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DEAD WOOD, FOREST FRAGMENTATION AND ELEVATION INFLUENCES MACROFUNGAL DIVERSITY ON DOWNED COARSE WOODY DEBRIS IN BEECH AND OAK OLD FOREST ECOSYSTEMS FROM NORTHEASTERN ROMANIA

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Abstract: Coarse woody debris is often highlighted as the most important microhabitat for numerous saproxylic species, including macrofungi. Providing valuable nutrients, stable microclimatic conditions and development space, logs and large branches are considered of great ecological value for macrofungal diversity conservation. Old forests are especially rich in downed coarse dead wood both at quantity and quality level. Unfortunately, these forests are also affected by human interventions, through wood extraction and forest fragmentation. The main objective of this study was to find the factors that best explain the macrofungal diversity on downed coarse woody debris (DCWD). For this, we sampled 21 plots in forests dominated by beech or oak from Northeastern Romania, where we collected data about fungi, forest structure, and dead wood. We completed the variables set with forest fragmentation and topographic indices. In order to find the best models and predictors, we used generalized linear models (GLM). We found 163 taxa, polypores and agarics being the most frequent. The two most important predictors had a positive effect, increasing macrofungal diversity: 2'nd and 3'rd decay stages DCWD volume and elevation while the third one had a hump-shape effect on diversity. In old forests, downed dead wood quality and quantity is a vital component for numerous species of fungi to survive and develop. Elevation is a known proxy of macroclimatic conditions, furthermore creating new rich-resources niches because increasing humidity and taxonomic diversification by conifers occurrence. Patch shape can have divergent effects on fungi, as increasing perimeter is associated from one point on, with human deforestation and accessibility. Overall, we believe that Northeastern Romania's old forests hosts a great lignicolous macrofungal richness, which will be protected through silvicultural practices such as keeping valuable dead wood on site.

Keywords: broadleaved dominated forest, forest structure, lignicolous fungal richness, logs and large branches, shape index, topography.

Introduction

Coarse woody debris (CWD) is one of the most important types of microhabitats found in forest ecosystems [HEILMANN-CLAUSEN & CHRISTENSEN, 2003]. Numerous groups of organisms depend on food and/or shelter provided by this type of wood, including lichens, bryophytes, insects and fungi [ABREGO & SALCEDO, 2011; GOIA & GAFTA, 2018; HEILMANN-CLAUSEN & CHRISTENSEN, 2003].

The most important forest types characterized by high dead wood volume and high-decay wood volume are the old forests [MORRISSEY & al. 2014]. Numerous studies carried out in these forests across the Northern hemisphere highlighted the importance of those habitats for lignicolous fungal high diversity conservation [RUOKOLAINEN & al. 2018;

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RUNNEL & LÕHMUS, 2017; SAAR & al. 2007]. Furthermore, this importance was sustained by studies comparing natural/old-growth forests with managed ones, silvicultural practices usually changing lignicolous fungal composition and reducing diversity [ABREGO & al. 2014; JUUTILAINEN & al. 2014; KEBLI & al. 2012]. Unfortunately, old forests take a long time to develop, period during which human intervention should be restricted and driven by special conservative measures focused on retaining large dead wood (including both DCWD and dead trees) and large living trees [SIITONEN & al. 2000].

Dead wood characteristics were studied in lignicolous fungal diversity or composition-related researches in forest habitats, either at plot-level: volume, dead wood species diversity [RUNNEL & LÕHMUS, 2017] or substrate-level: species, diameter, decay class, bark cover, moss cover, age, complexity, microclimatic conditions [HEILMANN-CLAUSEN, 2001; HEILMANN-CLAUSEN & CHRISTENSEN, 2003; HEILMANN-CLAUSEN & al. 2005; HEILMANN-CLAUSEN & al. 2014; ABREGO & al. 2017; RUOKOLAINEN & al. 2018]. Different forest characteristics have been studied in relation to fungal diversity and composition of lignicolous fungi in Europe: tree richness, relative volume of dominant, codominant or non-dominant trees [KUTSEGI & al. 2015]; or structure: tree density, large tree density, tree basal area, mean tree DBH, tree DBH coefficient of variation, snags volume, cover of understorey vegetation [KUTSEGI & al. 2015]. Also, forest fragmentation was included in lignicolous fungal-related studies, using characteristics such as forest area, broadleaved or coniferous forest area [RUNNEL & LÕHMUS, 2017], forest connectivity at different spatial scales, reserve size [ABREGO & al. 2015].

This study tries to respond to the following questions: i) does forest structure influence lignicolous fungal diversity? ii) is the forest fragmentation important in beech/oak old forests from Northeastern Romania for wood-inhabiting fungi? iii) does dead wood high quality and quantity increases the number of lignicolous fungal species?

Material and methods

Study area

The study was conducted in beech- and oak-dominated forests from Northeastern Romania (Figure 1). These forests are situated in the Moldavian Plateau, Sub-Carpathians Hills and the Eastern part of Eastern Carpathians. The main soils are cambisoils and luvisoils. The climate is temperate continental, with an increasing continentality towards the eastern-most located studied forests. The studied forests are dominated either by *Fagus sylvatica* L. (European beech) or species of *Quercus* (oak), ones of the most important tree genera in Europe [PETRITAN & al. 2012] and Romania [MILESCU & al. 1967]. Region's forests are prone to deforestation and illegal logging [ANDRONACHE & al. 2017]. Also, even if there measures for old-growth forests protection were taken, logging, invasive species, and climate change are still important threats [KNORN & al. 2012].

Datasets

In beech and oak forests we chose circular plots of 1,000 m for forest and dead wood data inventory. The plots were chosen using the 50% threshold in terms of tree basal area of beech/oak from the total basal area. Each plot had at least one big branch or log (diameter at larger end > 10 cm). Within each plot, all living and dead trees with a diameter at breast height (DBH) > 10 cm were measured for diameter. Old or large-sized trees were considered those trees with DBH > 50 cm [LOMBARDI & al. 2012]. For old-forests delineation, we chose only plots in which old trees basal area proportion was at least 50% of the total tree basal area.

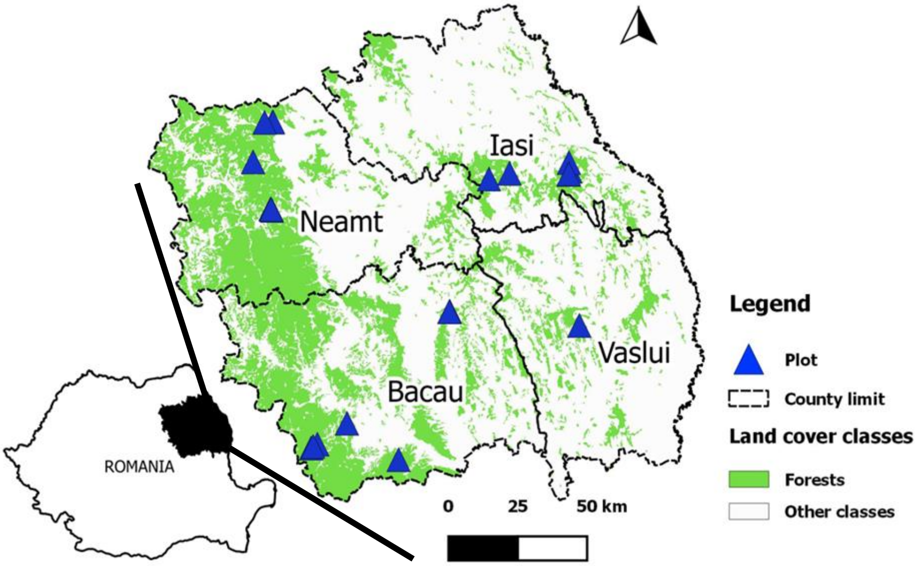

Figure 1. Plots location in Northeastern Romania

In each plot, we measured all logs and large branches with the diameter at large end > 10 cm, the diameter of both ends, length and decay stage using 3 classes. The decay classes are an adaptation of the classification proposed by HEILMANN-CLAUSEN & CHRISTENSEN (2003): (i) incipient stage – intact bark, twigs presence, hard texture, original color of wood, the knife penetrates less than 1 cm into the wood; (ii) intermediary stage – absent bark, absent twigs, hard and soft texture, changed wood color, the knife penetrates up to 6 cm into the wood; (iii) advanced stage: absent bark, absent twigs, completely change wood color, wood crashes in hand when humid, the knife penetrates fully into the wood.

For each plot, forest structure-specific variables were assessed (Table 1): tree richness, tree density, young tree density, tree basal area, tree diameter coefficient of variation, snags basal area, snags density, beech basal area proportion, and oak basal area proportion.

Dead wood characteristics were also calculated (Table 1): DCWD volume, DCWD taxonomic diversity, DCWD decay diversity, DCWD volume in middle and late decay stages. DCWD volume was calculated using frustum of cone formula. DCWD decay and taxonomic diversity were calculated following RUNNEL & LÕHMUS (2017).

Forest fragmentation was based on Corine Land Cover 2018 raster with 100 m resolution (https://land.copernicus.eu). The classes were reclassified such that CLC forest classes were grouped in 'forest class' and the others in 'other classes'. In circular areas of 2,000 m radius having in the center the forest plot, we calculated indices at class level: patch area mean index and edge density index, or at patch level: shape index.

Main topographic variables were obtained for each plot: slope, positive openness, aspect index, and elevation. The derived topographic indices were calculated based on SRTM at 30 m resolution, downloaded from the official database of United States Geological Survey's EarthExplorer [www.earthexplorer.usgs.gov].

Table 1. Variables considered in the analysis

Abbreviation	Name	Range	Mean	Units	GLM
Forest structure					
TREE_RICH	tree richness	1 – 7	4	None	1
TREE_N	tree density	160 - 410	285	trees ha^{-1}	0
TREE_U50_N	young tree density	50 – 320	190	trees ha^{-1}	1
TREE_DBH_CV	tree diameter coefficient of variation	0.4 – 1.9	0.9	None	1
TREE_BA	tree basal area	22.7 – 68.2	50.5	m^2	1
TREE_BA_MN	mean tree basal area	0.1 – 0.3	0.2	m^2	0
SNAG_BA	snags basal area	0 – 14.2	0.6	m^2 ha^{-1}	1
SNAG_N	snag density	0 – 60	10	snags ha^{-1}	1
BEECH	beech trees basal area proportion	0 – 100	51.7	%	0
OAK	oak trees basal area proportion	0 – 82.1	7.2	%	0
Downed dead wood					
DCWD_DIV	DCWD taxonomic diversity	0 – 0.9	0.2	None	1
DCWD_DECAY	DCWD decay diversity	0 – 0.9	0.6	None	1
DCWD_VOL	DCWD volume	0.1 – 148.8	2.8	m^3	1
DCWD_VOL23	DCWD volume in 2'nd and 3'rd decay stages	0 – 68.1	1.1	m^3	1
Forest fragmentation					
AREA_MN	mean of patch area index	54.6 – 1600.0	388.7	ha	1
SHAPE	shape index	5.9 – 33.4	15.6	None	1
ED	edge density index	0 – 23.3	13.5	m ha^{-1}	0
Topography					
ALT	elevation	186 – 706	450	m	1
SLOPE	slope	0.7 – 30.4	7.7	°	0
ASPI	aspect index	6.7 – 156.0	56.3	°	1
PO	positive openness index	1.2 – 1.5	1.4	None	1

In a concentric plot of 2,000 m^2, each macrofungal species found on downed coarse woody debris was identified at species or genera level. Those which couldn't be determined *in situ* were identified in the laboratory using mycological literature [BERNICCHIA, 2005; BREITENBACH & KRÄNZLIN, 1986; COURTECUISSE & DUHEM, 2013; GERHARDT, 1999; RYVARDEN, 1991; SĂLĂGEANU & SĂLĂGEANU, 1985; TĂNASE & al. 2009]. Index Fungorum [http://www.indexfungorum.org/Names/Names.asp] was used for fungal nomenclature.

Data and analysis

We used R software version 3.5.1 (R Core Team 2012) in data exploration and statistical analysis. The R packages used were: landscapemetrics, MuMIn, MASS, reshape, rsq. Packages ggplot2 and RColorBrewer were used for graphical representation of relationships. For topographical and CLC processing, we used QGIS [QGIS Development Team (2018). QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org] and SAGA GIS software [CONRAD & al. 2015].

We tested the 20 variables for collinearity with Pearson correlation and removed the variables from collinear pairs so that only one remained using the correlation coefficient threshold of 0.7. Using 15 non-correlated variables, we made GLM (Generalised Linear Models) with Poisson probability distribution and tested them for overdispersion. The resulted models were selected based on AIKc (Akaike Information Criterion corrected) value, using the method proposed by BURHNHAM & ANDERSON (2002). These models were used to select the most important variables that explained the lignicolous macrofungal diversity.

Results and discussions

Taxonomic diversity

We found 163 species in approximately 500 records, on 249 logs and large branches. The diversity was higher than other studies made in similar habitats – 44 [BÎRSAN & al. 2014], 72 [ŽUPANIC & al. 2009]. In a study made in beech forests in the same region, the authors [COPOȚ & al. 2018] found 110 species, but they only gathered data from fine woody debris (FWD), with diameter less than 10 cm. In similar studies, like those from Danish deciduous forests, the authors [HEILMANN-CLAUSEN, 2001; HEILMANN-CLAUSEN & CHRISTENSEN, 2003] found a higher number of species on beech logs. Still, the logs had more than 70 cm in diameter and consequently, the higher richness could be explained, besides other factors, by the log diameter, as it is known that diameter and associated-big log characteristics (e.g. better microclimate for mycelial development) is highly associated with lignicolous fungal diversity [HEILMANN-CLAUSEN & CHRISTENSEN, 2003].

The species belong to 113 genera, of which *Mycena* and *Pluteus* were the richest. The majority of the species (159) belongs to 58 families (4 species were included in *Incertae Sedis*), from which the most important in diversity were: Polyporaceae and Mycenaceae, each of them with 15 taxa. 162 species belong to 22 orders and one to *Incertae Sedis*, from which Agaricales (36.2% of total), Polyporales (19.0%), Xylariales (8.5%) and Hymenochaetales (7.3%) where the richest. Basidiomycota phylum comprises 79.1% of total diversity, while Ascomycota, 20.9%.

Half of the species (88) were identified in a single plot and another 24 in two plots. The most frequent found taxa in terms of plots presences were: (a) saproparasites: *Fomes fomentarius*, *Fomitopsis pinicola*; (b) saprotrophes of first decay stages: *Jackrogersella* *cohaerens*, *Schizophyllum commune*, *Stereum hirsutum*, *Trametes versicolor*; or (c) middle and late decay stages: *Chlorociboria* sp., *Mollisia* sp., *Orbilia* sp., *Scutellinia scutellata*, *Pluteus cervinus*. Those species were also frequently found growing on logs, especially beech [ABREGO & SALCEDO, 2011; HEILMANN-CLAUSEN, 2001], but can also grow on other tree genera [BREITENBACH & KRÄNZLIN, 1986; TĂNASE & al. 2009]. Among the most frequently found species on fresh dead wood, *F. fomentarius* is a common sight on stem/large branches, of living, dying or fallen trees [BAUM & al. 2003], as it is one of the main decay fungi of beech [SCHWARZE, 1994].

Models that explain macrofungal diversity on DCWD

Following model selection, we obtained two models that best explain the macrofungal diversity on downed coarse woody debris in beech or oak-dominated forests (Table 2).

Table 2. Best explaining models of macrofungal diversity found on downed coarse woody debris in beech or oak-dominated forests

Intercept	ALT	DCWD_VOL	DCWD_VOL23	SHAPE	R^2	R^2 adj.	AICc	delta	weight
1.784	0.003	-	0.015	-0.031	0.99	0.99	140.04	0	0.67
1.775	0.003	0.003	0.012	-0.036	0.99	0.99	141.48	1.44	0.33

The variables found important were: SHAPE (Shape Index), DCWD_VOL_D23 (DCWD volume in 2'nd and 3'rd decay stages) and ALT (elevation), (Table 3). Together, they explained 76% of the fungal richness variation.

Table 3. Linear models highlighting effect of the most important variables on macrofungal richness

Variable	Estimate	Standard Error	Explains (%)	p-value (< 0.05)	Sign	Importance
Elevation	0.032	0.014	17	< 0.05	↑	0.90
2'nd and 3'rd decay DCWD volume	0.484	0.121	42	< 0.001	↑	0.63
Shape Index	5.713 -0.137	1.227 0.028	50	< 0.0005 < 0.0005	∩	0.62

Predictors that influence macrofungal diversity on DCWD

Elevation

In this study, as the elevation is increasing, the macrofungal richness is higher (Figure 2.A). The elevation is considered as a proxy for macroclimatic conditions, especially mean annual precipitations and mean annual temperatures [VAN GILS & al. 2012]. As a consequence, it is possible that the high richness associated with higher altitudes is in fact an effect of precipitations and temperature regimes. Indeed, the plots associated with higher diversity are found in mountainous forests, at elevations above 600 m. Because of the mountain encampment, higher precipitations and lower temperatures create more humid conditions in the forests, which enhance and keep for long periods of time, the deadwood humidity. This can be a decisive factor, especially in carpophore-based studies, when fungi produce a large amount of carpophores during rich-pluvial seasons [BRAZEE & al. 2014; RUDOLPH & al. 2018]. Linked to the next found predictor is the fact that in temperate forests, the regions with colder summers (like mountains) are associated with higher dead wood quantities [WOODALL & LIKNES, 2008]. Thus, the higher elevation plots can host a higher lignicolous macrofungal richness due to higher dead wood volumes.

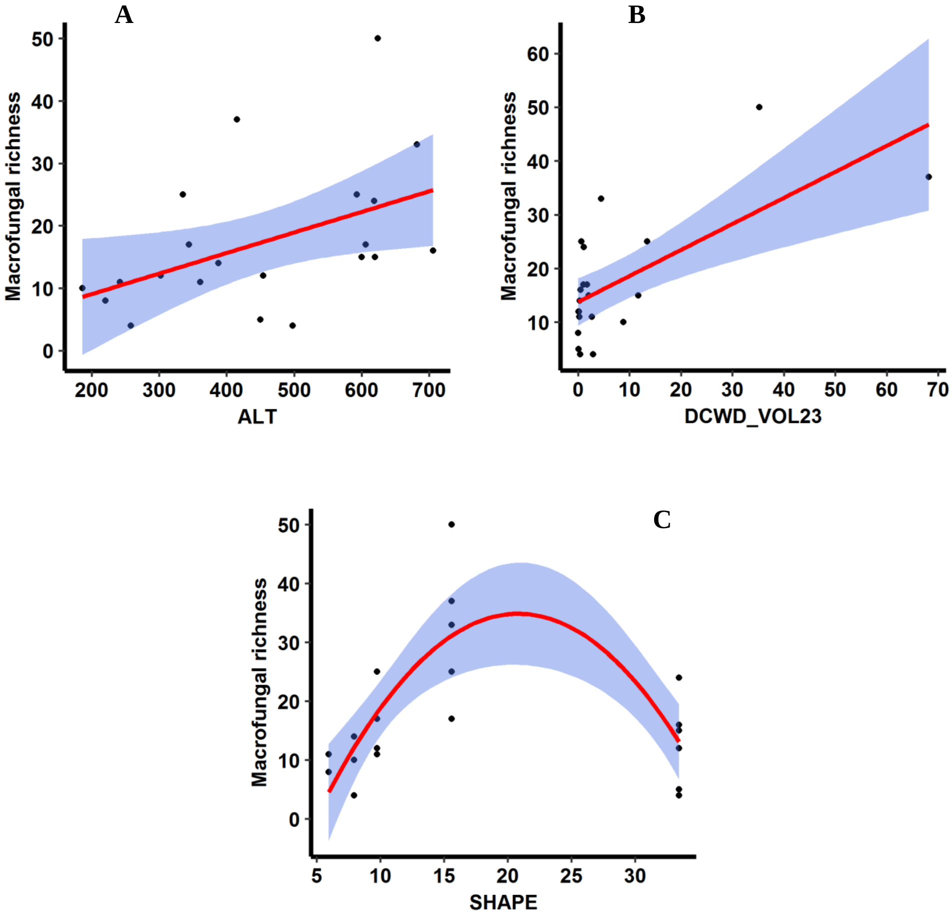

Figure 2. Relationship between macrofungal diversity and the most important variables: A. elevation (m); B. 2'nd and 3'rd decay stage of downed coarse woody debris (m^3); C. Shape Index

Another effect of elevation on forest plots composition differentiation is the occurrence of conifers in Romanian forests. Thus, at higher altitudes, the presence of coniferous dead wood creates important ecological niches which do not exist in forests dominated by pedunculate oaks (*Quercus robur*), like in Moldavian Plateau. Those niches are colonized both by some broadleaved-associated fungi and especially by coniferous-specific fungi, thus increasing total diversity on DCWD.

Middle and late stage decayed DCWD volume

In our study, the DCWD volume in the middle and last decay stages was positively and significantly influencing the macrofungal diversity (Figure 2.B). This variable was calculated taking into account two assumptions: (i) one of the main old-growth forests characteristics is the presence of dead wood in large volumes [BRUNET & al. 2010; DVOŘÁK & al. 2017]; the main reason behind this is represented by the protective status of those forests, as silvicultural measures tend to keep dead trees on-site [ÇOLAK & al. 2010] – the source of downed dead wood [DOMKE & al. 2013]; thus, the presence of large quantities of middle and late decayed wood is a measure of continuous forest protection; pro-conservative forest management proved to positively influence lignicolous fungal diversity in old-growth hardwood forests [BRAZEE & al. 2014]; (ii) middle and last decay stage of wood hosts a diverse variety of macrofungi, many of them decay-stage specialists [HEILMANN-CLAUSEN & CHRISTENSEN, 2003; HEILMANN-CLAUSEN & al. 2014].

Here, this volume alone explains approximately 40% of total macrofungal richness. The species-richest plots are found in Nemira mountains (Eastern Carpathians, Bacău county), in a beech-silver fir forest. This habitat is rich in downed deadwood of both beech and coniferous trees, thus completing the previous predictor explanation.

Shape Index

In our study, the macrofungal richness follows a hump-shaped relationship with the Shape Index (Table 2). Initially, as the index is increasing, so is the diversity, until it approaches a mid-value of approximately 20, after which the diversity is decreasing as the index is increasing (Figure 2.C). It is the variable that explains the most of macrofungal diversity, counting approximately 50% of the total variation.

According to authors [HESSELBARTH & al. 2019], the Shape Index is calculated as the ratio of patch perimeter and the minimum perimeter. Consequently, it takes values from 1 beyond, rising as the patch shape becomes more complex. Through reducing patch complexity, there are created rectangular patches, characterized by regularity and straight borders [MOSER & al. 2002].

In order for the macrofungal diversity-shape index complex relationship to be understood, patch shape values variation causes must be known. There are three main groups of factors that influence patch complexity: (i) historical human intervention; (ii) topography; (iii) forest composition [DORNER & al. 2002; SAURA & CARBALLAL, 2004]. Shape Index can be used as a direct measure of human interventions, complexity usually decreasing as human activity increased [SAURA & CARBALLAL, 2004]. On the other side, topographical factors (slope, aspect, terrain rugosity) where found to increase forest patch shape irregularity in Galicia (Spain) [SAURA & CARBALLAL, 2004]. Also, mountainous forest habitats are characterized by increasing elevation and steep slopes, which hinder human accessibility [SAURA & CARBALLAL, 2004], which in turn translates through less extracted dead wood and consequently more available wood resources to macrofungi. Thus, increasing shape complexity results in macrofungal diversity increasing, in the up-section of hump-shaped relationship (Figure 2). Irregular shapes and consequently higher Shape Index values can also result from increasing tree diversity [SAURA & CARBALLAL, 2004]. In our case, the oak-dominated forests from mountainous areas in Neamț County are characterized by higher tree diversity, even if they have high shape index values. In those plots, the macrofungal diversity is lower than in less-rich beech-fir forests from Nemira Mountains. This can explain the second down-section of hump-shaped relationship (Figure 2). Still, this phenomenon might raise a question because high tree diversity is often associated with increasing niche variation, because of macrofungal association with particular genera, thus rising fungal diversity [BÎRSAN & al. 2014]. But forest stands with a higher number of species is less vulnerable to climatic hazards [JACTEL & al. 2017], represented in the Carpathians by strong winter winds and long snow periods [ANM, 2008]. Therefore, there are more chances for climatic hazards to manifest in mountain beech-dominated stands, represented here in the middle of the hump-shaped relationship. This will increase downed dead wood volume in beech-dominated stands, but less in oak-dominated ones, a situation which confirms in our study.

Conclusions

This is the first study in which diferent types of predictors explain the macrofungal richness found on dead wood in Northeastern Romania. Dead wood quality, elevation and forest fragmentation proved to be key factors in explaining the differences between the total number of fungi in broadleaved-dominated forests. It is the first study that shows the importance of patch shape to macrofungal diversity conservation. Also, dead wood-associated silvicultural practices proved to be of high importance in macrofungal preservation success. As a consequence, it is important to properly manage old forests, keeping high quality downed dead wood, especially in regular forest patches.

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