



## Environmental drivers of forest biodiversity in temperate mixed forests – A multi-taxon approach



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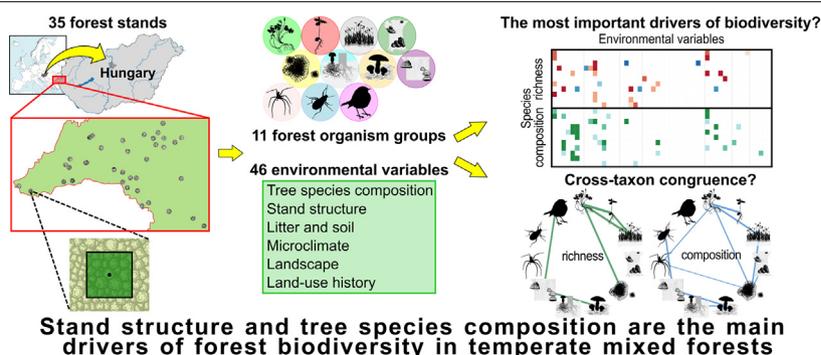
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### HIGHLIGHTS

- Forest biodiversity conservation needs knowledge about the environmental drivers.
- We studied forest stand, microclimate, soil, litter, landscape, and land-use history.
- The response of eleven forest-dwelling organism groups was evaluated.
- Stand structure and tree species composition were the most important drivers.
- Management has the potential to ensure favorable conditions for biodiversity.

### GRAPHICAL ABSTRACT



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### ABSTRACT

Harmonization of timber production and forest conservation is a major challenge of modern silviculture. For the establishment of ecologically sustainable forest management, the management-related environmental drivers of multi-taxon biodiversity should be explored. Our study reveals those environmental variables related to tree species diversity and composition, stand structure, litter and soil conditions, microclimate, landscape, and land-use history that determine species richness and composition of 11 forest-dwelling organism groups. Herbs, woody regeneration, ground-floor and epiphytic bryophytes, epiphytic lichens, terricolous saprotrophic, ectomycorrhizal, and wood-inhabiting macrofungi, spiders, carabid beetles, and birds were sampled in West Hungarian mature mixed forests. The correlations among the diversities and compositions of different organism groups were also evaluated.

Drivers of organism groups were principally related to stand structure, tree species diversity and composition, and microclimate, while litter, soil, landscape, and land-use historical variables were less influential. The complex roles of the shrub layer, deadwood, and the size of the trees in determining the diversity and composition of

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Soil  
Stand structure  
Tree species composition

various taxa were revealed. Stands with more tree species sustained higher stand-level species richness of several taxa. Besides, stands with different dominant tree species harbored various species communities of organism groups. Therefore, landscape-scale diversity of dominant tree species may enhance the diversity of forest-dwelling communities at landscape level. The effects of the overstory layer on forest biodiversity manifested in many cases via microclimate conditions. Diversity of organism groups showed weaker relationship with the diversity of other taxa than with environmental variables.

According to our results, the most influential drivers of forest biodiversity are under the direct control of the actual silvicultural management. Heterogeneous stand structure and tree species composition promote the different organism groups in various ways. Therefore, the long-term maintenance of the structural and compositional heterogeneity both at stand and landscape scale is an important aspect of ecologically sustainable forest management.

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## 1. Introduction

Forests hold most of the Earth's terrestrial biodiversity, therefore preserving forest biota is crucial for global biodiversity conservation (FAO and UNEP, 2020). According to the regional assessment of biodiversity and ecosystem services, there is a strong and continuous biodiversity loss in European forests (IPBES, 2018). At the same time, the demand for timber is increasing; thus, the purposes of timber production and conservation within forest management practice must be harmonized (Bouget et al., 2012). To contrive how biodiversity can be preserved during forest management, as a first step, we must find the key determinants of forest biota.

A significant number of environmental drivers have been revealed to be important for the different components of the forest biota. However, the results are various and often context-dependent (Blondeel et al., 2019). The studied forest types, forestry systems, the involved organism groups, and environmental variables all influence the results (Paillet et al., 2010; Gossner et al., 2014; Sabatini et al., 2014; Lelli et al., 2019). In management guidelines and strategies, among the environmental characteristics, only a few structural variables are used as biodiversity indicators (EEA, 2016). Deadwood is the most common one since it serves as a habitat, substrate, or hiding, breeding, or feeding place for numerous saproxylic, epixylic, and other organisms (Stockland et al., 2012). Large trees are also often considered based on their importance for epiphytic species and cavity-nesting birds and bats (Mollet et al., 2013; Hofmeister et al., 2015). Intensive studies of deadwood and large trees can be explained also by the fact that both are strongly reduced in managed forests, thus organisms related to them are especially threatened (Stockland et al., 2012; Bütler et al., 2013). However, if not only the demands of these deadwood- and large tree-associated organisms are considered but also those of a wider variety of the biota occurring in forests, the simultaneous investigation of a broader range of potential environmental drivers is necessary.

Tree species composition of forest stands proved to be the main driver of forest biodiversity in numerous studies (Penone et al., 2019; Ampoorter et al., 2020). It can directly determine the diversity and composition of the regeneration layer (Ádám et al., 2013), of the epiphytic taxa (Mezaka et al., 2012), and of the parasitic or symbiotic fungi (Smith and Read, 2008). Understory vegetation is related to the tree species composition via complex pathways (light, throughfall, litter, etc., Barbier et al., 2008; Chamagne et al., 2016). Many insects are related to specific tree species (Horák, 2011), and herbivorous mammals also show a preference for certain woody species (Ohse et al., 2017). Stand structure and tree species composition usually affect forest organisms indirectly through microclimate factors; for instance, the presence of a secondary canopy or a shrub layer influences the light conditions, which is one of the main drivers of understory herbs and tree regeneration (Plue et al., 2013). Besides, temperature and humidity are also determined by the stand structure and may be crucial for several taxa (Renvall, 1995; Oxbrough et al., 2006; Nordén et al., 2012). Understory vegetation offers heterogeneous habitats for animals living near the

ground (Riechert and Gillespie, 1986; Mollet et al., 2013), while due to trophic relationships understory species richness and cover may influence the diversity and composition of herbivores and taxa on higher trophic levels (Tews et al., 2004). Soil and litter conditions may determine the plant assemblages (Hofmeister et al., 2019) and the soil-inhabiting fungi (Ferris et al., 2000), while mainly litter characteristics can influence the ground-dwelling arthropods such as carabids (Skłodowski, 2014) and spiders (Ziesche and Roth, 2008). The surrounding landscape can be relevant for taxa acting on larger areas, such as birds or larger mammals (Mollet et al., 2013), or for taxa with good dispersal ability (Seibold et al., 2019). Land-use history may be crucial for species with low dispersal because they can hardly recolonize if the forest continuity is breaking (Hermý and Verheyen, 2007).

Most of these environmental variables can be influenced by forest management directly (stand structure and tree species composition) or indirectly via the stand characteristics (microclimate, litter, and top-soil variables). Landscape characteristics (such as spatial connectivity of forests, heterogeneity of management systems or tree species compositions, presence of meadows and shrublands in the landscape) are influenced by human activities as well, even if usually they are not considered in the course of forest planning that focuses on stand-scale considerations. Landscape characteristics are especially neglected in landscapes that are composed by small private forests with numerous different owners.

Our aim was to explore the most important drivers of forest biodiversity among those factors that can be influenced by forest management. We emphasize the key characteristics of the studied temperate mixed forests that should be preserved during ecologically sustainable, multi-purpose forest management. The responses of many organism groups to the environmental conditions have already been thoroughly studied during our project, based on the same data, in individual, single-taxon-focused publications (vascular understory: Márialigeti et al., 2016; woody regeneration: Tinya et al., 2019; ground-floor bryophytes: Márialigeti et al., 2009; epiphytic bryophytes: Király et al., 2013 and Ódor et al., 2013; lichens: Nascimbene et al., 2012; fungi: Kutszegi et al., 2015, 2021; spiders: Samu et al., 2014; and birds: Mag and Ódor, 2015). In the present multi-taxon study, we synthesize our findings and focus on the comparisons of the main drivers of different organism groups, analyzing only the species richness and general composition, as well as the correlation among the organism groups. The strengths of this study are i) the variety of studied tree species combinations, ii) the broad spectrum of investigated environmental variables, and iii) the significant number of organism groups involved.

Investigated stands were chosen based on the presence and proportion of ecologically and economically important tree species such as the broadleaved beech (*Fagus sylvatica*) and oaks (*Quercus petraea* and *robur*), and the coniferous Scots pine (*Pinus sylvestris*). We sampled stands with various combinations of these species and their monodominant stands also. Besides, admixing species were also present in different proportions. The Őrség region of Hungary gave an excellent opportunity to this study, because—for land-use historical reasons—forest stands of this

hilly area are quite heterogeneous with respect to their tree species composition and dominant tree species, while macroclimatic and geographical conditions are rather uniform. Recent forest management of the stands is various, both even-aged and uneven-aged management occur in the region. As our aim was to investigate the effects of management-driven environmental variables, separated from edaphic effects, we did not include sites with special edaphic conditions (e.g., alluvial forests, mire forests, or stands on rocky hill-sides).

The involved environmental variables describe not only the tree species diversity and composition and stand structure, but also numerous other characteristics that are influenced by the recent forest stand, such as litter, topsoil, and microclimate, or by management activities at landscape scale (Table 1). The 11 investigated organism groups (understorey herbs, regeneration of woody species, ground-floor and epiphytic

bryophytes, epiphytic lichens, terricolous saprotrophic, ectomycorrhizal, and wood-inhabiting macrofungi, spiders, carabid beetles, as well as birds) cover a broad range of ecological demands and functions from the forest biota. In many studies, one or few taxa are used as surrogates for the whole forest biodiversity (Lewandowski et al., 2010); however, this approximation is strongly controversial (de Groot et al., 2016; Sabatini et al., 2016; Jokela et al., 2018). Our multi-taxon approach enables the comparison of the diversity pattern of the various organism groups and the evaluation of whether their response to the different environmental conditions is similar.

Our main questions were as follows:

- 1) Which environmental characteristics are the most important drivers of forest biodiversity? How are the species richness and composition

**Table 1**

Potential explanatory variables. Values are given for the 35 studied plots. In order to fulfill normality assumption for the residuals, and to avoid heteroscedasticity, the marked explanatory variables that have skewed distributions were ln-transformed before the analyses.

Explanatory variables	Abbreviations	Mean (min. – max.)	Transform.
<b>Overstorey tree species diversity and composition</b>			
Tree species richness	TreeS	5.63 (2–10)	ln
Tree species Shannon diversity (H')	TreeH	0.847 (0.097–1.802)	ln
Relative volume of beech (%)	Beech%	27.9 (0.0–94.4)	ln
Relative volume of hornbeam (%)	Hornbeam%	3.9 (0.0–21.8)	ln
Relative volume of oaks ( <i>Q. petraea</i> , <i>Q. robur</i> , and <i>Q. cerris</i> , %)	Oaks%	36.4 (1.1–98.0)	ln
Relative volume of Scots pine (%)	Pine%	26.2 (0.0–76.9)	ln
Relative volume of other admixing trees (%)	Admixing%	0.02 (0.00–0.17)	ln
<b>Stand structure</b>			
Density of trees (stems/ha)	TreeDensity	593.39 (217.75–1392.75)	–
Density of large trees (> 50 cm DBH, stems/ha)	LargeTrees	17.14 (0.00–56.25)	ln
Density of shrubs (> 50 cm height, < 5 cm DBH, stems/ha)	ShrubDensity	952.14 (0.00–4706.25)	ln
Basal area of trees (m <sup>2</sup> /ha)	BA	32.87 (21.49–42.26)	–
Mean DBH of trees (cm)	dbhM	26.65 (13.70–40.75)	–
Variation coefficient of DBH	dbhCV	0.480 (0.172–0.983)	–
Volume of snags (m <sup>3</sup> /ha)	Snags	8.99 (0.90–65.02)	ln
Volume of logs (m <sup>3</sup> /ha)	Logs	10.51 (0.17–59.48)	ln
Cover of deadwood (m <sup>2</sup> /ha)	DWCov	261.57 (79.44–729.99)	ln
Cover of understorey vegetation (m <sup>2</sup> /ha)	UnderstoreyCov	740.80 (19.19–4829.30)	ln
Cover of ground-floor bryophytes (m <sup>2</sup> /ha)	BryophyteCov	247.37 (16.57–2201.59)	ln
<b>Litter and soil</b>			
Cover of litter (m <sup>2</sup> /ha)	LitterCov	9367 (7815–9834)	–
Litter weight (g/900 cm <sup>2</sup> )	LitterWeight	147.66 (105.41–243.08)	–
Proportion of deciduous litter (%)	DecidLitter	14.71 (2.54–32.80)	–
Proportion of decayed litter (%)	DecayLitter	67.71 (51.58–84.16)	–
Litter pH	LitterpH	5.29 (4.86–5.68)	–
Litter carbon content (%)	LitterC	65.69 (42.87–78.09)	–
Litter nitrogen content (%)	LitterN	1.28 (0.83–1.84)	–
Cover of mineral soil (m <sup>2</sup> /ha)	SoilCov	146.75 (8.56–472.22)	–
Soil pH	SoilpH	4.33 (3.96–4.84)	–
Soil fine texture (clay and silt) proportion (%; 0–10 cm)	Clay%	51.95 (27.60–68.60)	–
Soil carbon content (%; 0–10 cm)	SoilC	6.45 (3.30–11.54)	–
Soil nitrogen content (%; 0–10 cm)	SoilN	0.22 (0.11–0.34)	–
Soil phosphorus content (mg P <sub>2</sub> O <sub>5</sub> /100 g; 0–10 cm)	SoilP	4.29 (1.96–9.35)	–
Soil potassium content (mg K <sub>2</sub> O/100 g; 0–10 cm)	SoilK	7.74 (4.00–13.10)	–
<b>Microclimate</b>			
Mean relative diffuse light (%)	LightM	2.93 (0.62–10.36)	ln
Variation coefficient of relative diffuse light	LightCV	0.51 (0.12–1.23)	ln
Temperature difference (K)	TempM	–0.10 (–0.93–0.73)	–
Temperature range difference (K)	TempR	0.94 (–0.42–2.49)	–
Air humidity difference (%)	HumidM	0.84 (–1.83–3.32)	–
Air humidity range difference (%)	HumidR	1.89 (–2.27–6.58)	–
<b>Landscape</b>			
Proportion of forests in the landscape (%)	Forest%	89.80 (56.92–100.00)	–
Proportion of regenerating areas in the landscape (%)	RegenAreas%	5.73 (0.00–23.03)	ln
Proportion of open areas in the landscape (%)	OpenAreas%	4.72 (0.00–45.25)	–
Landscape diversity (H')	LandscapeH	1.114 (0.108–1.858)	–
<b>Land-use history</b>			
Proportion of forests in the landscape in 1853 (%)	PastForest%	76.58 (24.03–100.00)	–
Proportion of meadows in the landscape in 1853 (%)	PastMeadows%	7.26 (0.00–40.73)	–
Proportion of arable lands in the landscape in 1853 (%)	PastArable%	16.16 (0.00–61.27)	–
Plot was forest in 1853 (binary)	PlotWasForest	0.800 (0–1)	–

of 11 forest organism groups related to these environmental variables?

- 2) How strongly are the studied organisms groups correlated regarding their species richness (alpha diversity) and species composition?

## 2. Material and methods

### 2.1. Study area

The study area is located in the Őrség National Park, West Hungary (N 46°51'–55', E 16°07'–23', ca. 13 km × 24 km, Fig. 1). The topography consists of hills and wide valleys, and the elevation varies between 250 and 350 m a.s.l. The mean annual temperature is 9.0–9.5 °C, and the mean annual precipitation is 800 mm (Dövényi, 2010). Alluvial gravel forms the bedrock, mixed with loess. The soil of the area is acidic and nutrient poor. On hills, pseudogleyic brown forest soil (Planosol or Luvisol) is the most common soil type, while in the valleys, mire and meadow soils (Gleysols) are typical (Krasilnikov et al., 2009).

The particularity of the area is that forests with various tree species compositions and stand structures occur under similar climatic, topographical, and bedrock conditions (see Appendix A regarding the historical reasons of this phenomenon). Beech, sessile, and pedunculate oak, hornbeam (*Carpinus betulus*), and Scots pine are the dominant species, creating both monospecific and mixed stands. Admixing species (e.g., silver birch—*Betula pendula*, common aspen—*Populus tremula*, sweet chestnut—*Castanea sativa*, wild cherry—*Prunus avium*) are present in a relatively high proportion (Tímár et al., 2002). The height of the trees varies from 20 m to 30 m, while the living stock is 300–600 m<sup>3</sup>/ha. The shrub layer is mainly composed of tree regeneration, with about 80% hornbeam and beech.

### 2.2. Data collection

Investigated stands were selected from the stand structural database of the Hungarian National Forest Service by stratified random sampling (Fig. 1). The 35 selected stands represent different tree species combinations of the typical species of the region (Fig. A.1, Table A.1). As a first step, we selected mature, closed stands with similar site conditions, based on the following criteria: age of the dominant tree layer was between 70 and 100 years, they grew on relatively level ground, sites

had absence of direct water influence, the canopy closure was minimum 70% and spatial independence of the sites was achieved by using a minimum distance 500 m between them. As a second step, stands were selected based on their main tree species (sessile and pedunculate oak, beech, and Scots pine) covering monodominant stands and mixed forests with a broad range of proportions of these overstorey species. Among stands with similar tree species compositions, the sampled stand was selected randomly. Although the sample is representative for the mixed forests of the Őrség region, we suppose that the explored relationships have broader relevance since such mixed forests occur in many lowland and hilly regions in Europe (EEA, 2007). Most of the investigated stands were managed either by spontaneous or standardized selection or shelterwood forestry systems; furthermore, three unmanaged reserves were also sampled (Fig. A.1, Table A.1). The management systems used were connected to the ownerships and not to the tree species combinations: private forests were managed mainly by uneven-aged system, while in state forests, even-aged management was applied (Table A.1). However, independently from the current management system, most forests in the region (even the reserves) are secondary forests, because the area was deforested for extensive farming in the 13th century. From the 19th century, agricultural use was repressed, and reforestation of the area began. Farming and other land-use activities, such as litter collection and ridging (a special form of tillage) resulted in the acidification and erosion of the soil. Detailed management history of the area can be found in Appendix A.

A total of 11 organism groups and numerous environmental variables were recorded in the 35 stands by means of various sampling methods. The basic sampling unit of the sites was always a 40 m × 40-m block. It was representative of the stand's general tree species composition, canopy structure and closure and did not contain forest roads or other human disturbances. Its distance from the forest edge was minimum 100 m. In the center of each block, a 30 m × 30-m plot was designated, which was divided into 36 contiguous 5 m × 5-m quadrats. Some variables were recorded at quadrat level (in all 36 quadrats), or in several points within the plot, but in all cases, data were merged for block (i.e., site) level.

Data collection took place between 2006 and 2012. Understorey herbs, woody seedlings, bryophytes, lichens, and birds were sampled in 2006–2007, fungi, were studied in 2009–2010, while spiders and carabids were collected in 2009–2010 and 2012. There was no forestry

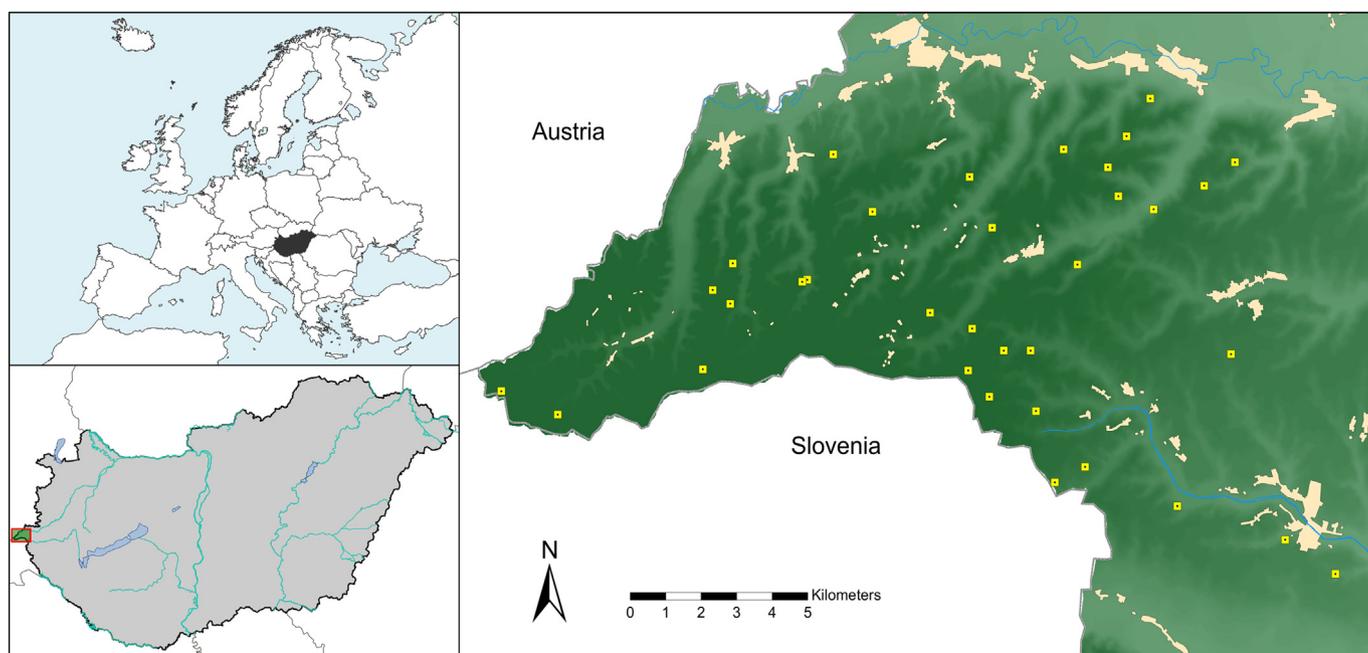


Fig. 1. Location of the study area in Őrség region, West Hungary (N 46°51'–55' and E 16°07'–23'). Sampling plots are signed with squares.

intervention in the studied stands in this period. In those samplings in which repeated campaigns are not mentioned in the description of the sampling, only one sampling per plot was performed.

### 2.2.1. Environmental variables

Environmental variables could be categorized as variables related to i) overstory tree species diversity and composition, ii) stand structure, iii) litter and soil, iv) microclimate v) landscape, and vi) land-use history. The specific variables belonging to these categories are listed in Table 1. The methods applied for the collection of these data are described in detail in Appendix B. We calculated the tree species richness and diversity, the relative volume of the main tree species, respectively, and the proportion of admixing species. The used stand structure variables describe the density of the stand, the size of the trees, the abundance of large trees, shrubs, understory, and deadwood. Both physical and chemical variables of the litter and topsoil were involved. We measured the mean and heterogeneity of light, air temperature, and air humidity. To characterize the landscape and land-use history, the proportion of the various land-use types in the present and in the past, and landscape diversity were applied.

### 2.2.2. Organism groups

**2.2.2.1. Understory herbs, woody seedlings, and ground-floor bryophytes.** The absolute cover ( $\text{dm}^2$ ) of each species was estimated in all of the  $5 \text{ m} \times 5\text{-m}$  quadrats, and summarized for the  $30 \text{ m} \times 30\text{-m}$  plots. Woody seedlings were defined as individuals of woody species shorter than 50 cm. We did not discriminate between *Quercus petraea* and *Q. robur* seedlings (considering both as *Q. petraea*). Ground-floor bryophytes were defined as bryophytes occurring on the soil, on lying deadwood and on above-ground roots. The nomenclature follows The Plant List (2013) for vascular plants and Hodgetts et al. (2020) for bryophytes.

**2.2.2.2. Epiphytic bryophytes and lichens.** Epiphytic bryophytes and lichens were recorded in the  $30 \text{ m} \times 30\text{-m}$  plots. The absolute cover ( $\text{dm}^2$ ) of bryophyte and lichen species was recorded on every living tree with a minimum of 20-cm diameter at breast height (it means ca. 20–40 trees/plot), from the base to 1.5-m height. The nomenclature follows Hodgetts et al. (2020) for bryophytes, and Nimis (2016) for lichens.

**2.2.2.3. Terricolous saprotrophic, ectomycorrhizal, and wood-inhabiting macrofungi.** Macrofungal assemblages were investigated based on sporocarp incidences. We sampled basidiomycetes (excluding most of the resupinate non-poroid taxa) and ascomycetes that develop sporocarps visible to the naked eye ( $> 2 \text{ mm}$ ). Sporocarps were sampled three times in each sampling plot: in August 2009, May 2010, and during September–November 2010. The species identity of taxa was recorded in each quadrat of each plot, in each sampling period. The local frequency value was calculated as an abundance measure for each collected fungal species. The data of the three sampling periods were pooled, thus the maximum value of the local frequency of a species was  $36 \times 3 = 108$  (36 quadrats, three sampling periods). Species identification procedures are detailed in Siller et al. (2013). Nomenclature follows Knudsen and Vesterholt (2012) and MycoBank (2013). Macrofungal taxa were classified into three main functional groups, namely terricolous saprotrophic fungi living on litter or any kind of buried plant debris in the uppermost 10 cm of the soil, ectomycorrhizal fungi, and wood-inhabiting fungi colonizing dead branches, twigs, logs, snags, and trunks or roots of living trees (Tedersoo et al., 2014).

**2.2.2.4. Spiders.** Pitfall trapping and suction sampling were employed to collect spiders from each plot. Sampling was conducted in four campaigns corresponding to the highest activity regime of the species, namely summer and autumn. In each campaign, five pitfall traps were deployed in a plot (in the center, and on the corners of a square of ca.

15-m sides positioned symmetrically around the center). Plastic cups of 75-mm upper diameter were filled with 70% ethylene glycol as a preservative, with some detergent added. The traps were open for a month.

A hand-held motorized suction sampler fitted with a  $0.01\text{-m}^2$  orifice was applied for the suction sampling (Samu and Sárospataki, 1995). Samplings lasted for ca. 60 s/plot. During this time, various microhabitats of the stands of up to 1.5-m height were sampled such as leaves from shrubs and lower branches of trees, trunks, deadwood surfaces, gravel surfaces, patches of terricolous mosses, litter, and soil. Since the number of specimens caught was smaller than initially expected, the number of samples per plot was increased over the campaigns (from three to eight samples per plot). Due to the various catches per sample, all samples from a plot across methods and dates were lumped and used as abundance data. The nomenclature of spiders follows the World Spider Catalogue (2020).

**2.2.2.5. Carabid beetles.** Carabid beetles were collected with the same pitfall traps as spiders. The samples from the five traps of the same plot and the different sampling campaigns were merged; the sum of the numbers of individuals per plot was used as abundance data for each species. Nomenclature of carabid beetles follows Löbl and Löbl (2017).

**2.2.2.6. Birds.** Bird data were collected by double-visit fixed radius point count technique (Gregory et al., 2004) in the center of each plot. The first count was conducted between April 15 and May 10, while the second was carried out between May 11 and June 10. In all cases, at least two weeks passed between the two counts. Each survey was conducted for 10 min between sunrise and 10.00 a.m., when there was no rain or strong wind blowing. We noted all the passerine, woodpecker, and columbiformes birds seen or heard within a 100-m radius circle. Birds of prey and corvids were excluded from the analysis due to the large size of their territories. Common cuckoo (*Cuculus canorus*) was also excluded due to its special reproductive behavior. For each species, the maximum of the two counts was used as abundance data. Nomenclature for birds follows Hagemeyer and Blair (1997).

### 2.3. Data analysis

We investigated the effects of the various environmental variables on the species richness of the different organism groups by general linear models (GLM) and species compositions by redundancy analysis (RDA). The same set of environmental variables (listed in Table 1) was used both for the richness and composition models. In order to fulfill normality assumption for the residuals, and to avoid heteroscedasticity, some explanatory variables that have skewed distributions were ln-transformed. Prior to the analyses, all explanatory variables were standardized.

General linear models were built to find the most important drivers of species richness of the organism groups (Faraway, 2005). If the dependent variable (species richness) deviated from the normal distribution (understory herbs and woody seedlings), ln transformation was applied.

Before the statistical selection procedure, pairwise correlations and scatterplots between the dependent and explanatory variables were investigated, and multicollinearity was also considered. In the models, only those explanatory variables were used that showed a strong and consistent (homogeneous) linear relationship with the dependent variable (it was checked visually based on the scatterplots), and whose intercorrelations with other explanatory variables were weak ( $|r| < 0.5$ , Faraway, 2005, Borcard et al., 2011). From the intercorrelating variables, the ones with stronger and more homogeneous relationship with the dependent variable were selected for further analyses. This process reduced the number of potential variables to 4–11 before statistical selection procedure. The correlations and the manual preliminary selection of the variables are detailed in Appendix D. Model selections were performed by backward elimination; the minimal adequate

models were determined by deviance analysis with F-test (Type-III ANOVA, Faraway, 2005). After model selection, the linearity between the dependent and explanatory variables, the normal distribution of the residuals, and the homogeneity of the residual error variance were verified. Multicollinearity was also checked by variance inflation factor (Faraway, 2005). In the case of fungi groups, the third field sampling campaign had a long run (from early September to late October in 2010) because it was an extremely wet year, resulting in extraordinary high sporocarp production. Since the sampling date could influence the number of detected sporocarps in the different sites, its effect was excluded from the models by the use of partial regression (Legendre and Legendre, 2012).

The effects of the explanatory variables on species composition were investigated by redundancy analysis (Borcard et al., 2011). Preliminary detrended correspondence analysis detected short gradient length (lower than 3) along the first axes for each taxon that supported the use of the linear RDA method for constrained ordination (ter Braak and Šmilauer, 2002). To avoid the distortion effect of rare species (Borcard et al., 2011; Legendre and Legendre, 2012), only species occurring at least in four plots were included. Abundance was variously defined at the different groups (cover for plants and lichens, local frequency for fungi, number of individuals for animal groups). The abundance data were ln-transformed. As a preliminary selection, the explained variance of each explanatory variable was calculated and tested separately, and only those variables that had significant individual explained variance were used for further selection process. Among intercorrelating variables only one was used, similarly to the GLMs. The process of this preliminary variable selection is detailed in Appendix D. From the pool of the remaining potential variables, the minimal adequate model was selected by manual backward elimination with permutation based on pseudo-F tests with 9999 permutations (Borcard et al., 2011; Oksanen et al., 2019). To check the manually-built models, Akaike Information Criteria-based automatic forward and backward selection was applied. The significance of the final model and the canonical axes were tested by permutation test. In the case of fungi groups, the sampling date of the third sampling campaign was used as a covariable within a partial RDA model (Borcard et al., 2011). From the analyses of understory herbs and woody seedlings, one stand was excluded due to its extreme data. Consequently, only 34 sites were involved in these cases.

The cross-taxon correlations were also investigated. For species richness data, correlation analysis with Holm correction was performed (Zar, 1999), and for species compositions, matrix correlation and Mantel test were used (Podani, 2000).

All analyses were implemented in the R environment (R Development Core Team, 2019). We used the package “vegan” for the RDA (Oksanen et al., 2019), “corrplot” for the correlation matrix (Wei and Simko, 2017) and “ggplot2” (Wickham, 2016) for constructing heatmaps.

### 3. Results

Altogether, 1125 species were identified from the 11 organism groups (Table 2, Table C.1–C.11). The two most species-rich groups were the ectomycorrhizal and wood-inhabiting macrofungi, considering both the total species richness and the mean species richness per plot. The species richness of understory herbs, terricolous saprotrophic macrofungi, and spiders was intermediate, while other organism groups showed lower values (Table 2).

#### 3.1. Response of species richness of the organism groups to the environmental variables

The explained variance ( $R^2$ ) of the species richness models of the organism groups was above 0.4, except for ectomycorrhizal macrofungi, carabids, and birds (Table E.1). The strongest models were obtained for the epiphytic lichens and the ground-floor bryophytes. In most

**Table 2**  
The species richness of the studied organism groups.

Organism groups	Species richness	
	Total	Mean $\pm$ SD/plot
Understory herbs	132	21.1 $\pm$ 13.5
Woody seedlings	39	9.7 $\pm$ 4.2
Ground-floor bryophytes <sup>a</sup>	74	19.2 $\pm$ 7.0
Epiphytic bryophytes <sup>a</sup>	60	14.0 $\pm$ 5.0
Epiphytic lichens	44	9.8 $\pm$ 3.7
Terricolous saprotrophic macrofungi	127	18.3 $\pm$ 11.6
Ectomycorrhizal macrofungi	290	41.2 $\pm$ 17.1
Wood-inhabiting macrofungi	245	40.1 $\pm$ 13.3
Spiders	91	17.6 $\pm$ 4.9
Carabid beetles	34	8.0 $\pm$ 2.9
Birds	33	9.4 $\pm$ 3.0

<sup>a</sup> Ground-floor and epiphytic bryophyte assemblages contain 44 overlapping species.

cases, two to four environmental variables were included in the final model, except for wood-inhabiting macrofungi that were determined by six variables (Fig. 2). The most frequent drivers that occurred in the final models were related to stand structure, tree species diversity and composition, and microclimate (they occurred in the models of seven, six, and six organism groups respectively). Litter and soil variables were intermediately frequent (present in the models of four organism groups). Landscape and land-use history variables were not significant for any group (Fig. 2, Table E.1).

#### 3.2. Response of species composition of the organism groups to the environmental variables

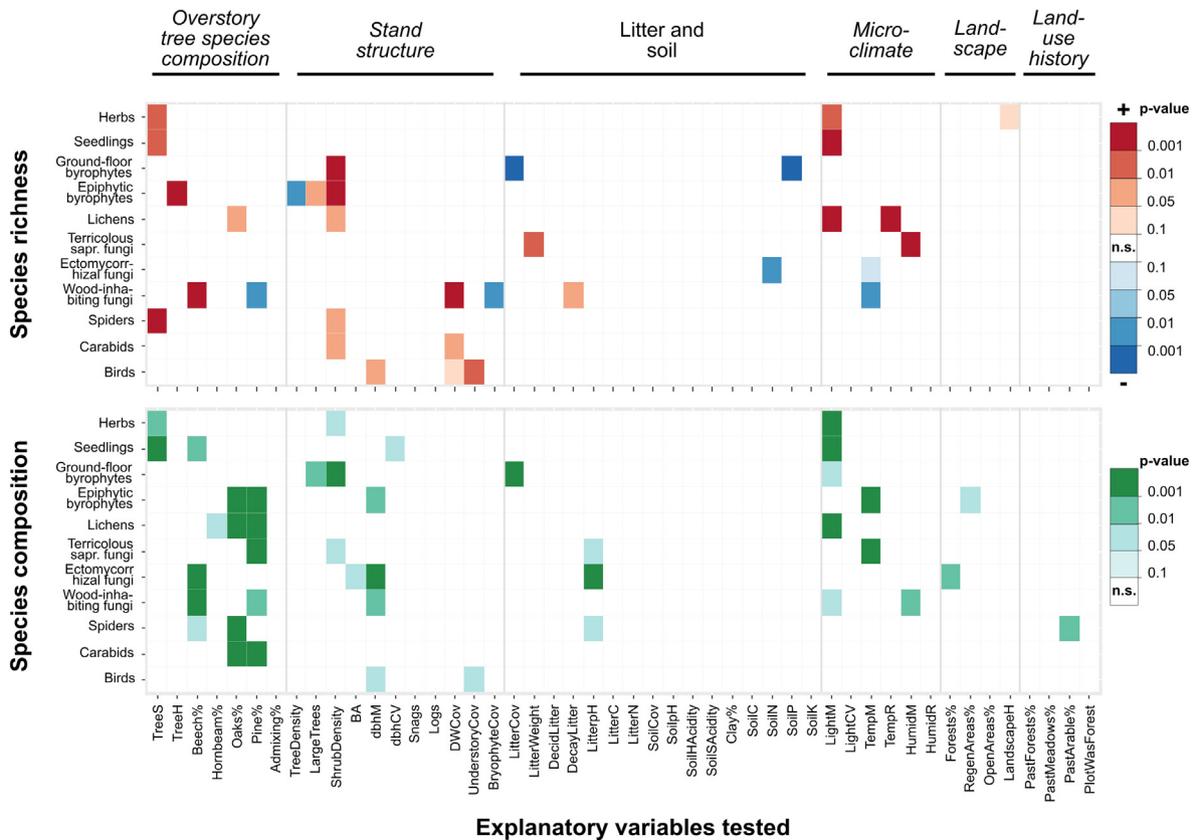
In the RDA models (Table E.2, Fig. E.1–E.11),  $R^2$  was above 0.4 only in one model (epiphytic lichens). It was intermediate for most of the organism groups and below 0.2 for wood-inhabiting macrofungi, carabids, and birds. Most of the models contained a higher number of explanatory variables (usually four or five) than the species richness models (Fig. 2). Overstory species composition, stand structure and microclimate variables were the most frequent ones in the models (occurring in models of nine, eight, and seven organism groups). Litter and soil, landscape, and land-use history variables were present only in few models (in the case of four, two, and one organism groups respectively, Fig. 2, Table E.2). Detailed interpretation of the species composition models of each taxon is provided in Appendix E.

#### 3.3. Relationships between the investigated organism groups

The correlations between the species richness values of the 11 organism groups and the Mantel tests on the species compositions of the groups showed weak relationships among the studied taxa (Fig. 3). Several significant correlations occurred between the photosynthetic organisms (herbs, seedlings, ground-floor and epiphytic bryophytes, and lichens), concerning both the species richness and composition. There were significant relationships among the different fungal groups: in the case of terricolous saprotrophic and wood-inhabiting fungi, both measures correlated, and the composition of terricolous saprotrophic fungi was also related to that of ectomycorrhizal fungi. Animal groups did not correlate with each other. We found few significant correlations between organism groups that are taxonomically far from each other (spiders—lichens, spiders—seedlings, wood-inhabiting fungi—birds, wood-inhabiting fungi—carabids). There were no significant negative correlations between any organism groups.

### 4. Discussion

The strongest models were obtained for the substrate-specialist sessile organism groups, while mobile taxa and taxa from higher trophic levels resulted in weaker relationships. The studied organism groups



**Fig. 2.** Significance of the explanatory variables a) for the species richness of the studied organism groups, based on the GLM, and b) for the species compositions based on the redundancy analysis (RDA). Red indicates positive and blue indicates negative effects. Abbreviations of the explanatory variables are explained in the Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

were driven by miscellaneous environmental variables; however, some general patterns can be drawn. Stand structure, tree species diversity and composition, and microclimate conditions (influenced by forest stand) proved to be the most important determinants of forest organisms. Litter and soil conditions, landscape characteristics, and land-use history had much weaker effects.

Stand-level species richness of the organism groups was mainly increased by the presence of shrub layer, the species richness of overstory tree species, the cover of lying deadwood, the amount of light, and by the cool, wet microclimate. The importance of stand structural variables for forest biodiversity is affirmed by numerous other multi-taxon surveys. It seems to be a universal phenomenon that is valid from boreal forests (Jokela et al., 2018), through maritime pine plantations (Barbaro et al., 2005) to temperate deciduous stands (Blasi et al., 2010). The importance of within-stand tree species richness on stand-level multi-taxon biodiversity was also confirmed by the European-level study of Ampoorter et al. (2020). Microclimate was an essential determinant of forest biodiversity also in temperate mountain forests (Janssen et al., 2018).

Species composition of the organism groups was influenced mainly by the relative volumes of the main tree species, the mean size of the trees (which reflects the presence or absence of a secondary canopy layer), and the litter pH. Species compositions were also influenced by microclimate conditions (light, temperature, and humidity). Accordingly, the heterogeneity of these variables among stands may ensure the occurrence of various communities of the forest organisms in different stands, and thus, increases their diversity at landscape level. Several recent multi-taxon studies also emphasized the importance of landscape-level heterogeneity (Hilmers et al., 2018; Seibold et al., 2019; Schall et al., 2020). In beech-dominated landscapes, Schall et al. (2018) found that management systems enhancing structural and microclimate heterogeneity between stands instead

of within stands maintain higher biodiversity at landscape level. Penone et al. (2019) concluded from the same project that tree species composition of the stands should be kept heterogeneous not only within stand, but also at landscape level.

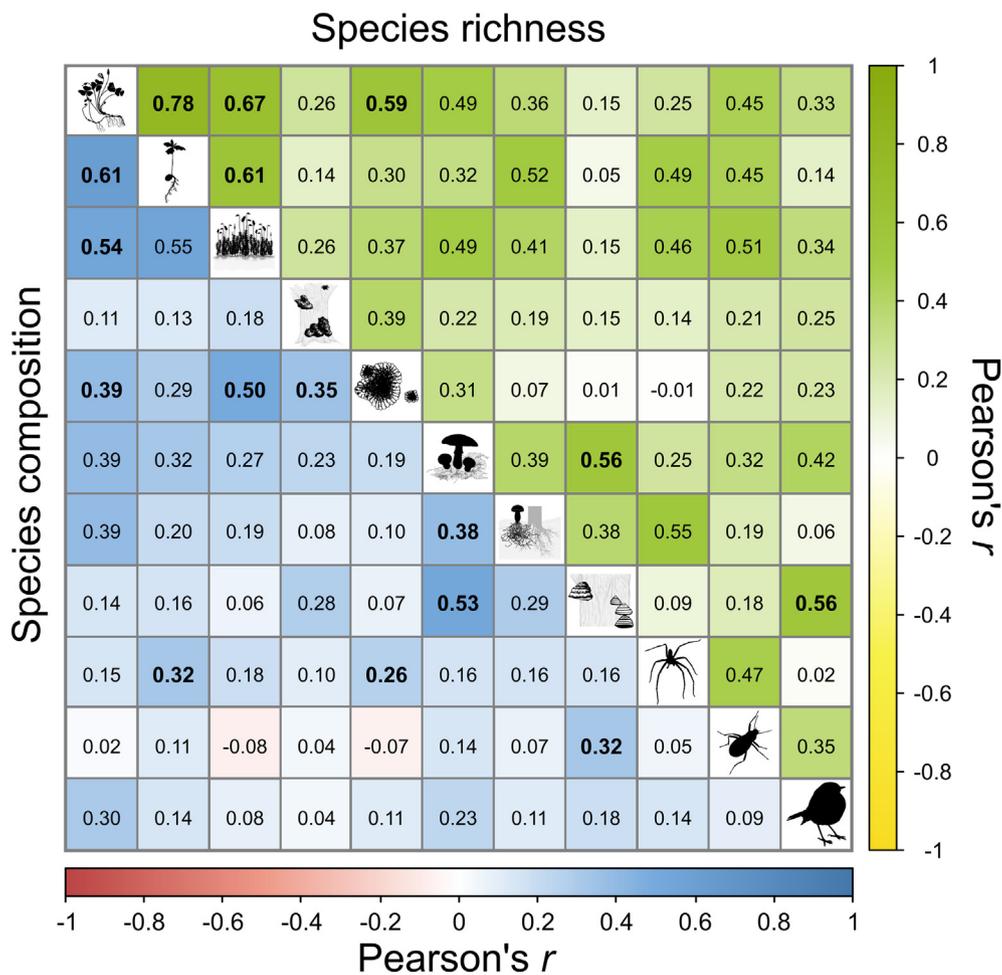
In our study, all correlations between the different organism groups were weak, but always positive.

Hereinafter, we discuss the differences between the strength of the models first; then, we discuss the most important drivers in detail. We evaluate the correlations between the different organism groups, we also emphasize the limitations of the study, and as a conclusion, we give implications for forest management practices. Structural elements that should be enhanced within the stands or kept heterogeneous at landscape level to preserve biodiversity even in managed forests are highlighted.

#### 4.1. The strength of the models for the different organism groups

The investigated environmental variables best explained the species richness and composition of epiphytic lichens, ground-floor, and epiphytic bryophytes. Besides, the species richness model of wood-inhabiting fungi also covered a high proportion of variance. All of these organisms are substrate-specialists and are, thus strongly determined directly by the trees (species composition, tree size, and litter quality) (Renvall, 1995; Dzwonko and Gawroński, 2002). Since they are sessile, they proved to be highly exposed to the local microclimate conditions (air temperature/humidity, light), which is in line with previous studies (Moora et al., 2007; Thorn et al., 2018).

Birds and carabid beetles provided the weakest models. Birds are the most mobile organisms in this study; they can easily move between stands (e.g., for foraging). As a result, we can suppose that they are less determined by the conditions of the local stand (Mitchell et al., 2006). Based on a landscape-level analysis done by Mag (2019) in



**Fig. 3.** Correlations between the species richness of the studied organism groups (upper half of the matrix); correlation coefficients of distance matrices based on species compositions (lower half of the matrix). Significant correlations are typed as bold.

Hungary, birds are sensitive to the proportion of forests in the landscape at a larger scale than was studied in our project, and to several variables of the stands at the landscape level (e.g., to the age of the stands and to the diversity of forest types in the landscape). In our study, among the stand-level variables, birds were the most driven by features that influence their nesting, namely the mean diameter of the trees for cavity-nesters, and the understory cover for ground-nesting species.

Carabid beetles are generalist predators, and live mainly on the ground layer. They may be sensitive to other characteristics of their environment (presence and abundance of prey taxa, specific microhabitats, and so on) that were not measured. [Ampoorter et al. \(2020\)](#) also found that taxa on higher trophic levels are less affected by the stand characteristics than producers and primary consumers, for them the effects can prevail more directly. [Jouveau et al. \(2020\)](#) found that the diversity of forest vegetation increased the activity-density of carabid beetles because it improved the habitat heterogeneity and ensured a larger amount and higher diversity of available food. Coarser-scale stand characteristics (e.g., the presence of gaps) also influence them ([Andrés et al., 2018](#)). Mobility may also play a role in this case since forest stands in this region are small-sized and arranged in a quite fine-scaled mosaic; thus, carabid beetles may have been able to move between the stands ([Elek et al., 2018](#)).

#### 4.2. Importance of the various environmental factors

##### 4.2.1. Stand structure

Variables related to the stand structure were determining for all organism groups. The importance of stand structure have been emphasized

for several taxa by earlier studies (e.g., [Bereczki et al., 2014](#) for birds, [Chen et al., 2017](#) for bryophytes, or [Tomao et al., 2020](#) for fungi). Nevertheless, the relative weights of the different structural elements are varying. Shrub density was an important driver for seven out of 11 organism groups investigated. The density of shrubs in the stands increased the species richness of five organism groups. Besides, it also influenced the species composition of some groups indicating that its various amount in the different stands may supports the between-stand diversity of communities. Presumably, it affects organisms via the modification of a wide variety of microclimate variables, such as mean and extremes of air temperature and humidity, light, and wind speed, as was shown by [Kovács et al. \(2017\)](#) based on the same dataset. [Friedel et al. \(2006\)](#), with the same conclusions, also found the shrub layer as the main driver of epiphytic species. Shrub density might affect the species composition of terricolous saprotrophic macrofungi also via the increased and more heterogeneous dead plant material accumulated under the shrubs ([Berg and McClaugherty, 2014](#)). For ground-floor bryophytes, the connection with the shrub layer may also be indirect in the region, due to land-use historical reasons (see Appendix A). A dense shrub layer typically occurs in open, pioneer pine forests that harbor a richer ground-floor bryophyte community with a specific species composition. A denser shrub layer may enhance the structural complexity of the habitat for spiders (e.g., it helps to create webs; [Mcnett and Rypstra, 2000](#)) and promotes a higher diversity of herbivorous insects serving as prey for carabids ([Jouveau et al., 2020](#)), thus increasing the species richness of these taxa.

Tree size (variables “mean diameter of the trees” or “density of large trees”) was important driver not only for wood-inhabiting organisms (it

influenced the species richness of epiphytic bryophytes and the composition of wood-inhabiting fungi), but it also influenced the species composition of ground-floor bryophytes, ectomycorrhizal fungi, and birds. Earlier studies showed that larger trees offer more time for colonization and that there is a compositional shift during this process (Fritz et al., 2008). Large trees provide also larger surface for colonization (Madžule et al., 2012), and have more complex bark structure, i.e., higher habitat diversity for epiphytes (Friedel et al., 2006). They may influence the species composition of ground-floor bryophyte assemblages because on their above-ground roots and fallen branches certain epiphytic species can reach a substantial share in the total bryophyte cover. They can also affect ectomycorrhizal fungal species composition by acting as hubs in common mycorrhizal networks (Simard et al., 2012). For birds, larger trees provide nesting places, and high amount and diversity of food (Bereczki et al., 2014). The upper canopy layer of the studied stands was always mature (70–100 years old); thus, low mean diameter values indicate a secondary canopy layer. Stands with such heterogeneous tree size categories (i.e., with low mean diameter) hosted communities with different species compositions from stands with only one canopy layer (i.e. with higher mean diameter). It implies that in order to increase overall diversity of numerous organism groups, structural heterogeneity should be maintained also between stands, and the presence of stands both with one or more canopy layer are necessary at landscape level.

Among deadwood-related variables, the cover of lying deadwood (that consisted mainly dead branches) increased the diversity of wood-inhabiting fungi, as their main substrate, and of carabid beetles, perhaps by increasing the diversity of their habitat. It had a marginally significant importance for bird diversity, presumably because deadwood elements on the ground provide habitats and food for insects serving as forage for birds. However, the amounts of snags and logs did not influence any organism groups, which is contradictory to the general findings of several other studies (Ohlson et al., 1997; Jokela et al., 2018). In our study, it can be explained by the general low amount of snags (9 m<sup>3</sup>/ha) and logs (10 m<sup>3</sup>/ha) in almost all sampled stands and by the actually missing coarse units (thicker than 30 cm). However, the amount of deadwood in our study is similar or even a bit higher than in managed forests in other regions of Europe (Stockland et al., 2012; Puletti et al., 2019). Presumably, the amounts of snags and logs would be more important drivers if their broader gradient would be sampled, i.e. if more natural forests with higher amounts of dead trees were included in the sample (Paillet et al., 2010; Penone et al., 2019). Another explanation for the low importance of snags and logs in our case might be the lack of strictly deadwood-related taxa investigated. It is also important to stress that additional deadwood characteristics (e.g., diversity of deadwood types) can be also influential (Penone et al., 2019). Jokela et al. (2018) found that deadwood is a relevant driver even in managed forests with low amounts of deadwood. However, in the studied region, due to the long history of forest management, a considerable amount of dead trees has been lacking for a long time; thus, species with obligatory connections to deadwood may have been diminished from the species pool.

Birds were also related to the understory vegetation cover, which can offer habitat, as well as nesting and feeding places (Zellweger et al., 2017). We did not find any effect of understory cover on invertebrates; however, some studies emphasized its role for these taxa (Oxbrough and Ziesche, 2013; Pakeman and Stockan, 2014). In Italian forests, Blasi et al. (2010) found that understory vegetation is an important structural indicator for forest biodiversity. Nonetheless, our results suggest that it cannot be considered as a general relationship.

#### 4.2.2. Tree species diversity and composition

Variables related to the tree species diversity and composition of the stands were drivers for nine organism groups out of the 11. Stands containing more tree species sustained higher species richness of many taxa. It indicates the importance of admixing species on within-stand

diversity of forest-dwelling taxa, as was also shown by Vockenhuber et al. (2011) for herbs, Ziesche and Roth (2008) for spiders, Ganault et al. (2021) for the soil macrofauna, and Penone et al. (2019) for multi-taxon biodiversity. Besides, stands with different proportions of the main tree species (beech, oaks, and the coniferous Scots pine) hosted various species compositions. It is in agreement with Penone et al. (2019), who emphasizes that the demands of all specialist species cannot be satisfied within one stand. Therefore, to increase landscape-scale biodiversity, stands with various dominant tree species are needed. The role of hornbeam and other admixing species was much smaller: only hornbeam was included in the model of lichen composition due to its special, smooth bark texture that hosts peculiar and diverse lichen assemblages (Mezaka et al., 2012; Łubek et al., 2020). In the case of the other taxa, admixing tree species (which occurred in relatively low proportion) might determine only certain specialist species but not the assemblages. The obtained weak effect of admixing species on biodiversity can also be explained by their low variance, i.e. their low proportion in the studied stands (Ampoorter et al., 2020), even if they were relatively species-rich forests of Hungary.

The impact of tree species may also prevail via the functional differences among the species, as—due to their different architecture—they ensure various microhabitats, light, or chemical conditions (Ampoorter et al., 2020). For the understory herbs and woody regeneration, heterogeneous light, litter, soil, and microclimate conditions under the different tree species can be determinant (Vockenhuber et al., 2011). Moreover, woody seedlings are directly driven by the tree species since distance from parent trees has a substantial effect on the regeneration (Ádám et al., 2013; Tinya et al., 2020). For epiphytic bryophytes, lichens, and wood-inhabiting fungi, different tree species offer various substrates, with their distinct bark texture and chemical environment (Chen et al., 2017; Jagodziński et al., 2018; Tomao et al., 2020). Ectomycorrhizal fungi are related to certain tree taxa as to primary hosts that are essential for their fruiting body formation (Kernaghan et al., 2003). Spiders and carabids can be affected by tree species through complex indirect ways (e.g., via litter, microclimate, or through prey assemblages; Oxbrough and Ziesche, 2013).

#### 4.2.3. Microclimate

Eight organism groups were related to microclimate variables. These variables influenced both the species richness and composition of these organism groups, suggesting that heterogeneous microclimate conditions should be maintained both within and between stands in order to offer favorable conditions for a high number of species within a stand, and for various communities in the different stands.

Photosynthetic organisms were strongly determined by light, despite its narrow gradient in the studied stands (0–10%, Table 1). Macek et al. (2019) found that above a canopy cover of 75% the canopy openness (which is a widely-used proxy of light) did not have strong effect on understory plant communities. However, numerous studies confirmed our findings regarding light as a significant driver of vegetation, even in closed stands with narrow range of canopy openness/light values (Janssen et al., 2018; Dormann et al., 2020). In the case of bryophytes, light determined only the species composition of the ground-dwelling communities. This was also shown by Tinya et al. (2009) who focused on the effect of light on these assemblages. Epiphytic bryophyte species (that can occur within the ground-dwelling assemblages as well, on roots, or on lying deadwood) are less related to the light conditions than species living on soil or mineral soil, which can explain the fact that the ground layer of shady stands keeps a similar number of bryophytes species but with different compositions. Jagodziński et al. (2018) also found that light was one of the most important predictors for bryophyte guilds, except epiphytes.

Epiphytes and fungi were sensitive to humidity/temperature, as also shown by Friedel et al. (2006) in the case of bryophytes and lichens. The strong relation of lichens with light and temperature range shows their connection to the more open stands. This is in line with Nordén et al.

(2012) and Nascimbene et al. (2012) who stated that lichens need opening patches in the closed stands. For terricolous saprotrophic fungi, temperature can be crucial for the activity of cellulose- and ligninolytic enzymes (Berg and McLaugherty, 2014).

Microclimate was not determinative for any animal groups. Oxbrough and Ziesche (2013) also stated that stand structure and microhabitats are more important for spiders than microclimate, but they also emphasize the role of light, temperature, and humidity for this taxon. Microclimate is more important for the less mobile soil-dwelling organisms, such as enchytraeid worms (Uhiá and Briones, 2002), or for gastropods whose species composition is strongly dependent from microclimate, even within the stand, towards the edges (Kappes, 2013). For mobile organisms, local conditions may play a less important role. Park et al. (2017) found that carabid communities are sensitive to microclimate mainly at environmentally more unfavorable sites. In our case, the relatively buffered microclimate of all sites did not influence the carabid communities.

#### 4.2.4. Litter and soil conditions

Variables related to litter and soil were less important for the studied components of forest biodiversity than the above-mentioned variable-groups. Five organism groups were driven by litter characteristics and only two groups by soil variables.

For ground-dwelling bryophytes, the cover of broadleaved litter limits the available substrate, thus, influencing the species richness and composition of this assemblage. A similar result was obtained by Dzwonko and Gawroński (2002) in a litter removal experiment. Startsev et al. (2008) stated that litter influences the bryophytes via shading and allelopathy. For terricolous saprotrophic fungi, litter is the primary nutrient source and its amount and pH are crucial for survival (Reverchon et al., 2010). Litter pH is also important for ectomycorrhizal fungi, triggering or suppressing their digestive enzymes in the soil (Baar and ter Braak, 1996; Talbot et al., 2013). Among the investigated animal groups, only spiders were driven by litter pH, which is in line with the findings of Oxbrough and Ziesche (2013). However, Oxbrough and Ziesche (2013) emphasize the role of further litter variables (e.g., thickness, composition) that we could not support. Presumably involving additional litter-dwelling taxa (e.g., gastropods, further beetle groups, or mites) to the study would increase the obtained importance of litter variables (Kappes, 2013; Urbanowski et al., 2018).

Soil nitrogen content decreased the species richness of ectomycorrhizal fungi, which is in line with the findings of Cox et al. (2010). Nevertheless, we did not detect any substantial effects of soil conditions on other taxa that are presumably sensitive to soil heterogeneity on a coarser scale than it was observable within this region.

#### 4.2.5. Landscape and land-use history

Landscape and historical variables had minor prediction power for any organism groups. We received only a few, weak, and hardly explainable relationships. Janssen et al. (2018) and Hofmeister et al. (2019) stated that the landscape and land-use history effects depend on the scale of the movement of a taxon and the scale of pattern of the land-use mosaics. In our region, land-use is heterogeneous at a very fine scale and there is a huge amount of—heterogeneous—forests around all investigated stands. However, the temporal continuity of the given stands is usually low because most of the forests were used as arable fields in the past. The different land-use types varied at a fine scale in the past as well. Thus, species sensitive to local continuity might have diminished from the study area, while species with better dispersal ability could move to the adjacent stands and survive as forests were continuously present in the landscape. The temporal continuity of habitats at landscape-scale and the high current spatial connectivity of forests may explain why dependence from the landscape and historical characteristics was not detectable. In such cases, the features of the current forest stand are more important drivers of forest biodiversity than historical variables (Janssen et al., 2018).

#### 4.3. Limitations of the study

It is hard to estimate the spatial representativeness of the relationships found. Some of the interactions might have only regional relevance. However, our most important results about the importance of stand structure, tree species composition and diversity, and microclimate variables are also supported by other multi-taxon studies from different regions (Blasi et al., 2010; Janssen et al., 2018; Jokela et al., 2018; Penone et al., 2019; Ampoorter et al., 2020); thus, we suppose that our main findings could be useful for management implications.

Although 11 organism groups were investigated, only their species richness and composition, which are two general measures of forest biodiversity, were analyzed in this study. Lelli et al. (2019) stated that the use of various metrics can modulate the results and that a functional approach is important. Such detailed single-taxon analyses, including functional groups, have been published from the dataset of our study in separate papers. The explanation of the RDA biplots also details the different responses of functional groups within taxa (Appendix E). We have found that, for all organism groups, the richness of forest specialist species had the same drivers as general species richness, even for vascular plants. Vascular plant diversity often shows a positive response to management intensity, because of the occurrence of non-forest, disturbance-tolerant species (Paillet et al., 2010; de Groot et al., 2016). However, in our case, forest specialist vascular plants had a similar positive response to the main factor (light) as the general species richness, because the studied stands were relatively closed, and light was the main limiting factor even for them (Tinya et al., 2009; Márialigeti et al., 2016). For many organisms groups (such as epiphytic bryophytes and lichens, and wood-inhabiting fungi), species richness is a good proxy for conservation status of the community, because all of the recorded species were forest specialists.

Another limitation of our study is that some functional groups (e.g., soil invertebrates and microbes, litter- or deadwood-inhabiting decomposers, and herbivores), were excluded while photosynthetic groups (understory herbs, woody regeneration, bryophytes, and lichens) were overrepresented. This could cause some biased importance of different environmental factors on multi-taxon diversity (Penone et al., 2019), e.g., including saproxylic beetles could increase the importance of deadwood (Stockland et al., 2012), while studying soil organism groups would enhance the significance of soil conditions and microclimate (Boros et al., 2019).

Moreover, within-stand relationships mean only one spatial scale. Several environmental variables (such as soil conditions) show a natural spatial heterogeneity at coarser scale, and the applied management system strongly influences the scale of the environmental heterogeneity, as well. The different taxa are sensitive to the environmental conditions also at various scales, depending on numerous traits (such as mobility, dispersal, or habitat specificity). Some of our result suggest the importance of landscape-scale heterogeneity on biodiversity, that is supported by other studies (Burrascano et al., 2018; Schall et al., 2018), but to verify them landscape-scale analyses would be necessary.

The strength of the obtained connections can be weakened by the delayed response of organisms to the changing environment (Hofmeister et al., 2019). In the studied area, forest stands are in intensive alteration due to the cessation of traditional land-use forms. Thus, in some cases, the current condition of the taxa may reflect certain circumstances of the past.

#### 4.4. Relationships between the investigated organism groups

Only a few and weak, but always positive correlations were found between the different organism groups (both in the case of species richness and composition), which is in accordance with our expectations. At a fine (stand) scale, other studies had similar experiences (Sabatini et al., 2016; Burrascano et al., 2018; Jokela et al., 2018). Zellweger et al. (2016) stated that the relationships between animal and plant

groups were weak even at the landscape scale. In some studies, understory plants or their subgroup proved to be good indicators for other components of forest biodiversity (Blasi et al., 2010; Hofmeister et al., 2019). However, our results affirm that diversity of forest taxa is more related to structural variables than to the diversity of other organism groups (Blasi et al., 2010; Sabatini et al., 2016), thus studying numerous taxa at the same time is necessary in order to evaluate overall forest biodiversity (de Groot et al., 2016; Jokela et al., 2018).

There is no consensus in the literature whether the similar diversity pattern of two or more taxa is a consequence of their similar response to certain environmental variables or is caused by cross-taxon functional interactions (Toranza and Arim, 2010; Gioria et al., 2011; Ampoorter et al., 2020). Our results support the first hypothesis. The correlations between the ground-floor plant groups (herbs, woody regeneration, and bryophytes) and lichens can be explained by their common demand for light and mixed tree species composition. The correlation among the different fungal groups may be the result of their similar environmental requirements and dependence on certain tree species. Only few taxonomically independent groups were correlating, but in these cases, there was a common driver in the background as well. Such joint driver can be the proportion of oaks for lichens and spiders, or the cover of deadwood for wood-inhabiting fungi and birds. The lack of negative correlations between organism groups also support the larger importance of common environmental demands against the relevancy of interactions such as competition. The obtained correlations were usually detectable in both the species richness and composition.

#### 4.5. Conclusions – implications for management

For the conservation of a selected organism group or target species, specific conservation strategies are necessary that primarily focus on the limiting factor of the given taxon. However, if close-to-nature forestry would like to harmonize timber production with the maintenance of forest biodiversity in general, the exploration of drivers connected to many organism groups might be more useful. According to our results, forest biodiversity is driven by environmental variables that are under the direct control of the actual silvicultural management. Thus, forest management has an important responsibility and, at the same time, a huge opportunity to preserve (or even improve) the biodiversity of forests. None of the environmental variables had both positive and negative effect on the different organism groups, and there were no significant negative correlations between taxa. It means that management actions that enhance an important element of the stand can support multiple organism groups without trade-offs (Ampoorter et al., 2020). Complex stand structure (e.g., the presence of the shrub layer and lying deadwood) is an exceedingly important driver of multi-taxon biodiversity within the stands, while stands with different structures ensure heterogeneous habitats for various communities. The other outstanding factor is the heterogeneous tree species composition. Overstory tree species diversity itself increases the species richness of some organism groups within the stand, but a more pronounced effect is that stands with different dominant tree species host different compositions of numerous organism groups, and, thus, contribute to the preservation of diverse elements of biodiversity at landscape level (Penone et al., 2019). As shown above, both various stand structure and tree species composition promote several organism groups in different ways, such as through the heterogeneous light and other microclimate conditions and accessible microhabitats. Thus, maintaining the structural and compositional heterogeneity is a robust tool to conserve multi-taxon biodiversity, even if in the practice, we cannot consider all individual relationships. Besides, it has positive effects also on the stability of the stands (Jactel et al., 2005) as well as on their resistance to the effects of climate change and herbivore gradations (Bereczki et al., 2014; Brang et al., 2014).

Continuous cover forestry ensures the occurrence of the above-mentioned important structural elements within the stands by its nature, and also compositional heterogeneity can be easily achieved during the

fine-scaled interventions of this forestry system (Pommerening and Murphy, 2004). The required structural and compositional diversity can be created directly as well, within the framework of conservation-oriented management (Bauhus et al., 2009). However, most of the necessary structural elements and the mixed composition can be retained or established even during rotation forestry: the prolonged regeneration period, retention of trees or tree groups after final cutting, or the use of an irregular shelterwood forestry system can help to achieve these goals (Raymond et al., 2009; Lindenmayer et al., 2012; Schall et al., 2020). Moreover, shrubs can be saved even during a conventional shelterwood forestry system, if they are not removed during the thinnings. In some patches, or on edges or side slopes admixing shrub species can be retained even during the regeneration period.

At the same time, to preserve biodiversity and to maintain ecosystem processes is necessary not only within stands but also at landscape level (van der Plas et al., 2016; Kuuluvainen et al., 2021). Not all requirements of the different components of the forest biota can be ensured within one stand type (Penone et al., 2019; Ampoorter et al., 2020). According to our result, stands with different proportions of the main tree species and with different structure can harbor diverse species assemblages. Therefore, maintaining heterogeneous stand structure and tree species composition at landscape level, and using various conservation aims and management strategies in the different forest stands could increase the complementarity of stands within the landscape and enhance the biodiversity of forests (Sitzia et al., 2017; Schall et al., 2020; Tomao et al., 2020; Kuuluvainen et al., 2021).

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#### CRediT authorship contribution statement

**Flóra Tinya:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Bence Kovács:** Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **András Bidló:** Methodology, Investigation. **Bálint Dima:** Methodology, Investigation. **Ilidkó Király:** Methodology, Formal analysis, Investigation. **Gergely Kutszegi:** Methodology, Formal analysis, Investigation, Writing – review & editing. **Ferenc Lakatos:** Methodology, Investigation. **Szuzsa Mag:** Methodology, Formal analysis, Investigation. **Sára Márialigeti:** Methodology, Formal analysis, Investigation. **Juri Nascimbene:** Methodology, Formal analysis, Investigation. **Ferenc Samu:** Methodology, Formal analysis, Investigation. **Irén Siller:** Methodology, Investigation. **Győző Szél:** Methodology, Investigation. **Péter Ódor:** Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

#### Declaration of competing interest

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

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