

**LIGNICOLOUS FUNGI ECOLOGY – BIOTIC AND ABIOTIC
INTERACTIONS IN FOREST ECOSYSTEMS**

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Lignicolous macromycetes are of great importance for the functionality of forest ecosystems. These fungi work as the main carbon reintegrating agents in the soil or as keepers of forest vitality. Under the biotic and abiotic changes, fungi species reacts differently, the main effects being seen at the level of numbers and composition structure of fungal communities. In the context of human actions on forest ecosystems, numerous studies show the detrimental effects on lignicolous mycodiversity, at both European and local levels. In order to protect mycodiversity, it is vital to understand the way the relation between fungi and forest works.

Keywords: lignicolous macromycetes, abiotic and biotic factors, forest ecosystems

1. INTRODUCTION

Besides bacteria, fungi are the most abundant terrestrial organisms on Terra [Miller & Lodge, 1997]. Even if global fungal diversity registers about 108.000 known fungi [Dai *et al.*, 2015], there are estimations of about 712,000 [Schmidt & Muller, 2007] to 1,5 million taxons [Kutorga *et al.*, 2012; Boa, 2004] or even more – even 3.5 up to 5.1 million species [Rudolph *et al.*, 2018].

In general, except the known accepted species, fungal diversity richness is deduced with the Hawksworth index [Rudolph *et al.*, 2018] and also from cryptic species considerations [Schmidt & Muller, 2007]. Mostly represented by *Ascomycotina* and *Basidiomycotina*, macromycetes represent approximately 10% of the whole global diversity [Gómez-Hernández *et al.*, 2012].

Lignicolous fungal diversity represents an important part of terrestrial mycodiversity. Percentages reach 40% in Polish riparian forests [Nita, 2007], 41.7% in Czech beech forests [Dvořák *et al.*, 2017], up to 44% in Polish fir-dominated mixed forests [Kałucka, 1995], which makes it the leading fungal trophic group in forest ecosystems in terms of diversity [Dvořák *et al.*, 2017].

Lignicolous fungi are responsible for wood decay and forest ecosystems organic matter reintegration [Lonsdale *et al.*, 2008], carbon being the main component in the forest-lignicolous fungi relationship [Buée *et al.*, 2011].

As dead wood represents an equal or higher C-source than living trees [Baldrian *et al.*, 2016], saprotroph and saproparasite lignicolous fungi are of great value in the nutrient cycling in world's forests.

Wood decay is releasing CO₂ into the atmosphere at the same rate as fossil-fuel combustion does. Nevertheless, high lignicolous fungal diversity was associated with low CO₂ emissions, more diverse communities being forest's "CO₂ keeper" [Yang *et al.*, 2016].

Lignicolous fungi can be saprotrophic, when feeding on decaying organic substances, or saproparasites, compulsorily when they live only on living trees, or facultatively when they can live both on living and dead wood [Tănase & Mititiuc, 2001].

The main drivers of lignicolous fungi are the abiotic ones: forest type [Buée *et al.*, 2011], soil conditions [Tedersoo *et al.*, 2014], forest landscape [Abrego & Salcedo, 2014], tree diversity [Buée *et al.*, 2011], woody debris variety in terms of decay, dimensions and genera [Abrego & Salcedo, 2014; Heilmann-Clausen & Christensen, 2003; Hottola & Siitonen, 2008; Sefidi & Etemad, 2015; van der Wal *et al.*, 2017].

Considering the multiple interactions manifested between the forest and the topographic and climatic conditions [Sharma *et al.*, 2010], abiotic characteristics such as elevation, precipitations and temperature have a great influence, directly on saprotroph fungal diversity and composition [Tedersoo *et al.*, 2014] through substrate microclimate [Heilmann-Clausen & Christensen, 2003; Bässler *et al.*, 2010] and indirectly, through tree geographical distribution [Angelini *et al.*, 2014].

Unfortunately, human interventions in the last 8,000 years have transformed forested lands into farmlands and other use [Fyfe *et al.*, 2015]. In the remaining forests, extraction of all logs – the main habitat for forest saproxylic species – causes fast wood depletion, thus endangering lignicolous fungi [Preikša *et al.*, 2015].

Other wood types (*e.g.*, fine woody debris – FWD, or other types of coarse woody debris – CWD) are also important for lignicolous mycodiversity [Bässler *et al.*, 2010; Gates *et al.*, 2007].

As a consequence of the abiotic-biotic, anthropic-natural and fungal-forest multilateral ecosystem relations that dominate the environment in a variety of forms, it is important to understand the complexity of the interactions between forest and lignicolous fungi, and to take responsible actions for preserving forest legacy.

2. BIOLOGICAL MECHANISMS INFLUENCING LIGNICOLOUS FUNGAL ECOLOGY

Once the lignicolous fungal species starts its development on the freshly colonized substrate, it has to face a variety of challenges for surviving. For nutrient

absorption, it needs complex enzymatic packages with which it will transform the organic macromolecules in low weight molecular compounds. Nutrients such as monosaccharides, amino acids and salts can be easily absorbed, once the decaying process starts.

From the beginning, the fungus must compete with other organisms for the food source, so that it must develop a strategy for the dry periods of time. The biochemical reactions are slowed down as the enzymes cannot diffuse in wood cells in the absence of liquid water [Kirk & Cowling, 1984]. Also, fungi must face the various biochemical substances present in the wood (low nitrogen and phosphorous contents, presence of tannins, terpenes or flavonoids, low levels of oxygen) [Petre *et al.*, 2014]. To overcome competition and environmental adverse conditions, fungi have developed different strategies.

While ruderal species can develop fast on the substrate using low molecular weight compounds, stress-tolerant species can face unfriendly environmental conditions (low levels of humidity or high levels of heat). Other species secrete inhibitory compounds or have an overgrowth mycelium to compete other fungal neighbours [Petre *et al.*, 2014].

One of the best adaptations of saprotrophic fungi is their capability of developing a net-like mycelium that will use the space available in the substrate in search for water and organic substances [Webster & Webber, 2007]. Most of lignicolous basidiomycetes use rhizomorphs – hyphal aggregates – to transport water and nutritive substance through the mycelium [Webster & Weber, 2007]. Along with their ability to degrade many types of organic substances, such properties make lignicolous fungal species ubiquitous.

As the enzymes, once produced, do not have the property to diffuse over large distances, the fungus must extend its hyphal system into the new wood [Petre *et al.*, 2014].

Lignicolous fungi will produce energy using oxidative mechanisms [Petre *et al.*, 2014], and a considerable amount of nitrogen or phosphorus [Petre *et al.*, 2014].

The main biochemical ability of lignicolous fungi is the degradation of lignin, considered one of the most recalcitrant organic compounds found in nature [Knežević *et al.*, 2013]. It is the second most abundant natural polymeric carbon source on earth [Paliwal *et al.*, 2015], while the microbial breakdown of lignin opens the stage for carbon utilization by various microorganisms [Paliwal *et al.*, 2015]. Considering that only fungi and bacteria can break lignin [Paliwal *et al.*, 2015], this essential ecological function of fungi becomes obvious.

Lignin is a high molecular weight biopolymer, chemically formed from phenyl-propanoid units linked by covalent bonds [Paliwal *et al.*, 2015], which stocks high amounts of carbon [Schmidt, 2006], making it critical in the global carbon cycle [Paliwal *et al.*, 2015]. The cell wall is composed of cellulose micro-fibrils and the space between them is occupied by an amorphous complex made of lignin and hemicellulose [Schmidt, 2006].

To degrade lignin, an insoluble and unhydrolysable substance [Jurcoane *et al.*, 2006], lignicolous fungi resort to their cellulosic and ligninolytic poly-enzymatic system, under rich oxygen conditions [Petre *et al.*, 2014], thus causing microbial ligninolysis or bioligninolysis [Paliwal *et al.*, 2015].

The manner in which wood-rotting basidiomycetes decay wood is the reason for dividing the group into: white-rot fungi and brown-rot fungi [Ryvarden, 1991].

White rot and brown rot fungi evolution is linked to that of angiosperms and gymnosperms [Watkinson *et al.*, 2016]. White rot fungi capacity to degrade lignin was highlighted as the main cause of an early development of terrestrial invertebrates as, through cellulose and hemicellulose release, many living beings (nematodes, molluscs, insects and arachnids) could use it as food [Watkinson *et al.*, 2016].

White rot fungi are predominating in the first decay stages, because they break lignin, cellulose and hemicellulose. They form the main rot fungi found on hardwood species, being therefore very important in broad-leaved forest ecosystems carbon reintegration.

An interesting insight is given by *Quercus*, a hardwood genus with which some brown-rot fungi are associated. It seems that this tree genus belongs to a primitive angiosperm group [Ryvarden, 1991].

White rot species are capable of degrading wood completely [Ryvarden, 1991], but they differentiate in the extent of cellulose decay. Some species scarcely decay cellulose (*Bjerkandera adusta*), some degrade lignin and hemicellulose prior to cellulose (*Heterobasidion annosum*), while others decay simultaneously all the 3 substances, as it is the case of aggressive saproparasites (*Fomes fomentarius*, *Phellinus igniarius*) [Schmidt, 2006].

The modifications taking place are different from a piece of wood to another. White-rot fungi, like *Heterobasidion annosum* on spruce or *Xylobolus frustulatus* on oak, will create a surplus of cellulose, as lignin and hemicellulose are decayed [Schmidt, 2006]. The fungi that will colonize later on (*e.g.* *Merulius tremellosus*, *Inonotus dryophilus*) [Schmidt, 2006] might continue or not the high degradation of lignin [Otjen & Blanchette, 1982; Blanchette & Reid, 1986].

On the contrary, brown rot fungi can only decay cellulose and hemicellulose [Krzyszowska-Waitkus *et al.*, 2005], leaving behind lignin [Nakasone, 1993; Watkinson *et al.*, 2016]. Brown rot fungi are found primarily on coniferous woods [Watkinson *et al.*, 2016], a major part of them being polyporales [Nakasone, 1993], known as playing an important ecological role in boreal forests. Because of this, most brown rot fungi have a boreal distribution, few polyporales genera being found in the tropical mountain regions of US or South-East Asia [Ryvarden, 1991].

White rot degradation leaves the wood spongy, stringy, or laminated, while the brown rot leaves the wood crumbly, brown cubical pieces being observed [Ryvarden, 1991]. The resulting white rot wood components are not stable in the soil, while the brown rots are [Ryvarden, 1991].

Another type of rot fungi resembles the brown rot ones through their preference for cellulose and hemicellulose – the soft rot fungi [Paliwal *et al.*,

2015], showing limited lignin degradation capabilities [Gao *et al.*, 2018]. These fungi belong to ascomycetes and *fungi imperfecti* and, through the decay process, form cavity chains within the secondary cell walls [Daniel *et al.*, 1992; Paliwal *et al.*, 2015].

With the exception of *Mucidula mucida*, no other Basidiomycetes were found to form characteristic cavities in wood [Daniel *et al.*, 1992]. They prefer moist wood, with less lignin – therefore partially decayed [Goodell *et al.*, 2008]. Soft rot fungi have the ability to decay wood under unfavourable conditions for Basidiomycetes – from dryness to high humidity to almost water saturation [Schmidt, 2006].

Therefore, species like aquatic ascomycetes, *e.g.* freshwater submerged logs, play an important role in water sunken wood decay, where they can represent up to 2/3 of the decaying microbial diversity [Simonis *et al.*, 2008]. Among soft rot fungi, *Kretzschmaria deusta* [Paliwal *et al.*, 2015] is a broad-leaved wood decayer, especially of beech [Tănase *et al.*, 2009]. In a dry and cold environment (*i.e.* Svalbard), brown rot and soft rot fungi were found as the main decayers of soil-contacted wood [Mattsson *et al.*, 2010]. Worth mentioning is that both white rot (*Trametes versicolor*) and brown rot fungi (*Gloeophyllum trabeum*) can furthermore decay freshwater submerged wood [Laurençon *et al.*, 2016], like the logs fallen in rivers, thus contributing to overall decay in forest ecosystems.

As a result of the ecological amplitude in the boreal zone, brown rot and soft fungi can be considered as the main decay agents in forest ecosystems.

Wood decay is therefore a complex process that depends on multiple factors, being accelerated or reduced, depending on the fungal species presented. In its complex dependence on previous decay and type of wood, the presence of a particular fungal species is assured as long as it can survive the microhabitat living conditions.

As the fungal species decay wood, depletion of the substances necessary for survival and growth of other organic substances concentrations creates a new niche available for other species, thus producing a succession of fungal species, the success of which depends on the previous one [Hiscox *et al.*, 2015].

The decay stage-fungal species relationship is so strong, that secondary invading fungi cannot develop if a particular decay stage is not assured [Ryvarden, 1991]. Some species act as path breakers (*i.e.*, *Fomes fomentarius* and *Fomitopsis pinicola*), facilitating the development of the next lignicolous fungal generations [Niemelä *et al.*, 1995]. The main reason is represented by the physical and chemical parameters of wood, with effects on lignicolous fungal communities [Perry & Herms, 2017].

This assertion is valid not only for fungal assemblages but for a single species. Hiscox *et al.* (2015) observed that *Biscogniauxia nummularia* or *Hypoxylon fragiforme*, respectively *Vuilleminia comedens*/ *Trametes versicolor*/ *Bjerkandera adusta*/ *Hypholoma fasciculare* did not evolve in different next decay stage assemblages, while *Stereum hirsutum* did.

Another aspect of the fungal communities present on wood is the presence of opportunistic species that live besides the decomposer species. Even if they are not actively involved in wood decay and live on the products resulted from the neighbouring decaying fungi, the opportunistic species may be more dependent on

the previous species than the actual dominant ones. The explanation of this assertion is the passive dependence on the substance complexes resulted from the previous decay stage [Hiscox *et al.*, 2015].

Wood physical changes can be quantified as mass loss, species like *Trametes versicolor*, *T. hirsuta*, *Bjerkandera adusta* registering high weight losses in the first stage of beech wood decay. Species from *Trichoderma* *agg.* complete the wood loss in the intermediate and well-decay stages [Fukasawa *et al.*, 2010].

Often seen as more important for the existence of lignicolous fungal species than forest composition [Kałucka, 1995], the quality and quantity of the substrate are primary factors in fungal communities composition and diversity.

Decayed wood has different nutrient concentrations, depending on the decay stage. The *Populus*, *Acer*, *Betula*, *Fraxinus* and *Abies* woody debris collected from American broad-leaved forests showed higher levels of nutrients (except potassium) while decay advanced [Klockow *et al.*, 2014]. At diameter level, VFWD (very fine woody debris) and FWD have higher nutrient concentrations than CWD. Considering that VFWD duramen is richer in nutrients than CWD, the higher bark surface/ wood volume ratio in the case of smaller woody debris explains the higher nutrient content of FWD, with effects on the colonization of fungal species [Klockow *et al.*, 2014].

The decay-dependence of lignicolous fungi has another effect, as explained by Heilmann-Clausen & Christensen (2003). They show that an advanced decayed log has a higher mycodiversity, because of the higher number of ecological niches present, resulted from the different decay processes produced in the log in time.

Analysis of wood decay faces different difficulties. For example, the number of decay classes is different in CWD and in FWD. While most of the studies use 5 [Abrego & Salcedo, 2011; Fukasawa *et al.*, 2010; Heilmann-Clausen & Christensen, 2003] or 3 classes [Pedlar *et al.*, 2002] to delineate the decay stage of CWD, FWD decay is delineated by 2 classes [Klockow *et al.*, 2014]. The lower number for FWD decay classes is caused by the difficulty of identifying the classes, due to wood integration in the litter [Ostrogović *et al.*, 2015].

Another issue to solve is the time passed until the woody debris is fully decayed. In one of the most wide-spread tree species in Temperate Europe – *Fagus sylvatica* [Küffer *et al.*, 2004], FWD is decayed within 18 years, while the CWD - in 35 years [Müller-Using & Bartsch, 2009]. One can assume that the longer the time, the greater the chances for the communities to shift, and for diversity to grow.

3. RELATIONS BETWEEN FOREST AND LIGNICOLOUS FUNGI: FROM TREE SPECIES TO FOREST ECOSYSTEMS

The distribution of forest trees and shrub species is closely linked to climate and pedologic substrate [Walthert & Meier, 2017]. Thus, at community level, soil influences the lignicolous and white rot fungi through its pH, phosphorous concentration and C/N ratio [Tedersoo *et al.*, 2014]. Also, calcium, carbon and

nitrogen concentrations influence lignicolous and white-rot fungi at diversity level [Tedersoo *et al.*, 2014].

The vast distribution of some tree species, hosts for the lignicolous fungi, shows that numerous fungal species are also well-distributed across the landscape. Extrapolating from mycorrhizal fungi, distribution of some fungi might be dependent on the distribution of forests with the dominant tree as the the most important tree-host for fungal species [Copoř *et al.*, 2016]. They have numerous adaptations through which they can colonize new lands. For example, some species spores can travel up to 500 km and develop on a completely new site, if the conditions are suitable [Mattias & Gunnar, 2001].

The spore dispersal capacity of polyporales may be the main reason for the wide distribution of some fungal species. Otherwise, a paradox is formulated, namely the vast majority of polyporales have evolved rapidly before the Gondwana split, within only 100 million years, followed by a slow evolution in the next 100 million years [Ryvarden, 1991].

The fact that species like *Heterobasidion annosum* can produce up to 7,000 spores/ square cm/ min [Mattias & Gunnar, 2001] shows how big are the chances of this species to colonize new uninhabited wood, throughout the forest. Being a potent saproparasite, *H. annosum* is of great concern among particular habitats. Over 90% of *Pinus mugo* individuals were infected with *H. annosum* or another strong saproparasite, *Armillaria sp.* [Dobbeertin *et al.*, 2001].

Out of the total number of 132 accepted polyporales genera, 30 have a cosmopolitan distribution, while the rest are climatically restricted [Ryvarden, 1991]. Generalist species have the capability of colonizing large geographic regions or continents. According to Simmel *et al.* (2017), species like *Bjerkandera adusta*, *Clavulina corraloides*, *Dacrymyces stillatus*, *Diatrype disciformis*, *D. stigma s.l.*, *Diatrypella favacea*, *Fomitopsis pinicola*, *Heterobasidion annosum*, *Hypholoma fasciculare*, *H. lateritium*, *Lycoperdon pyriforme*, *Mycena galericulara*, *Nectria cinnabarina s.l.*, *Panellus stipticus*, *Pluteus cervinus*, *Schizophyllum commune*, *Stereum hirsutum*, *Trametes hirsuta*, *T. versicolor*, *Hymenopellis radicata*, *Xylaria hypoxylon* are present across all Europe.

However, this capacity of large-scale dispersal capacity is found in generalist species, the red-listed species being dependent on both forest connectivity and wood source dissemination through the forest [Nordén *et al.*, 2013]. This means that the higher diversity depends not only on the tree-host distribution, but also on their wood spatial allocation.

In a study devoted to the drivers of saproparasite fungi in French forests [Vacher *et al.*, 2008], host trees' diversity did not influence fungal diversity. The same study also showed that host tree abundance and woody composition are important drivers for saproparasite fungal diversity. Still, fungal composition is strongly influenced by tree species, as van der Wal (2017) found out in a *Larix* and *Quercus* dominated forest, at log/ stump-plot level [van der Wal, 2017].

As a consequence of the nitrogen/ phosphorous ratio changes occurring in soil, beech vitality in Europe is dropping [Talkner *et al.*, 2015]. Side effects include changes in beech forest composition and woody debris pool volume, with indirect influences on the distribution of lignicolous fungi [Lassauce *et al.*, 2011]. At log-plot level, tree species were considered as main predictors of lignicolous fungal community variation in a *Quercus-Pine* forest of China [Yuan *et al.*, 2017].

Lignicolous fungal species have different preferences on host-trees, some being specialised, while others are generalists [Gerhardt, 1999; Sălăgeanu & Sălăgeanu, 1985; Tănase *et al.*, 2009]. This situation is also found in Romania, where the lignicolous species are either specialised on the main dominant tree genera (*Fagus*, *Quercus*, *Abies*, *Picea*) or on the less common genera (*Salix*, *Populus*, *Fraxinus*, *Pinus*), or grow on multiple hosts (Table 1).

Table 1

Some macromycetes preferences on host-trees in Continental Europe [Gerhardt, 1999; Ryvardeen, 1978; Sălăgeanu & Sălăgeanu, 1985; Tănase *et al.*, 2009]

Fungal species	Trophic type	Host tree/shrub
<i>Ascotremella faginea</i>	Lign. saprotroph	<i>Fagus</i> , <i>Alnus</i>
<i>Auriscalpium vulgare</i>	Lign. fruit saprotroph	<i>Pinus sylvestris</i>
<i>Bulgaria inquinans</i>	Lign. saprotroph	<i>Quercus</i> , <i>Fagus</i>
<i>Cytidia salicina</i>	Lign. saprotroph	<i>Salix</i>
<i>Daedalea quercina</i>	Lign. saprotroph	<i>Quercus</i> , <i>Castanea</i>
<i>Fomitopsis betulina</i>	Lign. saproparasite	<i>Betula pendula</i>
<i>Gloeophyllum odoratum</i>	Lign. saprotroph	<i>Abies</i> , <i>Picea</i>
<i>Gymnopilus picreus</i>	Lign. saprotroph	<i>Pinus sylvestris</i>
<i>Hymenochaete cruenta</i>	Lign. saprotroph	<i>Abies alba</i>
<i>Peniophora piceae</i>	Lign. saprotroph	<i>Picea abies</i>
<i>Phellinus pomaceus</i>	Lign. saprotroph	<i>Prunus</i> , <i>Pyrus</i> , <i>Malus</i>
<i>Phellinus hartigii</i>	Lign. saproparasite	<i>Abies</i> , <i>Picea</i> , <i>Pinus</i>
<i>Phellinus pini</i>	Lign. saproparasite	<i>Pinus sylvestris</i>
<i>Phellinus robustus</i>	Lign. saproparasite	<i>Quercus</i>
<i>Phellinus tremulae</i>	Lign. saproparasite	<i>Populus tremula</i>
<i>Pholiota destruens</i>	Lign. saproparasite	<i>Populus</i>
<i>Mucidula mucida</i>	Lign. saprotroph	<i>Fagus</i> , <i>Ulmus</i>
<i>Xylaria carpophilla</i>	Lign. fruit saprotroph	<i>Fagus</i>
<i>Xylodon sambuci</i>	Lign. saprotroph	<i>Sambucus</i>

While the ecological amplitude of fungal lignicolous species is diverse, there is a situation that proposes another view on the relations between fungi and host-plants – the spatial scale. At local or regional scale, one may see that a species is maintaining its ecological preferences. This situation changes as the species is found in another place, hundreds or thousands kilometres away.

Except the situation in which the tree-host is not present in that particular area, and therefore there are other tree species/genera on which the fungal species grow, a particular situation occurs when the fungi are growing on another host, even

if the most frequent host, as established, is there, too. For example, in Continental Europe, *Fomes fomentarius* grows especially on *Fagus sp.* while, in Great Britain, the main saproparasites for these trees are species of *Ganoderma* or *Stereum*. Moving north on the British Island, *Fomes fomentarius* shifts from *Fagus* to *Betula*, where it replaces *Fomitopsis betulina* as the main lignicolous saproparasite [Schwarze, 1994].

An interesting application refers to the capacity of fungal species to develop in forests dominated by one species. As one host-tree species concentrate in a forest ecosystem, the chances for the associated fungal pathogens to spread grow [Nguyen, 2015]. To count the effect of endemic trees on polyporales species, an index can be established, calculated as the density of endemic trees [Hottola & Siitonen, 2008], which leads to another conclusion: the more tree species are present in the forest, the higher is the resistance of trees against pathogens. A recommendation can be suggested here: increasing tree diversity will significantly reduce spreading of pathogen fungi [Pärvi, 2010]. Species like *Fomes fomentarius*, *Heterobasidion annosum* or *Armillaria mellea*, well-known as aggressive fungal saproparasites, could be stopped from ravaging healthy trees in monodominant forests, and especially in plantations.

Tree diversity is considered highly important for mycodiversity, numerous studies showing the significant and positive correlation between them [Buée *et al.*, 2011]. This relation is sustained by the structural hypothesis which proves that the number of available niches for a colonizing fungal species grows as the structural complexity of a forest stand is larger [Carroll, 1993].

The importance of tree genera can be also highlighted thorough the way in which wood is decayed. For example, hornbeam FWD (*Carpinus betulus*) is more rapidly decayed than ash FWD (*Fraxinus angustifolia*). As some authors suggested [Ostrogović *et al.*, 2015], these differences come from the different preferences of fungal species for the tree-host.

As expected, from the lignicolous fungal composition viewpoint, the differences between forest ecosystems are also visible among different types of broad-leaved forests. For example, Bîrsan *et al.* (2014) showed that, in beech, oak and oak-poplar-willow dominated forests, the fungal species were gathered in 3 distinct clusters, according to their host preferences. They observed that the fungi attached to a particular tree-host were shaping the fungal communities in their respective forest ecosystem, as follows: *Daedalea quercina*, *Peniophora quercina*, *Ganoderma lucidum* in oak-dominated forests, *Fomes fomentarius*, *Bjerkandera adusta*, *Pleurotus ostreatus* in beech-dominated forests and *Pluteus salicinus*, *Phellinus igniarius*, *Laetiporus sulphureus* in broad-leaved meadow forests, respectively.

As Lilleleht *et al.* (2014) observed, increasing coniferous trees ratio in mixed forests also grows the risk of tree breaking or uprooting. They concluded that, as tree diversity increases, the chance of forest damage decreases. Some tree species have extra-resistance to climatic or biological hazards resulting in overall forest resistance [Jactel *et al.*, 2017], which reduces the woody debris quantity and lignicolous mycodiversity.

The above data showed that not only tree diversity is important to lignicolous mycodiversity, but also forest composition.

The ratio of rot type woods can vary in different types of ecosystems, as tree composition changes. For example, Zhou & Dai (2012) found out that white rot fungi exceed the brown rot ones in a forest dominated by angiosperms. As angiosperm lignin is easier to degrade than the gymnosperm one [Hammel & Cullen, 2008], it is obvious that most of the white rot fungi grow on angiosperms [Zhou & Dai, 2012].

Extended at sub-continental scale, this situation can lead to the dominance of polyporales species upon angiosperms in an area in which most forests are dominated by broad-leaved or evergreen angiosperms, as is China. Here, 74% of the total polyporales species are growing on angiosperm trees [Zhou & Dai, 2012].

The composition of lignicolous fungal species in broad-leaved forests, different from the one in coniferous forest, can be observed all over the world. In this respect, studies have been devoted to oak and beech forests, *vs.* coniferous ones, in Hungary [Kutsegi *et al.*, 2015], or to broad-leaved *vs.* coniferous species, in Lithuania [Runnel & Lõhmus, 2017] or Poland [Kałucka, 1995].

Lignicolous mycodiversity has different outcomes in broad-leaved *vs.* coniferous forests from the necromasis perspective, as well. Generally, in boreal ecosystems, the total volume of dead wood is higher than in the temperate ones, with a strong positive correlation as to the number of fungal lignicolous species [Lassauce *et al.*, 2011].

Another cause of coniferous forests' different lignicolous fungal composition is the effect of the tree upon floor humidity. Higher levels of soil and litter moisture will create better microhabitats for fungi' spreading through and colonization of deep incorporated-litter wood [Kałucka, 1995; Kubartová *et al.*, 2009].

An interesting observation refers to the fungal diversity of stumps. Mycodiversity is lower on stumps in boreal forests than in broad-leaved forests [Lassauce *et al.*, 2011], which can be explained by the lower boreal forest diversity, a situation outlining the importance of tree diversity upon fungal diversity.

4. THE RELATIONS BETWEEN ABIOTIC CHARACTERISTICS AND LIGNICOLOUS FUNGI: ECOLOGICAL ASPECTS OF WOOD DECAY

While the tree-host and forest composition have an important effect on both fungal lignicolous diversity and composition, other environmental factors, like the abiotic-derived ones, can have an interesting impact on fungi, at different geographic scales.

To understand abiotic factors' involvement and the natural chronological evolution of the wood-lignicolous fungi relation in a stable ecosystem forest with no forest fires, few powerful storms or heavy snow falling should be elucidated.

4.1. DECAY INITIATION

Once a living tree is dying, some parts of its crown begin to dry, losing fine branches which, in turn, will enrich the FWD pool under the tree. Furthermore, crown's thinning will allow more and more light to reach the lower layers of the forest. This will cause drying of upper litter and woody debris, especially of fine woody debris, through increasing radiation and wind exposure [Sharma *et al.*, 2005], once known that high soil and litter humidity is associated with fast decay [Fravolini *et al.*, 2018], quantified in high mass losses [Kubartová *et al.*, 2009]. In turn, the fungal capacity to decay wood will be reduced to a half, whereas the quantity of fine woody debris will grow even further [Fatsh *et al.*, 2011].

In such wood materials, the lignicolous fungal communities are probably dominated by xerophile species, associated with first-decay stages, instable microclimate, and limited and hardly diverse living supplies. A closely related situation is found in the high canopy of living trees, where few species can survive, due to aridity.

In *Fraxinus*, *Quercus* and *Tilia* high canopies, Unterseher *et al.* (2003) found out that 60% of all records were represented by *Cryptosphaeria*, *Diatrypella*, *Nitschkia*, *Peniophora* genera. As the height lowered, the fungal lignicolous diversity increased. Still, no less than 85 species were found in tree canopies [Unterseher *et al.*, 2003], which may continue the decay on the fallen woody debris.

Lignicolous species' composition is similar in tree canopy and freshly fallen wood, especially FWD. The species continuing the decay from the canopy to the ground are diverse, depending on tree-genera: for *Quercus* – *Peniophora quercina*, *Vuilleminia comedens*, *Hyphoderma setigerum* [Iršénaitė & Kutorga, 2006], while others are freshly installed on fallen wood, like *Bulgaria inquinans* for *Quercus* [Iršénaitė & Kutorga, 2006].

This situation is enhanced on southern areas, the scientific proofs obtained showing that beech wood is decaying slower in Mediterranean ecosystems [Fravolini *et al.*, 2018]. Also, on southern sites, stumps nutrient' concentrations were higher [Hellsten *et al.*, 2013], which might be a proof of various fungal communities living on the opposite slopes.

Also, a higher decay might occur in topographic humidity-friendly areas. In the temperate hemisphere, northern aspects are considerably prone to lower solar energy which, in turn, corroborated with a larger slope degree, will favour preserving soil and substrate humidity [Sharma *et al.*, 2010] and higher soil nitrogen, phosphorous and carbon concentrations [Sharma *et al.*, 2010].

The aspect and slope characteristics of topographic surfaces act upon plant distribution in forests [Sharma *et al.*, 2010; Måren *et al.*, 2015]. Consequently, the more xerophytic tree species will grow preponderantly in southern sites, while the more mesophilic species will grow in northern areas [Måren *et al.*, 2015]. Thus, fungal lignicolous distribution will be indirectly influenced by topography.

The slope can inhibit or favour the decaying process. The litter and FWD included in it [Ostrogović *et al.*, 2015] will decay faster on different slope positions and aspects [Sariyildiz, 2015]. Another topographic parameter, terrain rugosity, can influence wind's direction and intensity [Hengl & Reuter, 2009], capturing humidity in sheltered places, at soil level [Sharma *et al.*, 2005].

The momentum of falling is important for the development of fungal species. Considering that, during winter or autumn, the living wood is richer in nutrients because of the tree stocking strategy for spring [Klockow *et al.*, 2014], the fallen FWD will offer a lush quantity of food resources for fungi. Besides the fact that, during winter, saprotroph fungi are less active in decaying newly fallen branches, this will favour spring specific fungi to colonize and develop, thus generating a different fungal community than in spring and summer-fallen wood.

Depending on the variety of humidity substrate, some species are specialised to grow on FWD under xeric conditions, like *Diatrype disciformis* [Abrego & Salcedo, 2011], *Schizophyllum commune*, *Trametes hirsuta* and *Lentinus arcularius* [Simmel *et al.*, 2017]. Other species, like ascomycetes: *Bisporella citrina* [Abrego & Salcedo, 2011; Tănase *et al.*, 2009] or basidiomycetes: *Trametes pubescens*, *T. ochracea*, *Chlorociboria aeruginascens*, *Flammulina velutipes* and *Daedaleopsis confragosa* [Simmel *et al.*, 2017] need humid FWD.

After small branches' falling, which will generate more light, the neighbouring trees will develop new branches that will slowly reduce crown gap. Also, forest's first layer will enrich in herbaceous species, followed by tree saplings. Therefore, the amount of light will decrease and wood humidity will grow, accelerating wood decay, enabling new fungal species to colonize the wood, increasing FWD fungal diversity and therefore integrating the organic material into the litter.

Heilmann-Clausen & Christensen (2004) pointed out the cause of the high diversity associated with the FWD total volume. According to them, a larger FWD volume causes a larger surface-to-volume ratio, which means that the fungal species have better chances to colonize wood. However, from their perspective, this means that the dying trees must be preserved in totality, in order to assure a constant supply of FWD, and finally the main source of CWD.

While the vast majority of studies on lignicolous fungal ecology had been made on CWD, FWD being the less studied category in terms of fungal species [Debeljak, 2006], more and more numerous studies have evidenced the growing importance of FWD for mycodiversity [Bässler *et al.*, 2010; Gates *et al.*, 2007].

Even if, *per se*, the vast majority of species are not found on FWD, study of this type of woody debris is recommended for improving mycodiversity recording, for pointing out the real numbers [Kruys & Jonsson, 1999] and for preserving this dead wood on the ground [Heilmann-Clausen & Christensen, 2004]. Besides, in a study on temperate natural forests in Sweden, Nordèn *et al.* (2004) found out that FWD can represent up to 45% of the total dead wood.

4.2. FROM FINE WOODY DEBRIS TO COARSE WOODY DEBRIS – EFFECTS ON FUNGAL SPECIES AND COLONIZING STRATEGIES

In the process of tree dying, after the initial stage in which the fine branches were falling, the main trunk decay will continue, branches of larger sizes falling to the ground. As a consequence, the diameter profile of the woody debris will change, new size woods becoming available for colonization. Thus, the CWD quantity shows a Gaussian curve, larger and larger size wood becoming available [Perry & Herms, 2017].

As a consequence, the ratio between FWD and CWD changes, making the FWD-CWD relation variable over time and from one place to another. No wonder that a negative correlation can be found between FWD's total volume and mycodiversity [Kebli *et al.*, 2012].

Fungal diversity will grow even more as decay continues, especially in polyporales [Purhonen *et al.*, 2017], the different trunk parts developing slightly different fungal lignicolous communities. The intermediate and advanced decay stages are associated frequently with higher mycodiversity, both in mixed broad-leaved coniferous [Yuan *et al.*, 2017], coniferous [Rajala *et al.*, 2015] and broad-leaved forests [Sefidi & Etemad, 2015].

Changing of WD profile will increase fungal diversity, as species that prefer a particular wood type will develop. This assumption is especially valid with CWD, as in the case of early-colonizer fungi dominance on logs. Here, the within-log diversity was higher, as the new species were occupying different positions within the log [Kubartová *et al.*, 2015]. The longer the earlier colonizer remained on the log, the least the decay stage will be [Kubartová *et al.*, 2015], a situation closely related to low humidity [Kubartová *et al.*, 2015], thus emphasising the particular local climate.

As Abrego & Salcedo (2011) discovered, species like *Diatrype disciformis* and *Bisporella citrina* on VFWD, respectively *Fomes fomentarius* and *Kretzschmaria deusta* on CWD were loyal species, as they were growing especially on a particular diameter category type.

From a different perspective, Bîrsan *et al.* (2014) showed that the preference of some species for a particular WD diameter was explained by the more-resource argument. This is the case of large-bearing sporome fungi, like *Fomes fomentarius*, *Laetiporus sulphureus* or *Ganoderma applanatum*. On the contrary, small-bearing fruit-bodies fungi, like *Pycnoporus cinnabarinus*, *Exidia glandulosa* or *Plicaturopsis crispa* preferred smaller WD, because of their reduced food and space needs.

The way fungi colonize wood may explain the different values of mycodiversity, on different WD types. Some species have an advantage, induced by their type of colonization strategy. Other lignicolous species have the ability to exclude others if high populations on WD like stumps [Driver & Ginns, 1969] are reached. Polycentric species start colonization from different spatial points, while the monocentric ones start from one point [Bîrsan *et al.*, 2014].

Substrate's colonization is especially important for the fungi whose evolution produces further morphological modifications, spore ornamentation and size being associated with trophicity, lignicolous fungi having elongated spores that reduce the wash out risk caused by precipitations [Calhim *et al.*, 2018].

Other species are well-adapted to a particular microclimate, so that they will prevail in wood colonization. As in the case of FWD loyal fungi, species growing on logs more exposed to sun have the first hand in taking the niche. For example, on spruce logs situated in forest gaps, *Gloeophyllum sepiarium* was found to aggregate on closely distanced logs [Mattias & Gunnar, 2001].

The litter plays a key role in nutrients cycle and in humus formation in forest ecosystems [Kubartová *et al.*, 2009], and an important role in the colonization of some lignicolous fungi of litter contact woody debris. Considering that approximately 20% of the plant litter in forest ecosystems is represented by lignin [Paliwal *et al.*, 2015], the strategy used by some fungi to develop their mycelia into forest litter is obvious.

As known, forest litter contains a considerable quantity of nutrients that are scarcely present in CWD [Ottosson, 2013]. This means that some fungi will search for food in the litter and eventually find another coarse woody piece, on which to develop fruiting bodies. Lignicolous saprotrophs like *Trametes versicolor*, *Phanerochaete sordida*, *Phlebia albida* were found in more than ¼ of the litter samples [Kubartová *et al.*, 2009], which evidences mycelia's spreading adaptation.

Soil's chemical properties, especially pH and humus properties, together with litter chemical properties, strongly influence litter saprotrophs [Kaľucka, 1995; Kubartová *et al.*, 2009] which can also influence the soil and litter-migrating lignicolous fungi.

Litter-soil migration was observed in *Coniophora olivacea*, a mycelium spreading species, which was found to aggregate if the distance between logs was less than 25 m [Mattias & Gunnar, 2001]. Also, *Coniophora olivacea* stump and soil-contacted wood preferences showed that this species has an active display in litter [Kubart *et al.*, 2016].

Some fungi, like *Trametes sp.*, *Phanerochaete sp.*, *Pleurotus sp.*, have the ability to grow in soil and to modify particular soil characteristics, such as permeability [Petre *et al.*, 2014]. On the other side, the competition for a unoccupied niche is huge as, besides such fungi, air-carrier spores will develop fast in mycelia, occupying the wood.

The changes in wood quantity can have multiple causes, depending on the spatial scale, management type or manifestation of climatic phenomena. Also, the type of rot that fungi exert over wood determines whether it will be a fast or slow decay. As known, a wood colonized by brown-rotting fungi will lose weight much faster and in larger quantities than if it had been colonized by white-rotting fungi [Ryvarden, 1991]. Besides this capacity, a brown-rotting fungal adaptation to a tree's shorter growing season might be manifested, as it is the case in boreal regions [Ryvarden, 1991].

Considering that many brown rot fungi also grow on *Quercus* [Ryvarden, 1991], an unequal decay rate may be registered between oak-dominated forests and boreal forests on an elevation gradient. As mountainous forests have higher humidity than the lowland oak-dominated ones, the woody debris might decay faster if colonized by a monodominant brown rot fungus, under favourable microclimatic conditions. One should not forget that decay is inhibited at low temperatures [Kubartová *et al.*, 2009], which might rise the importance of southern slopes or open canopies.

A particular example is the ecological situation created by clear-cutting, similar to the one induced by great winds, heavy snows or landslides. In both situations, a great amount of fine fresh wood results. The newly resulted wood is ready for being colonized by the same species, which means that, from a particular management perspective, the lignicolous fungal communities will not be highly different [Lindhe *et al.*, 2004].

Also, the first decay stage wood volume–advanced decay stage wood volume ratio is higher in a recently clear-cut forest, defining the structure of lignicolous communities by the dominance of pioneer fungi [Abrego & Salcedo, 2011]. Differences in community's structure appear on CWD, where log collecting in clear-cut areas vs. natural decaying of fallen trunks creates differences between managed and natural forests [Juutilainen *et al.*, 2014].

The total or diametric categories wood volumes are well-known important factors influencing fungal colonization and, consequently, fungal diversity and composition [Abrego & Salcedo, 2011; Birsan *et al.*, 2014; Heilmann-Clausen & Christensen, 2003; Hottola & Siitonen, 2008; Juutilainen *et al.*, 2014; Lassauce *et al.*, 2011; Runnel & Löhmus, 2017; Sefidi & Etemad, 2015].

The diameter profile of the woody debris is of great importance, once known that the different CWD – to – TWD volume creates various effects upon mycodiversity. As the total CWD volume ratio increases, mycodiversity increases, as well [Kruys & Jonsson, 1999]. The positive correlation of total wood volume and lignicolous mycodiversity has been found not only in boreal hemisphere, but also in austral one [Allen *et al.*, 2000].

4.3. COARSE WOODY DEBRIS – THE MYCODIVERSITY KEEPER

CWD – whose main forms in a forest are logs, stumps and roots – is considered a valuable old growth forests indicator [Tobin *et al.*, 2007]. Many red-listed species are associated with CWD – 40%, in Sweden, for example [Kubart *et al.*, 2016].

Numerous studies associated larger diameter wood to a higher mycodiversity [Kebli *et al.*, 2012; Birsan *et al.*, 2014; Juutilainen *et al.*, 2014].

In a complex study, in which no more than 6 diameter types were accounted, the 6th category showed the greatest diversity and abundance of lignicolous fungi in boreal Finnish forests [Juutilainen *et al.*, 2014]. In boreal aspen forests of Eastern

Canada, larger and advanced decayed logs housed approximately 9% more mycodiversity than smaller or medium decayed logs [Kebli *et al.*, 2012].

The most important type of woody debris in a forest is the log. Zhou & Dai (2012) found out that 65% of the total polyporales species preferred fallen trunks, therefore the last death stage of a tree. This stage is often associated with higher humidity, because of the neighbouring trees crown closing gap and forest first layer growing.

As humidity grows, the fungal community on woody debris is changing. Low-moisture species like *Megacollybia platyphylla*, *Peniophorella paraetermissum*, *Conferticium ochraceum* are replaced by *Junghuhnia luteoalba*, *Kneiffiella alutacea*, *Hyphodontia abieticola*, which are moisture-loving ones [Kubartová *et al.*, 2015]. Some of these species show even more particular environmental requirements – for example, *M. platyphylla* and *P. praetermissum*, known as low-density wood decomposers [Kubartová *et al.*, 2015] – preferring more decayed wood, yet growing in sunny or windy places. On the contrary, *J. luteoalba* and *K. alutacea* prefer the lowest density wood [Kubartová *et al.*, 2016], namely humid rotten wood found in shady places parasite.

Depending on the particular site moisture regimes, some species will prevail in colonizing wood, while others will not. Species like *Bjerkandera adusta*, *Trametes pubescens*, *T. ochracea*, *T. versicolor*, *Heterobasidion annosum*, *Cerrena unicolor*, *Fomitopsis pinicola* are hygrophilic [Soloviev, 2007], meaning that they will colonize the wood of rather humid places, as it is the case of some saprotrophic and saproparasite species growing in mountainous boreal or riparian forests [Sălăgeanu & Sălăgeanu, 1985; Tănase *et al.*, 2009].

Besides litter-integrated wood, either FWD or CWD, within the “hidden” wood category, roots are of great importance for forest carbon cycle, as they are the most important C-stock source [Tobin *et al.*, 2007]. Aggressive root pathogens, like *Heterobasidion agg.* or *Armillaria agg.*, are especially important in forest ecology [Lygis *et al.*, 2010], due to their ability of disseminating across soil through their root system.

In the natural process of tree death, one of the main organic remains is the stump. On long-term, stumps are nutrient pools, as they increase the P and Mg amount [Palviainen *et al.*, 2010], being therefore of special importance for the saproxylic species. Also, stumps are the main CWD types remaining from a clear-cutting [Måren *et al.*, 2015].

In various studies, stumps have been associated with various results in relation with mycodiversity. While van der Wal *et al.* (2017) showed that stumps can be a precious wood type for numerous fungal species, Lindhe *et al.* (2004) found out that log mycodiversity is higher than that of stumps. Also, stump mycodiversity is characterized by generalists, red-listed species being less frequently found, as in Sweden [Kubart *et al.*, 2016].

Even so, many species detected on stumps do not grow or are more rarely met on logs – for example, *Coniophora puteana*, *Phlebia gigantea*, *Ischnoderma benzoinum*, *Resinicium furfuraceum*, recorded always on stumps and only rarely on soil-contacted logs - in Sweden [Kubart *et al.*, 2016].

While stump mycodiversity's variation still has ambivalent explanations, stump fungal composition is more clearly influenced by particular stump characteristics. For example, Norway spruce stump lignicolous fungal composition is strongly influenced by stump age and latitudinal gradient [Kubart *et al.*, 2016]. On the other side, fungal species forming communities on *Pinus mugo* stumps showed similarities between non-burned and burned stumps [Lygis *et al.*, 2014].

5. MANAGEMENT AND NATURAL DISTURBANCES EFFECTS ON LIGNICOLOUS FUNGI

Defined as a physical-chemical phenomenon that affects habitat's functionality, disturbance phenomena can be of multiple types, from anthropogenic to natural ones [Miller & Lodge, 1997].

Forest management has modified stand's structure and composition, which enhanced even more the effects of natural disturbances over forests. By removing all logs, logging residues and stumps, fungal diversity and abundance have been drastically reduced [Brazee *et al.*, 2014]. Natural disturbances have polyvalent effects as, in time, mycodiversity is recovering [Kutorga *et al.*, 2012; Penttilä *et al.*, 2013].

5.1. MANAGEMENT EFFECTS ON LIGNICOLOUS FUNGI

Managed forests always have lower quantities of CWD, especially large logs and snags [Kebli *et al.*, 2012]. As a consequence, many saproxylic species, fungi included, are endangered in many parts of Europe [Kebli *et al.*, 2012].

In managed aspen forests, FWD was found as negatively correlated with CWD pool and mycodiversity, as such forests are exploited for logs, which leads to the reduction of wood's main habitats [Kebli *et al.*, 2012].

Mycodiversity can be influenced by management history – for example, in Finland, spruce forests were exploited before the pine ones. As a consequence, mycodiversity in spruce forests was 1.5 lower than in those of pine [Juutilainen *et al.*, 2014].

The time since humans interfered within the forest is considered a good indicator of aphylloroid fungi [Senn-Irlet *et al.*, 2007].

Widely used in the spatial modelling of species [Copoț & Tănase, 2017], land cover can be an important factor in the distribution of fungal lignicolous species. According to literature [Gerhardt, 1999; Sălăgeanu & Sălăgeanu, 1985; Tănase *et al.*, 2009], fungi prefer a variety of environments, from parks and gardens to humid natural forests. The anthropic activities have a valent effect on species, some of them growing well in anthropically modified environments, while others are threatened with extinction [Siitonen, 2001].

In Finland, reduction of CWD volume in managed forests is considered the main cause for the prognosticated disappearance of more than 50% of saproxylic

species [Siitonen, 2001], including lignicolous fungi. The more forest CWD is extracted, the more are chances for fungal species not to survive in their full original diversity [Hottola & Siitonen, 2008].

High diversity reduction has been also observed in spruce and fir forests, up to 28% of the polyporales species missing in the managed forests *vs.* the protected ones [Zhou & Dai, 2012]. Forest stand area provided an important explanation for lignicolous fungal diversity, especially the red-listed species, in Norway's spruce dominated forests [Berglund & Jonsson, 2009].

In a study about the influence of forest fragmentation on mycodiversity, Berglund & Gunnar (2001) found out that the isolation degree of forest fragments was not representative for the number of lignicolous fungi. Fungi were dispersed across fragmented forest landscape if the distance between fragments was less than 500 m. Still, Nordén *et al.* (2013) observed that, in fragmented forests, lignicolous fungal composition is formed especially of generalists, the red-listed species being too specialized, and therefore requiring continuous natural forests.

In another study [Abrego & Salcedo, 2014], the uniformity of forest fragments was considered as significant for mycodiversity variation. As forest fragments have an irregular perimeter, mycodiversity was dropping. Another observation was that the distance to forest margin was not significantly correlated with lignicolous mycodiversity, which confirms the ease of this group of fungi to spread across forest landscape. Negative influences of forest fragmentation were highlighted by other researches, as well, disruption of life cycle leading to local populations' disappearance [Senn-Irlet *et al.*, 2007].

5.2. DISTURBANCE'S EFFECTS ON LIGNICOLOUS FUNGI

Fungal lignicolous populations are influenced by topographic and climatic parameters, at different spatial scales. Topographic characteristics, such as slope and aspect, have a direct effect on radiative energy and soil humidity distribution [Méndez-Toribio *et al.*, 2017] and impact on the vegetation spreading across forest landscape, both at diversity and composition levels [Sharma *et al.*, 2010].

Climatic factors play a major role in lignicolous fungal distribution [Tedersoo *et al.*, 2014]. Medium annual precipitations influence numerous types of fungi, in relation with both their diversity and abundance (saprotrophic fungi, white rot fungi, pezizas). Medium annual temperatures also influence fungi as to their diversity (white rot fungi) or abundance (saprotrophs, white rot fungi). Such climatic variables are, as known, correlated to elevation, which in turn is considered as a proxy for them [Hijmans *et al.*, 2005; van Gils *et al.*, 2012].

The climate has an important influence on lignicolous fungi through the accumulation or decay of downy wood. In the US, the largest mean stocks were found in dry/ cool climates, while the lowest wood pools were associated with dry/ hot climates [Woodall & Liknes, 2008]. Higher values of temperature and humidity increase wood production in forests, while decreasing the time dead wood can resist until fully decay [Woodall & Liknes, 2008].

Elevation was found as a good predictor for explaining the composition of saprotrophic and white-rot fungi [Tedersoo *et al.*, 2014]. In a study devoted to an important medicinal mushroom – *Ganoderma lucidum*, elevation was seen as one of the main factors influencing the distribution across broad-leaved dominated forests. Species' preference for lower altitudes, correlated with warmer sites, was confirmed by species' Ellenberg index [Copoț *et al.*, 2017]. Still, this might be also an effect of the distribution of their main habitat dominated by their preferred host in Romania – *Quercus* [Tănase *et al.*, 2009].

On the other side, the distribution of rich medium precipitations and lower maximum temperatures was correlated with the high woody debris number, in all US forests [Woodall & Liknes, 2008].

Often in nature, climatic phenomena have an unexpected effect on forest development. It is the case of natural hazards, represented especially by the mechanical ones (powerful storms, intense winds, heavy snows). As known, such phenomena increase the quantity of woody debris of all types. Some tree genera are susceptible to these hazards.

One of the main effects of the strong disturbances affecting forests is shifting, which occurs on fungal lignicolous communities. It is known that, in the case of severe phenomena, fungal species better equipped to stress will prevail, to the detriment of the less provided ones. As a result, communities can shift from rich rare species to lesser generalists, granting to autochthonous fungi small chances to survive and develop in the newly modified environment [Miller & Lodge, 1997].

A shift from the balanced ecosystems scenario is cascade dying back, caused by climatic phenomena. During powerful winds, in the forest, multiple isolated trees are falling to the ground floor. For each tree, a natural clearing is formed. More and more trees will fall, as other powerful winds will develop the next months or years. As a result, the wood pool is regenerating with newer logs and smaller woody debris. This also means that older falling trees various decay stages host different fungal communities [Mattias & Gunnar, 2001].

Stormy winds' effect has also an interesting result on litter and litter-integrated wood mycodiversity and composition. After a healthy tree's fall down, the litter will rapidly enrich in volume and mass. It is expected that, in the first months, the litter mass loss be different, depending on tree species, once shown that soluble inhabiting substances will decrease the decay rate, as in the case of beech litter [Kubartová *et al.*, 2009].

However, as suggested by the same authors, other inhibiting substances (like tannins) widely present in oak litter, might not influence the decay rate, if the stand was a humid and warm one [Kubartová *et al.*, 2009]. Considering that particular lignicolous fungi are also growing in the soil, the question about the special importance of tree species over climatic and microclimatic-induced characteristics may be formulated.

The above case shows that, in a stable ecosystem, with cyclic climate manifestations, fungal lignicolous diversity is maintained properly and the forest is changing without losing its biodiversity.

Even if the perturbing effect is heavy, as time passes and the ecosystem is soon but steadily recovering, the old communities are reviving. Fire is an interesting natural disturbance as, in time, it triggers different effects upon mycodiversity [Kutorga *et al.*, 2012; Penttilä *et al.*, 2013].

In a study on juniper shrub land in Estonia, Kutorga *et al.* (2012) showed that fire had severely changed the fungal lignicolous community in the first year, after which the pyrophilic species were seen as decreasing, leaving the older ones to regain their place in the environment.

In another study on Finnish boreal *Pinus sylvestris* forests [Penttilä *et al.*, 2013], it was shown that the immediate effect of fire was to drop polypore diversity. This situation changed within 6 years as, during the last year, mycodiversity was fully recovered. Furthermore, 13 years from the initial fire, mycodiversity was higher, because of the large quantities of woody debris available.

From another perspective, the influence of another climatic disturbance – drought, can have a short-time positive effect on the number of fungal lignicolous species. Reduced total summer precipitations [Pešková *et al.*, 2012] or the precedent year total precipitations [Ferretti *et al.*, 2014] induce a powerful stress on forest trees, manifested in a reduced foliar system, drying of smaller branches, dying of large trees, etc. All these might considerably increase the wood supply on the ground floor. During droughty periods, the absence of humidity will inhibit fungi development, a situation changing when precipitations reach the respective area.

Biological disturbances have different effects upon fungi distribution, being closely related to mechanic hazards. Strong winds produce structural damages to trees, which in turn opens a gateway to insect and fungal attack [Beldeanu, 1999].

Lignicolous fungal communities developed on wind-fallen logs are different from those present on logs resulted from insect attacks [Bače *et al.*, 2012]. As Stursova *et al.* (2014) observed, the quantity of woody debris resulted from *Ips typographus* attack grows, resulting in fungal communities shifting.

6. MYCOCONSERVATION AND POTENTIAL LIGNICOLOUS FUNGAL-DERIVED APPLICATIONS

In order to protect *lignicolous* macrofungi, it is important to delineate the habitats. Some wood-inhabiting fungi can be used as valuable indicators for forest biodiversity status [Christensen *et al.*, 2005]. For old-growth forests, lignicolous fungi are often seen as good species indices: both ascomycetes, such as *Ascocoryne sarcoides* [Gates *et al.*, 2007], or basydiomycetes – *Ganoderma applanatum* [Gates *et al.*, 2007]. For natural beech forests, species like *Dentipellis fragilis*, *Flammulaster muricatus*, *Hericium erinaceum* or *Pluteus umbrosus* are considered good saproxylic diversity indices [Christensen *et al.*, 2005].

Among the actions taken in Scandinavian countries, some had a favourable impact on lignicolous mycodiversity. The most important was harvesting practices diversification [Kebli *et al.*, 2012].

The main silvicultural measure that could be taken is of maintaining wood of different dimensions in the forests, as both downy wood and snags. As logs have been proven important for lignicolous fungal diversity, partial harvesting might be a good pro-bioconservation management method that had already registered favourable effects in numerous countries [Kebli *et al.*, 2012].

As tree diversity was shown of great importance for lignicolous mycodiversity [Vacher *et al.*, 2008], and considering the high capacity of forest fungi to establish on new areas placed far away [Mattias & Gunnar, 2001], increasing the number of tree genera had an upper-mycodiversity effect in Fennoscandia's forests [Kebli *et al.*, 2012].

Other measures might be the introduction of shade-tolerant tree species in low-light forests [Kebli *et al.*, 2012], for increasing diversity in monodominant coniferous forests.

Being positively and significantly related to mycodiversity, stump decay [van der Wal *et al.*, 2017] is influenced by stump diameter and the time passed since cutting [Melin *et al.*, 2008]. This means that, in the cases of clear-cuts, the more diameter variation, the more mycodiversity. However, in selective cutting, according to which trees are cut only when they reach a particular age, this might create stumps of approximately same decay stage, thus leading to reduced stump mycodiversity. In managed forests, cutting trees of different dimensions might favour mycodiversity increase.

An interesting proposal is burning of forest stands, once seen that, in time, mycodiversity exceeds pre-fire numbers and increases red-listed species [Penttilä *et al.*, 2013]. Also, from an economic perspective, burning of *Heterobasidion annosum* s.s. infected *Pinus mugo* plantations, possibly reduces its incidence in the respective areas [Lygis *et al.*, 2010]. Equally, infected stump removal could reduce *H. annosum* propagation through the root system from approximately 17% to 1% [Stenlid, 1987].

Investigations on the management of a forest ecosystem for both economic and myco-conservation applications, cause dual, sometimes even contradictory effects. Preserving dead wood in the forest, yet eliminating the infected one, means that complex evaluations must be done in order to apply proper silvicultural techniques and assure the conservation of lignicolous fungal diversity and composition.

7. CONCLUSIONS

Through their ability to degrade wood components, lignicolous fungi integrate carbon and other nutrients into the forest ecosystem, thus maintaining the natural habitat and indirectly keeping alive forest's living beings - from small saproxylic organisms to trees.

Numerous ecological situations preserved by the complex forest biotic and abiotic interactions diversify the decay mechanism, with implications upon fungal diversity and composition.

The most important biotic interactions of lignicolous fungi here analysed involve tree taxons, starting from diversity to forest composition and fungi-to-fungi interactions, from competition to peaceful cohabitation.

In terms of forest-fungi interactions, wood necromass is generally accepted as the most important forest component, supporting lignicolous fungal diversity and composition.

Each type of lignicolous fungi, either decay pioneers or final stage wood decayers, white rot or brown rot, belonging to either *Ascomycota* or *Basidiomycota*, demonstrate that their relations with forest dead wood is at the core of forest functionality.

Ecosystem's abiotic components diversify even more such interactions, as topography-derived local to regional characteristics and climatic differentiation have a great influence on substrate humidity and temperature regimes, affecting considerably the living conditions of lignicolous fungi.

Even more, disturbances have multiple effects on the diversity and composition of lignicolous fungi, through their capacity of dramatically changing the stable environmental conditions.

As nature prevails in cases of climatic disturbances, through mycodiversity recovering, anthropic actions over the forest have been generally described as unfavourable on long term.

In all temperate forest ecosystems, human interventions, such as clearings or structural and compositional changes, reduced mycodiversity and caused the extinction of numerous fungi.

Therefore, it is important to apply responsible management measures over forest ecosystems to maintain their large mycodiversity, for preserving carbon and for conserving the largest land ecosystem on Earth.

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