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Exploring the relationship between macrofungi diversity, abundance, and vascular plant diversity in semi-natural and managed forests in north-east Hungary

Kinga Rudolf¹, Tamás Morschhauser¹, Ferenc Pál-Fám², Zoltán Botta-Dukát³

1. Department of Plant Taxonomy and Geobotany, University of Pécs, Ifjúság u. 6, Pécs 7624, Hungary
E-mail: morsi@gamma.ttk.pte.hu
2. Department of Botany and Plant Production, University of Kaposvár, Guba S. u. 40, Kaposvár 7400, Hungary
3. Institute of Ecology and Botany, MTA Centre for Ecological Research, Alkotmány u. 2-4, Vácrátót 2163, Hungary

Abstract

The diversity of easy-to-study organisms (e.g. vascular plants) is often used as a proxy for the diversity of other organisms whose investigation needs more effort, time and specialist knowledge. Some previous studies have found positive relationships between plant and macrofungal diversity and thus support this approach, while others question this practice. Our aim was to explore the possibility of using plant diversity as surrogate for macrofungal diversity in the forests of the Pannonian ecoregion. A total of 19 permanent plots in north-east Hungary were sampled for vascular plants and macrofungi. The effect on macrofungal abundance and diversity, of plant evenness and richness as well as degradation level was tested using generalized linear models. Species richness of macrofungi assemblages proved to be independent of the diversity and naturalness of vascular plant communities; however, there was congruence in the composition of the two communities. In contrast to diversity, macrofungi abundance was significantly negatively correlated to plant species richness. There was a hump-backed relationship between the abundance of terricolous macrofungi and the degradation level estimated on the basis of the occurrence of vascular plants, although degradation did not influence the abundance of lignicolous macrofungi. Our results question the reliability of decisions on nature conservation actions based on a few groups of easy-to-observe organisms, and underline the necessity of studying as wide a range of taxonomic groups as possible.

Keywords

Habitat degradation, Intermediate Disturbance Hypothesis, Macrofungi diversity, Plant richness, Sporocarp abundance

Introduction

Human activities cause loss of biodiversity by degradation, fragmentation and over-utilisation of habitats, introduction of alien species as well as the spread of infectious diseases (Primack 1998). These negative effects are well-documented for some components of biodiversity (e.g. birds, reptiles, mammals, plants; Oleksyn and Reich 1994; Findlay and Houlihan 1997; Lenzen et al. 2009) while we have only scarce information on the influence of human activities on many other organisms.

Macrofungi are an often neglected component of biodiversity; however, there is evidence that habitat degradation adversely influences the number of fruiting bodies of macrofungi and diminishes the diversity of the fungal community (Arnolds 1988, 1991; Ohenoja 1988; Zak 1992; Miller and Lodge 1997).

The main reasons that macrofungi are neglected when making decisions on nature protection activities (including selection of protected areas) are the lack of information on their abundance and distribution, and their unexplored taxonomic diversity. Researchers have attempted to solve these problems through the use of better-known surrogate taxa, such as vascular plants. Vascular plants are often used as a surrogate for estimating the diversity of other taxa because they are fundamental components of the structure of terrestrial ecosystems, reflecting environmental conditions and providing habitat for other organisms. Moreover, sampling of vascular plants is easier (Ryti 1992; Pharo et al. 2000; Chiarucci et al. 2005; Santi et al. 2010). The practice of using plant communities as a proxy for fungal communities is supported by the congruence in composition between them reported in several studies (e.g. Nantel and Neumann 1992; Packham et al. 2002; Saetersdal et al. 2003; Chiarucci et al. 2005; Brown et al. 2006; McMullan-Fisher et al. 2010). However, there is no clear evidence that higher plant diversity indicates higher fungal diversity. In a continental-scale metaanalysis Schmit et al. (2005), and in regional analyses Villeneuve et al. (1989), Gabel and Gabel (2007), and McMullan-Fisher (2008) have found significant positive correlation. On the other hand, studies by Chiarucci et al. (2005) and Santi et al. (2010) found that the species richness of the two communities were not correlated in spite of the positive correlation between their compositions in earlier studies. More recently, Gómez-Hernández and Williams-Linera (2011) reported a negative correlation between macrofungi and overstorey tree richness. Simulation studies (Virolainen et al. 2000; Chiarucci et al. 2005; McMullan-Fisher et al. 2010) showed that site-selection optimised based on plant communities cannot maximize fungal diversity, even if there is a statistical relationship between the compositions of the two groups. In studies by Virolainen et al. (2000) and McMullan-Fisher et al. (2010), random selection performs better than selection based on plant species. Several factors may underlie these contradictory results: (1) the studies were performed at different scales (Flather et al. 1997) (from continental scale meta-analysis to comparing degradation stages of the same vegetation type); (2) different fungal groups may respond differently to environmental factors and may correlate with different proxies (cf. Villeneuve et al. 1989); (3) previous studies focussed on species composition and species richness and neglected other components of fungal diversity (e.g. evenness).

The aim of the present study was to overcome the limitations in our knowledge in relation to the last two points. Therefore, we investigated the relationship between abundance and diversity of macrofungi (and its two main subgroups) and diversity of vascular plants using different diversity measures (species richness, Shannon-diversity, evenness). Furthermore, we studied the consequences of habitat degradation on fungal communities using plant species as degradation indicators.

The study area is situated in the Carpathian Basin, whose biodiversity represents a very unique ecological entity in comparison with other European regions. For this reason, it is considered as a distinct ecological region (Pannonian ecoregion) in the Natura 2000 programme. Only some preliminary investigations of macrofungi–plant interactions have been published for the Pannonian ecoregion (Benedek et al. 2005; Pál-Fám et al. 2007).

Materials and methods

Study area

Our study was performed in the Cserehát—a hilly landscape in north-east Hungary (Fig. 1). The climate is rather cool, with an annual mean temperature 8–8.5 °C. The annual mean precipitation is about 600 mm, but about 400 mm falls during the growing season, which is important for fungal fructification. The most characteristic soil type is brown forest soil with clay illuviation on loess (Dorgai 1986).

The landscape is dominated by agricultural cultivation. Its forest vegetation has been changed significantly as a result of excessive forestry management, hunting and grazing. The area can be characterised by fragmented forest stands and alien tree plantations with invasive plant species in the herb layer. The study was carried out in five locations 50–80 km away from the city of Miskolc, at 200–250 m altitude above sea level near the villages Abaújlak (48°24'N, 20°57'E), Nyésta (48°23'N, 20°58'E), Irota (48°24'N, 20°52'E), Szendrőlád (48°20'N, 20°44'E) and Büdöskútpuszta (48°22'N, 20°44'E). Stands of beech (*Melittio-Fagetum* Soó 1964 emend. 1971), zonal Turkey oak (*Quercetum petraeae-cerris* Soó 1963), and extrazonal hornbeam-oak (*Carici pilosae-Carpinetum* Neuhäusl et Neuhäuslová-Novotná 1964 emend. Borhidi 1996), as well as oak wood-pastures, Scotch pine (*Pinetum sylvestris cultum*) and Norway spruce plantations (*Piceetum cultum*) were investigated and characterised (Rudolf et al. 2008) (Table 1). The nomenclature of the plant associations follows the work of Borhidi (2003).

Sampling

Two sampling sites were selected in the most common forest type (i.e. zonal Turkey oak forest) and one site in other main forest types. In larger (1–3 ha) and more heterogeneous sites, five plots were selected, while in the smaller (<1 ha) and more homogeneous stands only 1 plot was sampled. Thus, in seven sites of the six vegetation types, 19 sample plots (1,200 m²/plot) were selected and marked. In the sites located at Nyésta and Abaújlak, the plant surveys were made in the spring and summer of 1995–1996; however, in the other locations (Irota, Szendrőlád and Büdöskútpuszta), sampling took place in 2004–2005. For each plot, all vascular plants (both woody and herbaceous) were recorded and their cover estimated visually in the herb, shrub, and canopy layers separately (Bullock 2006). The work of Simon (2000) was used for the identification of vascular plants. Fungi were sampled in the years 1995, 1996, 1998, 2002 in the sites at Nyésta and Abaújlak and in 2004–2006 at the other locations. Macrofungi species were recorded and fruit bodies were counted as measure of species abundance on six to eight occasions in each year between July and November. We investigated only epigeous macrofungi. These belong to following groups: soil saprotrophic, mycorrhizal, wood saprotrophic, necrotrophic parasites and saprotrophic on other plant remains. The literature used for determination of 'semipileate' species provides a measure of each species when they grow separately (Hansen and Knudsen 1997). Thus, we estimated abundance using these measures separately for each semipileate species; macrofungi were determined by K.R. and F.P.-F. Species names followed the work of Krieglsteiner (1991) and the Index Fungorum (CABI 2008). Many macrofungal species are known to fruit sporadically, with diverse patterns of occurrence from year to year (Watling 1995) due to different factors such as climatic and edaphic conditions. Accordingly, many years of intensive surveys are necessary to describe the macrofungal communities of a vegetation unit (Tofts and Orton 1998). On the other hand, vegetation composition dominated by long-lived perennials was recorded for only 1 year in each plot, thus the difference between years due to environmental fluctuations is negligible relative to differences between vegetation types. The proportion of disturbance indicator plant species (hereafter called degradation level) was calculated using species categorization of Social Behaviour Types (Borhidi 1995). This measures the level of degradation caused by human activities or natural processes and indicated by changes in species composition (Morschhauser 1995). Social Behaviour Types categories are a refinement of Grime's (1979) strategies adapted to Hungarian Flora. Plant species indicating degradation belong to Grime's 'ruderal' category, except pioneer species of primary succession, which belong to the 'natural pioneers' category in Borhidi's classification.

Applied diversity indices

There are a lot of diversity indices (Magurran 2004), and different indices may be sensitive to different aspects of abundance distribution, and thus may rank communities in different ways (Hurlbert 1971; Tóthmérész 1995). This problem can be solved by using parametric diversity families (Rényi 1961; Hill 1973; Aczél and Daróczy 1975; Patil and Taillie 1979; Keylock 2005) instead of a single diversity index (Tóthmérész 1995). Indices of these families show varying sensitivities to rare

and abundant species as the scale parameter (α) changes. Jost (2006) suggested that, instead of entropy, “the effective number of species” or “numbers equals” (i.e. the number of equally abundant species that would result in the same entropy value) should be used as the unit of diversity. It can be proved that, if this suggestion is followed, all the above-mentioned diversity families lead to the same form (Jost 2006):

$$D_\alpha = \left(\sum p_i^\alpha \right)^{1/(1-\alpha)} \quad \text{if } 0 \leq \alpha < 1 \text{ or } \alpha > 1$$

$$D_1 = \exp \left(- \sum p_i \ln p_i \right)$$

where p_i is the relative abundance of the i th species, and α is the scale parameter.

Plotting diversity values (D_α) as a function of scale parameter (α) is a useful tool with which to compare communities (Tóthmérész 1995), but lots of correlated diversity values related to similar α values cannot be used as independent variables in statistical modeling. Therefore, in this study, three scale parameter values were chosen: $\alpha = 0$, which leads to species richness; $\alpha = 1$, which corresponds to Shannon entropy; and $\alpha = 2$, which corresponds to the Gini–Simpson index. If $\alpha > 0$, diversity can be split into two components: species richness and evenness of the species abundance values (Pielou 1977). Evenness was measured by the ratio of diversity and richness:

$$E_\alpha = \frac{D_\alpha}{D_0}$$

In this paper, we use the term diversity in general statements that are valid for any component of diversity. When referring to diversity values at $\alpha = 1$ or $\alpha = 2$, we use term ‘diversity value’. Plant diversity was calculated from visually estimated cover data, while fungal diversity was calculated from abundance (number of sporocarps) data.

Large differences in total macrofungi abundance (which ranged from 119 to 8,961 for all species; from 47 to 1,131 for terricolous macrofungi; and from 24 to 8,460 for lignicolous macrofungi) might distort differences in diversity, resulting in high diversity in sample plots with high abundance (Gotelli and Colwell 2001). To eliminate this artifact, macrofungi richness, diversity and evenness values were calculated in 50 random subsamples and the averages were used in subsequent analyses. Random subsamples were generated by random selection of fruitbodies without replacement. The subsample size was set to slightly lower than the lowest abundance: 100 individuals for the whole macrofungi assemblage, 40 for terricolous macrofungi, and 20 for lignicolous macrofungi.

Statistical analysis

Species composition of plant and fungal communities was compared using the Mantel test based on Sorensen (binary data) and Bray-Curtis (abundance data) dissimilarities (Legendre and Legendre 1998) using 9,999 randomizations. Diversity values calculated with different scale parameters (Hill 1973), and components of diversity (Stirling and Wilsey 2001) may be strongly correlated. Correlation among independent variables results in inaccurate estimation of regression coefficients, while correlation among dependent variables may lead to over-interpretation of the results. To avoid these problems, correlations (see Appendix) were calculated within variable sets (plants, macrofungi, terricolous macrofungi, lignicolous macrofungi), and uncorrelated variables (Table 2) were selected for the analyses. The relationships between independent and dependent variables were studied by generalized linear models (Crawley 2007), which reveal non-monotonic (e.g. hump-backed) relationships. In each model, one dependent variable, and linear and quadratic terms of independent variables within one variable set, were entered. In the case of diversity, evenness and richness values, Gaussian distribution (according to the central limit theorem, the distribution of averages is approximately Gaussian) and identity link function were used; in the case of abundance data, quasi-Poisson distribution and log link function were used. The quasi-Poisson distribution allows over-dispersion (higher variance than mean), thus it is suitable if the spatial distribution of the individuals

is aggregated. The effect of independent variables was tested by Type II F test (Fox 2009). All analyses were carried out in R version 2.9.2 (R Development Core Team 2009) using the vegan package (Oksanen et al. 2009) for rarefaction and calculating diversity and evenness values, and the car package (Fox 2009) for F tests.

Results

In all, 276 vascular plants and 266 macrofungi species were recorded in the 19 sample plots; 50 species of the vascular plants were trees or shrubs. According to the Mantel tests, there was congruence between the composition of plant and fungal communities; however, the correlations were higher if dissimilarities were calculated from binary data. Composition of terricolous fungal communities was related more strongly to plant communities than to lignicolous fungal communities (Table 3).

Species richness of macrofungi assemblages proved to be independent of the diversity and degradation of vascular plant communities (Tables 4, 5). An exception was the quadratic relationship between evenness of plant communities and richness of lignicolous macrofungi (Table 4). However, even this relationship becomes nonsignificant after removing the plot with highest plant evenness from the analysis (Table 4). Improved fit of residuals to the normal distribution supports exclusion of this outlier point.

The total abundance of macrofungi seems to equal the quadratic function of evenness of plant communities (Table 4; Fig. 2). However, after excluding the plot with highest macrofungi abundance, which proved to be an outlier, the pattern changed: macrofungi abundance is negatively related to plant richness and is independent of plant evenness (Table 4; Fig. 3). There is a hump-backed relationship between the abundance of terricolous macrofungi and the degradation level estimated by the occurring vascular plants (Table 5; Fig. 4), but degradation does neither influence abundance of lignicolous macrofungi nor species richness in any macrofungi group.

Discussion

Composition of fungal and plant communities Similar to previous studies (e.g. Nantel and Neumann 1992; Packham et al. 2002; Chiarucci et al. 2005; Saetersdal et al. 2003; Brown et al. 2006; McMullan-Fisher et al. 2010), we found that there is congruence between plant and fungal communities. This relationship is stronger for terricolous than for lignicolous fungal communities because, due to forest management, dead wood is almost absent from the studied plots except in the beech forest, which was richest in dead wood from both a qualitative and quantitative point of view.

Macrofungi diversity versus vegetation Our results suggest that diversity of vascular plants (including richness and evenness) cannot be used as a proxy for macrofungi diversity; neither can diversity values or their components, i.e. species richness and evenness. These results coincide with those of Chiarucci et al. (2005) and Santi et al. (2010), while others (e.g. Schmit et al. 2005; Gabel and Gabel 2007; McMullan-Fisher 2008) have found significant positive correlations.

In some previous studies, the lack of positive correlation may be attributed to methodological shortcomings: e.g. the sampling of Santi et al. (2010) covered only 1 year, which is not sufficient for macrofungi examinations. However, that is not the case in Chiarucci et al. (2005) and our study. In both these latter studies, small-sized habitats were sampled within a relatively small area. There are different possible explanations for the positive correlation between diversity of different groups of organisms. To understand the lack of correlation in our case, we should explore why these possible mechanisms did not act. It could be that the expected diversity of both plants and macrofungi is influenced by habitat microheterogeneity, causing a positive correlation between these diversities. In European temperate forests, the species pool of woody species is small, thus the richness of vascular plants is determined mainly by the richness of the herb layer. Plant species richness was highest in the oak wood-pasture plots with the lowest canopy cover and a high variation of light availability, while it was lowest in Norway spruce plantations with evenly low light availability. This suggests that plant species richness (especially the richness of the herb layer) was influenced by

the amount of, and variation in, light availability, which has a lower influence on heterotrophic macrofungi.

Another chain of events that could create a positive correlation between plant and macrofungi diversity is the following: higher plant diversity generates higher diversity of substrate for macrofungi, which generates higher macrofungi diversity. This is probably why the diversity of tree species is a promising surrogate for macrofungal diversity at the global scale (Schmit et al. 2005). The lack of positive correlation in our data is not evidence against this mechanism. Thus, it is possible that this mechanism operates in the Cserehát forests but its effect is overwhelmed by other factors. Due to the pauperisation of European flora during the Ice Age, even the most diverse European forests are more speciespoor than temperate forests in other continents. This narrower range of tree diversity values makes it hard to find a significant relationship. Gabel and Gabel (2007) showed a significant relationship between species diversity of macrofungi and plants in an area less influenced by glaciation.

Macrofungi abundance versus vegetation Contrary to macrofungi diversity, macrofungi abundance is significantly correlated to plant diversity. Plots in Piceetum and Pinetum communities showed low plant evenness, while the abundance of macrofungi had high values. In both young plantations, the species pools of the canopy, shrub, and herb layers are small and fallen needles form a barely decayable layer of litter. The richness and productivity of terricolous saprotrophs (main litter decomposers) is known to depend on the quantity and quality of litter and is related significantly to the diversity of vascular plants (Villeneuve et al. 1989). In addition, the local abundance of a species is correlated with the size of its geographic range (Gaston 1994; Johnson 1998; Straatsma and Krisai-Greilhuber 2003). Therefore, in these fungal assemblages, a few less demanding, unspecific, higher-production species dominate. However, in the Norway spruce plots, the higher abundance values are caused mainly by the number of fruitbodies of lignicolous species. This fungal community is dominated by species living on Norway spruce deadwood (*Trichaptum fuscoviolaceum*, *Marasmius androsaceus*, *Baeospora myosura*) and widespread litter decomposers (*Rhodocollybia butyracea*, *Lepista flaccida*, *Mycena filopes*, *Mycena pura*). In macrofungal communities of artificial spruce forests examined by Kost (1992), the common litter decomposing and widespread lignicolous macrofungi can be found in abundance. The old-growth beech forests, rich in arboreal species, showed greater evenness but low abundance of macrofungi. In most unmanaged beech forest plots, besides highly productive and frequent species such as the lignicolous *Bisporella citrina*, *Trametes hirsuta*, *Micromphale foetidum*, *Schizophyllum commune*, the more rare ectomycorrhizal fungi with low abundance such as *Cortinarius alboviolaceus*, *C. terpsichores*, *Inocybe asterospora*, *I. furfurea*, *Lactarius flavidus*, *Russula fellea* and *Thelephora palmata* can be found in greater proportion, presumably because of the host trees and forest structure (Bujakiewicz 1992; Pál-Fám et al. 2007) as well as the physical and chemical properties of the humus (Nantel and Neumann 1992).

The abandoned oak wood-pasture is the richest in vascular plants, but fungal abundance is low there. There are several possible explanations for low sporocarp abundance. This habitat is characterised by alternation of old trees (in small groups or standing alone) and patches of grass, thus it has an open canopy. This results in more extremes of temperature and lower humidity (Brown et al. 2006), which decreases the number of sporocarps. Due to the warmer and drier microclimatic conditions, the litter decomposes slowly, therefore, the abundance of the terricolous species may be reduced. The abandonment of grazing may be unfavourable for many macrofungi (Arnolds 1992). The total species richness is high but the species richness of trees and shrubs is low in this vegetation type. Low numbers of ectomycorrhizal partners and small quantity of fallen deadwood may also cause low sporocarp production. The evenness of vegetation was greatest in the two Turkey oak forests. This results in a relatively high number of species and abundance of macrofungi due to the forest structure, quality of litter and edaphic conditions.

Effect of degradation

At low disturbance level (indicated by the degradation of vegetation) the number of sporocarps of terricolous macrofungi is low. The increase in degradation of vegetation is followed by increasing abundance of terricolous macrofungi up to a moderate disturbance level. In fungal communities living on soil of different vegetation types, the proportion of higher-productive species increases. However, further increase of disturbance causes a decrease in the number of sporocarps. According to the Intermediate Disturbance Hypothesis (Grime 1973; Connell 1978; Hobbs and Huenneke 1992), a moderate disturbance leads to highest diversity; diversity is decreased by too low or high a level of disturbance.

This hypothesis has been proven for vascular plants (Kim et al. 2002; Rejmánek et al. 2004) and birds (Lepczyk et al. 2008). Sobek and Zak (2003), examining the functional diversity of soil fungal communities in a Georgia forest disturbed by human activity, have shown that a medium amount of disturbance (a greater complexity of carbon substrate of sites) results in the highest soil fungal functional diversity. Surprisingly, although we did find such a relationship between disturbance and abundance, we did not find species richness of macrofungi. Obviously fructification of macrofungi speeds up in case of increased disturbance, in response to this pressure. However, beyond a certain disturbance level, the fructification is blocked then ceases. This pattern appears only in terricolous macrofungi, because the occurrence of lignicolous macrofungi depends strongly on the presence, quantity and quality of dead wood (Kost and Haas 1989; Hřiland and Bendiksen 1996; Siller 2004), which overwhelms the other factors (e.g. disturbance).

In conclusion, the vascular plant diversity cannot be used for proxy of macrofungi diversity in Pannonian forests and forest plantations. This result questions the reliability of decisions on nature conservation actions (including selection of protected areas) based on only a few groups of easy-to-observe organisms and underlines the necessity of studying as wide range of taxonomic groups as possible.

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Table 1 Characteristics of the sampled vegetation types

Vegetation type; status; location	Bedroc; soil type; soil pH(H ₂ O)	Cover of canopy layer (%); Dominant species (cover >5 %) in canopy layer (c); shrub layer (s); herb layer (h); plant species number	Age of trees (years)	Cover and quality of deadwood	Orientation; slope
Turkey oak forest, site 1 (1 plot); zonal, managed; Nyésta	Loess; brown forest soil; pH 5.20	65–75; c: <i>Quercus cerris</i> , <i>Qu. petraea</i> ; s: <i>Acer campestre</i> , <i>A. tataricum</i> , <i>Crataegus monogyna</i> , <i>C. oxyacantha</i> , <i>Ligustrum vulgare</i> ; h: <i>Campanula rapunculus</i> , <i>Fallopia convolvulus</i> , <i>Galium aparine</i> , <i>Viola hirta</i> ; 36	Two cohorts: 30 and 60	<1 %, hard, less decomposed	SE 18°
Turkey oak forest, site 2 (1 plot); zonal, managed; Nyésta	Loess; brown forest soil; pH 4.71	65–70; c: (upper): <i>Quercus cerris</i> , <i>Qu. petraea</i> , <i>Qu. robur</i> ; c (lower): <i>Qu. petraea</i> , <i>Fraxinus exelsior</i> ; s: <i>Acer campestre</i> , <i>C. oxyacantha</i> , <i>Ligustrum vulgare</i> ; h: <i>Poa angustifolia</i> ; 54	Several age groups (40, 60 and 80)	<1 %, hard, less decomposed	NW 20°
Hornbeam-oak forest (1 plot); extrazonal, managed; Nyésta	Loess; brown forest soil with clay illuviation; pH 4.85	80–90; c:(upper): <i>Quercus cerris</i> , <i>Qu. petraea</i> ; c (lower): <i>Carpinus betulus</i> ; s: <i>Acer campestre</i> ; h: <i>Ficaria verna</i> , <i>Galium aparine</i> , <i>Viola cyanea</i> ; 43	Two age groups: 30 and 60	1–5 %, uniformly decomposed	SE 8°
Oak wood-pasture (5 plots); Turkey and Hornbeam oak forests with deforestation and grazing; Irota	Loess; brown forest soil with pseudogley; pH 4.59–5.10	40–55; c: <i>Quercus cerris</i> trees standing alone or in small groups; s: <i>Crataegus monogyna</i> , <i>Prunus spinosa</i> , <i>Rosa canina</i> ; h: <i>Anthoxanthum odoratum</i> , <i>Agrostis tenuis</i> , <i>Carex praecox</i> , <i>C. pallescens</i> , <i>Festuca pratensis</i> , <i>F. rupicola</i> , <i>F. valesiaca</i> , <i>Fragaria vesca</i> , <i>F. viridis</i> , <i>Lysimachia nummularia</i> , <i>Qu. cerris</i> , <i>Trifolium alpestre</i> ; 93–115	Several hundred years	<1 %, hard, less decomposed	ESE-NE 3–6°
Beech forest (5 plots); extrazonal, unmanaged; Szendrőlád	Limestone; shallow brown rendzina with calcareous screes; pH 6.49–7.17	60–90; c: physiognomy of the stand is characterized by old trees of <i>Fagus sylvatica</i> , <i>Carpinus betulus</i> ; s: In the gaps formed by the falling of old trees: <i>Acer campestre</i> , <i>Tilia platyphyllos</i> , and: <i>Cornus mas</i> , <i>Corylus avellana</i> ; h: <i>Mercurialis perennis</i> , <i>Aegopodium podagraria</i> , <i>Asarum europaeum</i> , <i>Convallaria majalis</i> , <i>Polygonatum multiflorum</i> ; 50–84	Several age groups; 200-year-old trees	1–5 %, decomposed in different degrees	NNW-NNE 28–40°
Scotch pine plantation (1 plot); managed, formerly grazed; Abaújlak	Loess; brown forest soil with clay illuviation; pH 4.36	70–75; c: (upper and lower): <i>Pinus sylvestris</i> ; s: <i>Crataegus monogyna</i> ; h: <i>Fragaria vesca</i> ; 39	Two age groups 30–50	<1 %, hard, less decomposed	SW 7°
Norway spruce plantation; (5 plots) Búdöskútpuszta	Loess; brown forest soil with clay illuviation; pH 4.75–5.50	92–98; c: (upper and lower): <i>Picea abies</i> ; s: absent, in most of the plots; h: sparse, h: <i>Anthriscus sylvestris</i> ; 13–37	40	>5 %, decomposed in different degrees	WSW-NE 14–30°

Table 2 Uncorrelated variables selected for the analysis

Role of variables	Variable set	Selected variables
Independent variables	Diversity of vascular plants	Species richness (S) Evenness with $\alpha = 2$ (E)
	Degradation level of the vegetation	Degradation % (D)
Dependent variables	Fungal diversity	Species richness
	Diversity of terricolous macrofungi	Species richness
	Diversity of lignicolous macrofungi	Species richness
	Macrofungi abundance	Evenness with $\alpha = 2$ Total abundance Abundance of terricolous macrofungi Abundance of lignicolous macrofungi

Table 3 Relationship between plant and macrofungal communities tested by Mantel-test

Macrofungal communities	Sorensen dissimilarity (binary data)		Bray–Curtis dissimilarity (abundance data)	
	Correlation (r)	P value	Correlation (r)	P value
All macrofungi	0.6097	0.0001	0.3081	0.0012
Lignicolous macrofungi	0.3736	0.0001	0.1706	0.0239
Terricolous macrofungi	0.5589	0.0001	0.3346	0.0012

*P values were calculated based on 9,999 randomizations

Table 4 Effect of species richness (S) and evenness (E) of plant communities on the richness and abundance of macrofungi

Macrofungi	Dependent variable	Dataset ^a	P value				R ²
			S	E	S ²	E ²	
All	Richness (D ₀) Abundance	Complete	0.874	0.113	0.889	0.311	0.190
		Complete	0.057	0.003*	0.890	0.038*	0.663
		Excluding the highest abundance	<0.001*	0.621	0.787	0.797	0.631
Terricolous	Richness (D ₀) Abundance	Complete	0.260	0.868	0.051	0.873	0.261
		Complete	0.033*	0.918	0.413	0.653	0.323
Lignicolous	Richness (D ₀)	Complete	0.616	0.059	0.251	0.048*	0.358
		Excluding the highest plant evenness	0.711	0.618	0.792	0.075	0.424
	Evenness (E ₂) Abundance	Complete	0.590	0.678	0.999	0.821	0.070
		Complete	0.141	0.001*	0.632	0.061	0.661
		Excluding the highest abundance	0.007*	0.690	0.616	0.829	0.496

* Significant at P < 0.05

^a Some cases analyses were repeated by excluding one outlier point where indicated

Table 5 Effect of the degradation level of plant communities (D) on the richness, evenness and abundance of macrofungi

Macrofungi	Dependent variable	P value		R ²
		D	D ²	
All	Richness	0.817	0.797	0.008
	Abundance	0.961	0.052	0.277
Terricolous	Richness	0.085	0.211	0.240
	Abundance	0.187	0.002*	0.464
Lignicolous	Richness	0.214	0.823	0.098
	Evenness	0.056	0.792	0.212
	Abundance	0.703	0.173	0.178

*Significant at P < 0.05

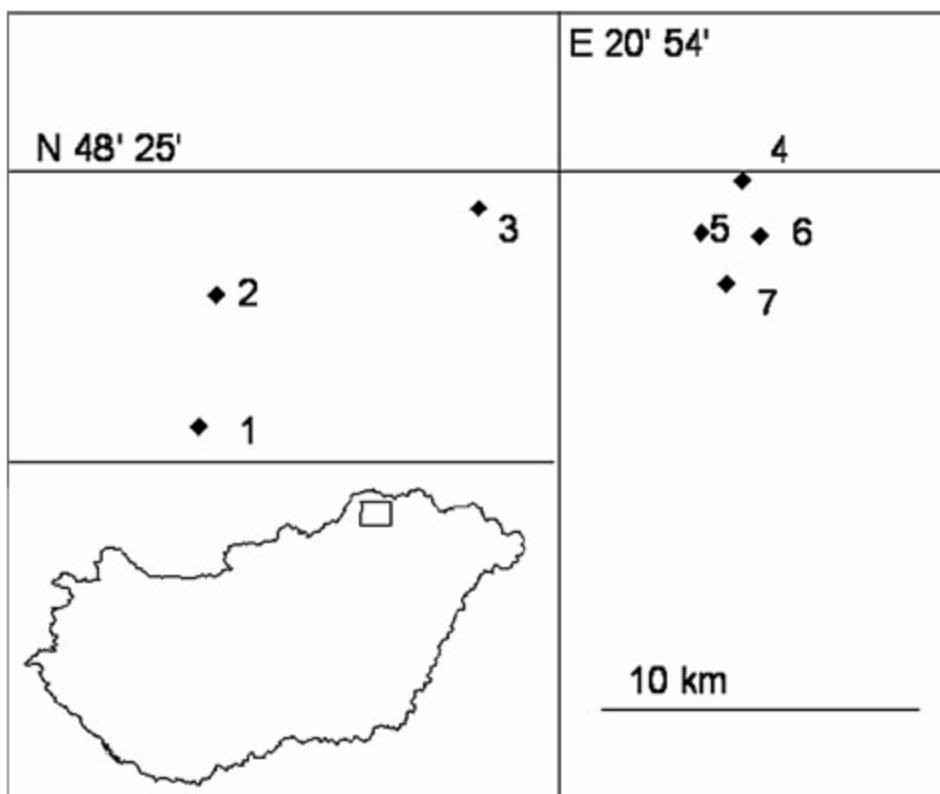


Fig. 1 Location of the study area and the investigated sites. 1 beech forest, 2 Norway spruce plantation, 3 oak wood-pasture, 4 Scotch pine plantation, 5 Turkey oak forest 1, 6 hornbeam-oak forest, 7 Turkey oak forest 2

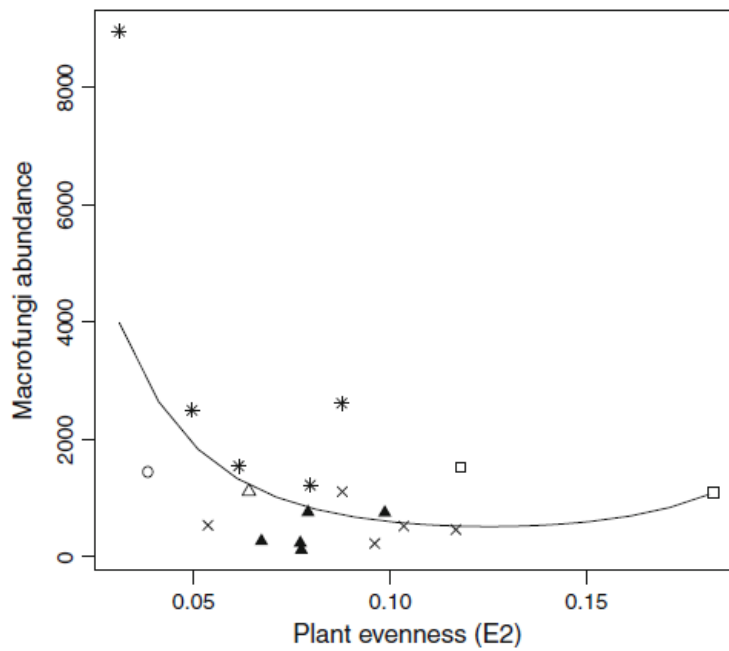


Fig. 2 Relationship between evenness of plant communities and total abundance of macrofungi. Different forest types: open squares Turkey oak forest, open circle Scotch pine plantation, open triangle hornbeam-oak forest, crosses beech forest, asterisks Norway spruce plantation, filled triangles oak wood-pasture

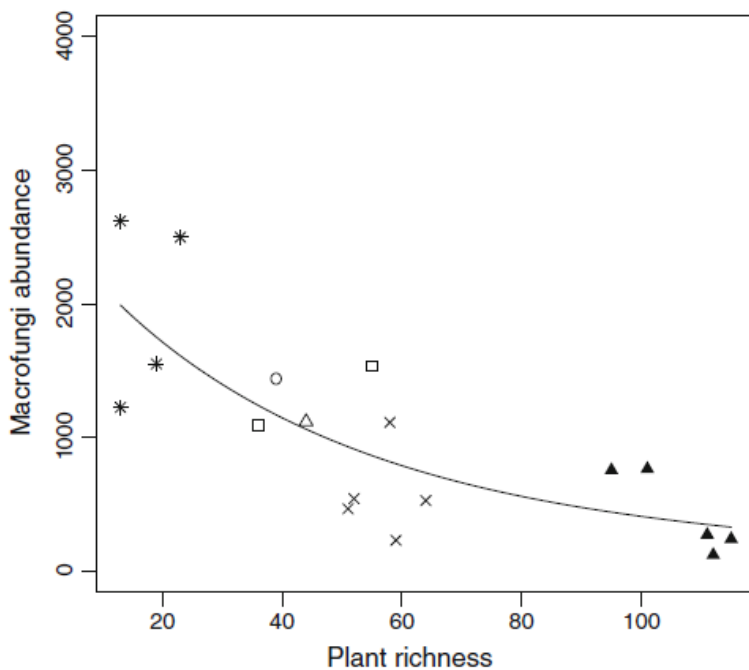


Fig. 3 Relationship between species richness of plant communities and total abundance of macrofungi. Different forest types: open squares Turkey oak forest, open circle Scotch pine plantation, open triangle hornbeam-oak forest, crosses beech forest, asterisks Norway spruce plantation, filled triangles oak wood-pasture

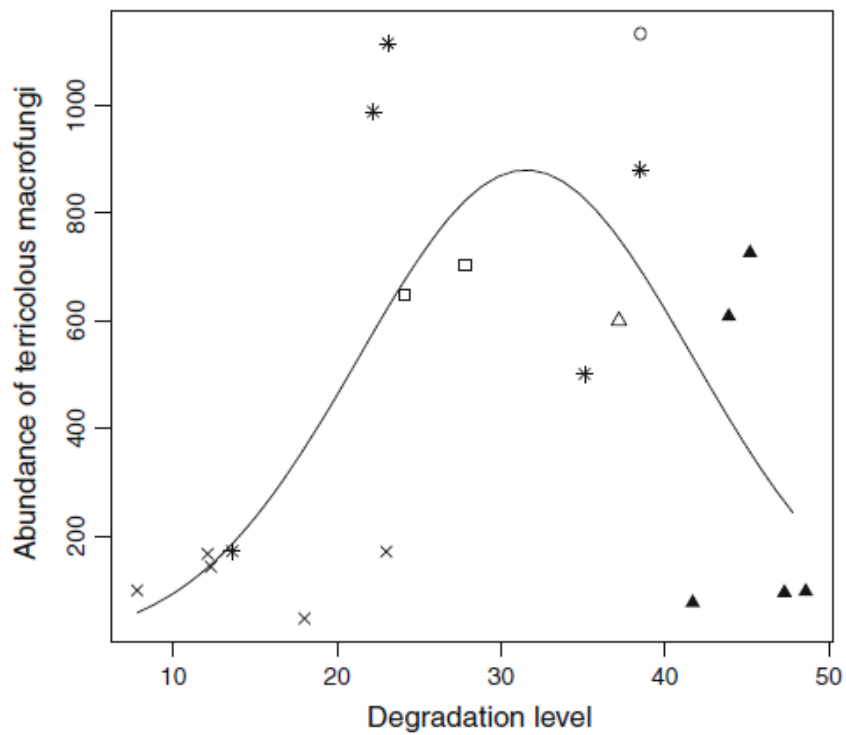


Fig. 4 Relationship between degradation level % and abundance of terricolous macrofungi. Different forest types: open squares Turkey oak forest, open circle Scotch pine plantation, open triangle hornbeam-oak forest, crosses beech forest, asterisks Norway spruce plantation, filled triangles oak wood-pasture

Appendix

See Table 6.

Table 6 Correlations within variable sets

	D0	D1	D2	E1
Diversity of vascular plants				
D1	0.94636			
D2	0.876632	0.968753		
E1	0.437517*	0.682372	0.776212	
E2	0.03731*	0.327585*	0.492462	0.882539
Macrofungal diversity				
D1	0.923743			
D2	0.811818	0.967714		
E1	0.770027	0.938857	0.9607	
E2	0.615768	0.859948	0.948178	0.96111
Diversity of terricolous macrofungi				
D1	0.971748			
D2	0.935317	0.9915		
E1	0.784483	0.89295	0.918737	
E2	0.705208	0.845691	0.893239	0.983578
Diversity of lignicolous macrofungi				
D1	0.954523			
D2	0.906786	0.990238		
E1	0.312672*	0.571762	0.657776	
E2	0.095193*	0.380168*	0.487839	0.967258

See formulas in the main text. D0, D1, D2 Hill's diversity with scale parameter 0, 1 and 2, respectively, E1, E2 evenness calculated from D1 and D2

*Non-significant correlations ($\alpha = 5\%$)