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Soil fungal communities reflect aspect-driven environmental structuring and vegetation types in a Pannonian forest landscape

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ABSTRACT

In temperate regions, slope aspect is one of the most influential drivers of environmental conditions at landscape level. The effect of aspect on vegetation has been well studied, but virtually nothing is known about how fungal communities are shaped by aspect-driven environmental conditions. I carried out DNA metabarcoding of fungi from soil samples taken in a selected study area of Pannonian forests in northern Hungary to compare richness and community composition of taxonomic and functional groups of fungi between slopes of predominantly southerly vs. northerly aspect. The deep sequence data presented here (i.e. 980 766 quality-filtered sequences) indicate that both niche (environmental filtering) and neutral (stochastic) processes shape fungal community composition at landscape level. Fungal community composition correlated strongly with aspect, with many fungi showing preference for either south-facing or north-facing slopes. Several taxonomic and functional groups showed significant differences in richness between north- and south-facing slopes and strong compositional differences were observed in all functional groups. The effect of aspect on fungal communities likely is mediated through contrasting mesoclimatic conditions, that in turn influence edaphic processes as well as vegetation. The compositional differences observed in fungi are largely consistent with the coenologically described forest types, which indicates the usefulness of these habitat types as a framework to better understand environmental differences that influence fungal community composition at landscape level. Finally, the data presented here provide unprecedented insights into the diversity and landscape-level community dynamics of fungi in the Pannonian forests.

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1. Introduction

In temperate regions, slope aspect is among the most influential factors that drive the physical environment at the landscape level. The aspect effect is driven primarily by the variation in the amount of solar radiation per surface area, which is a function of the angle of incidence of solar radiation (McCune and Keon, 2002). As a result, slopes oriented toward the Equator receive higher intensity and greater duration of solar radiation, which can be 50% higher on south-facing than on north-facing slopes in the northern hemisphere (Geiger, 1965; Rosenberg et al., 1983; Gilliam et al., 2014). These contrasting energy inputs can profoundly alter mesoclimatic conditions, particularly air and upper soil temperature, which, in turn, affect relative humidity, evapotranspiration, soil moisture and edaphic processes (Fekedulegn et al., 2003). As a result, slopes with poleward (in this case, northerly) aspect generally are cool and more humid, while slopes with southerly aspect tend to be markedly warmer and drier, particularly in mid- and high latitudes (Holland and Steyn, 1975; Méndez-Toribio et al., 2016). For example, Rorison et al. (1986) reported a 2.5–3 °C annual mean temperature difference recorded adjacent north- and south-facing slopes in a British calcareous grassland, a difference roughly equivalent to that encountered in a shift of 5° in latitude or 500 m in altitude (Barry, 1992).

Such aspect-related contrasts in the abiotic environment are intuitively expected to have influence on the composition of biotic communities. Indeed, the effects of aspect on vegetation are well known and clear compositional differences have been found between north- and south-facing slopes in various ecosystems, e.g., in temperate and Mediterranean forests (Whittaker, 1956; Sternberg and Shoshany, 2001; Gilliam et al., 2014), temperate grasslands

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(Schmidt, 2013), boreal forests (Hollingsworth et al., 2006), and arctic tundra (Walker et al., 1994). On the other hand, virtually nothing is known about the influence of aspect on richness and community composition of fungi at landscape level, except two recent studies focusing on arbuscular mycorrhizal fungal richness in boreal forests and arid steppes in China (Chu et al., 2016; Liu et al., 2017). Therefore, how slope aspect affects richness and community composition of various taxonomic and functional groups of fungi remains unknown.

According to the macroecological study of Tedersoo et al. (2014), global-scale fungal diversity and distribution patterns are primarily influenced by climatic factors, mainly mean annual temperature and precipitation, followed by edaphic factors, particularly pH, and spatial patterns due to dispersal limitation. On the other hand, the coupling between vegetation and soil fungal community composition and richness appears to be much weaker, with the exception of ectomycorrhizal (ECM) fungi (Tedersoo et al., 2014; Peay et al., 2016). Therefore, it is reasonable to hypothesize that the above-mentioned aspect-driven environmental differences are expected to influence the diversity and distribution of fungal communities at landscape level as well.

In this study, I tested the effects of aspect on the richness and composition of taxonomic and functional groups of fungi at a selected study area in northern Hungary, where regional climatic conditions and geological parent material were uniform in order to minimize confounding factors. Within the purposefully small study area, I sampled various Pannonian forest types that are consistently formed in relatively specific environmental conditions that are mostly influenced by topography, particularly slope aspect (Vojtkó, 2002; Borhidi, 2003; Vojtkó et al., 2010; Bölöni et al., 2011). The Pannonian biogeographical region represents unique ecosystems in Europe (Sundseth, 2009), with numerous sub-Mediterranean, continental, Pontic and Balkanian species as well as Pannonian endemics (Fekete et al., 2016). The study area is located in the Északi-középhegység (North Hungarian Mountains), which is characterized by high habitat diversity, due to the wide variety of calcareous, volcanic and igneous rocks (Pelikán, 2010) and diverse topography that create a broad spectrum of edaphic and mesoclimatic conditions. This diversity of habitats allows the coexistence of sub-Mediterranean, continental, Atlantic, and Carpathian floristic and faunistic elements often in close proximity, depending on slope aspect, elevation, and geological parent material (Suba, 1983; Vojtkó, 2002; Vojtkó et al., 2010). With respect to macrofungi, there is a long history of sporocarp-based studies in various areas of the Északi-középhegység (Bohus and Babos, 1960; Takács and Siller, 1980; Rimóczi, 1992, 1994; Tóth, 1999; Siller et al., 2002, 2005; Albert and Dima, 2005; Egri, 2007; Pál-Fám et al., 2007; Rudolf et al., 2008; Siller, 2010; Siller and Dima, 2014). In addition, morphological and molecular analyses of roots colonized by ECM genera *Humaria*, *Genea*, *Tomentella*, and *Tuber* have been carried out in a well-preserved montane beech forest reserve (Kovács and Jakucs, 2006; Erős-Honti *et al.* 2008; Jakucs et al., 2015). However, the diversity and distribution of fungi, particularly microscopic fungi, in various habitat types are still unexplored and I am not aware of any molecular study assessing the richness and community composition of fungal communities in the Pannonian forests.

The goals of this DNA metabarcoding study were to provide the first insights into the kingdom-wide taxonomic and functional diversity of fungi in different Pannonian forest types on a landscape scale and to compare richness and community composition of fungi in forest types characteristic of predominantly south- or north-facing slopes. Although the effect of slope aspect on fungal community composition has not been specifically tested before, there is accumulating knowledge with regard to the richness and composition of fungal communities among habitat types in different regions. At the landscape level, most studies report comparable fungal richness values, but also substantial compositional turnover among habitats with different mesoclimatic and/or edaphic conditions (e.g., Geml et al., 2014b; Timling et al., 2014; Grau et al., 2017). Therefore, while aspect was not expected to affect total fungal richness, I hypothesized that fungal community composition would differ significantly between north- and south-facing slopes due to environmental filtering according to contrasting environmental conditions, i.e. community turnover will be greater among sites with different aspects than among sites of similar aspect (Hypothesis 1). Moreover, I expected that fungi with different life strategies would be favored by different environmental conditions (Hypothesis 2). For example, drought-tolerant fungi are often regarded as generalists, instead of dry specialists, with respect to their ability to grow along a broad moisture gradient (Lennon et al., 2012), while drought-intolerant fungi are considered specialists to a narrow range of mesic conditions, where they likely have competitive advantage over the generalists (Crowther et al., 2014). The resulting competitive dynamics is expected to force most drought-tolerant fungi to the more xeric south-facing slopes, while fungi with a stronger competitive ability under mesic conditions are expected to dominate the mesophilous forests on the north-facing slopes in the study area. Therefore, regarding saprotrophic fungi, I hypothesized that opportunistic generalist saprotrophs (predominantly ascomycetes) will dominate the communities on south-facing slopes in terms of both proportional richness and abundance, while litter and wood decomposers (particularly basidiomycetes) will be more diverse and abundant on north-facing slopes (Hypothesis 2a). Similarly, in ECM fungi, I hypothesized that greater drought stress in southerly aspect will result in higher proportional richness and abundance of ECM fungi with little extramatrical mycelium, i.e. taxa with contact and short-distance hyphal exploration types, that have minimal carbon cost to their host plants (Agerer, 2006; Castaño et al., 2018). In contrast, the proportion of ECM fungi with extensive extramatrical mycelium, i.e. taxa with medium- and long-distance hyphal exploration types, will be more diverse and abundant in northerly aspect. Furthermore, because ECM communities have been reported to be dominated by ascomycetes in arid and semiarid environments, while basidiomycetes tend to dominate more moist habitats (Cavender-Bares et al., 2009; Gehring et al., 2014), I hypothesized that the proportional richness of ECM ascomycetes will be higher in the more xerotherm oak forests, while that of ECM basidiomycetes will be greater in the mesic forests of the north-facing slopes (Hypothesis 2b).

2. Materials and methods

2.1. Study area

Within the broader region of the Északi-középhegység characterized above, the focal area of this study is located in the valley of the Tarna creek situated between the Mátra and the Bükk mountains in Hungary. The area is characterized by rolling hills of low elevations (200–400 m a.s.l.), mostly covered with secondary forests, with a subcontinental climate: mean January and July temperatures ca. −3 °C and 20 °C, respectively, and mean annual precipitation of ca. 580 mm (Tóth, 1983; Horváth and Gaálová, 2007).

Pannonian-Balkanic turkey oak – sessile oak forests (*Quercetum petraeae-cerris*, Natura 2000 code 91M0) form the zonal vegetation type on gentle slopes and in placor settings in the study area as well as in other colline (200–450 m a.s.l.) areas of the Északi-középhegység. They are dominated by oaks, such as *Quercus*

dalechampii, *Q. petraea*, and *Q. cerris*, and can attain 15–25 m canopy height. Within the turkey oak – sessile oak zone, Pannonian thermophilous downy oak forests (*Corno-Quercetum pubescentis*, 91H0) generally develop on shallow and rocky soil on steep (>20°), south-facing slopes with particularly warm and dry mesoclimate. These xerothermic forests are also dominated by the same oak species as the zonal forest type, but the canopy remains low or medium tall (8–10 m), with the characteristic appearance of *Q. pubescens* (Vojtkó, 2002; Borhidi, 2003; Vojtkó et al., 2010; Bölöni et al., 2011).

North-facing, gentle slopes are mostly covered by Pannonian sessile oak – hornbeam forests (*Carici pilosae-Carpinetum*, 91G0), that are predominantly mesophilous, submontane (400–600 m a.s.l.) forests, characteristic of cool, relatively humid habitats on deep soils, with a canopy height of 25–30 m. These mixed forests are dominated by *Carpinus betulus* and *Quercus petraea*. In the low-elevation landscape of the study area, extrazonal submontane beech forests (*Melittio-Fagetum*) occur very sporadically and are restricted to steep, north-facing slopes with the coldest mesoclimatic conditions. These tall (25–35 m), mesic forests are dominated by *Fagus sylvatica* and occur zonally between 400 and 750 m a.s.l. in the region.

The fourteen sampling sites were evenly distributed in two hills (Kis-várhegy and Nagy-várhegy) just south of the village of Sirok, Heves county, Hungary (Fig. 1, Table 1). The location was chosen because it features, in an unusually small area (<2 km^2), the above-mentioned major Pannonian forest types of northern Hungary. The forest types were sampled on both hills, except the submontane beech forest, which is restricted to the northern slope of the Nagy-várhegy (Fig. 1). Potentially confounding factors that often limit the interpretation of ecological studies in natural habitats are minimal: (1) the Kis-várhegy and Nagy-várhegy are uniformly composed of Jurassic calcareous limestone (Pelikán, 2010); (2) the regional climate is uniform throughout the small study area; (3) all forest types are represented by mature (>70 y) secondary forests that have already achieved the characteristic canopy heights of the corresponding forest types; (4) the elevation differences among the sampling sites are minor (<60 m) and are not related to aspect or to any other environmental conditions; and (5) the spatial proximity and the continuous natural or semi-natural landscape are expected to facilitate unrestricted dispersal of fungal propagules among the sites by wind, water and wildlife. Therefore, any observed compositional differences among the samples are expected to be the result of niche-based and stochastic processes, with the former primarily referring to environmental filtering according to differences in abiotic factors (mesoclimatic and edaphic) and biological communities (i.e. vegetation, meso- and microfauna and other soil biota) driven by topography: predominantly northerly vs. southerly aspect and to a lesser extent by slope angle.

2.2. Sampling and molecular work

For this study, fourteen sites were chosen that represented forests of northerly and southerly aspects on both the Kis- and Nagy-várhegy. At each site (ca. 10 × 25 m), 20 samples (5 cm^3 each) of top soil were taken from underneath the litter layer, and at least 2 m from each other. For each site, I estimated canopy cover using a densitometer and calculated the relative abundance of the two dominant tree genera (*Carpinus* and *Quercus*) that were distributed throughout the majority of the sites. Soil samples collected at a given site were pooled, mixed and sieved (2 mm), resulting in a composite soil sample for each site. Ca. 20 g of each composite sample was kept frozen until DNA extraction, while the rest was used for soil chemical analyses to measure pH (water-based), and total carbon (C) and nitrogen (N) contents following Sparks et al. (1996).

Genomic DNA was extracted from 0.5 ml of soil from each composite sample using NucleoSpin® soil kit (Macherey-Nagel Gmbh & Co., Düren, Germany), according to manufacturer's protocol. The ITS2 region (ca. 250 bp) of the nuclear ribosomal DNA repeat was PCR amplified using primers fITS7 (Ihrmark et al., 2012) and ITS4 (White et al., 1990). The ITS4 primer was labelled with sample-specific Multiplex Identification DNA-tags (MIDs). The amplicon library was sequenced at Naturalis Biodiversity Center (Naturalis) using an Ion 318™ Chip and an Ion Torrent Personal Genome Machine (Life Technologies, Guilford, CT, U.S.A.). Detailed protocols of the molecular work are described in Geml et al. (2014b).

2.3. Bioinformatic work

The initial clean-up of the raw data was carried out using Galaxy (https://main.g2.bx.psu.edu/root), in which the sequences were sorted according to samples and adapters (identification tags) were removed. The primers were removed and poor-quality ends were trimmed off based on 0.02 error probability limit in Geneious Pro 8 (BioMatters, New Zealand). Subsequently, sequences were filtered using USEARCH v.8.0 (Edgar, 2010) based on the following settings: all sequences were truncated to 200 bp and sequences with expected error > 1 were discarded. For each sample, sequences were collapsed into unique sequence types, while preserving their counts. The quality-filtered sequences from all samples were grouped into operational taxonomic units (OTUs) at 97% sequence similarity and putative chimeric sequences were removed using USEARCH. I assigned sequences to taxonomic groups based on pairwise similarity searches against the curated UNITE + INSD fungal ITS sequence database (version released on October 10, 2017), containing identified fungal sequences with assignments to Species Hypothesis (SH) groups delimited based on dynamic sequence similarity thresholds (Kõljalg et al., 2013). After excluding OTUs with <80% similarity or <150 bp pairwise alignment length to a fungal sequence, 6216 fungal OTUs were retained, representing a total of 980 766 quality-filtered sequences, including 1930 global singletons. Global singletons are routinely excluded from metabarcoding studies, because the vast majority of them represent erroneous sequences (Lindahl et al., 2013; Geml et al., 2016, 2017). However, this practice likely results in the exclusion of some real high-quality data on locally rare species. Because, to my best knowledge, this is the first metabarcoding study in the Pannonian forests, I intended to keep all high-quality data, including 342 singletons with >98% sequence similarity to a reference fungal SH, a conservative threshold for conspecificity in most fungal groups (Kõljalg et al., 2013), and excluded the remaining 1588 singletons from further analyses. DNA sequences have been deposited in the NCBI database under BioProject: PRJNA436601 and associated Biosamples: SAMN08628702.

Only OTUs with >90% similarity to a fungal SH with known ecological function were assigned to one of the following functional groups: animal pathogens, ECM fungi, lichens, litter decomposers, mycoparasites, plant pathogens, root-associated fungi (non-ECM orchid and ericoid mycorrhizal fungi and root endophytes), saprotrophs (generalists), and wood decomposers. Arbuscular mycorrhizal fungi were not included in the analyses, because only one representative OTU was found in the quality-filtered dataset. The initial functional assignments were made by FunGuild (Nguyen et al., 2015) and were manually checked afterwards. For genera that are known to comprise species from multiple functional guilds (e.g., *Amanita*, *Entoloma*, *Ramaria*, and many SH groups in the Sebacinales), I assigned ecological function for each OTU individually, based on available ecological information for the matching SH in the UNITE database. To further examine patterns of functional

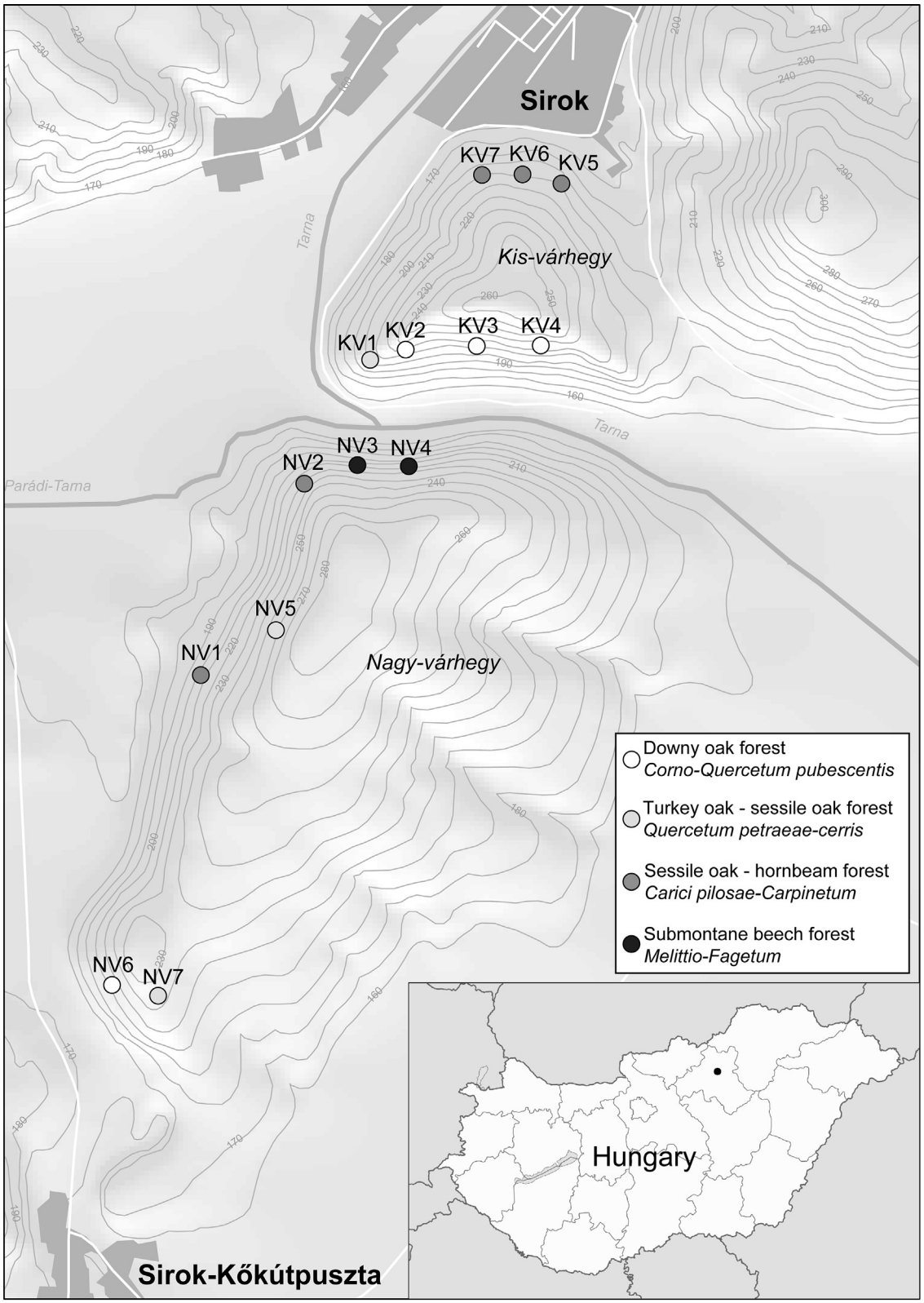


Fig. 1. A map of the sampling localities, with the location of the region of study in Hungary (inset). Full names, vegetation types, topographic variables, and geographic coordinates corresponding to the sampling localities are listed in Table 1.

Table 1
Sampling sites included in this study with code, locality, forest type, dominant tree species, slope aspect, northerly aspect expressed in degrees (south = 0, north = 180), slope angle, and geographic coordinates. Abbreviations for tree genera are: *C.*: *Carpinus* (Betulaceae), *F.*: *Fagus* (Fagaceae), and *Q.*: *Quercus* (Fagaceae). Locations are displayed in a map in Fig. 1.

Site code	Locality	Forest type	Dominant tree species	Aspect	Northerly aspect (degrees)	Slope angle (degrees)	Latitude (degrees)	Longitude (degrees)
KV1	Kis-várhegy	*Quercetum petraeae-cerris*	*Q. dalechampii, Q. petraea, Q. cerris*	SW	13	22.85	47.918885	20.187345
KV2	Kis-várhegy	*Corno-Quercetum pubescentis*	*Q. dalechampii, Q. petraea, Q. pubescens*	S	5	5.71	47.918840	20.188193
KV3	Kis-várhegy	*Corno-Quercetum pubescentis*	*Q. dalechampii, Q. petraea, Q. pubescens*	S	2	29.71	47.919033	20.190292
KV4	Kis-várhegy	*Corno-Quercetum pubescentis*	*Q. dalechampii, Q. petraea, Q. pubescens*	S	10	24	47.918927	20.192524
KV5	Kis-várhegy	*Carici pilosae-Carpinetum*	*C. betulus, Q. petraea*	N	175	19.43	47.921958	20.193339
KV6	Kis-várhegy	*Carici pilosae-Carpinetum*	*C. betulus, Q. petraea*	N	170	22.86	47.921977	20.192281
KV7	Kis-várhegy	*Carici pilosae-Carpinetum*	*C. betulus, Q. petraea*	N	165	25.14	47.921792	20.191034
NV1	Nagy-várhegy	*Carici pilosae-Carpinetum*	*C. betulus, Q. petraea*	WNW	115	17.14	47.912658	20.181935
NV2	Nagy-várhegy	*Carici pilosae-Carpinetum*	*C. betulus, Q. petraea*	NW	145	33.14	47.916270	20.184321
NV3	Nagy-várhegy	*Melittio-Fagetum*	*F. sylvatica*	N	178	37.71	47.917315	20.186580
NV4	Nagy-várhegy	*Melittio-Fagetum*	*F. sylvatica*	N	179	38.85	47.917191	20.188443
NV5	Nagy-várhegy	*Quercetum petraeae-cerris*	*Q. dalechampii, Q. petraea, Q. cerris*	WNW	115	22.85	47.913477	20.183917
NV6	Nagy-várhegy	*Corno-Quercetum pubescentis*	*Q. dalechampii, Q. petraea*	SW	15	24.28	47.906740	20.180339
NV7	Nagy-várhegy	*Quercetum petraeae-cerris*	*Q. dalechampii, Q. petraea, Q. cerris*	SW	18	8	47.906650	20.181740

categories within ECM fungi, I classified ECM fungal OTUs into two aggregate extramatrical mycelial exploration type categories: contact/short-distance/medium-distance smooth with hydrophilic hyphae (C/SD/MDS) and medium-distance mat/medium-distance fringe/long-distance with hydrophobic hyphae (MDM/MDF/LD) following Agerer (2006), Tedersoo and Smith (2013), and the DEEMY database (http://deemy.de). In addition to the morphological differences, the above categories also indicate differences in nutrient acquisition strategies: ECM fungi with C/SD/MDS hyphae preferring labile N pools and ECM fungi with MDM/MDF/LD exploration types having greater ability to break down complex organic compounds (Hobbie and Agerer, 2010).

2.4. Statistical analyses

I normalized the OTU table for subsequent statistical analyses by rarefying the number of high-quality fungal sequences to the smallest library size (36 946 reads). The resulting matrix contained 517 244 read counts of 4312 fungal OTUs. Total fungal richness as well OTU richness and proportional richness of taxonomic and functional groups were compared among the four aspect-driven forest types using ANOVA and Tukey's HSD test in R (R Development Core Team, 2015). I also compared proportional abundance of the fungal functional groups, based on the sequence counts of OTUs assigned to each functional group. In addition, linear regression analyses, also in R, were used to examine relationships between aspect and richness of taxonomic and functional groups of fungi as well as between aspect and environmental variables, i.e. edaphic factors (pH, C, N, and C/N), canopy cover, and the relative abundance values of the two dominant tree genera (*Carpinus* and *Quercus*). When aspect is treated as a continuous variable from 0° to 360°, the two extreme values of this interval refer to the same aspect in the landscape (north). Therefore, aspect was expressed as northerly aspect in degrees (south: 0°, north: 180°) following Calef et al. (2005), which better reflects the well-known ecological differences between north- and south-facing slopes.

To visualize fungal community turnover among the samples, I used the *vegan* R package (Oksanen et al., 2013) to run non-metric multidimensional scaling (NMDS) on the Hellinger-transformed OTU table and a secondary matrix containing environmental variables, which were standardized using the *scale* function in R. Ordinations were run separately for functional groups as well as for all fungi Bray-Curtis distance measure. I used the *envfit* R function to calculate the correlation of the above-mentioned environmental variables with fungal community structure and fit them onto the NMDS ordination plots. In addition, I plotted isolines of northerly aspect on the NMDS ordinations using the *ordisurf* function. In addition, I tested whether fungal communities were statistically different among forest types using the multiresponse permutation procedure (MRPP) and determined any preferences of individual OTUs for forest types and for north- or south-facing slopes using indicator species analyses (Dufrêne and Legendre, 1997) in PC-ORD v. 6.0 (McCune and Grace, 2002).

A series of mantel tests were carried out in PC-ORD to reveal any spatial autocorrelation in environmental variables as well as fungal community composition among the sampling sites and to measure correlation between fungal community composition and environmental variables. Furthermore, partial mantel tests were applied to estimate the effects of northerly aspect, relative abundance of tree genera, and edaphic factors on fungal community structure. The expectation in purely neutral (stochastically assembled) communities is no correlation between the environmental distance and the community dissimilarity of two sites (Smith and Lundholm, 2010). Permutational multivariate analysis of variance was carried out for each functional group, using the *adonis* function in *vegan*, to estimate the relative importance of forest type (categorical) and environmental (continuous) variables as sources of variation in fungal community composition. Finally, to account for correlations among environmental variables, I performed a forward selection of parameters, including only significant environmental variables in the final model.

3. Results

3.1. Patterns of fungal richness

In total, the quality-filtered and rarefied dataset contained 4312 fungal OTUs. Total fungal richness was similar in all forest types, with mean per-plot OTU richness of 1228 ± 90. However, there were substantial differences among the taxonomic groups with respect to richness in the four forest types. Because both absolute and proportional richness values showed practically identical patterns, only the results of the proportional richness analyses are shown. In general, basidiomycetes tended to show higher proportional richness in the mesic and relatively cool forest types. This was particularly true for Agaricomycetes, where the differences between predominantly southern and northern slopes were

significant. Conversely, ascomycetes in general showed higher proportional richness in the warmer and drier forest types, with corresponding significant differences observed in Dothideomycetes, Eurotiomycetes, and Sordariomycetes, while proportional richness was comparable across forest types in Leotiomycetes and Pezizomycetes. Finally, representatives of the phyla Mortierellomycota and Mucoromycota, both formerly classified in Zygomycota, had significantly higher proportional richness on north-facing slopes (Fig. 2).

With respect to functionality, 2196 OTUs representing 345547 reads (50.93% of OTUs and 66.81% of reads) were assigned to functional groups. Four out of the nine functional groups exhibited significant differences among the four forest types in terms of proportional richness. Namely, lichens showed greatest proportional richness in the zonal turkey oak – sessile oak forest and lowest in the mesic sessile oak – hornbeam forest. Plant pathogens and generalist saprotrophs had higher proportional richness in the oak-dominated forests of the south-facing slopes, while wood decomposers showed an opposite trend with lowest proportional richness in the xerothermic downy oak forest and highest in the submontane beech forest (Fig. 2). Despite the differences in proportional richness, most functional groups showed no statistical difference among the forest types with respect to proportional abundance. The only exception was the group of generalist saprotrophs that was significantly more abundant on south-facing slopes, particularly in the downy oak forest, than on north-facing slopes (Fig. S1). Although there were no significant differences in the proportional richness and abundance of ECM fungi among the forest types, there were some differences at the phylum level and in terms of mycelial exploration types. Namely, proportional richness of ECM basidiomycetes was significantly higher in the mesic oak – hornbeam forests than in the zonal and xerotherm oak forests. This pattern was driven by an increase in the proportional richness of ECM basidiomycetes with C/SD/MDS exploration types (e.g., *Inocybe*, *Laccaria*, *Lactarius*, *Russula*, *Sebacina*), while proportional richness of ECM ascomycetes (all C/SD/MDS) and ECM basidiomycetes with MDM/MDF/LD exploration types did not differ significantly among the forest types (Fig. S2). With respect to proportional abundance, there were no differences observed in any phylum or exploration type category of ECM fungi.

3.2. Correlation of aspect with fungal richness and environmental variables

Richness values of most functional groups showed significant ($p < 0.05$) or marginally ($p < 0.1$) significant correlation with

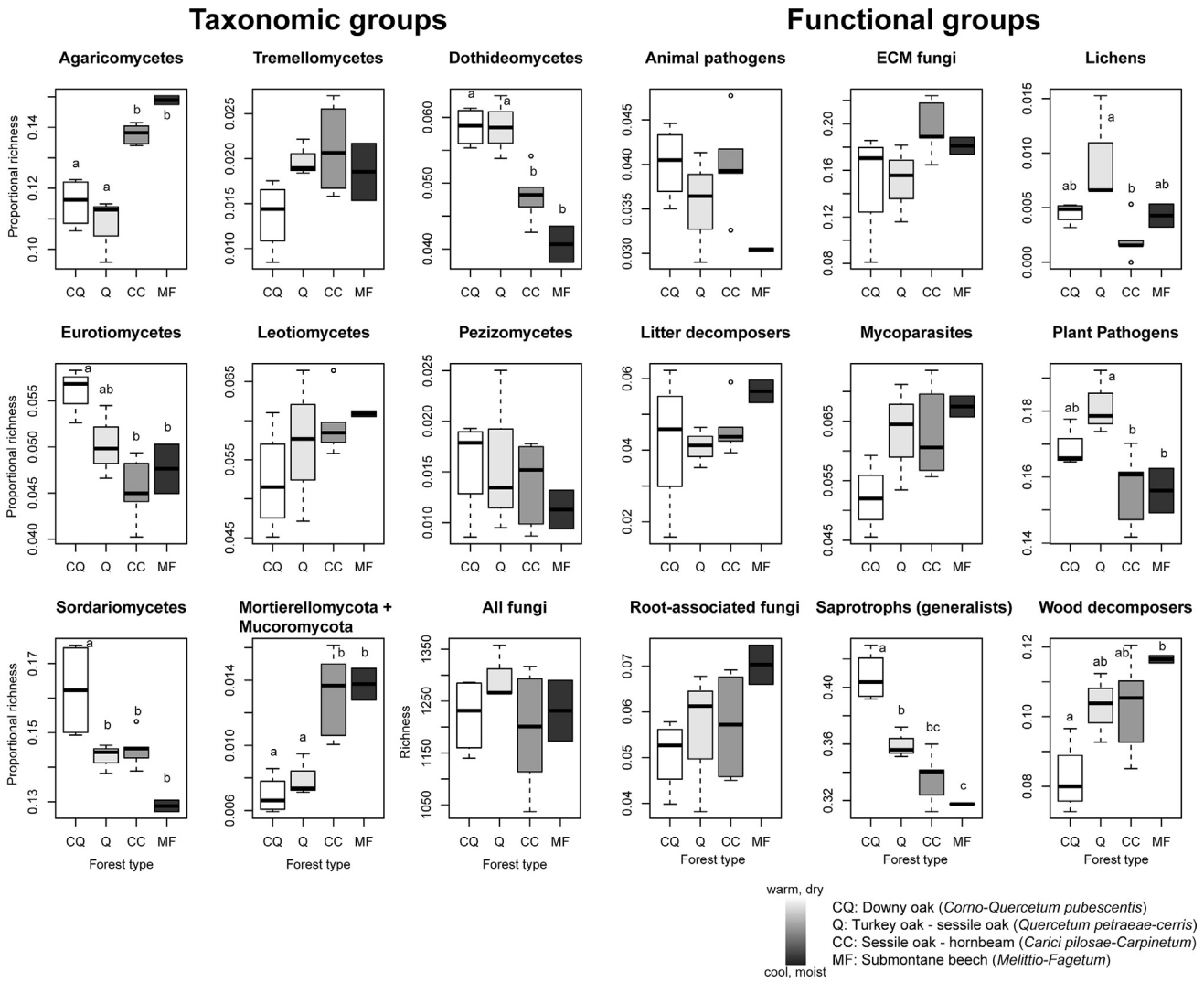


Fig. 2. Comparison of total fungal richness and proportional richness of taxonomic and functional groups across the four sampled forest types. Means were compared using ANOVA and Tukey's HSD tests, with letters denoting significant differences. Forest types are described in detail in the text.

northerly aspect. For example, I found positive correlation in root-associated fungi ($r^2 = 0.231$; $p = 0.047$), mycoparasites ($r^2 = 0.148$; $p = 0.096$), and wood decomposers ($r^2 = 0.204$; $p = 0.059$) with northerly aspect, while negative correlation was observed in lichens ($r^2 = 0.154$; $p = 0.091$), plant pathogens ($r^2 = 0.231$; $p = 0.047$), and generalist saprotrophs ($r^2 = 0.615$; $p < 0.001$) (Fig. S3). Richness of several taxonomic groups also correlated with northerly aspect with varying significance, positively in Agaricomycetes ($r^2 = 0.261$; $p = 0.036$), Tremellomycetes ($r^2 = 0.211$; $p = 0.056$), Leotiomycetes ($r^2 = 0.166$; $p = 0.083$), and Mortierellomycota and Mucoromycota that had formerly been classified to Zygomycota ($r^2 = 0.465$; $p = 0.004$), and negatively in Dothideomycetes ($r^2 = 0.605$; $p < 0.001$), Eurotiomycetes ($r^2 = 0.523$; $p = 0.002$), and Sordariomycetes ($r^2 = 0.386$; $p = 0.011$) (Fig. S3). Among the measured edaphic factors, only pH correlated significantly with northerly aspect, showing strong negative correlation ($r^2 = 0.516$; $p = 0.002$). With respect to forest structure, the relative abundance of *Quercus* ($r^2 = 0.804$; $p < 0.001$) correlated negatively, while the relative abundance of *Carpinus* ($r^2 = 0.258$; $p = 0.037$) and total canopy cover ($r^2 = 0.783$; $p < 0.001$) correlated positively with northerly aspect (Fig. S3).

3.3. Comparing fungal community composition among the sampling sites

NMDS ordinations revealed strong structuring of fungal communities according to aspect and indicated a clear separation among the four forest types. Community composition of all fungi in the sampling sites structured according to aspect, which represented the first axis ($r = 0.999$) (Fig. 3). Pairwise Bray-Curtis distance values among sites of similar aspect were practically identical for both southerly and northerly aspects with no statistical difference: mean distance of 0.526 and 0.529, respectively (*t*-test, $p = 0.8333$). In contrast, when comparing all sites, linear regression analysis indicated a significant positive relationship ($r^2 = 0.547$; $p < 0.001$) between pairwise differences in northerly aspect and community turnover (Bray-Curtis dissimilarity), confirming the strong effect of aspect on community composition (Fig. 4). Soil pH ($r = -0.993$) correlated strongly with the first axis in that south-facing slopes had higher pH than north-facing ones. With respect to vegetation characteristics, relative abundance of oaks ($r = -0.932$) correlated negatively, while canopy cover ($r = 0.999$) and relative abundance of both hornbeam ($r = 0.646$) and beech ($r = 0.311$) correlated positively with northerly aspect. The second axis seemed to represent the differences in C, N, and particularly in C/N ratio ($r = 0.998$) among the sites as well as the varying dominance of hornbeam ($r = -0.764$) *versus* beech ($r = 0.951$) on the north-facing slopes. Richness of only two functional groups showed significant correlation with the NMDS ordinations: generalist saprotrophs correlating negatively with both the first ($r = -0.835$) and second axes ($r = -0.551$), while lichens predominantly correlated with the second axis ($r = 0.934$) and to a lesser extent with the first axis ($r = -0.356$). As for taxonomic groups with significant results, richness values of Dothideomycetes ($r = -0.976$), Eurotiomycetes ($r = -0.848$), and Sordariomycetes ($r = -0.753$) were negatively, while that of Mortierellomycota and Mucoromycota ($r = 0.921$) was positively, correlated with northerly aspect (Fig. 3).

NMDS plots of the datasets corresponding to the functional groups of fungi showed similar correlations with aspect, forest types, and edaphic variables as detailed above. The NMDS ordinations of the four largest functional groups in terms of OTU richness, i.e. ECM fungi, plant pathogens, generalist saprotrophs, and wood decomposers, are shown in Fig. 5, while those of the three less species-rich functional groups, i.e. animal pathogens, litter decomposers, mycoparasites, and root-associated fungi are shown in Fig. S4. Richness values of taxonomic families (or genera, when a family was represented by a single genus) of ECM fungi that correlated with northerly aspect were as follows: only ascomycete genera, i.e. *Elaphomyces*, *Helvella*, and *Tuber* showed negative correlations with northerly aspect, while only basidiomycetes, i.e. *Amanita*, Atheliaceae, *Cortinarius*, *Inocybe*, *Laccaria*, Russulaceae, and *Sebacina* correlated positively with northerly aspect. In addition, *Cenococcum*, *Clavulina*, and Thelephoraceae showed positive correlation with axis 2. Vectors representing the richness of taxonomic groups of plant pathogens seemed to be relatively evenly distributed in the ordination plot. Of these, Bionectriaceae and Mycosphaerellaceae showed preference for hornbeam forests, while *Leptodontitidum*, Taphrinaceae, and Venturiaceae seemed to favor beech forests, both on north-facing slopes. Conversely, richness in Coniochaetaceae, Didymellaceae, Massarinaceae, Phaeosphaeriaceae, *Pyrenochaeta*, and Spizellomycetaceae correlated strongly with southerly aspect. With regard to generalist saprotrophs, the majority of taxa showed clear preference for south-facing slopes, such as *Acremonium*, Aspergillaceae, Chaetomiaceae, Didymosphaeriaceae, Gomphaceae, Helotiaceae, Lasiosphaeriaceae, Microascaceae, Onygenaceae, Sporormiaceae, Stachyobotryaceae, *Tetracladium*, Trichocomaceae, Tricholomataceae, Trichomeriaceae, and Trichosporonaceae, while Mortierellaceae, Tremellaceae, Umbellopsidaceae, and to some extent Cunninghamellaceae tended to have higher richness in sites of northerly aspect. In wood decomposers, Corticiaceae, Hyaloscyphaceae, Lophiostomataceae, and *Pluteus* correlated negatively, while Chaetosphaeriaceae, Crepidotaceae, Helotiaceae, *Trechispora*, and Xylariaceae correlated positively, with northerly aspect. MRPP confirmed the importance of aspect in shaping fungal community composition (effect size $A = 0.084$, probability $p < 0.001$). There were 137 and 174 significant ($p < 0.05$) indicator fungal OTUs characteristic of north- and south-facing slopes, of which, 46 and 69 were assigned to functional groups, respectively (Table 2).

3.4. Assessing the effects of environmental factors on fungal community composition

Mantel tests showed that neither spatial proximity nor slope angle had any significant correlation with fungal community composition or with aspect, relative abundance of tree genera, and edaphic factors. On the other hand, aspect was strongly correlated with the relative abundance of tree genera ($r = 0.526$; $p < 0.001$) and weakly with the measured edaphic factors ($r = 0.151$; $p = 0.046$), while there was moderate correlation between tree genera and edaphic factors ($r = 0.266$; $p = 0.035$) (Table 3). Fungal community composition was strongly correlated with aspect ($r = 0.743$, $p < 0.001$), relative abundance of tree genera ($r = 0.558$, $p < 0.001$), and edaphic factors ($r = 0.535$, $p < 0.001$). Partial mantel tests indicated that aspect in itself had a strongly significant effect on community structure ($r = 0.637$, $p < 0.001$) when the abundance of tree genera was accounted for (control matrix), while the effect of tree genera was substantially weaker, though still significant ($r = 0.295$, $p = 0.018$) when aspect was controlled. Conversely, the correlations of aspect ($r = 0.793$, $p < 0.001$) and edaphic factors ($r = 0.639$, $p < 0.001$) with fungal community composition were both strong when edaphic factors or aspect were controlled for, respectively (Table 3).

Forest type was a significant source of variation in fungal community composition in the total fungal dataset as well as in most functional groups, explaining 39.39% of the variation in all fungi and between 33.27% and 51.64% in the functional groups (Table 4). The only two exceptions were lichenized and litter fungi with non-significant results. With respect to continuous environmental variables, northerly aspect explained the greatest variation, followed

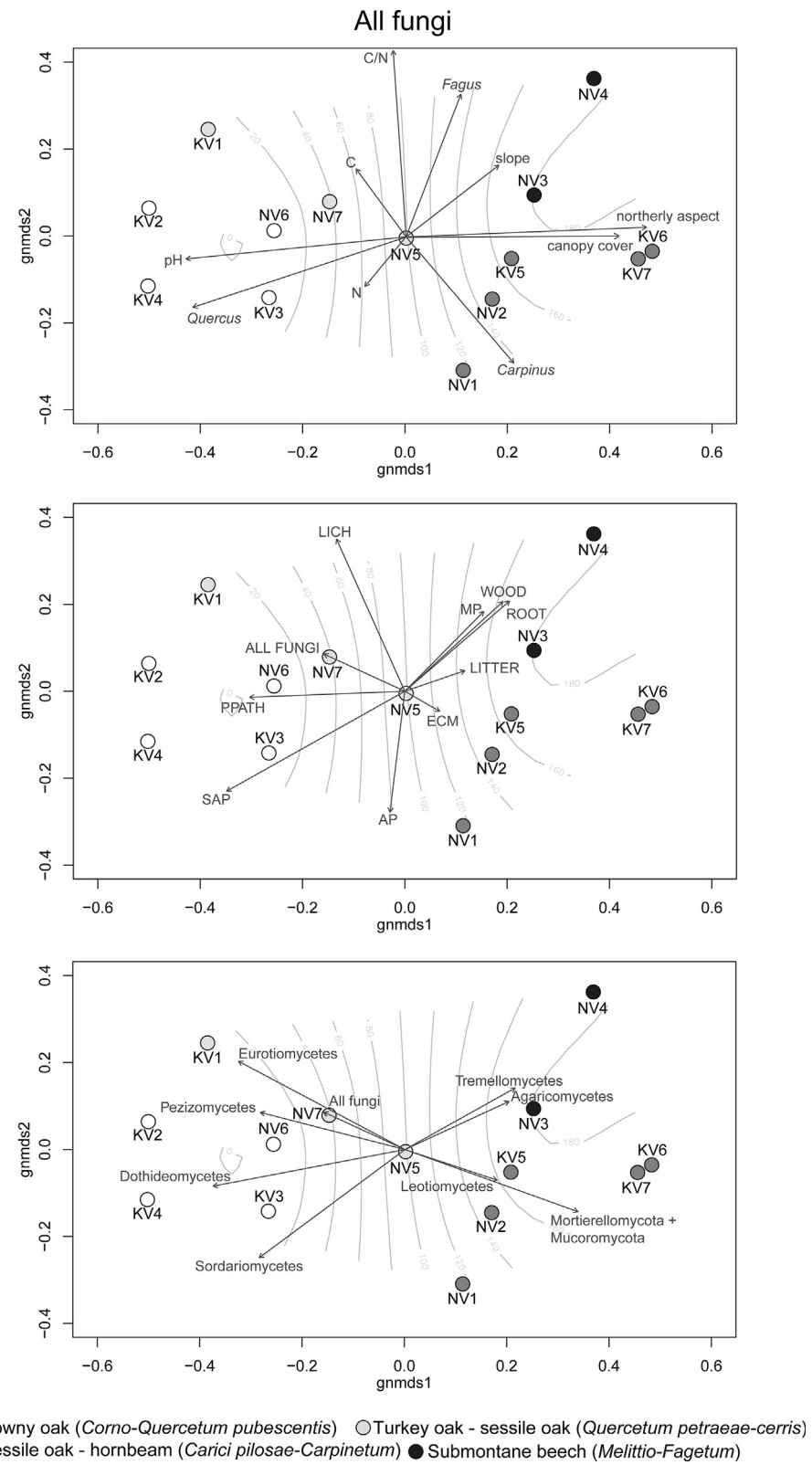


Fig. 3. Non-metric multidimensional scaling (NMDS) ordination plot (final stress: 0.0693) of the fungal communities in the sampled forest types based on Hellinger-transformed data, with northerly aspect displayed as isolines. Labels, localities and descriptions of the sampling sites are given in Table 1. Vectors of environmental variables and richness of functional and taxonomic groups of fungi correlated with ordination axes are displayed in three identical ordination plots. Abbreviations for functional guilds: AP = animal pathogen, ECM = ectomycorrhizal fungus, MP = mycoparasite, PPATH = plant pathogen, ROOT = root-associated (non-ECM) fungus, SAP = generalist saprotroph, WOOD = wood decomposer.

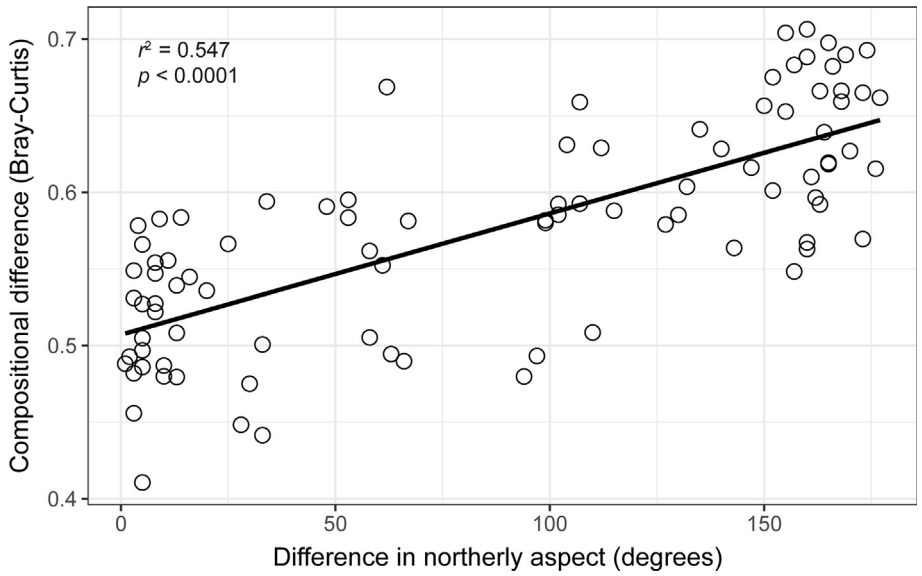


Fig. 4. Correlation between differences in northerly aspect (degrees) and fungal community composition (Bray-Curtis dissimilarity) based on pairwise comparisons among the sampled Pannonian forest sites.

by the relative abundance of *Quercus*, canopy cover, pH, the relative abundance of *Carpinus*, all with statistical significance in almost all fungal groups. The remaining variables, the relative abundance of *Fagus*, slope angle as well as C and N contents played less important roles (Table 4). When the parameters were combined in a model to account for correlation among them, northerly aspect was the single significant contributor of variance in all fungi (24.72%, $p = 0.0001$), mycoparasites (29.79%, $p = 0.0003$), plant pathogens (36.99%, $p = 0.0001$), root-associated fungi (23.09%, $p = 0.0003$), generalist saprotrophs (24.16%, $p = 0.0001$), and wood decomposers (18.44%, $p = 0.0003$). In three functional groups, both northerly aspect and relative abundance of oaks explained significant proportions of the models: 26.96% ($p = 0.0001$) and 10.93% ($p = 0.0229$) in animal pathogens, 21.19% ($p = 0.0001$) and 8.52% ($p = 0.0441$) in ECM fungi, and 23.09% ($p = 0.0003$) and 12.88% ($p = 0.0185$) in root-associated fungi, respectively. In litter fungi, only the relative abundance of *Carpinus* explained a significant proportion of variation in community composition (12.71%, $p = 0.0159$).

4. Discussion

4.1. Effects of aspect on fungal communities

The deep sequence data presented here clearly show that fungal community composition at the selected Pannonian forest sites are strongly structured according to slope aspect. Although total fungal richness is not statistically different between north- and south-facing slopes, the data clearly show a strong emerging pattern driven by slope aspect in all fungal groups. Fungal community turnover is greater among sites with different aspects than among sites of similar aspect, as also suggested by the numerous indicator species on south- or north-facing slopes. Therefore, the data confirm Hypothesis 1, i.e. fungal community composition differs significantly between north- and south-facing slopes due to environmental filtering according to contrasting mesoclimatic and edaphic conditions as well as differences in vegetation. Similarly, fungi with different life strategies seem to be favored by different environmental conditions, as indicated by the functional differences between slopes of northerly or southerly aspect. Even in functional groups with no significant differences in richness, I observed strong compositional differences between slopes of northerly and southerly aspects (confirming Hypothesis 2 in general).

The results presented here confirmed Hypothesis 2a based on the competitive dynamics model, i.e. opportunistic, drought-tolerant generalist saprotrophic fungi are favored by environmental conditions present on south-facing slopes, while forest specialist litter and wood decomposers, and to a lesser extent mycoparasites and non-ECM root-associated fungi, are more diverse on north-facing slopes, presumably as a result of their competitive advantage in mesic conditions. The cooler microclimate in particular may be more advantageous for root-associated fungi, because this group has been shown to be more diverse at higher elevations in altitudinal gradient studies (Geml et al., 2014b). On the other hand, although richness of wood decay fungi and mycoparasites have been shown to decline with decreasing temperature in elevation gradients (Geml et al., 2014b), considering the given moisture limitation in this study area, their higher richness on north-facing slopes may be more strongly driven by the greater availability of moisture. Lichens and plant pathogens were more species rich in the oak-dominated forests. With regard to lichens, this may be a consequence of the more open canopy of the oak forests that allow more light to penetrate and apparently fosters the growth of the generally shade-intolerant and drought-tolerant lichens. On the other hand, plant pathogens and generalist saprotrophs may benefit more from the higher temperatures characteristic of the south-facing slopes, as richness values of these groups generally correlate positively with temperature in altitudinal as well as in global studies (Geml et al., 2014b; Tedersoo et al., 2014). In addition, based on the above-mentioned theory on competitive dynamics, drought-tolerant generalist saprotrophic fungi may be outcompeted on the north-facing slopes by mesophilic specialists.

Conversely, I did not find statistical support for Hypothesis 2b, as neither proportional richness, nor proportional read abundance of ECM ascomycetes were statistical different among the forest types. Only the greater proportional richness of ECM basidiomycetes in the mesic forests was in agreement with my expectations, but even this was driven by an increase in taxa with C/SD/MDS mycelial

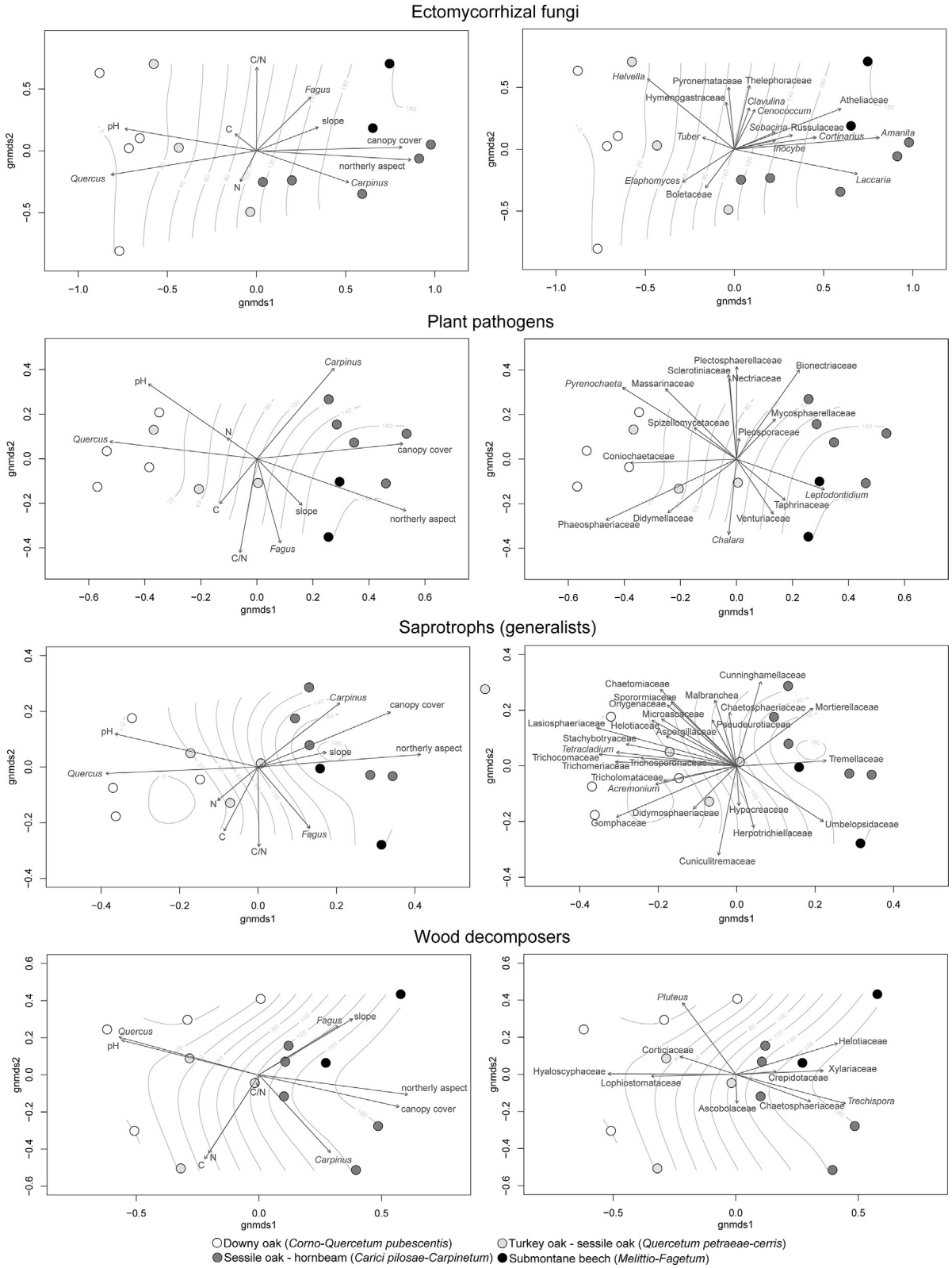


Fig. 5. Non-metric multidimensional scaling (NMDS) ordination plots of the four most diverse functional groups of fungi in the sampled forest types based on Hellinger-transformed data, with northerly aspect displayed as isolines. Vectors of environmental variables and OTU richness of fungal families correlated with ordination axes are displayed. Where a certain family was represented by only one genus, the genus name is shown. Final stress values: ECM fungi (0.1046), plant pathogens (0.0679), saprotrophs (0.0947), and wood decomposers (0.1471).

Table 2
Fungal OTUs considered as significant indicators of northerly (N) or southerly (S) slope aspects with corresponding *p*-values, assigned functional guild, matching Species Hypothesis, ITS2 rDNA sequence similarity (%) and taxonomic classification of the most similar matching sequence in the UNITE + INSD dynamic Species Hypotheses database (version released on October 10, 2017). Only indicators with a known function are shown, displayed in the order of aspect, functional guild, and decreasing significance of indicator value. Abbreviations for functional guilds: AP = animal pathogen, ECM = ectomycorrhizal fungus, MP = mycoparasite, PPATH = plant pathogen, ROOT = root-associated (non-ECM) fungus, SAP = generalist saprotroph, WOOD = wood decomposer.

OTU	Aspect	*p*	Function	Species Hypothesis	%	Matching taxon	Phylum	Class
OTU_2513	S	0.0116	AP	SH007609.07FU	95.5	*Arthroderma insingulare*	Ascomycota	Eurotiomycetes
OTU_892	S	0.0186	AP	SH012485.07FU	99.4	*Beauveria* sp.	Ascomycota	Sordariomycetes
OTU_4940	S	0.0192	AP	SH193551.07FU	95.6	*Metacordyceps chlamydosporia*	Ascomycota	Sordariomycetes
OTU_423	S	0.0262	AP	SH196109.07FU	97.5	*Simplicillium minatense*	Ascomycota	Sordariomycetes
OTU_1990	S	0.0488	AP	SH214395.07FU	100	*Metarhizium flavoviride*	Ascomycota	Sordariomycetes
OTU_178	S	0.0036	ECM	SH182661.07FU	98.8	*Melanogaster ambiguus*	Basidiomycota	Agaricomycetes
OTU_462	S	0.0036	ECM	SH182459.07FU	99.4	*Scleroderma areolatum*	Basidiomycota	Agaricomycetes
OTU_3	S	0.0046	ECM	SH220826.07FU	100	*Russula insignis*	Basidiomycota	Agaricomycetes
OTU_674	S	0.0068	ECM	SH629220.07FU	95.5	*Helvella* sp.	Ascomycota	Pezizomycetes
OTU_20	S	0.0144	ECM	SH214605.07FU	96.9	*Sebacina incrustans*	Basidiomycota	Agaricomycetes
OTU_722	S	0.02	ECM	SH497502.07FU	98.2	*Helvella latispora*	Ascomycota	Pezizomycetes
OTU_219	S	0.0208	ECM	SH222268.07FU	99.4	*Membranomyces spurius*	Basidiomycota	Agaricomycetes
OTU_138	S	0.0208	ECM	SH006539.07FU	100	*Helvella* sp.	Ascomycota	Pezizomycetes
OTU_112	S	0.0414	ECM	SH190455.07FU	98.3	*Astraeus telleriae*	Basidiomycota	Agaricomycetes
OTU_2018	S	0.0228	MP	SH495246.07FU	92.5	*Cosmospora* sp.	Ascomycota	Sordariomycetes
OTU_501	S	0.0012	PPATH	SH443332.07FU	96.3	*Fusarium concentricum*	Ascomycota	Sordariomycetes
OTU_541	S	0.0032	PPATH	SH198276.07FU	99.4	Nectriaceae sp.	Ascomycota	Sordariomycetes
OTU_435	S	0.0056	PPATH	SH175284.07FU	99.4	*Myrothecium* sp.	Ascomycota	Sordariomycetes
OTU_434	S	0.0062	PPATH	SH217882.07FU	99.4	*Pyrenochaeta* sp.	Ascomycota	Dothideomycetes
OTU_279	S	0.0068	PPATH	SH202579.07FU	96.9	*Pyrenochaeta* sp.	Ascomycota	Dothideomycetes
OTU_1610	S	0.0096	PPATH	SH177600.07FU	100	*Microbotryum anomalum*	Basidiomycota	Microbotryomycetes
OTU_1629	S	0.0108	PPATH	SH213880.07FU	99.4	*Gibberella tricincta*	Ascomycota	Sordariomycetes
OTU_4998	S	0.0112	PPATH	SH345969.07FU	97.5	*Stagonosporopsis dorenboschii*	Ascomycota	Dothideomycetes
OTU_1425	S	0.0154	PPATH	SH196352.07FU	100	*Spizellomyces pseudodichotomus*	Chytridiomycota	Spizellomycetes
OTU_2945	S	0.0192	PPATH	SH175285.07FU	95.7	*Myrothecium inundatum*	Ascomycota	Sordariomycetes
OTU_5594	S	0.0194	PPATH	SH191389.07FU	97.5	*Coniochaeta ligniaria*	Ascomycota	Sordariomycetes
OTU_525	S	0.0224	PPATH	SH174362.07FU	100	*Lectera longa*	Ascomycota	Sordariomycetes
OTU_2810	S	0.0246	PPATH	SH180770.07FU	100	*Helminthosporium solani*	Ascomycota	Dothideomycetes
OTU_1113	S	0.0032	ROOT	SH020834.07FU	96.3	*Phialocephala compacta*	Ascomycota	Leotiomycetes
OTU_1268	S	0.0238	ROOT	SH204998.07FU	94.3	*Acephala* sp.	Ascomycota	Leotiomycetes
OTU_890	S	0.0246	ROOT	SH008258.07FU	96.6	*Cadophora* sp.	Ascomycota	Leotiomycetes
OTU_748	S	0.0276	ROOT	SH216991.07FU	95.7	*Oidiodendron pilicola*	Ascomycota	Leotiomycetes
OTU_185	S	0.0012	SAP	SH180481.07FU	98.8	*Knufia tsunedae*	Ascomycota	Eurotiomycetes
OTU_1707	S	0.0012	SAP	SH176700.07FU	100	Hypocreales sp.	Ascomycota	Sordariomycetes
OTU_935	S	0.0012	SAP	SH180772.07FU	98.1	*Corynespora* sp.	Ascomycota	Dothideomycetes
OTU_3865	S	0.003	SAP	SH629325.07FU	94.9	*Chaetomium homopilatum*	Ascomycota	Sordariomycetes
OTU_368	S	0.003	SAP	SH216342.07FU	98.1	*Kavinia alboviridis*	Basidiomycota	Agaricomycetes
OTU_350	S	0.0068	SAP	SH213544.07FU	98.8	Hypocreales sp.	Ascomycota	Sordariomycetes
OTU_5475	S	0.0076	SAP	SH527119.07FU	98.1	*Cladophialophora* sp.	Ascomycota	Eurotiomycetes
OTU_367	S	0.0114	SAP	SH217071.07FU	100	*Podospora* sp.	Ascomycota	Sordariomycetes
OTU_388	S	0.0118	SAP	SH008915.07FU	98.2	Hypocreales sp.	Ascomycota	Sordariomycetes
OTU_1557	S	0.013	SAP	SH184177.07FU	98.3	*Preussia persica*	Ascomycota	Dothideomycetes
OTU_1071	S	0.015	SAP	SH640120.07FU	91.3	*Durella macrospora*	Ascomycota	Leotiomycetes
OTU_682	S	0.0154	SAP	SH021128.07FU	99.4	Hypocreales sp.	Ascomycota	Sordariomycetes
OTU_479	S	0.0188	SAP	SH205999.07FU	100	*Acrostalagmus luteoalbus*	Ascomycota	Sordariomycetes
OTU_5347	S	0.0192	SAP	SH527119.07FU	95.7	*Cladophialophora* sp.	Ascomycota	Eurotiomycetes
OTU_3468	S	0.0196	SAP	SH014661.07FU	96.9	Hypocreales sp.	Ascomycota	Sordariomycetes
OTU_96	S	0.0206	SAP	SH204873.07FU	99.4	*Chaetomium nigricolor*	Ascomycota	Sordariomycetes
OTU_1105	S	0.0208	SAP	SH019302.07FU	95	Hypocreales sp.	Ascomycota	Sordariomycetes
OTU_409	S	0.0216	SAP	SH201192.07FU	100	*Schizothecium carpinicola*	Ascomycota	Sordariomycetes
OTU_2009	S	0.022	SAP	SH003731.07FU	98.8	*Articulospora* sp.	Ascomycota	Leotiomycetes
OTU_3406	S	0.022	SAP	SH026623.07FU	100	*Trichoderma delicatulum*	Ascomycota	Sordariomycetes
OTU_1576	S	0.0224	SAP	SH007110.07FU	100	Hypocreales sp.	Ascomycota	Sordariomycetes
OTU_3912	S	0.0228	SAP	SH194607.07FU	97.2	*Penicillium christenseniae*	Ascomycota	Eurotiomycetes
OTU_1178	S	0.0228	SAP	SH183440.07FU	99.4	*Plectania melastoma*	Ascomycota	Pezizomycetes
OTU_1694	S	0.023	SAP	SH128133.07FU	95.7	*Microcera larvarum*	Ascomycota	Sordariomycetes
OTU_1502	S	0.0246	SAP	SH207979.07FU	96.4	*Acremonium persicinum*	Ascomycota	Sordariomycetes
OTU_1025	S	0.0332	SAP	SH197542.07FU	92.5	*Didymosphaeria* sp.	Ascomycota	Dothideomycetes
OTU_1444	S	0.0342	SAP	SH204465.07FU	94.4	Hypocreales sp.	Ascomycota	Sordariomycetes
OTU_680	S	0.0344	SAP	SH175276.07FU	95.2	Stachybotryaceae sp.	Ascomycota	Sordariomycetes
OTU_878	S	0.035	SAP	SH029684.07FU	90.4	*Arachnomyces gracilis*	Ascomycota	Eurotiomycetes
OTU_1550	S	0.0366	SAP	SH030697.07FU	94.4	*Myrmecridium phragmitis*	Ascomycota	Sordariomycetes
OTU_425	S	0.0404	SAP	SH213541.07FU	97.2	Hypocreales sp.	Ascomycota	Sordariomycetes
OTU_165	S	0.0428	SAP	SH014661.07FU	98.8	Hypocreales sp.	Ascomycota	Sordariomycetes
OTU_1223	S	0.0442	SAP	SH194321.07FU	99.4	*Dictyochaeta simplex*	Ascomycota	Sordariomycetes
OTU_1337	S	0.0478	SAP	SH184969.07FU	90.1	Hypocreales sp.	Ascomycota	Sordariomycetes
OTU_1810	S	0.0012	WOOD	SH492473.07FU	96.3	*Monodictys capensis*	Ascomycota	Dothideomycetes
OTU_1642	S	0.0178	WOOD	SH216764.07FU	100	*Lophiostoma cynaroidis*	Ascomycota	Dothideomycetes
OTU_1194	S	0.039	WOOD	SH216909.07FU	95.7	*Arachnopeziza aurata*	Ascomycota	Leotiomycetes

(*continued on next page*)

Table 2 (*continued*)

OTU	Aspect	*p*	Function	Species Hypothesis	%	Matching taxon	Phylum	Class
OTU_108	N	0.0012	AP	SH184964.07FU	99.4	*Tolypocladium cylindrosporum*	Ascomycota	Sordariomycetes
OTU_895	N	0.0118	AP	SH192574.07FU	100	*Pochonia bulbillosa*	Ascomycota	Sordariomycetes
OTU_344	N	0.0034	ECM	SH642176.07FU	94.6	*Laccaria* sp.	Basidiomycota	Agaricomycetes
OTU_6	N	0.0052	ECM	SH214650.07FU	98.2	*Sebacina* sp.	Basidiomycota	Agaricomycetes
OTU_57	N	0.0056	ECM	SH186707.07FU	100	*Russula cyanoxantha*	Basidiomycota	Agaricomycetes
OTU_37	N	0.0056	ECM	SH204757.07FU	97.5	*Tarzetta* sp.	Ascomycota	Pezizomycetes
OTU_1741	N	0.0076	ECM	SH016378.07FU	100	*Piloderma* sp.	Basidiomycota	Agaricomycetes
OTU_60	N	0.0154	ECM	SH214626.07FU	99.4	*Sebacina* sp.	Basidiomycota	Agaricomycetes
OTU_67	N	0.0202	ECM	SH210482.07FU	95.4	*Paxillus cuprinus*	Basidiomycota	Agaricomycetes
OTU_182	N	0.0212	ECM	SH195878.07FU	100	*Inocybe maculata*	Basidiomycota	Agaricomycetes
OTU_450	N	0.0228	ECM	SH188589.07FU	100	*Cortinarius decipiens*	Basidiomycota	Agaricomycetes
OTU_15	N	0.0242	ECM	SH214721.07FU	96.8	*Sebacina* sp.	Basidiomycota	Agaricomycetes
OTU_312	N	0.0398	ECM	SH220557.07FU	99.4	*Russula chloroides*	Basidiomycota	Agaricomycetes
OTU_111	N	0.041	ECM	SH185240.07FU	100	*Tomentella* sp.	Basidiomycota	Agaricomycetes
OTU_2977	N	0.021	MP	SH190871.07FU	96.6	*Trichoderma harzianum*	Ascomycota	Sordariomycetes
OTU_1367	N	0.0212	MP	SH211287.07FU	98.8	Cephalothecaceae sp.	Ascomycota	Sordariomycetes
OTU_570	N	0.0368	MP	SH628832.07FU	100	*Tremella* sp.	Basidiomycota	Tremellomycetes
OTU_731	N	0.0404	MP	SH195954.07FU	100	*Hypomyces perniciosus*	Ascomycota	Sordariomycetes
OTU_43	N	0.0032	PPATH	SH211202.07FU	100	Bionectriaceae sp.	Ascomycota	Sordariomycetes
OTU_841	N	0.0052	PPATH	SH211202.07FU	96.3	Bionectriaceae sp.	Ascomycota	Sordariomycetes
OTU_699	N	0.0056	PPATH	SH218629.07FU	98.8	*Chalara* sp.	Ascomycota	Leotiomycetes
OTU_1254	N	0.0142	PPATH	SH194809.07FU	100	*Gnomonia virginianae*	Ascomycota	Sordariomycetes
OTU_1572	N	0.016	PPATH	SH213283.07FU	96.9	*Cladosporium* sp.	Ascomycota	Dothideomycetes
OTU_3715	N	0.018	PPATH	SH217194.07FU	98.3	Nectriaceae sp.	Ascomycota	Sordariomycetes
OTU_2484	N	0.0214	PPATH	SH187445.07FU	100	*Erysiphe arcuata*	Ascomycota	Leotiomycetes
OTU_2587	N	0.0242	PPATH	SH211202.07FU	90.9	Bionectriaceae sp.	Ascomycota	Sordariomycetes
OTU_340	N	0.0262	PPATH	SH209885.07FU	94.4	Nectriaceae sp.	Ascomycota	Sordariomycetes
OTU_870	N	0.0354	PPATH	SH116565.07FU	97.8	*Passalora californica*	Ascomycota	Dothideomycetes
OTU_5159	N	0.0382	PPATH	SH202969.07FU	96.9	*Nectria ramulariae*	Ascomycota	Sordariomycetes
OTU_387	N	0.0056	ROOT	SH207784.07FU	99.4	*Meliniomyces* sp.	Ascomycota	Leotiomycetes
OTU_5186	N	0.0056	ROOT	SH216990.07FU	93.8	*Oidiodendron chlamydosporicum*	Ascomycota	Leotiomycetes
OTU_1785	N	0.0096	ROOT	SH217001.07FU	98.2	*Oidiodendron* sp.	Ascomycota	Leotiomycetes
OTU_937	N	0.0134	ROOT	SH217004.07FU	99.4	*Oidiodendron echinulatum*	Ascomycota	Leotiomycetes
OTU_970	N	0.0336	ROOT	SH181589.07FU	93.8	*Chloridium* sp.	Ascomycota	Sordariomycetes
OTU_489	N	0.0104	SAP	SH193250.07FU	98.2	*Cladophialophora* sp.	Ascomycota	Eurotiomycetes
OTU_1409	N	0.0118	SAP	SH013614.07FU	100	*Wardomyces humicola*	Ascomycota	Sordariomycetes
OTU_780	N	0.0128	SAP	SH180117.07FU	99.4	*Mortierella* sp.	Mortierellomycota	Mortierellomycetes
OTU_1191	N	0.0146	SAP	SH019878.07FU	90.1	*Curreya* sp.	Ascomycota	Dothideomycetes
OTU_2865	N	0.0192	SAP	SH199695.07FU	99.4	*Absidia cylindrospora*	Mucoromycota	Mucoromycetes
OTU_1876	N	0.0236	SAP	SH213264.07FU	97.5	*Cladophialophora chaetospira*	Ascomycota	Eurotiomycetes
OTU_332	N	0.024	SAP	SH196089.07FU	100	*Umbelopsis dimorpha*	Mucoromycota	Umbelopsidomycetes
OTU_655	N	0.0242	SAP	SH200349.07FU	90.8	*Malbranchea dendritica*	Ascomycota	Eurotiomycetes
OTU_1528	N	0.036	SAP	SH028610.07FU	98.8	*Leuconeurospora* sp.	Ascomycota	Leotiomycetes
OTU_471	N	0.048	SAP	SH216098.07FU	99.4	*Umbelopsis changbaiensis*	Mucoromycota	Umbelopsidomycetes
OTU_859	N	0.0042	WOOD	SH205445.07FU	100	*Nectriopsis rexiana*	Ascomycota	Sordariomycetes
OTU_1116	N	0.0052	WOOD	SH198389.07FU	97	*Hymenoscyphus fructigenus*	Ascomycota	Leotiomycetes

Table 3
Correlation of environmental and spatial variables with each other and with fungal community composition of the sampling sites. Correlations among standardized environmental variables and with Hellinger-transformed fungal community matrix were tested individually using Mantel tests showing correlation coefficients (r) and significance values (p). Non-significant results (n.s.) are not shown. In addition, to disentangle the 'pure' effects of environmental variables on fungal community composition, partial Mantel tests were used in all combinations of tested and controlled environmental variables.

Correation among environmental variables				
	aspect	slope	tree genera	edaphic factors
aspect	–			
slope	n.s.	–		
tree genera	$r = 0.5256$; $p < 0.0001$	n.s.	–	
edaphic factors	$r = 0.1508$; $p = 0.0461$	n.s.	$r = 0.2661$; $p = 0.0354$	–
spatial	n.s.	n.s.	n.s.	n.s.

Correlation with fungal community composition						
Tested variables	Mantel test	Control variables for partial mantel test				
		aspect	slope	tree genera	edaphic factors	spatial
aspect	$r = 0.7429$; $p < 0.0001$	–	$r = 0.7395$; $p < 0.0001$	$r = 0.6368$; $p < 0.0001$	$r = 0.7928$; $p < 0.0001$	$r = 0.7449$; $p < 0.0001$
slope	n.s.	n.s.	–	n.s.	n.s.	n.s.
tree genera	$r = 0.5584$; $p < 0.0001$	$r = 0.2949$; $p = 0.0178$	$r = 0.5486$; $p = 0.0002$	–	$r = 0.5108$; $p = 0.0002$	$r = 0.5579$; $p = 0.0001$
edaphic factors	$r = 0.5347$; $p < 0.0001$	$r = 0.6388$; $p < 0.0001$	$r = 0.5247$; $p = 0.0002$	$r = 0.4828$; $p = 0.0006$	–	$r = 0.5397$; $p < 0.0001$
spatial	n.s.	n.s.	n.s.	n.s.	n.s.	–

Table 4
Proportion of variation in fungal community composition explained by forest type (categorical) and continuous environmental variables calculated independently with permutational multivariate analysis of variance, based on Hellinger-transformed fungal community matrix. Significant results are in bold. Significant variables were included in the final model for each fungal group (results shown in the text).

Variable	All fungi		Animal pathogens		Ectomycorrhizal fungi		Lichenized fungi		Litter fungi	
	Variance (%)	*p*	Variance (%)	*p*	Variance (%)	*p*	Variance (%)	*p*	Variance (%)	*p*
Forest type	**39.59**	**0.001**	**40.36**	**0.002**	**34.33**	**0.002**	26.12	0.27	24.50	0.31
aspect	**24.71**	**0.001**	**26.96**	**0.001**	**21.19**	**0.001**	12.84	0.078	10.14	0.111
Quercus	**22.68**	**0.001**	**25.08**	**0.001**	**20.11**	**0.002**	10.34	0.164	8.54	0.272
Canopy	**22.47**	**0.001**	**23.60**	**0.001**	**19.83**	**0.001**	10.38	0.187	10.57	0.08
pH	**20.77**	**0.001**	**24.53**	**0.001**	**17.92**	**0.001**	10.95	0.17	9.19	0.178
Carpinus	**16.19**	**0.007**	**21.51**	**0.001**	**13.42**	**0.017**	8.35	0.338	**12.71**	**0.017**
Fagus	**11.66**	**0.034**	8.50	0.329	**11.22**	**0.031**	4.88	0.714	6.21	0.774
slope	11.23	0.087	6.14	0.673	**11.93**	**0.043**	12.48	0.098	5.09	0.95
CN	9.64	0.167	10.96	0.12	9.41	0.145	8.80	0.321	5.49	0.92
C	9.49	0.157	5.48	0.807	7.08	0.525	8.68	0.363	8.73	0.254
N	9.03	0.186	7.00	0.526	7.57	0.461	7.56	0.461	7.67	0.469
latitude	9.59	0.15	9.14	0.222	11.01	0.05	4.60	0.834	10.60	0.082
longitude	8.58	0.263	7.77	0.383	10.70	0.079	3.57	0.917	10.24	0.105
	Mycoparasites		Plant pathogens		Root-associated fungi		Saptrotrophs		Wood decomposers	
Variable	Variance (%)	*p*	Variance (%)	*p*	Variance (%)	*p*	Variance (%)	*p*	Variance (%)	*p*
Forest type	**40.23**	**0.013**	**51.64**	**0.001**	**34.46**	**0.013**	**39.55**	**0.001**	**33.27**	**0.002**
aspect	**29.80**	**0.001**	**37.00**	**0.001**	**21.96**	**0.002**	**24.16**	**0.001**	**18.44**	**0.001**
Quercus	**27.60**	**0.004**	**32.26**	**0.001**	**22.02**	**0.003**	**22.43**	**0.001**	**17.51**	**0.001**
canopy	**23.94**	**0.005**	**33.91**	**0.001**	**20.28**	**0.003**	**21.89**	**0.002**	**17.53**	**0.001**
pH	**26.36**	**0.003**	**25.59**	**0.001**	**23.09**	**0.001**	**20.32**	**0.001**	**18.33**	**0.001**
Carpinus	10.94	0.159	**23.67**	**0.005**	**15.87**	**0.02**	**15.37**	**0.01**	**12.97**	**0.013**
Fagus	11.62	0.113	11.68	0.12	10.17	0.168	11.65	0.084	10.42	0.117
slope	14.53	0.059	10.90	0.144	10.38	0.181	10.44	0.097	**12.01**	**0.034**
CN	7.46	0.386	10.78	0.155	8.15	0.351	9.50	0.167	7.90	0.38
C	8.04	0.349	11.63	0.114	10.09	0.192	10.93	0.078	**12.29**	**0.019**
N	9.32	0.24	8.44	0.326	10.37	0.151	9.38	0.201	**11.52**	**0.036**
latitude	5.03	0.78	9.66	0.21	6.93	0.579	9.34	0.192	9.05	0.197
longitude	6.56	0.488	6.29	0.586	7.17	0.471	8.20	0.331	7.24	0.545

exploration types, contrary to my hypothesis and to the findings of Castaño et al. (2018) in a Mediterranean pine forest. However, it is worth mentioning that only ascomycete ECM genera showed clear preference for south-facing slopes (*Elaphomyces*, *Helvella*, and *Tuber*), while almost all ECM genera that preferred mesic forests of northerly aspect were basidiomycetes: *Amanita*, *Clavulina*, *Cortinarius*, *Inocybe*, *Laccaria*, *Sebacina* as well as those in Atheliaceae and Russulaceae, which lends some weak support to the difference in habitat preferences between ECM ascomycetes and basidiomycetes in Hypothesis 2b. It is plausible that the increase in C/SD/MDS ECM basidiomycetes in the mesic forests may be related to differences in rooting density. Sites with high rooting density, such as mature forests, generally are dominated by short- and medium-distance exploration types as opposed to early-successional forests with lower rooting density, where the proportion of long-distance exploration types often is higher (Peay et al., 2011). While all study sites in this project were mature forests and were dominated by C/SD/MDS mycelial exploration types, it is possible that the higher richness of C/SD/MDS ECM fungi on the north-facing slopes may be caused by higher rooting density in the mesic forests, when compared to the more xerothermic oak forests. Leuschner et al. (2004) found that beech forests in Germany had a higher number of root tips per square meter in sites with higher precipitation, suggesting indeed a positive relationship between soil moisture and rooting density. Somewhat surprisingly though, I did not find a statistical difference between proportional abundance among the south- and north-facing slopes despite the prevailing mesic conditions on the latter, which presumably are more conducive to mycelial growth and rooting density. There appear to be substantial functional and ecological variations at various taxonomic scales that can result in contrasting patterns within the above categories (e.g., between C/SD/MDS ascomycetes and basidiomycetes) that could drive the observed patterns. Certainly, more studies on the environmental and functional components of the ecological niches of these fungi are needed.

4.2. Environmental drivers

The effect of slope aspect on fungal community composition and richness is mediated through abiotic and biotic factors that are driven either directly or indirectly by the differences in net solar radiation received in north- and south-facing slopes (McCune and Keon, 2002). For example, aspect strongly influences local air and surface temperature, soil moisture, relative humidity, and soil chemical processes (Gilliam et al., 2014). Consequently, the habitats found on north- and south-facing slopes have distinct meso- and microclimatic as well as edaphic conditions. These differences are particularly marked regarding available moisture and pH, as had been observed in the study region previously (Dobos, 2010), which, in turn, influence the composition of biotic communities and their interactions.

The availability of soil moisture is one of the most important environmental conditions that determines richness as well as community composition in fungi (Crowther et al., 2014; Tedersoo et al., 2014). At landscape scale, as in the study area, annual precipitation is considered uniform across the sampling sites due to their close proximity. Therefore, topography likely is the most important factor that influences moisture availability through contrasting levels of evapotranspiration between north- and south-facing slopes, as has been observed in several biomes (Fekedulegn et al., 2003; Méndez-Toribio et al., 2016).

Soil pH also plays an important role in shaping fungal communities (Porter et al., 1987; Coughlan et al., 2000; Lauber et al., 2008; Rousk et al., 2010; Geml et al., 2014a; Tedersoo et al., 2014; Glassman et al., 2017) and is often influenced by slope aspect (Gilliam et al., 2014; Chu et al., 2016). Because many fungal species

have a relatively wide pH optimum (e.g. Wheeler et al., 1991; Nevarez et al., 2009), it is likely that the observed correlation of pH with community composition is mainly indirect, e.g., via altering nutrient availability and competitive interactions between soil fungi and bacteria (Rousk et al., 2010), and other soil biota. In the study sites, there was a strong negative correlation of soil pH with northerly aspect and it is difficult to disentangle the 'pure' effect of pH from that of aspect. Nevertheless, for some fungal groups that are known to be influenced by soil pH, the data presented here are in agreement with previous results. For example, several species of true truffles (*Tuber* spp.) are known to prefer high soil pH (García-Montero et al., 2006), which is in agreement with the data presented here (Fig. 5). Furthermore, root endophytic fungi had been shown to prefer low soil pH (Postma et al., 2006) and the strong preference of non-ECM root-associated fungi for the northerly sites with lower pH in this study confirms the above trend (Fig. 3).

The only other edaphic factors with strong correlation with fungal community structure was C/N ratio, which was not related to aspect. Instead, changes in C/N ratio appeared to be related to different forest types on the north-facing slopes, i.e. oak – hornbeam and submontane beech forests. Because C/N is considered a direct measure of resource quality (Nielsen et al., 2010), it is possible that the higher C/N values in the beech forests are driven by differences in litter quality between beech and hornbeam and oak. Measurements from more beech and oak – hornbeam stands are needed to test this hypothesis.

Although the two dominant tree genera (*Carpinus* and *Quercus*) occur in most of the sites, their relative abundance is strongly influenced by aspect. Furthermore, as indicated by the strong positive relationship between northerly aspect and canopy cover, the forest structure is notably different between south- and north-facing slopes even in communities composed of the same tree genera, which further increases the mesoclimatic differences between the south- and north-facing slopes. Therefore, and because the vast majority of plant-associated fungi are not strictly specific to a tree genus or family, I argue that to a great extent the observed fungal community patterns are caused by a complex array of aspect-driven environmental variables and not by the tree composition alone.

The results of the partial mantel tests as well as the permutational multivariate analysis of variance suggest that northerly aspect by itself explained greatest proportion of variation in community composition in all fungi and in most functional groups, while the effect of the tree community, although still strong, is secondary, followed by soil chemical characteristics. It is likely that environmental variables not yet measured, may also contribute substantially to the environmental differences currently accounted for only under northerly aspect. For example, I did not measure soil and air temperature, relative humidity, and soil moisture at the sites, partly because it is already well-known that these factors correlate strongly with aspect on mesoclimate scale and partly because obtaining a realistic characterization of these variables would have required measurements taken throughout the growing season at the sampling sites, which was beyond the scope and logistic possibilities of this case study. Future studies should include site-specific microclimate data as well as a more extensive list of edaphic variables to obtain more insights into the variation of environmental factors at small spatial scales as well as their influence on fungal community composition and turnover.

In summary, a large proportion (33.27%–51.64%) of variation in community composition in all fungal groups was explained by forest types, which were described formerly based on detailed coenological studies of woody plants, forbs, graminoids as well as non-vascular plants and are used as a framework for vegetation and phytogeographic studies (Vojtkó, 2002; Borhidi, 2003; Vojtkó et al., 2010; Bölöni et al., 2011). These coenological habitat types seem to capture well the consistent and largely predictable environmental differences and their delimitation and mapping are useful to better understand the distribution and community dynamics of fungi at landscape scales.

4.3. Contribution to the knowledge on Pannonian forest fungi

This study shows a remarkably high fungal diversity in a small area (<2 km^2) of secondary forests in the eastern edge of the Mátra mountains. After the stringent quality filtering steps, the non-rarefied and rarefied datasets contained 4655 and 4312 fungal OTUs, respectively. Based on the rarefied data, well over 1000 OTUs occurred in any given sample (Fig. 2), each representing an area of ca. 250 m^2. In total, I detected representatives of 707 fungal genera, of which 467 belonged to Ascomycota, 225 to Basidiomycota, 6 to Chytridiomycota, and 7 represented early-diverging lineages formerly classified in Zygomycota. Nonetheless, the true generic diversity likely is even higher, because the vast majority of fungi in the sampled sites, as well as globally, are microfungi and many of them could only be assigned to families, orders or classes due to the lack of sufficiently identified reference data. Consequently, these represent species with unknown identity, several of which may still be undescribed. With respect to the identified microfungi, the results presented here may be the first data on their diversity and possible habitat preference in the Pannonian biogeographic region, serving as potential reference data for future studies as well. The full list of fungal OTUs of the non-rarefied dataset with their distribution among the samples and taxonomic classification (Table S1) will facilitate other mycological and fungal ecological studies in the region.

I was able to assign a relatively high proportion (51%) of fungal OTUs to functional groups, particularly in taxa with macroscopic fruiting bodies for which extensive reference data are available from Europe, e.g., agarics, boletes, coral fungi, polypores, and several true and false truffles. For example, the number of unique matching SHs in some of the most diverse basidiomycete genera were 69 in *Inocybe*, 48 in *Russula*, 18 in *Lepiota*, while somewhat surprisingly *Cortinarius* and *Lactarius* were only represented by 23 and 13 unique SHs, respectively. On the other hand, the data also showed a high diversity ECM basidiomycetes with inconspicuous fruiting bodies, such *Sebacina* (66 SHs) and *Tomentella* (83 SHs) that are notoriously underrepresented in sporocarp surveys (Gardes and Bruns, 1996; Kõljalg et al., 2000; Geml et al., 2012). Furthermore, I detected numerous hypogeous ECM fungi, such as *Elaphomyces muricatus* and *E. papillatus*, *Genea verrucosa*, *Hydnotrya* sp., *Hymenogaster australis*, *H. griseus*, *Hysterangium stoloniferum*, *Gautieria graveolens*, *Melanogaster ambiguus*, *M. broomeanus*, and *M. variegatus*, *Wakefieldia macrospora*, as well as several species of the charismatic *Tuber* genus (e.g., *T. aestivum*, *T. borchii*, *T. brumale*, *T. maculatum*, *T. puberulum*, *T. rapaeodorum*, *T. rufum* and possibly *T. fulgens*). Most of these are known to occur in Hungary, except for *Gautieria graveolens*, as this genus is only represented by an unidentified species in the list of hypogeous fungi for the Carpathian-Pannonian region compiled by Bratek et al. (2013). Representatives of these hypogeous fungi were found in all forest types, indicating that they probably are relatively common in Pannonian forests.

In addition, I want to emphasize the suitability of DNA metabarcoding to complement sporocarp-based assessments for biological monitoring and conservation of fungi. Specifically, studies such as this can provide valuable knowledge not only on the total diversity of fungi at any given site, but also on the distribution and habitat preferences of numerous species, including rare and/or protected species. For example, I found at least one of the thirty-five species of fungi protected by law in Hungary (Siller et al., 2005,

2006): *Strobilomyces strobilaceus*, which was detected on north-facing slopes of both the Kis- and Nagy-Várhegy, which confirms the habitat preference of this species for mesophilic beech and oak-hornbeam forests in Hungary (Siller et al., 2005). Furthermore, even though the retained global singletons that were >98% similar to a reference fungal SH had only minor contribution to richness values, and had practically no influence on the community structure patterns, many were identified to a genus or species (Table S1). Most of the macrofungi among these, such as *Baeospora myosura*, *Coprinopsis picacea*, *Coprinus comatus*, *Cortinarius infractus*, *Crepidotus mollis*, *Geastrum fornicatum*, *Mycena renati*, *Russula albonigra*, *Russula heterophylla*, *Russula sororia*, and *Tricholoma batschi*, have been found in sporocarp surveys in the Északi-középhegység (Bohus and Babos, 1960; Tóth, 1999; Siller et al., 2002, 2005; Egri, 2007; Rudolf et al., 2008; Siller and Dima, 2014). With respect to the rest, more sampling is needed to confirm their presence in the region.

Finally, soil communities are extremely diverse and there is increasing evidence pointing to soil biodiversity as having key roles in determining the structure and ecological responses of terrestrial ecosystems (Bardgett and van der Putten, 2014). Soil fungi in particular are known to drive plant diversity and productivity and are crucial for ecosystem functioning and resilience towards disturbance (van der Heijden et al., 2008). Because most fungi have high habitat specificity and tend to respond quickly to changes in environmental conditions (Nielsen et al., 2010; Geml et al., 2015, 2016; Morgado et al., 2015, 2016; Mundra et al., 2016; Semenova et al., 2015, 2016), fungi have a promising potential as indicators of habitat quality in biological monitoring programs. More specifically, assessments of richness and composition of fungal communities in a variety of habitats can inform decision-makers with respect to land use strategies that foster the sustainable preservation of diverse and resilient ecosystems with a wide range of ecosystem functions.

5. Conclusions

A prominent finding of this study is that fungal diversity and community structure are strongly influenced by vegetation type and environmental variables driven by slope aspect, despite the short distance separating north- and south-facing slopes. Even though this finding may appear trivial due to the well-known effects of aspect on vegetation, fungal communities have been surprisingly little studied in this regard, and the data presented here offer unprecedented insights into the landscape-level distribution of various taxonomic and functional groups with respect to topography. Furthermore, while aspect-driven differences in vegetation tend to be related to relative importance as opposed the presence/absence of plant species on slopes with different aspect (Gilliam et al., 2014), many fungal species were detected exclusively on either north- or south-facing slopes. This reflects the often-observed high habitat specificity exhibited by many fungi, which offers possibilities for biological monitoring and habitat characterization, and I strongly advocate incorporating fungi in biodiversity assessments and conservation efforts.

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Supplementary data

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