.002**
	Year	-	0.129	2.615	4, 40	**0.001**
	Stand age + Year	-	0.182	2.602	6, 38	**0.001**
	Stand age + Year + (Stand age: Year) **	-	0.223	1.883	14, 30	**0.001**
	Stand age	Year	0.052	2.251	2, 38	**0.001**
	Year	Stand age	0.136	2.718	4, 38	**0.001**
	Stand age: Year	Stand age + Year	0.041	1.244	8, 30	0.060

Note: R^2_{adj} = adjusted R^2, F = F-statistic, d.f. = degrees of freedom, P = significance values ($P < 0.05$ are in bold).

* Saprotrophic: The proportion of inertia constrained by the explanatory variables was 42.9%; total inertia = 3.154. The first two axes explained 24.0% (CCA1; F = 5.409, P = 0.001) and 13.4% (CCA2; F = 3.017, P = 0.177) of the accumulated constrained eigenvalues.

** Ectomycorrhizal: The proportion of inertia constrained by the explanatory variables was 46.8%; total inertia = 4.429. The first two axes explained 24.5% (CCA1; F = 6.447, P = 0.01) and 18.0% (CCA2; F = 4.739, P = 0.025) of the accumulated constrained eigenvalues.

Table 5 Outcomes of species analysis of the indicator (IndVal) for the abundance of saprotrophic and ectomycorrhizal species data surveyed at studied plots during the five years in the Vrchdobroč locality (Central Slovakia).

Fungal groups	**Year**	**Species Acronym**	**Specificity (A)**	**Fidelity (B)**	**Statistic**
Saprotrophic	2016	MyceAlca	0.6190	0.5556	0.586*
	2017	MaraAtro	0.5385	0.8889	0.692*
		PsatLaev	1.0000	0.3333	0.577*
	2019	RhodButy	0.5168	1.0000	0.719***
	2020	MyceCitr	0.6325	1.0000	0.795***
		HydrSuba	0.7647	0.7778	0.771***
		AmpuClav	0.7155	0.7778	0.746***
		MyceCine	0.6102	0.8889	0.736**
		ClitDico	0.6242	0.7778	0.697**
Ectomycorrhizal	2016	LaccBico	0.7500	0.5556	0.645**
		RussFirm	0.7547	0.4444	0.579*
	2017	RussXera	0.8609	0.8889	0.875***
		LactRufu	0.7199	0.8889	0.800***
		InocLace	0.7718	0.7778	0.775**
		HebeMeso	1.0000	0.5556	0.745***
		LactAura	0.6046	0.8889	0.733***
		CortCroc	0.6804	0.7778	0.727**
		LaccLacc	0.6315	0.7778	0.701**
		CortVari	0.5859	0.7778	0.675*
	2020	RamaForm	0.7242	1.0000	0.851***
		BoleEdul	0.4217	0.8889	0.612*
	Stand age				
Saprotrophic	31	LycoUmbr	0.5573	0.9333	0.721*
		MyceAura	0.7544	0.6000	0.673*
	51	LepiClyp	0.7500	0.4000	0.548*
		GymnConf	0.8507	0.3333	0.533*
		ClitOdor	0.8103	0.3333	0.520*
Ectomycorrhizal	21	SuilGrev	0.9540	0.6000	0.757***
		RussAeru	0.6644	0.6667	0.666*
		ChalPipe	0.8621	0.4667	0.634**
	31	BoleEdul	0.7229	0.8000	0.760***
		RussMust	0.7113	0.6667	0.689**
		GompGlut	0.5641	0.7333	0.643*
		RussFirm	0.7547	0.4000	0.549*
	51	AmanRube	0.8039	0.7333	0.768**
		ImleBadi	0.7368	0.8000	0.768**
		InocLace	0.8755	0.6000	0.725*
		AmanBatt	0.7949	0.4000	0.564*
		LaccAmet	1.0000	0.2667	0.516*

Note: Specificity (A) = the probability that the surveyed plot belongs to the target plot group if the species is found, Fidelity (B) = the probability of finding the species in plots belonging to the plot group for the species.

Fungal species acronyms: AmanBatt – *Amanita battarae*, AmanRube – *Amanita rubescens*, AmpuClav – *Ampulloclitocybe clavipes*, BoleEdul – *Boletus edulis*, ChalPipe – *Chalciporus piperatus*, ClitDico – *Clitocybe dicolor*, ClitOdor – *Clitocybe odora*, CortCroc – *Cortinarius croceus*, CortVari – *Cortinarius varius*, GompGlut – *Gomphidius glutinosus*, GymnConf – *Gymnopus confluens*, HebeMeso – *Hebeloma mesophaeum*, HydrSuba – *Hydropus subalpinus*, ImleBadi – *Imleria badia*, InocLace – *Inocybe lacera*, LaccAmet – *Laccaria amethystina*, LaccBico – *Laccaria bicolor*, LaccLacc – *Laccaria laccata*, LactAura – *Lactarius aurantiacus*, LactRufu – *Lactarius rufus*, LepiClyp – *Lepiota clypeolaria*, LycoUmbr – *Lycoperdon umbrinum*, MaraAtro – *Marasmiellus atropapillatus*, MyceAlca – *Mycena alcalina*, MyceAura – *Mycena aurantiomarginata*, MyceCine – *Mycena cinerella*, MyceCitr – *Mycena citrinomarginata*, PsatLaev – *Psathyrella laevissima*, RamaForm – *Ramaria formosa*, RhodButy – *Rhodocollybia butyracea*, RussAeru – *Russula aeruginea*, RussFirm – *Russula firmula*, RussMust – *Russula mustelina*, RussXera – *Russula xerampelina*, SuilGrev – *Suillus grevillei*.

Table 6 Interannual dynamics of ectomycorrhizal percentage values. Mean values are presented with their corresponding standard deviations (SD).

Plots	2016	2017	2018	2019	2020	Mean (SD)
A	36.07	45.59	44.19	47.54	32.82	41.24 (5.74)
B	34.29	41.89	48.84	43.1	40.7	41.76 (4.47)
C	31.25	37.5	38.85	43.66	37.21	37.69 (3.97)
Mean	33.87 (2.44)	41.66 (4.05)	43.96 (5.00)	44.76 (2.42)	36.91 (3.95)	40.23 (5.06)

Discussion

The study of the dynamics of macromycete communities in forest ecosystems is challenging, especially from a temporal point of view, due to the instability of the occurrence of macromycete fruiting bodies, which is mainly influenced by fluctuations in climatic conditions. The study of macromycete communities as important colonizers, growing on former abandoned or agricultural sites where symbiotic relationships between mycorrhizal fungi and woody plants were previously absent is particularly important.

The colonization of spruce stands at the Vrchdobroč site by ECM and SAP macromycetes has been studied in the past, e.g. by Gáper (1992) and Gáper & Lizoň (1995, 1997), who mention *Laccaria laccata* and the genus *Entoloma* as dominant species occurring in the youngest stands, while in older stands they reported species of the genera *Cortinarius* spp., *Lactarius* spp., *Hebeloma crustuliniforme* and *Chalciporus piperatus*; while the oldest stands, the species *Amanita rubescens, Hygrophorus pustulatus*, genus *Clitopilus* and others were described. Some of the same species, or genera, were also found in our study, e. g. *L. laccata, Cortinarius brunneus, Lactarius aurantiacus, L. rufus, Amanita muscaria, Hygrophorus pustulatus* and *Clitopilus prunulus, Inocybe lacera, Paxillus involutus, Suillus grevillei*.

During the present study, we found that in 50-year-old stands, the abundance of SAP fungi was lower than the abundance of ECM fungi, while in younger stands the ratio was the opposite (Table 3, Figure 1). The increase of ECM symbionts in the youngest spruce stands on former agricultural land was also reported by Pešková et al. (2009), who found that in the Orlické hory Mountains in the Czech Republic, the species spectrum of macromycetes and the quality of mycorrhizae increased in 10- to 50-year-old stands, which are similar in character to the mycocenosis in autochthonous forest stands. *Cortinarius anomalus, Gomphidius maculatus, Hebeloma crustuliniforme, Suillus grevillei* were typical species in the youngest spruce stands (10 years), whereas an increase of SAP fungi was observed in the oldest stands (80 years old). Pešková et al. (2009) found that the number of ECM species increased with the increasing of the stand age. Species of the genera *Amanita, Cortinarius, Lactarius, Russula* and *Xerocomus* were most abundant in the middle aged and the oldest stands, which was also confirmed by our research at the Vrchdobroč site. The species *Hygrophorus pustulatus* and *Paxillus involutus* were found in the Orlické Mountains mainly in middle-aged forest stands, while we found *H. pustulatus* in the oldest stands and *P. involutus* in the youngest stands.

Similarly, Unterseher et al. (2012) provided a comprehensive summary of the species richness and community structure of macromycetes in Mecklenburg-Vorpommern, Germany. They found that the species *Inocybe lacera, Laccaria amethystina, Russula decolorans, R. sardonia* and *Tricholoma imbricatum* belong to the five most prominent species of the conifer ectomycorrhizal community. We also found these species and nine species of the *Russula* genus in different proportions of species richness in our study plots, with a higher abundance in the oldest stands.

Stankevičiené & Kasparavičius (2007) presented interesting results of a study of species richness and the dynamics of fruiting bodies of ECM fungi in 50-year-old stands of *Pinus sylvestris* in Lithuania, where *Paxillus involutus* (average of 275 fruiting bodies/site), *Xerocomus badius* (98.4), *Lactarius rufus* (43.6) and *Tricholoma equestre* (10 fruiting bodies) were among the most frequently occurring fungi. These species were also found in our research plots. It should be added that Stankevičiené & Kasparavičius (2007) also reported relatively low levels of nitrogen (ranging from 0.029% to 0.197%) and humus (ranging from 2.05% to 8.02%) in their research areas, which should favour the development of ectomycorrhizal mycobiota. The values of nitrogen and humus from our research plots at the Vrchdobroč site are much higher (nitrogen ranging from 0.156% to 0.385%; humus ranging from 4.53% to 9.96%), which may be related to the intensive agricultural use of land at the Vrchdobroč locality in the past (Luptáková & Mihál 2018).

The interrelationships of fungal communities in different types of forest stands were studied by Hofmeister et al. (2014). The authors found a total of 1,413 macromyetes species at 106 sites in different forest types in the Czech Republic, with ECM species accounting for 29% of the species richness. The influence of forest stand management on the macromycete community was found to be statistically significant ($p < 0.001$). The authors stated that the species richness of macromycetes (β-diversity) increased with the age of the stands and decreased with the intensity of forest management. Outcomes from this study showed that from 2016 (Luptáková & Mihál 2018), in the group of ECM macromycetes, species richness increased from the youngest 21-year-old stands (coefficient of variation 31.1%) to 31-year-old stands (32.77%), while a significant decrease in the variation coefficient (only 4.33%) was recorded in the oldest 51-year-old stands. On the other hand, the abundance values of fruiting bodies of ECM macromycetes increased from the youngest ($p = 0.061$) to the oldest stands ($p = 0.026$).

The dynamics of fructification and abundance ratios of macromycetes are, in addition to species diversity, the most reliable indicators of the mycobiota structure of forest stands. Luptáková & Mihál (2018, 2020) found that the most abundant ECM species in the monitored stands in 2016 to 2018 at the Vrchdobroč site were: *Hygrophorus pustulatus* (340 fruiting bodies), *Russula aeruginea* (261), *Clitopilus prunulus* (186), *Paxillus involutus* (155), *Ramaria eumorpha* (145), *Laccaria bicolor* (111). The highest values of fruiting body abundance were found at the oldest locality, plot C (812 fruiting bodies). Interdependencies between species richness and abundance of ECM macromycete fruiting bodies at individual sites were found. The highest variability of values in the species richness was found in the middle-aged forest stand (B = 32.77%) and the smallest value in the oldest stand (C = 4.33%).

The greatest variability of values in the abundance was reported in the youngest stand (A = 100.11%) and the lowest in the middle-aged stand (B = 50.16%). Mihál & Luptáková (2016) also found similar values at the Vrchdobroč locality between 1993 and 2003. Higher values of the fruiting body abundance in general in younger forest stands were also found by Luptáková et al. (2018), who investigated macromycete abundance ratios in a fir-beech stand and found that up to 63% of fruiting bodies produced were produced in a young 28-year-old stand, and only 37% of fruiting bodies grew in an old 115-year-old stand.

At the same time, it is interesting that 27 species of SAP macromycetes produced more fruiting bodies than ECM species, especially *Mycena alcalina* agg. (52 fruiting bodies), *M. inclinata* (50), *Psathyrella laevissima* (38). The abundance of SAP species was significantly influenced by season, while there was also a significant interaction between site and season. The cause of this phenomenon may be low light availability in denser, youngest stands and limited photosynthesis, the amount of precipitation, but also the quality of the humification process, which is related to the decomposition of coniferous litter. Mihál (1998) investigated the biomass production of SAP macromycetes in spruce stands at the Vrchdobroč site. He found high biomass production in the oldest stands and the lowest in the youngest stands. The dynamics of production was mainly influenced by the type of humification processes in the soil and the microclimate in the stands.

The most productive SAP macromycetes included the species *Agaricus sylvaticaus, Clitocybe dicolor, Cystoderma amianthinum, Paralepista flaccida, Rhodocollybia butyracea* and *R. maculata*. These species together with some representatives of the genera *Agrocybe, Cystoderma, Lycoperdon, Micromphale, Omphalina* and *Otidea* prevailed in the dominance of SAP fungi in the oldest spruce stands at the Vrchdobroč locality in the 1990s (Gáper, 1994). Similarly, Wiklund et al. (1995) reprted that *Marasmius androsaceus, Micromphale* *perforans* and some *Clitocybe* and *Mycena* species predominated in 30-year-old Norway spruce stands in south-western Sweden. A higher frequency of the occurrence of SAP macromycetes in older stands was also described by Miyamoto et al. (2000), who found in 40-year-old spruce stands in Japan that among the most abundant SAP macromycetes were the species *Collybia pinastris, Gymnopus erythropus, Mycena pura, M. stylobates, M. vulgaris* and *M. wettsteinii* and - the species were also found in our collections.

Different levels and ratios of the ammount of chemical elements in soils newly colonized by macromycetes significantly influence the species composition, fructification and the ratio between ECM and SAP macromycetes (e. g. Jonsson et al. 2000, Arnolds et al. 2004). This is very important for the process of symbiosis formation and the subsequent survival of mycorrhizae. For example, the importance of phosphorus as an element supporting the abundance and overall structure of the fungal ECM community was highlighted by Burke et al. (2009). Similarly, Jonsson et al. (2000) found that the species diversity of ECM macromycetes was always lower in spruce stands where nitrogen was applied compared to trees without increased soil nitrogen content. Similarly, Arnolds et al. (2004) studied the mycoflora of young spruce monocultures growing on former non-forest land in the Netherlands and found lower levels of ECM fungi in trees that had a higher soil nitrogen and other nutrient levels than those grown on poorer peat soils. Among the most important dominant ECM macromycetes reporting *Amanita muscaria, Chalciporus piperatus, Cortinarius anomalus, C. cinnamomeus, Hebeloma mesophaeum, Hygrophorus agathosmus, Inocybe lacera, Laccaria proxima, Lactarius deterrimus*, these fungal species being also more or less dominant in our collections as well.

Peršoh et al. (2018) pointed to the importance of mycobiota in the process of carbon storage in forest landscapes; ECM and SAP macromycetes decompose organic matter and mobilize nutrients for host plants, and the competition between these two ecotrophic groups can cause the so-called Gadgil effect, i. e. a reduced rate of waste decomposition leading to increased carbon storage in the soil. Soil chemistry, as well as other ecological-climatic factors, also have a major influence on the ratio between ECM and SAP macromycetes. For example, during ten years of research in the Poľana region of central Slovakia, Mihál (2011) monitored the occurrence of macromycetes in a 150-year-old forest-like climax stand at the Zadná Poľana site and in an 80-year-old spruce monoculture (*Piceetum nudum*) at the Valaška site, planted on former pastures. He reported the occurrence of 177 macromycetes species, of which only 34 were ECM species, while it should be added that there were only 19 ECM species at the Valaška site. The oldest and primeval forest-like stand at the Zadná Poľana site was able to maintain a stable symbiotic mycoflora throughout the study period. In contrast to the Valaška site, we recorded a smaller number of ECM species compared to the Zadná Poľana site. However, it should be noted that at the Valaška site, under the conditions of a rich layer of acidic coniferous litter, the ectomycorrhizal mycoflora was displaced by terrestrial saprotrophs, which are ideally suited to such soil humification conditions. This fact was also described by Mihál & Gáper (1995), who stated that the commercial stand of nudal spruce at the Valaška site suffers from an acute lack of mycorrhizal symbionts, which also negatively affects the stability of its woody component (e. g. increased rotting of trees). This was also largely true for the soil humification conditions in the stands of the Vrchdobroč site. Similarly, Ujházy et al. (2018) confirmed that the species spectrum of macromycetes found at the Poľana locality was highest in unmanaged and old fir-beech forests, and significantly lower values of the species spectrum of macromycetes were found in spruce monocultures.

Vašutová (2004) studied macrophyte communities in different types of cultivated stands in the Czech Republic and found that 14-year-old cultures of spruce stands on former meadows (72 species) and 99-year-old waterlogged spruce stands (67 species) were the richest in species. In older 87 – 97 years old spruce stands, ECM species were dominant (44.2%), whereas in 14-year-old spruce stands, a high proportion of SAP species was also found (43%). The proportion of ECM fungi was positively correlated with the presence of spruce, the herb layer cover and the age of the trees, while the proportion of SAP fungi was positively correlated with the herb layer cover, the degree of naturalness of the forest and the heterogeneity of the surrounding vegetation.

In mycocenological studies, it is important to select the so-called bioindicator species of macromycetes, which are often species typical for the given type and nature of the habitat. The group of indicator species of macromycetes was listed, for example, in the work of Adamczyk (2011) for semi-natural biotopes of dry grasslands and in the work of Luptáková et al. (2018) for different managed foothill beech forests, with different macromycete bioindicator species occurring in each of these habitats. Egli (2011) stated that we currently do not know enough about macromycete species, especially ECM species, to be able to use them as bioindicators of tree health, or forest stands. Further research is needed, especially on the functional significance of ECM fungi at the species level. In the case of ECM macromycetes, he emphasized that, based on the current state of knowledge, there was no evidence that changes in the stand age or habitat characteristics affect the proportion of ECM fruiting bodies relative to other macromycete species. Klavina et al. (2022), studying the fungal communities of young spruce stands in Norway, identified some species of the genera *Cortinarius* and *Russula* as typical indicators of young spruce on former agricultural land.

In our collections, *Chalciporus piperatus* and *Suillus grevillei* were distinct indicative ECM species for the youngest stands; in the middle-aged stands it was *Boletus edulis* and representatives of the genus *Russula,* and *Amanita rubescens* and *Imleria badia* in the oldest stands. In the case of SAP species, in middle-aged stands there were *Lycoperdon umbrinum* and *Mycena aurantiomarginata*, and in the oldest stands the species *Lepiota clypeolaria, Gymnopus confluens* and *Clitocybe odora* (Table 5). It should be added that practically all ECM macromycetes have a high ability to indicate the type of the habitat in which they grow. For example, the importance of the symbiotic relationship between the larch *Larix kaempferi* and ECM fungi (in particular *Suillus cavipes, S. grevillei* and *S. laricinus*) was cited by Kwon & Tsuyuzaki (2016), who found that due to the symbiosis, nitrogen uptake by the larch increased from 5 to 76% depending on the exposure and location of the larch forest (5% on the ridge and 76% on the slope). In our case, the mycorrhizal relationship between *S. grevillei* and *Larix decidua* was also confirmed in the youngest stand at site A2. Rudawska et al. (2022) studied the species diversity of macromycetes in differently managed mixed forest ecosystems in Poland and reported that of the total macromycete species diversity recorded, the only ECM indicator in the managed stands was *Laccaria proxima*, a fungus that occurs as a pioneer together with other species associated with coniferous forests (Mueller 1992), but also found as a symbiont with many adult gymnosperm hosts and angiosperms (Li 1996). In our collections, we have recorded the related species *Laccaria amethystina, L. bicolor* and *L. laccata* as indicator macromycetes (Table 5).

It is generally accepted that the higher the percentage of mycorrhizal fungi or the higher the value of mycorrhizal potential is detected in a given forest stand, the better the stand's prospects in terms of its health status, vitality and ecological stability (Gáper & Mihál 2008, Mihál 2023). Important indicators of the structure of the mycobiota in forest stands are the values of ectomycorrhizal potential or values of mycorrhizal percentage (according to Gulden et al., 1992; Gáper & Mihál, 2008; Luptáková & Mihál, 2018). We consider the mycorrhizal percentage values found in this study (Table 6) to be very favourable in the conditions of the spruce stands at the Vrchdobroč locality.

In the past, the ectomycorrhizal potential values were determined in the same stands by Gáper & Mihál (2008), who found that the ectomycorrhizal potential values in the first ten years after planting varied in the youngest stands (from 0.85 to 7.0, exceptionally 11.0), which indicates that ECM species were more abundant than SAP species in the youngest stands. As the age of the stands increased, the ectomycorrhizal potential values decreased (0.15 to 0.87), indicating a more massive onset of species diversity of SAP macromycetes. A similar trend was also shown in the case of mycorrhizal percentage values, e.

g. Luptáková & Mihál (2018) found that in 2016 the values of mycorrhizal percentage in individual stands were more or less comparable - the youngest stand at site A = 34.5%, the middle-aged stand at site B = 35.9%, the oldest stand at site C = 32.2%. Similarly, Luptáková & Mihál (2020) reported that between 2016 and 2018, the highest mycorrhizal percentage values were recorded in the youngest (41.95%) and the lowest values in the oldest stands (35.86%).

Furthermore, Mihál & Luptáková (2018) compared the mycoflora of two spruce monoculture stands at the Poľana locality, planted on former pastures, and found that the younger 38-year-old stand at the Hriňová locality had a slighty higher ectomycorrhizal potential value (1.4) than the older 80-year-old stand at the Valaška locality (1.2). The higher value at the Hriňová locality is also evident from the mycorrhizal percentage values (Valaška: 37% and Hriňová: 70%). Directly in the spruce stands at the Vrchdobroč site, the ectomycorrhizal potential values ranged from 1.43 to 6.0 in the youngest (1 to 11 years old), and from 0.35 to 0.68 in the oldest stands (31 to 41 years old) from 1965 (year of planting) to 2006. This trend showed a gradual decrease of ectomycorrhizal potential values from the youngest to the oldest stands (Gáper & Mihál 2008). Luptáková & Mihál (2018) also found a similar trend of the ectomycorrhizal potential decrease in the oldest stands at the Vrchdobroč locality between 2016 and 2018.

Conclusions

Our study demonstrates pronounced inter-annual variability in macromycete species richness, diversity, abundance, and community composition in Norway spruce–dominated stands, with sampling year consistently explaining more variation than stand age for most response variables. Although stand age affected macromycete abundance in a group-specific manner, no direct interaction between stand age and sampling year was detected, indicating that macromycete communities are likely shaped by processes operating at broader spatial or temporal scales than those represented by the study plots and the five-year sampling period. Ectomycorrhizal communities were more heterogeneous than saprotrophic communities, and indicator species analysis confirmed clear year-to-year shifts in both functional groups. Together, these findings highlight that high inter-annual variability can obscure the effects of successional stage and other ecological drivers in short-term studies, underscoring the importance of long-term monitoring when assessing macromycete community dynamics.

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Author contribution

IM designed the study. IM carried out the fieldwork and provided the material. BJ carried out the statistical analyses. IM and BJ drafted the manuscript. All authors consented to the submission of the manuscript.

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