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Predictors of mushroom production in the European temperate mixed deciduous forest

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ABSTRACT

Mushrooms play an important role in the maintenance of ecosystem processes and delivering ecosystem services, including food supply. They are also an important source of income for many people worldwide. Thus, understanding which environmental factors influence mushroom productivity is a high practical and scientific priority. We monitored the production of mushrooms in temperate mixed deciduous forest in Białowieża Primeval Forest in eastern Poland for two yielding seasons. The research plots were set under similar environmental conditions (topography, geology, soil type) but differed by tree species composition and tree species richness. The main factor explaining mushroom production (close to 35% of the variation explained by the model) was the species richness of mushrooms. In turn, the species richness of mushrooms was mainly explained by soil properties (pH and C/N ratio) and stand characteristics (including tree species richness and wood increment) for ectomycorrhizal mushrooms and by soil pH for saprotrophic mushrooms. Higher precipitation in 2021 resulted in higher mushroom production than in 2020, while low levels of precipitation in 2020 resulted in stronger effect of ambient temperature. The differences in mushroom yield between years varied highly among plots. They were explained by stand characteristics, and in the case of saprotrophic mushrooms by tree richness and their own species richness. Our results suggest that promoting mushroom species richness is fundamental for increasing mushroom yield and should be taken into account in forest management.

1. Introduction

Wild forest mushrooms, represented in the temperate forest by two major fungal guilds - ectomycorrhizal (EM) and saprotrophic (SAP) species - play an important role both in maintaining ecosystem processes and delivering ecosystem services at local and global levels (Dighton, 2018). Ectomycorrhizal species form symbiotic associations with host plants (Brunner, 2001; Hartnett and Wilson, 2002), which is the dominating form of tree-fungus interactions in the temperate and boreal climatic zone (Steidinger et al., 2019), where 80–90 % of all tree species form this symbiotic relationship (Read, 1991; Brundrett, 2004). The importance of saprotrophic fungi in forest ecosystems is very high as well. They play the key role in the decomposition of organic matter and, through this, in carbon and nutrient cycling (Bahram and Netherway, 2022), as well as in the neutralization of organic and inorganic pollutants (Ceci et al., 2019).

One of the important provisional ecosystem services delivered by fungi is their sporocarps (mushrooms). Mushrooms have been used by humans as food and also as medicine, and in religious ceremonies since the earliest times (Chang and Miles, 2004; Nichols, 2016). Due to their wide availability in major parts of the world (Boa and Nations, 2004) and the high content of essential nutritional substances (e.g. a complete essential amino acids profile, source of antioxidant), in many regions mushrooms are still a key food and source of income (González et al., 2020; Valverde et al., 2015). They also might become a critical source of food in a circular economy, playing a role in climate change mitigation and in buffering food shortages (Kumar et al., 2022). Even in economically developed countries, harvesting mushrooms is still an important activity, although it is mainly recreational (Savoie and Largeteau, 2011). Despite such high importance, only 25 of close to 2000 mushroom species that are regarded as potentially edible worldwide are extensively used as food and cultivated for commercial purposes (Chang and Miles, 2004). This is caused by difficulties in mushroom cultivation on a mass scale, resulting in the need to harvest wild mushrooms from their natural

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environment – mostly forests (Savoie and Largeteau, 2011). Therefore, examining the environmental factors affecting mushroom production is a key element in enhancing the availability of mushrooms as an important element of the human diet and wellbeing.

The main factors affecting the production of forest mushrooms are weather conditions, access to nutrient sources, forest management, and forest stand characteristics. Ambient temperature, soil humidity, and especially precipitation in the summer and autumn seem to be the most important factors explaining differences in mushroom production between years (Karavani et al., 2018; Alday et al., 2017a; Taye et al., 2016). In a 21-year long survey carried out in Switzerland, a noticeable variation in the production and species richness of mushrooms between years was found. Only eight of 408 mushroom species occurred each year on research plots. The production of mushrooms was correlated with monthly sums of precipitation from June to October, while the time of fruitbodies' appearance was linked with mean temperatures in July and August (Straatsma et al., 2001). The high dependency of mushroom production seasonality on weather conditions is visible in their response to climate change: the mushroom season now starts earlier and finishes later than several decades ago (Kauserud et al., 2010; Büntgen et al., 2013; Kauserud et al., 2012). In spite of the longer period of sporocarp yielding, reports on the changes in mushroom production under the influence of climate change are contradictory, suggesting both increase or decrease, depending on the region (Büntgen et al., 2013; Yun and Hall, 2004).

Among other environmental characteristics, nitrogen concentration, pH, type of soil, slope, and elevation are listed as main predictors of mushroom production. The research carried out in the temperate forests of the USA revealed that long-term deposition of nitrogen affects the fungi species composition, leading to an increase of saprotrophs production and a decrease of ectomycorrhizal fungi production (Morrison et al., 2016). Other researchers confirmed the decline of mushroom production under high nitrogen concentrations (e.g.: Gillet et al., 2010). The type of soil also matters, as fewer mushrooms are observed in soils with decreasing proportion of sand (Taye et al., 2016). Soil acidity may have a contradictory influence on mushroom production, depending on species or group of species in question. Production of some species (e.g. *Lactarius* sp.) increases with the acidity of the substrate (Taye et al., 2016), while others (e.g. *Tuber aestivum* Vittad.) decrease (Bragato et al., 2022). Additionally, in mountains in Mediterranean region, mushroom production increases with increasing elevation (Bonet et al., 2008) but is lower on the steeper and southern slopes (Bonet et al., 2010).

Forest management practices modify stand structure that has an influence on the diversity of trees (Poudyal et al., 2019), understory plants (Battles et al., 2001), and microbiota (Colombo et al., 2016), and consecutively also the functioning of forest ecosystems. Thinning is the most common silvicultural practice, however despite many studies there are no clear conclusions on its impact on fungal communities. De-Miguel et al. (2014) showed that thinning positively affects the species composition of fungal communities and their productivity, whereas Parladé, Martínez-Peña, and Pera (2017) demonstrated negative correlation of these factors. In the same time, some other studies did not reveal any effect of thinning on mushroom production and their species richness (Salerni et al., 2020; Castaño et al., 2018). However, some researches indicate both increase (especially in the first years after thinning) and later decrease in fungal fruitbody production after thinning (Tomao et al., 2017).

Among basic tree stand characteristics, stand age, stand basal area, and canopy cover are most commonly reported to have the greatest impact on mushroom production. Mushroom yield is higher in younger stands, due to the faster growth rate of young trees (Tomao et al., 2017), although the transition between this stage is fluid and depends on the longevity of tree species and the fertility of the site (Martínez-Peña et al., 2012). In the mature forests, stand basal area is one of the best-studied predictors of mushroom production, however, a study conducted in Mediterranean pine forests suggests that stand basal area optimal from this point of view depends on tree species composition and soil properties (de-Miguel et al., 2014).

Despite many studies researching factors affecting mushroom production, knowledge on the impact of tree species composition on mushroom yield is scarce. Tree identity and tree species richness influence the fungal biomass and species composition of fungi. Urbanová et al. (2015) reported that in mixed temperate forests fungal taxa are often tree specific: 35–37 % of the dominant fungal operational taxonomic units (OTUs) were restricted only to one or two trees. In this study, numbers of observed dominant OTUs increased with the increasing number of trees, suggesting the great role of tree species richness in forming fungal communities. They also revealed that tree composition can explain a large proportion of variation in the species composition of fungal communities, even greater than soil properties. Similar results were obtained in Mediterranean forests, where fungi species richness was positively correlated with tree species richness, and the tree host species identity was the main driver of the fungal community composition (Saitta et al., 2018). In China's subtropical forest, the effect of tree species richness on fungi composition was examined on a larger biodiversity scale (1–12 tree species). The study revealed that beta diversity of trees and fungi are strongly coupled. However, the effects of tree species identity dominate over tree species richness on the diversity and composition of fungal communities (Chen et al., 2019). Similar results were also obtained by Otsing et al. (2021) in a boreal forest in a study on EM fungi, which revealed that tree species identity is an important determinant of species composition of the EM fungal community. All these studies confirm the importance of tree species identity and tree species richness for the development of fungal communities. However, there are very few studies dealing with the impact of these factors on mushroom yield. Most studies devoted to the factors affecting mushroom production were conducted in Mediterranean and boreal pine forests, which limited conclusions on tree species identity impact (Alday et al., 2017a; Karavani et al., 2018; Martínez de Aragón et al., 2007; Pinna et al., 2010; Tahvanainen et al., 2016; Bonet et al., 2010). Still, even in the studied pine monocultures, the impact of tree identity was found. In the pre-Pyrenees forests of Spain, plots with dominating *Pinus sylvestris* L. produce more mushrooms (60.26 kg ha^{-1}) than those with dominating *Pinus halepensis* Mill. (15.17 kg ha^{-1}) (Martínez de Aragón et al., 2007).

Bonet et al. (2004; 2008) revealed that mushroom production correlates with mushroom species richness. Similar result were obtained by Straatsma, Ayer, and Egli (2001) who showed positive relationship between yearly frequency of mushroom species and the average number of sporocarps. However, the evidence of direct linkage between tree species composition and mushroom production is very limited. There is also a knowledge gap on factors influencing mushroom production in mixed temperate forests, which have rarely been studied from this point of view. Taking into account the importance of fungi for human wellbeing and the functioning of forest ecosystems, we investigated factors affecting mushroom yield in Białowieża Primeval Forest (mixed temperate forest, northeastern Poland). We hypothesized that 1) tree species composition and tree species richness positively influence mushroom production via positive influence on fungal species richness. Additionally, we assumed that 2) this relationship is stronger for ectomycorrhizal fungi than saprotrophic, as the relationship between living trees and their mycorrhizal partners is more specific than between type of deadwood and saprotrophs, and also because trees provide their mycobionts access to carbohydrates, which may enhance the production of their sporocarps.

2. Methods

2.1. Study area

Our study was conducted in Białowieża Primeval Forest (approximately 1500 km^2), one of the best preserved forests in Europe

(Jaroszewicz et al., 2019; Sabatini et al., 2018). This forest massif stretches over the border between Poland and Belarus, in the eastern part of the Central European Lowland (52°41′ N; 23°49′ E) and covers the flat plain with a mean altitude of 170 m a.s.l. (Sokołowski, 2004). It is a zone of warm-summer humid continental climate (Kottek et al., 2006), with mean annual precipitation of 625 mm (for the period 1985–2015) and a mean annual temperature of 7.3 °C (range from 5.9 °C to 9.2 °C, but since 1997, it has never dropped below 6.6 °C) (Boczoń et al., 2018).

Białowieża Forest lies in the zone of hemiboreal and mixed broadleaved-coniferous forests according to the European Environment Agency classification (EEA, 2007). The western part of the forest (in the limits of Poland), where the study took place, is dominated by mesic and mesotrophic habitats of mixed deciduous forests, with a high share of oak-lime-hornbeam forest (*Tilio-Carpinetum* type). Tree species dominant in that part of Białowieża Forest include: *Pinus sylvestris* L. (27 %), *Picea abies* (L.) H.Karst (25 %), *Alnus glutinosa* (L.) Gaertn. (19,5%), *Quercus robur* L. (12 %), *Betula pendula* Roth (8 %), *Carpinus betulus* L. (4 %) and *Fraxinus excelsior* L. (3 %) (Sokołowski, 2004).

2.2. Sampling design

In 2020 and 2021 we carried out mushroom monitoring on 20 plots established for the needs of the EU-funded FunDivEUROPE project (https://project.fundiveurope.eu/) to study the effect of tree diversity on ecosystem multifunctionality. Within the project, 43 plots were set up, which varied in terms of tree species richness (1–5 tree species) and included *Picea abies*, *Pinus sylvestris*, *Quercus robur*, *Betula pendula*, and *Carpinus betulus*. The study plots were set in mature mixed deciduous forest of the oak-lime-hornbeam type (*Tilio-Carpinetum*) without signs of silvicultural activities for the last 10–20 years. All plots were located under similar environmental conditions (i.e. topography, geology, soil type) to minimize the influence of the variability of environmental factors on the subject of the study (Baeten et al., 2013). Each plot is 30 m × 30 m and is permanently marked in the field by wooden stakes at the corners to facilitate sampling. The plots are surrounded by a 10 m-wide buffering area with similar tree species composition and environmental conditions, which minimizes the edge effect of the surrounding stands.

Due to intensive dieback of spruce during 2015–2018 (Kamińska et al., 2020), all plots with spruce in the stand had been excluded from the monitoring of mushroom production to avoid the influence of the natural thinning of the stands. In effect, the investigation was carried out on 20 plots, encompassing four levels of tree diversity (1, 2, 3, and 4-tree species mixtures), including monocultures and mixtures of *Pinus sylvestris*, *Quercus robur*, *Betula pendula* and *Carpinus betulus* (not all species combinations were present in the field and not all existing combinations had replication: Table S.1).

2.3. Monitoring of mushrooms

All plots were sampled every ten days for two years (2020, 2021), from mid-June to the end of October (i.e. during the period of the highest intensity of production of sporocarps by edible species). We collected all mushrooms in the entire plot area, extended with a 2.5 m-wide strip of the land around to enlarge the sampling area to 35 m × 35 m. We harvested sporocarps of all soil-dwelling and epixylic macrofungi, excluding bracket fungi and those with the size of the sporocarp < 0.5 cm. All mushrooms were brought to the laboratory for cleaning, fresh weight measurements, and species identification. After identification and weighing we dried mushrooms in a food dehydrator at 50 °C for about 24 h to eliminate errors of biomass estimation caused by variations in the water content of fresh sporocarps, and weighed again with 0.01 g accuracy.

We determined the mushroom species to the lowest possible level, using our expertise, available online keys and atlases (https://www.grzyby.pl and https://www.nagrzyby.pl), and a book, “Fungi of temperate Europe: Volume 1 + 2” (Laessoe and Petersen, 2019).

2.4. Climate data

Custom-made microclimate stations were installed in 1- and 3-species plots ($n = 10$) at the plot’s centre. During the whole sampling period, these continuously monitored air temperature, air humidity, black globe temperature and wind speed, with a sampling frequency of one hour. As the stations were not installed in all plots and measures displayed no noticeable differences among plots, we decided to use the general meteorological data from Białowieża meteorological station (52°42′26″N 23°50′53″ E), located in the center of the forest. The hourly data of precipitation and daily mean, maximum and minimum temperatures of air were downloaded from the website of The Institute of Meteorology and Water Management (IMGW-PIB-2021).

2.5. Forest stand data

The plot-level forest inventory data for plots were obtained from FunDivEUROPE and Soil4Europe projects data portal (https://data.botanik.uni-halle.de/fundiveurope). The data were gathered in 2012 and 2018 according to the methodology described by Jucker et al. (2014) and included: tree species, diameter on breast height and wood increment (difference between wood biomass in 2012 and 2018).

The soil pH, C/N ratio, nitrogen and carbon concentration were measured in 2012 at the forest floor level (humus) and at the different depth of mineral soil (0–10, 10–20, 20–30, 30–40 cm). Taking into account that most of fungal mycelia biomass is located in litter (forest floor) and the upper 10 cm of soil (Brabcová et al., 2016), we used in our analysis data obtained for these two layers. Detailed procedure of the measurements of soil variables was described in Dawud et al. (2016). The understorey cover was estimated in June 2020 using the six-step Braun-Blanquet cover-abundance method (Braun-Blanquet, 1928) commonly used during plant surveys. The understorey was defined in this study as vegetation layer consisting of all herbaceous plants regardless of their height and trees and shrubs lower than 0.5 m.

2.6. Statistical analysis

Prior to statistical analysis, in addition to taxonomic identification, we categorized mushrooms for edible and non-edible (including poisonous) and for ectomycorrhizal (EM), saprotrophic (SAP) and other properties (parasites or mushrooms with unclear/unidentified ecological status). The online keys and atlases (https://www.grzyby.pl and https://www.nagrzyby.pl) and a book “Fungi of temperate Europe: Volume 1 + 2” (Laessoe and Petersen, 2019) were used to classify mushrooms to each category. Factors influencing the species richness of fungi were studied with the help of linear models (LM) implemented in the stats package (R Core Team, 2021). In all LMs, sums of mushroom dry mass (total, EM, SAP) from all harvests on each plot were used as a separate data record ($n = 20$). Since mushroom dry mass data were non-normally distributed, we used the logarithmic scale to normalize their distribution. Akaike’s information criterion (AIC) was used to choose the best model (Akaike, 1973), using the MuMIn package (Bartoń, 2020). To estimate the contribution of each variable in a multivariate model we used hierarchical decomposition of goodness-of-fit measures of regressions (hier.part) (Nally and Walsh, 2004).

We used a *t*-test to check for the significance of differences in the production of a specific group of mushrooms (SAP, EM, or total) between the years.

Due to the low descriptive power of the LMs, we used Generalized additive models (GAM) with integrated smoothness estimation from the mgcv package (Wood, 2003; 2004; Wood, Pya, and Säfken. 2016; Wood, 2011; 2017) to check the influence of climate factors on mushroom production between the years.

To study how production changed between the years and how it varied between the plots, we calculated the rate of collected mushroom biomass change between 2020 and 2021 in relation to mass in 2020 ((mass$_{2021}$-mass$_{2020}$)/ mass$_{2020}$) for total, EM, and SAP biomass. Next, we built the LMs to explain the variation of changes between the plots.

All statistical analyses were carried out in R software version 4.1.2 (R Core Team, 2021) using the RStudio version 2022.2.0.44 environment (RStudioTeam, 2022).

3. Results

Over a two-year study period we recorded 290 fungal species in total (149 species in 2020 and 238 in 2021), with 97 species recorded both years (Table S.2). *Xerocomellus chrysenteron* (Bull.) Šutara, *Armillaria mellea* (Vahl) P. Kumm. and *Mycena galericulata* (Scop.) Gray were the most frequent species both years (present on at least 75 % of plots). Additionally *Lycoperdon perlatum* Pers. was very frequent in 2020 but not in 2021 and *Mycena vitilis* (Fr.) Quél., *Mycena rosella* (Fr.) P. Kumm. and *Russula cyanoxantha* (Schaeff.) Fr. in 2021 but not in 2020 (Table S.2).

Out of all recorded mushroom species 116 were EM and 126 SAP. The remaining species were parasites or of unclear/unidentified ecological status. Ninety-one species were edible.

During the two years of monitoring, we collected in total (from all plots) 225.8 kg of mushrooms (fresh mass, mean 46.08 kg ha^{-1} per year), including 134.4 kg (27.4 kg ha^{-1} per year) of edible species, which translated into 22.4 kg (4.6 kg ha^{-1} per year) and 12.8 kg (2.6 kg ha^{-1} per year) of dry mass, respectively (Table S.3). EM species (14.4 kg of dry mass (2.95 kg ha^{-1} per year)) constituted 64 % of the total dry mass, whereas SAP 20.8 % (4.6 kg of dry mass (0.95 kg ha^{-1} per year)) (Table S.3).

In both years the most productive species were *Lactarius vellereus* (Fr.) Kuntze (1.82 kg and 1.81 kg of dry mass), *Armillaria mellea* (0.83 kg and 1.45 kg), and *Russula nigrescens* (Bull.) Fr. (0,73 kg and 1.51 kg) in 2020 and 2021, respectively. In 2021 *Russula cyanoxantha* was also highly productive (1.7 kg of dry mass) (Table S.2).

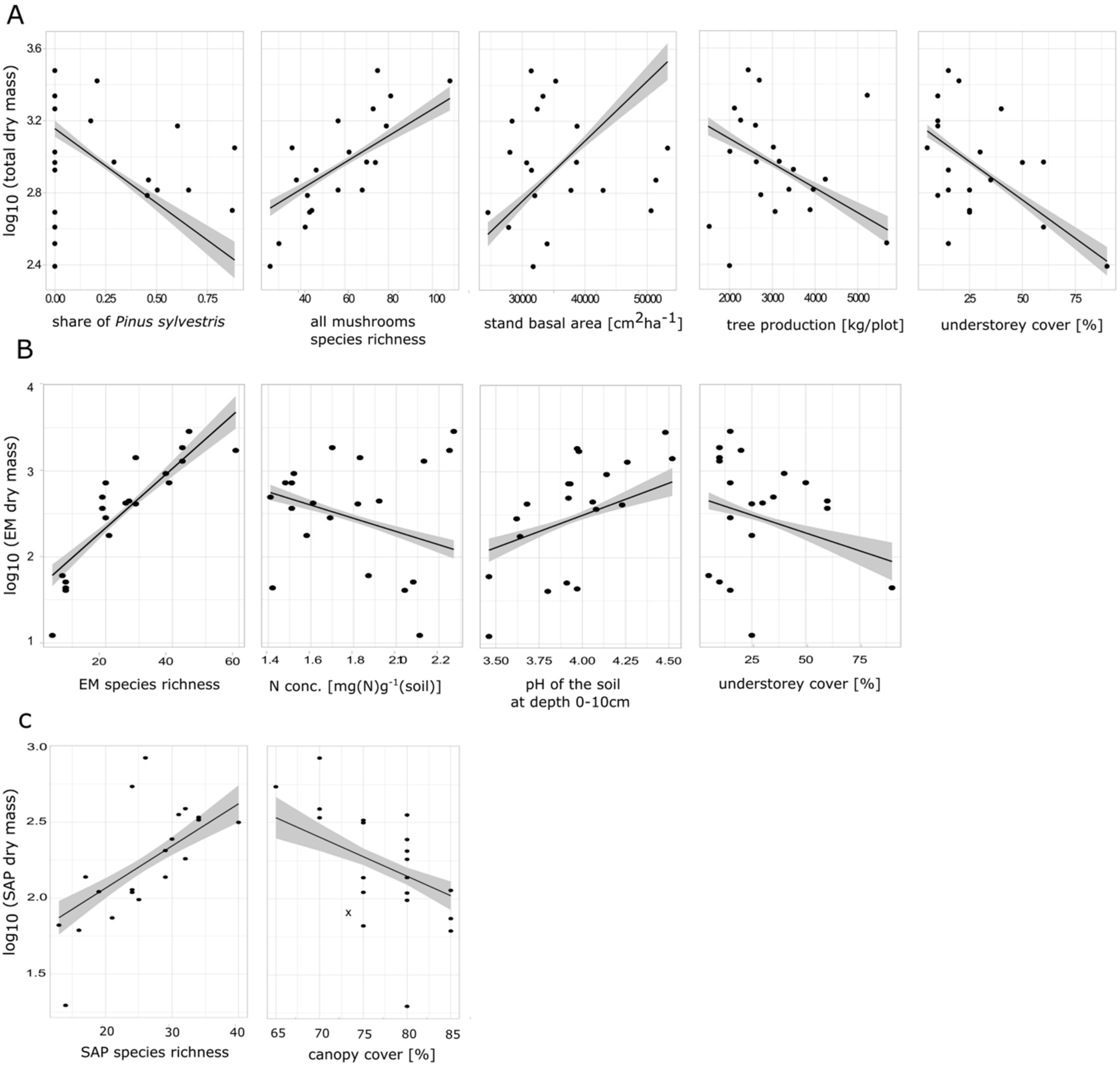

Fig. 1. Factors influencing the production of mushrooms in Białowieża Forest (North-Eastern Poland): A) all mushroom species (LM1), B) ectomycorrhizal species (EM) (LM2), and C) saprotrophic species (SAP) (LM3); only significant interactions are displayed (Table 1; Table S.4; Table S.6–7).

The total mushroom production in 2021 was 60 % higher than in 2020 ($m_{2020} = 3.5$ kg ha^{-1}; $m_{2021} = 5.6$ kg ha^{-1} of dry mass, respectively). The dry mass of EM mushrooms increased by 80 % ($m_{2020} = 2.1$ kg ha^{-1}; $m_{2021} = 3.8$ kg ha^{-1}), whereas dry mass of SAP fungi was similar between the years ($m_{2020} = 0.9$ kg ha^{-1}; $m_{2021} = 1$ kg ha^{-1}) (Table S.3).

3.1. *Effect of tree stand on mushroom production*

We revealed high variability of mushroom production between the plots. Total mushroom production increased with increasing stand basal area ($t = 5.822$, $p < 0.0001$) (with optimal area estimated at 30–35 m^2/ha) and mushroom species richness ($t = 5.823$, $p < 0.0001$), which turned out to be an essential variable, explaining around 35 % of variation of mushroom production. The second most important value was understorey cover negatively affecting sporocarps production ($t = -6.772$, $p < 0.0001$) and explaining around 17 % of its variation. Mushroom yield also increased with decreasing tree biomass increment ($t = -4.777$, $p \approx 0.0005$) and share of *Pinus sylvestris* in the stand ($t = -5.182$, $p \approx 0.0002$) (Fig. 1A; Table 1: LM1; Table S.4; Table S.5).

The species richness of both EM and SAP mushrooms was the key factor explaining 22 % of variation of EM mushroom production and 33 % of SAP production ($t = 6.222$, $p = 0.0002$; $t = 3.552$, $p = 0.003$, respectively5 (Table S.5). Additionally, EM species production also increased with increasing pH of the soil at depth 0–10 cm ($t = 2.786$, $p = 0.024$), decreasing nitrogen concentration in the soil ($t = -3.720$, $p = 0.006$), and decreasing understorey cover ($t = -2.314$, $p = 0.05$) (Fig. 1B; Table 1: LM2, Table S.6). The production of SAP fungi was negatively influenced by canopy cover ($t = -2.479$, $p = 0.03$) (Fig. 1; Table 1:LM3, Table S.7).

3.2. *Effects of tree stand on mushroom species richness*

The total species richness of mushrooms was not explained by any stand characteristics (Table 1: LM4, Table S.8). However, species richness of EM mushrooms increased with increasing forest floor pH ($t = 5.764$, $p < 0.0001$), plant species richness ($t = 4.528$, $p = 0.0007$), stand basal area ($t = 3.930$, $p = 0.002$), carbon to nitrogen ratio of the humus layer ($t = 4.458p = 0.0008$), tree species richness ($t = 2.199$, $p = 0.05$), and share of *Carpinus betulus* in the stand ($t = 3.398$, $p = 0.005$). It also decreased with increasing cover ($t = -4.244$, $p = 0.001$) (Fig. 2A, Table 1: LM5, Table S.9). Among them, pH, C/N ratio, and plant species richness were essential factors explaining 22 %, 16 % and 15 % of variation, respectively (Table S.5). The rest of the factors were less important and each of them explained less than 10 % of variation of EM species richness explained by the model (Table S.5). SAP species richness was influenced only by the pH of the soil at depths 0–10 cm ($t = -2.858$, $p = 0.01$) (Fig. 2B, Table 1: LM6, Table S.10).

3.3. *Year effects*

The mean change of the total mushroom production per plot between 2020 and 2021 was + 75 % (±107(SD)). The EM mushroom production changed by mean + 200 % (±322 (SD)). The enhancement of SAP mushroom production was on the mean change level of + 18 % (±101 (SD)) (Fig. S.1).

The change in total mushroom production in 2021 in comparison to 2020 (for all species) increased with increasing share of *Quercus robur* ($t = 4.935$, $p = 0.0004$), pH of the soil at depth 0–10 cm ($t = 2.806$, $p = 0.02$) and mushroom species richness ($t = 3.358$, $p = 0.006$), and with decreasing nitrogen concentration in the soil ($t = -5.097$, $p = 0.0003$), and decreasing plant species richness ($t = -3.561$, $p = 0.004$) (Fig. 3A, Table 1: LM7, Table S.11).

Higher increase in the production of EM mushrooms between the years was observed in plots with a lower share of *Pinus sylvestris* ($t = -2.296$, $p = 0.04$) and *Betula pendula* ($t = -2.192$, $p = 0.05$), lower plant species richness ($t = -2.800$, $p = 0.01$), and higher tree density ($t = 4.067$, $p = 0.001$) (Fig. 3B, Table 1: LM8, Table S.12). The bigger change in SAP mushroom production was related to higher SAP species richness ($t = 2.162$, $p = 0.05$) and lower tree species richness ($t = -3.322$, $p = 0.005$) (the change was higher in monocultures and also increased with the share of *Betula pendula* in the stand) (Fig. 3C, Table 1:LM9, Table S.13).

3.4. *Weather condition effects*

In 2021, the sum of precipitation during the mushroom yielding period was higher than in 2020 (324 mm and 251 mm, respectively), especially in July, when the monthly rainfall in 2021 was over two times higher than the year before (142.7 mm vs 67.2 mm, respectively). The mean monthly air temperature of the yielding period did not differ between the years (*t*-test; $t = 0.64032$, p-value $= 0.534$; $temp_{2020} = 16.29 \pm 3.85(SD)^{\circ}C$, $temp_{2021} = 15.78 \pm 5.44(SD)^{\circ}C$).

The gamma models revealed that in 2021 total mushroom production depended on the sum of precipitation from the month preceding the month of mushroom collection (i.e. the period 60 to 30 days before the date of sampling) but not on the temperature. In 2020 the mean temperature of the ten days before sampling explained mushroom production, but not the precipitation (Fig. 4; Table 2.).

4. Discussion

In our study we investigated factors affecting mushroom yield, mushroom species richness, and stability of mushroom production between years. Due to scrupulously selected plots (similar topology, geology, soil type; lack of thinning; stand's maturity) (Baeten et al., 2013), we minimized the influence of environmental factors other than stand characteristics and weather conditions. Therefore, tree stand composition should pose a prevailing impact on the functioning of the studied mushroom community. However, plots also differed in terms of other variables affected by tree stand characteristics like understorey cover, N concentration and pH (Ampoorter et al., 2016; Dawud et al., 2016).

The mean mushroom production differed between the 2020 and 2021, which is consistent with the previous studies revealing high

Table 1

Linear models explaining mushroom production (LM1-3), species richness (LM 4-6), and differences in mushroom productivity between years (LM7-9) for all mushrooms (LM1, LM4, LM7), EM mushrooms (LM2, LM5, LM8) and SAP mushrooms (LM3, LM6, LM9).

Model	Residual standard error:	Degrees of freedom	Multiple R-squared:	Adjusted R-squared:	F-statistic	p-value
LM1	0.0854	12	0.9482	0.918	31.39	8.58E-07
LM2	0.1878	8	0.9654	0.9179	20.32	0.000119
LM3	0.219	14	0.7591	0.6731	8.823	0.000588
LM4	14.77	13	0.6524	0.4919	4.066	0.01625
LM5	6.759	12	0.8745	0.8013	11.95	0.000147
LM6	5.348	12	0.6681	0.4745	3.451	0.02905
LM7	0.4317	12	0.9053	0.8365	13.15	1.26E-04
LM8	1.981	13	0.7417	0.6224	6.22	0.002905
LM9	0.7375	13	0.6363	0.4684	3.79	0.02095

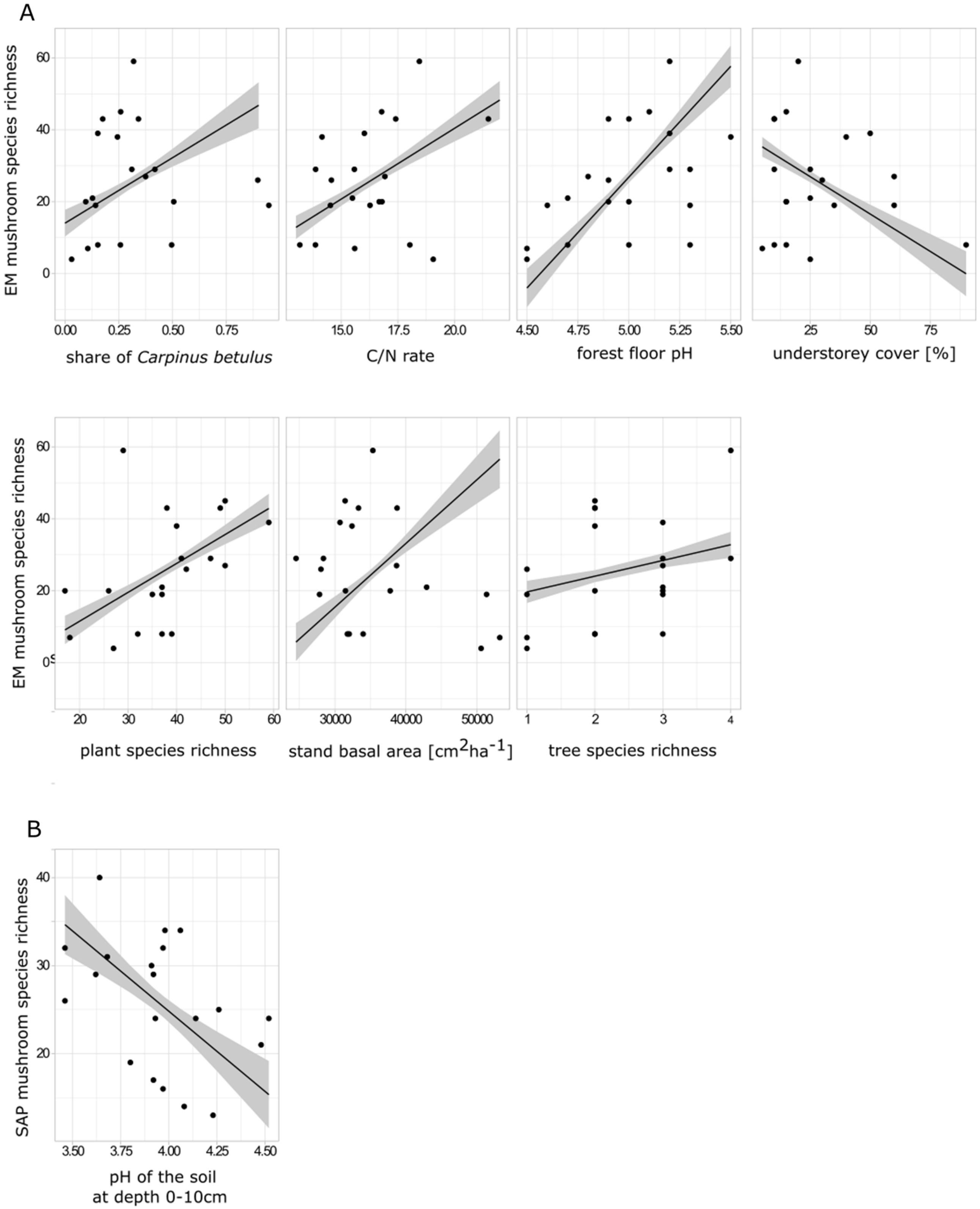

Fig. 2. Factors influencing A) ectomycorrhizal (LM5) and B) saprotrophic mushrooms species richness (LM6) in Białowieża Forest (North-Eastern Poland); only significant interactions are displayed (Table 1; Table S.9 and S.10).

variation of mushroom biomass between years (Büntgen et al., 2013; Alday et al., 2017a). The overall productivity revealed in our study is difficult to compare with other studies due to varied yielding times, groups of mushrooms included in analysis and forest characteristics like its management, continuity of forest cover or naturalness of ecosystem. Even in similar climate zones and time scales the differences are high. Alday et al. (2017a) collected around 130 kg ha^{-1} mushrooms per year, whereas Martínez de Aragón et al. (2007) reported several times lower annual sporocarp production, around 29.4 kg ha^{-1}, despite the fact that both studies were carried out in the Mediterranean climate zone with

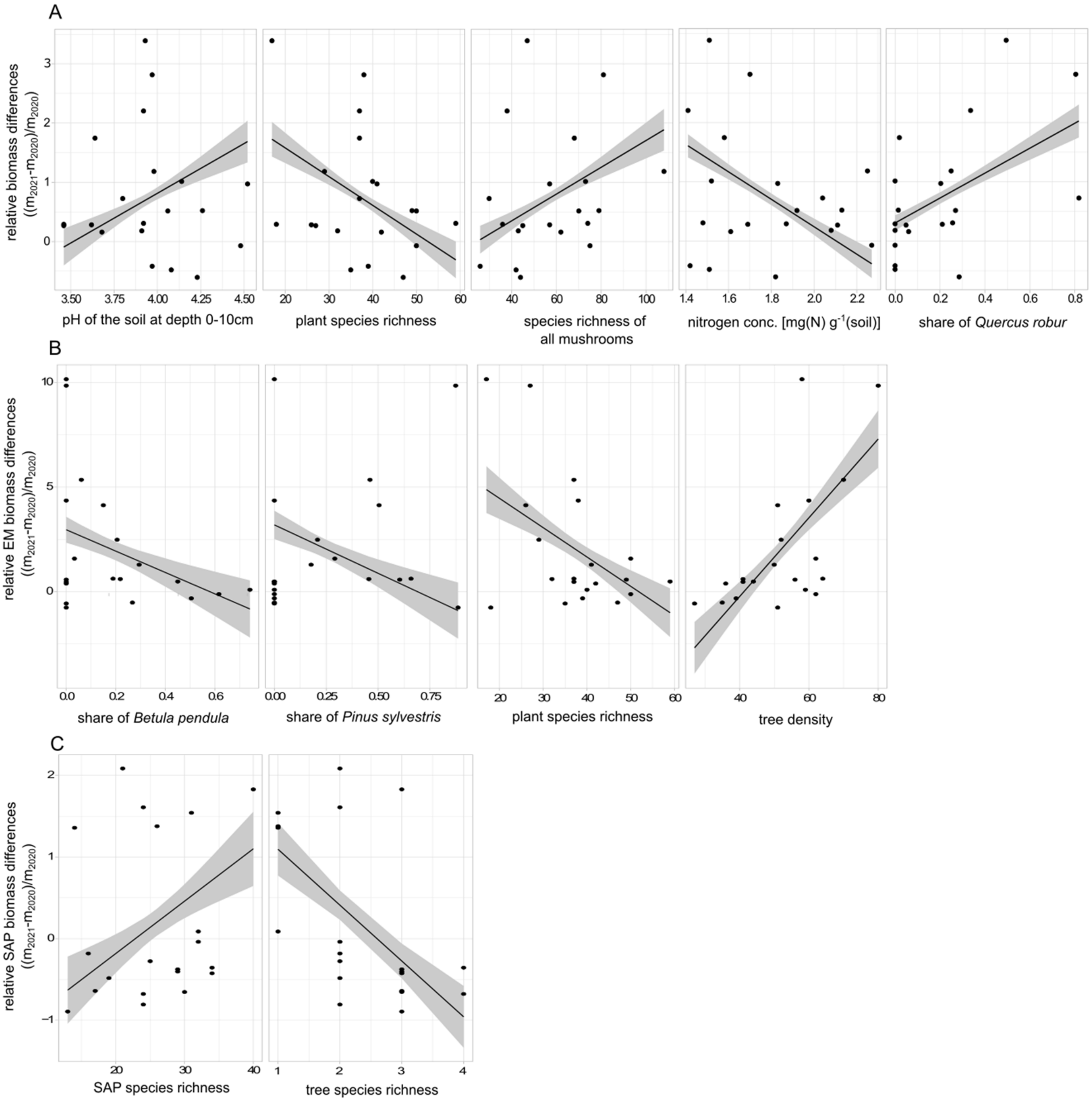

Fig. 3. Factors influencing A) all mushroom; B) ectomycorrhizal; C) saprotrophic mushroom production relative mean change between 2021 and 2020 in Białowieża Forest (North-Eastern Poland); only significant interactions are displayed (Table 1, Table S.11-S.13).

weekly harvesting from the beginning of September to the end of December. Our research was conducted in the temperate climate zone and in one of the most natural forest ecosystems in Europe, characterized by high species richness of mushrooms (Jaroszewicz et al., 2019). Our results suggest that high species richness of fungi should enhance the mushroom production, however, the mean production in our study (46,08 kg ha^{-1} per year) was similar to results obtained by Martínez de Aragón et al. (2007) from the Mediterranean zone.

4.1. Factors influencing mushroom production

Close to 95 % of variation in mushroom production was explained by stand characteristics (Table S.5). Stand basal area was one of the main factors affecting mushroom yield, which is consistent with papers from Mediterranean forests (Martínez-Peña et al., 2012; Bonet et al., 2010). From the point of view of mushroom production, the optimal stand basal area (resulting in the maximal mushroom yield) varies in the literature between 10 and 40 m^2/ha, depending on the study region, dominant tree species and soil properties, and can be different for specific mushroom species (Tomao et al., 2017). In our study, in the European mixed temperate forest, the stand basal area yielding the highest mushroom production was estimated at 30–35 m^2/ha. That is similar to the 35–40 m^2/ha suggested by Sánchez-González et al. (2019) based on studies carried out in *Pinus sylvestris* and *Pinus pinaster* Aiton stands in Northern Spain.

Our analyses revealed a decrease of mushroom yield with increasing tree increment (i.e. wood biomass production). This is the opposite of what was reported by Collado et al. (2019), who found a positive interaction of tree growth and mushroom yield in the Mediterranean region. This positive interaction was explained by the higher amount of

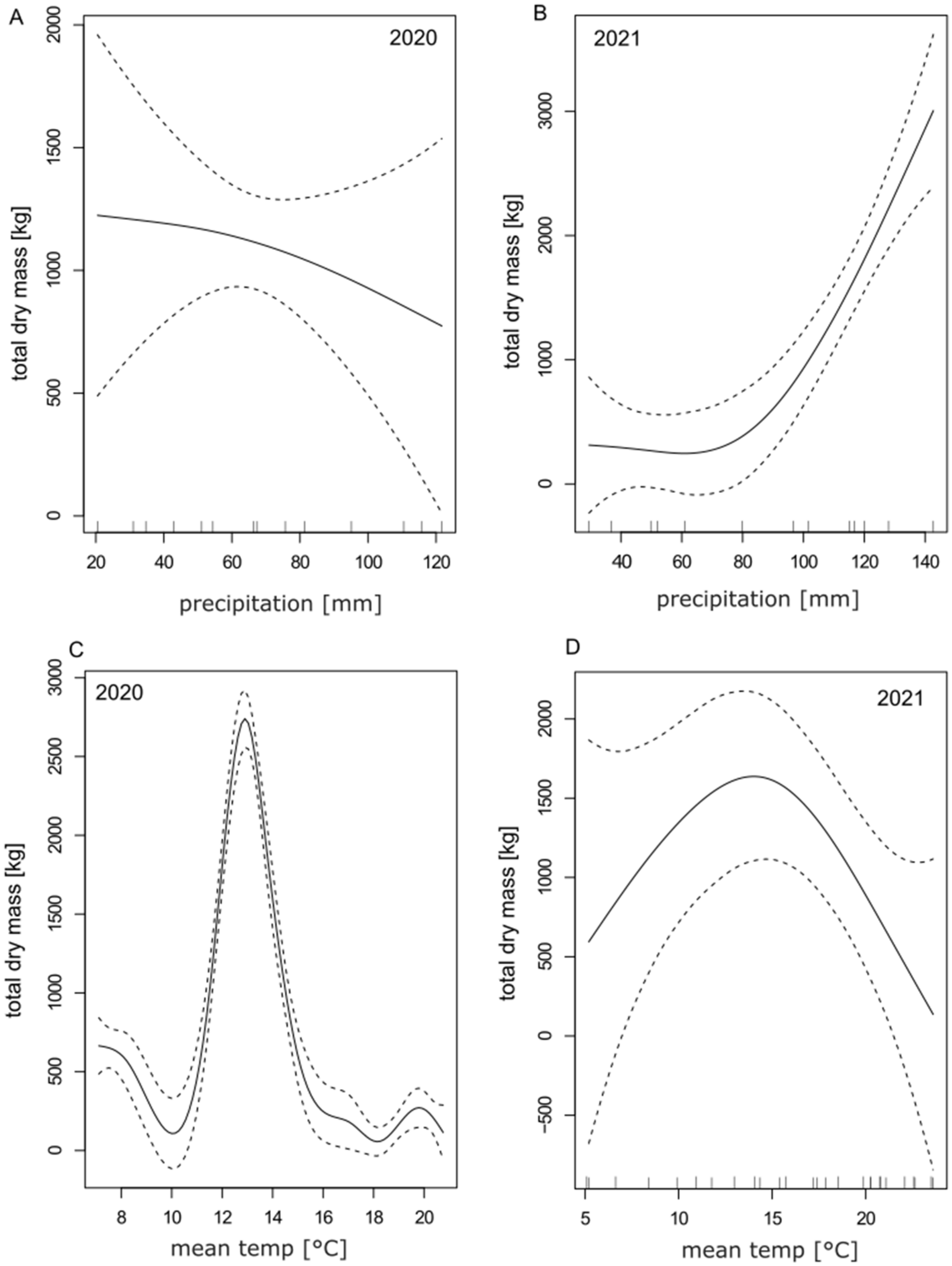

Fig. 4. Relationship between weather conditions and mushrooms production in Białowieża Forest in 2020 and 2021. A, B – sum of precipitation from the month preceding the month of mushroom collection; C, D - mean temperature of the ten days before mushroom collection.

Table 2
Gamma models explaining the relationship between mushroom production and weather conditions (the mean air temperature of the ten days before sampling, and the sum of precipitation of the previous month (period from 60 to 30 days before the date of sampling)); the significant models are marked in bold.

Variable	F-statistics	p-value	R-squared	Deviance explained
mean_temp_2020	**105.7**	**0.000218**	**0.986**	**99.6 %**
mean_temp_2021	2.081	0.16	0.296	41.7 %
precipitation_2020	0.24	0.633	−0.0286	6.34 %
precipitation_2021	**19.15**	**0.000173**	**0.831**	**86.6 %**

carbohydrates transferred from trees to mushrooms during periods of intensive tree increment. However, this correlation was revealed in the Mediterranean region under water-limited climate conditions, where both seasonal wood production and mushroom yields are more sensitive to precipitation events during the late growing season (Collado et al., 2019). At the same time, the authors did not find any linkages between these two factors in boreal and temperate forests, suggesting that this relationship is region-specific and caused by the high dependence of tree increment and mushroom production on precipitation. In our study, the negative impact of tree growth intensity on mushroom production may be the effect of high abundance of *Armillaria* spp. (Fr.) Staude, which accounted for close to 10 % of the dry mass of all collected mushrooms. *Armillaria* fungi are both facultative saprophytes and forest pathogens (Roll-Hansen, 1985), often affecting weakened trees and causing their death. Thereby, the stronger the trees, the lower sporocarp yield of this species. In our opinion, even with a 10 % share in the total yield, this species, in combination with saprotrophs, can change the lack of impact of tree growth on mushroom yield, observed in temperate forests by Collado et al. (2019), to a negative one revealed by us.

In our study, mushroom production was also negatively affected by understorey cover. A similar effect was observed in Finland in the case of *Tricholoma matsutake* S. Ito & S. Imai. Production of this mushroom decreased with density of understorey vegetation (Vaario et al., 2013), which was explained as an effect of several factors – light availability, inhibition of development of mycelium by herbs, and higher competition between plant roots and fungi. High understorey cover limits light availability, which is necessary for the development of fruiting bodies (Sakamoto, 2018). Gramss (1985) also proved that decaying grasses partly inhibit the growth of the mycelium, which can negatively affect mushroom production. Additionally, a denser understorey causes higher root competition (Coomes and Grubb, 2000), which means higher fungal competition for limited soil resources.

Soil nitrogen concentration negatively influenced EM mushroom yield, which was consistent with earlier observations (Buée et al., 2011) and experiments (Gillet et al., 2010). Many studies have shown that high nitrogen levels reduce EM mycelium growth, decrease their species diversity, and reduce sporocarp production, whereas SAP fungi are much less affected (Lilleskov et al., 2001; Peter et al., 2001; Hasselquist and Högberg, 2014). The difference is probably caused by diverse ways of carbon acquisition by these two groups of fungi. High nitrogen availability in the soil causes a reduction in the allocation of carbon to the roots by trees, which limits C supply for EM mushrooms (Demoling et al., 2008). SAP obtain carbon from dead biological matter, which decay rates increase with increased availability of nitrogen (Rinne et al., 2017).

Tree species composition did not affect total mushroom production on our study plots, which is contrary to our expectations based on the fact that at least mycorrhizal fungi are very often tree species specific. Only the share of *Pinus sylvestris* negatively impacted their yield. In plots with a higher share of pine, the biomass of mushrooms was lower than in plots with a lower share, whereas the yield of mushrooms in plots without pine varied but did not show any detectable trends. Most studies on mushroom production have been conducted in pine-dominated Mediterranean (Martínez-Peña et al., 2012; Karavani et al., 2018; Salerni et al., 2002) and boreal forests (Pinna et al., 2010; Tahvanainen et al., 2016), which did not allow an assessment of the importance of this tree species in comparison to others. A positive influence of an admixture of another tree species in pine stands on fungal species richness was found by Suz et al. (2017), who compared fungal communities of pine and pine-oak stands in Finland. Pure pine stands hosted on average 26 fungi species, while oak admixture increased their species richness to 38 species, but the authors did not take into account the exact share of pine in the studied stands. In our study, increasing abundance of *P. sylvestris* in stands negatively affected the yield of all mushrooms. In our opinion, this negative influence was mediated via litter and soil/substrate acidity. Pine is one of the species which has an acidifying effect on forest soils (Achilles et al., 2021), which negatively impacts mushroom production. Yamanaka (2003) found that higher pH of the substrate positively influences the production of many mushrooms, with the optimum at pH = 5–6 for EM and at pH = 7–8 for SAP mushrooms, while reaction of the pine litter is much lower (pH ≈ 4) (Smal and Olszewska, 2008). Our analysis revealed a similar positive relation between the pH of the soil and production of EM mushrooms, but lack of it for SAP mushrooms (only negative effect on SAP species richness). As pH gradient of soil at depth 0–10 cm was very short (3.5–4.5), the impact of pH on EM production could be more visible as their optimum is closer to the tested interval, whereas the differences between pH around 3.5 and 4.5 could be just to low to affect SAP production, whose optimum is much higher. The observed linkage between *P. sylvestris* and mushroom production could be very local, as the impact of tree species identity often has a local character, not extending too far beyond the crown or root range. This explains the importance of share of this tree species for mushroom production: the more pines, the bigger the share of the plot area, characterized by conditions not optimal for fungi. Adamo et al. (2021) demonstrated that mushroom yield does not differ between the studied pine species (*P. sylvestris*, *P. halepensis*, *P. nigra* Arn), which may be caused by the similar acidifying effect of all these species. However, Martínez de Aragón et al. (2007) showed that in *P. sylvestris* stands mushroom production is higher than in *P. halepensis* and *P. nigra* stands. The different results of this study may have been caused by variation of soil properties and other stand characteristic between plots not taken to account in the study, limiting the impact of trees to the local scale.

4.2. *Factors affecting species richness of fungi*

In our study, the production of all the studied groups of mushrooms (EM, SAP but also total) was positively related to the species richness of fungi. This is consistent with Bonet et al., 2004 and Bonet et al., 2008), who demonstrated similar links for many functional groups of mushroom: all, edible, marketed edible, *Lactarius* spp. In our study fungal species richness was the key factor, explaining around 35 % of variation of mushroom production (Table S.5, Table 1. (LM1)). The importance of this factor prompted us to find out which stand characteristics influence this variable.

The model explaining the species richness of all mushrooms did not reveal any factors affecting this variable. This is probably because different factors affect specific fungi species in ways contradictory to each other, and one may also expect many factors influencing just very specific species or species groups, like availability of spore vectors or high substrate specialization of fungi, etc. However, in the case of EM mushrooms, their species richness depended mainly on soil properties (pH of the forest floor explained 22 % of variation and C/N 16 % of variation; Table 1. (LM5); Table S.5) and some stand characteristics – plant species richness, stand basal area, understorey cover, tree species richness and share of *Carpinus betulus*. Our results were consistent with reports of Tedersoo et al. (2016) and Chen et al. (2019) describing soil properties as key drivers of fungal species richness.

Plant species richness and their cover also turned out to be important factors explaining 15 % and 8 % (respectively) of richness of EM mushrooms (Table 1. (LM5); Table S.5), which is consistent with the report of Hiiesalu, Bahram, and Tedersoo (2017), who suggested that plant species richness and their productivity may be the key factor explaining the diversity of fungi.

In our research, forest monocultures were characterized by lower EM mushroom species richness than mixed stands, which slightly increased with increasing tree species richness. This is consistent with studies suggesting the positive influence of tree diversity on the species richness of fungi (Saitta et al., 2018; Chen et al., 2019), and the study by Suz et al. (2017), reporting higher numbers of species of fungi in *Q. robur* – *P. sylvestris* forest than in a *P. sylvestris* monoculture. Additionally, we revealed that the share of *Carpinus betulus* also positively affected mushroom species richness, but only to the 30 % share of the basal area of all trees. The positive effect of *C. betulus* may be a result of its expansion in Białowieża forest and the high share of very young trees of this species under a canopy of mature-dominant trees of other species, which can cause accelerated transport of nutrients to mycelium and higher EM mushroom production.

The saprotrophic mushroom species richness was negatively affected by pH of the soil at depth 0–10 cm, which is in contradiction with reports from Amazonian forests, where Queiroz et al. (2021) found a direct, positive impact of pH on the species richness of saprotrophic fungi. The difference may be caused by the short gradient of measured pH (lack of positive impact of higher pH) and the influence of high inhibition of bacteria. In extremely low pH (around 3) the bacteria development declines severely and the fungal/bacterial ratio increases, as bacteria stop inhibit fungi growth (Bååth and Anderson 2003; Rousk, Brookes, and Bååth, 2010). The lack of inhibition, occurring in higher pH can explain the positive impact of extremely low pH on mushroom species richness.

4.3. Variation of mushroom production between the years

All our plots were located in a lowland area of approximately 30 × 40 km, and thus with similar amounts of precipitation and similar temperatures on each plot, which we confirmed by local monitoring of some meteorological characteristics. On the other hand, the weather conditions were the main factors explaining differences in mushroom yield between the two studied seasons. Similar effects were demonstrated in many earlier studies, with the special role played by precipitation, especially in the late summer-early autumn season (Alday et al., 2017a; Alday et al., 2017b; Taye et al., 2016; Karavani et al., 2018). In spite of the similar environmental conditions, on some plots mushroom production between 2020 and 2021 increased even three times, while on others decreased, which, taking into account the low variability of environmental factors, should be direct and indirect effects of the tree stand. We revealed that decreasing year-differences were linked with lower pH of the soil at depth 0–10 cm, species richness of all mushrooms, share of *Q. robur* and higher nitrogen concentration, and plant species richness. Higher differences between plots were observed in highly-dense stands, especially in the EM group of mushrooms, which could be interpreted as higher nutrient transfer from trees to mushrooms under better weather conditions in 2021 (more precipitation, lack of drought). Plants are reported to allocate up to 20 % of their photosynthetic production to mycorrhizal partners (Gorzelak et al., 2020), and the weather conditions conducive to woody biomass production can lead to greater transfers of carbon to mushrooms, and an increase in their productivity.

High mushroom species richness promoted not only mushroom production, but also larger differences in their production between years on the plot. This observation is contradictory to many plant studies, which revealed that high plant species richness increases the stability of their biomass production (Wang and Loreau 2014; Tilman et al., 2006; Isbell et al., 2009; Grime 1998). This effect is explained in plants by the asynchronous reaction of species to changing environmental conditions, e.g. increased temperature causes increase of biomass production in some species but reduction in others, resulting in total lower fluctuations in productivity on the community level. These effects are stronger in more diverse communities (Loreau and de Mazancourt 2008). On the other hand, the higher the species diversity of the community, the lower the chances that random loss or gain of a single (or few) species will cause change in the total biomass production at the community level (Wang and Loreau 2014). The explanation of the contradictory effect revealed in our study needs an experimental comparative approach to study the diversity-stability relation in plant and fungal communities. Here, we may only hypothesize that the studied fungal communities, in spite of high species richness, were not functionally diverse, and in effect most of the species reacted in a similar way to changes in temperature and precipitation, which resulted in a cumulative effect on productivity instead of a compensating one observed in plant communities by Loraeau and de Mazancourt (2008). That could also stem from the fact that species richness in our study was calculated only based on sporocarps, and thus it did not include the biomass of the mycelium of the unknown number of soil-dwelling species of fungi, which did not produce any sporocarps during the study. It must be taken into account that in our study we limited the monitoring of mushroom productivity only to sporocarps, neglecting the fact that an unknown share of biomass was also located in the growing mycelium. In effect, the mushroom production was a quite direct effect of the number of species capable of producing sporocarps under the environmental conditions of the given season.

The tree species composition, which did not influence EM mushroom production directly, affected the stability of mushroom yield between years, which may be connected to the higher stability of biomass production of the species-rich plant communities (Wang and Loreau 2014; Tilman et al., 2006; Isbell et al., 2009; Grime 1998). The sensitivity of plant biomass production to fluctuations in water availability differs between tree species, which may have a stabilizing effect on biomass production on the stand-scale, which in turn supports biomass production of their mycorrhizal counterparts. That is why the plots with a high share of *Betula pendula* and *Pinus sylvestris* were characterized by greater stability (lower level of differences in production) of mushroom production. These are pioneering tree species resistant to extreme weather conditions (Atkinson 1992; Alexe 1964), which results in higher, in comparison to other tree species, stability of their photosynthetic activity in the changing environment, and in effect also higher stability of the amount of carbohydrates delivered by them to mycorrhizal partners.

4.4. Weather conditions effects

The productivity of the studied fungal communities was moderated by the interplay between the precipitation and temperature. The mushroom production in 2021 was best explained by the precipitation from the month before the month of mushroom collection, which suggests that the effect of increased water availability had to be first assimilated by trees and then translated into increased sporocarp production of mainly EM fungi. A similar relationships linking mushroom production with the sum of precipitation in the 30 days before sampling was revealed by Karavani et al. (2018). The relationships between mushroom production and spring, all year (Salerni et al., 2002), or the previous year's sum of precipitation (Kauserud et al., 2010) were also reported, which suggests that importance of precipitation depends on local climate and type of soil.

In 2020 the mean temperature of the ten days before sampling explained the level of mushroom production. However, in 2020 the mushroom production was significantly lower and less variable between the plots in comparison to 2021. Salerni et al. (2002) revealed that in the Mediterranean area, abundant annual precipitation is necessary for the fungal mycelium to fruit. Thus, the much lower precipitation in 2020 seemed to be a limiting factor which kept mushroom production at a lower level, and allowed expression of the importance of temperature. The peak of productivity in 2020 was notable for the narrow range of the mean daily temperature of the yielding season, around 13–14 °C, which in our opinion allowed efficient sporocarp production without causing excessive increase of evapotranspiration, which would decrease water availability in the soil and slow down tree photosynthesis. Thus, due to the low availability of water, production of mushrooms in 2020 decreased rapidly with the increasing temperatures, while at the same time lower temperatures were also far from optimal for the development of sporocarps.

5. Conclusions

Our results revealed that stand characteristics, like understorey cover, tree production or stand basal area, play an essential role in sporocarp production. Tree species richness seemed not to be as important but still production of mushrooms was higher and more stable in more diverse stands. We also found that mushroom yield strongly depends on mushroom species richness, both in EM and SAP species groups. Therefore, if we would like to maximize mushroom production, it seems to be crucial to take into account the care of mushroom species richness in forest management, including by promoting factors affecting it, like tree species richness, which may also influence other important factors, e.g. plant species richness or soil pH.

The most baffling result was the lack of a stabilizing effect of mushroom diversity on their production. This may have been caused by the very short research period (two seasons) or by fact that in our study we defined mushroom species richness as the species richness of fruiting mushrooms and not all of the fungi present on plots. This aspect requires further research with the use of molecular techniques, allowing the determination of the total fungal diversity of forest soils and methods allowing estimation of the total biomass of soil dwelling mycelia. This topic is also worth exploration due to the role of fungi in the bonding and depositing of carbon in forests soils (Clemmensen et al., 2013).

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CRediT authorship contribution statement

Katarzyna Stojek: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Loïc Gillerot:** Data curation, Investigation, Writing – review & editing. **Bogdan Jaroszewicz:** Investigation, Methodology, Project administration, Supervision, Writing – review & editing.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120451.

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