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How does forest management affect fungal diversity and community composition? Current knowledge and future perspectives for the conservation of forest fungi

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ABSTRACT

The influence of forest management on fungal diversity and community composition has been the subject of a wide number of studies over the last two decades. However, the difficulty of studying the complex kingdom of fungi under real forest conditions has led to rather scattered scientific knowledge. Here, we provide the current state of knowledge suggesting future research directions regarding (i) stand structure attributes (age, tree cover, stand density, tree species composition), (ii) management history (managed vs unmanaged), (iii) silvicultural treatments (thinning, clearcutting, shelterwood methods, selective cutting) and (iv) other anthropogenic disturbances (mushroom picking, salvage logging, prescribed burning, fertilization) affecting fungal diversity and community composition. The reviewed studies reported a positive correlation between fungal diversity and stand structure variables such as canopy cover, basal area of the stand and tree species diversity, particularly for mycorrhizal species. Abundance and diversity in size, tree species and decomposition stage of deadwood are reported as positively related to richness of wood-inhabiting fungi. The main findings about the effects of silvicultural practices suggest that the higher is the management intensity the lower is the diversity of ectomycorrhizal and wood-inhabiting species, at least in the short term. We have therefore reported those silvicultural practices which may reduce trade-offs between timber harvesting and fungal diversity conservation. Indeed, fungal diversity can be conserved in managed forests if (i) low impact logging operations are performed; (ii) stand structural complexity and late-successional forest characteristics are enhanced; (iii) deadwood amount and diversity is promoted, (iv) landscape heterogeneity and connectivity is improved or maintained.

1. Introduction

Fungi are an extremely diverse group of organisms critically important to forest ecosystem functioning. Particularly, ectomycorrhizal and saprotrophic fungi play important roles in nutrient cycling (Cairney and Meharg, 2002) and are recognized as fundamental components of biodiversity and ecosystem functioning (Clemmensen et al., 2015, Steidinger et al., 2019). Indeed, ectomycorrhizal fungi are mutualists with plant roots but can also act as decomposers by oxidizing organic matter to obtain nitrogen (Lindahl and Tunlid, 2014), whereas saprotrophic fungi are the main responsible of hydrolytic degradation of organic matter (Hobbe et al., 1999). Preserving fungal diversity in forest ecosystems is important since (i) a positive relationship between microbial diversity (fungi and bacteria) and ecosystem multifunctionality has been shown in several ecosystems (Delgado-Vaquerizo et al., 2016; Duffy et al., 2017; Laforest-Lapointe et al., 2017). From a broad perspective along the successional forest ecosystem stages, (ii) forest ecosystem development and associated processes have been shown to be tightly linked to the composition of the fungal community (Clemmensen et al., 2015); therefore, maintaining diverse communities at landscape level should result in enhanced ecosystem succession. In addition, (iii) despite the specific functions from several fungi are still not known, a growing body of the literature is showing how specific fungal species develop crucial ecosystem processes. For example, specific *Cortinarius* species are involved in the oxidation of the organic matter in boreal ecosystems (Kyaschenko et al., 2017) and specific fungal species (i.e. *Meliniomyces*, *Cenococcum*) with structures resistant to degradation (e.g. melanin) may be contributing

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to soil C storage (Fernandez et al., 2019). In addiction, other fungal species (i.e. cord forming species such as *Suillus*) have been shown to efficiently transfer N to their hosts, promoting higher primary production (Clemmensen et al., 2015), as compared to other symbionts. Diversity and abundance of forest fungi also support diversity and abundance of other taxonomic groups. Thus, forest fungi are an important food source for wildlife (Worthen and McGuire, 1990). In addition, fungal fruit-bodies of these two functional groups also provide important provisioning and cultural ecosystem services, as they constitute the main resource of socioeconomic activities based on mushroom picking for both recreational and commercial purposes (Martínez de Aragón et al., 2011; Górriz-Mifsud et al., 2017). Moreover, soil fungal mycelium is also an important food source for other organisms living in soils, such as collembolan species (Heděnec et al., 2013) or fungal mycoparasites (Lindahl et al., 2010). Therefore, fungal diversity conservation is essential to maintaining the provision of multiple ecosystems services that are crucial to both forest ecosystem functioning and human well-being (Millennium ecosystem assessment, 2005; Heilmann-Clausen et al., 2014). Any loss of fungal diversity is potentially harmful, even though some functional redundancy may exist among several groups of fungi (Talbot et al., 2014). The taxonomic diversity of fungi is classically known from their reproductive structures, i.e., sporocarps. In the Eumycota, more than 140,000 species have been described (lndex Fungorum, 2019). However, Hawksworth and Lucking (2017) suggested a true diversity ranging from 2.2 to 3.8 Million species, while Larsen et al. (2017) estimated a number of fungal species higher than 150 Million. Hence, it is clear that much of global fungal diversity remains to be documented (Taylor et al., 2014). Most of fungal species depend on living or dead plants for their energy supply, and therefore there has long been an interest in comparing and relating plant and fungal diversity (Taylor et al., 2014).

Many different factors drive fungal species diversity and community composition. Forest landscape attributes, soil properties and climatic conditions are well-known drivers of both ectomycorrhizal and saprotrophic fungal diversity at multiple scales (Jansa et al., 2014; Andrew et al., 2016; Alday et al., 2017; Schappe et al. 2017). Moreover, forest fungi are also highly sensitive to vegetation composition, shifts and dynamics (Packham et al., 2002; Lauber et al., 2008; Landi et al., 2015). As a result, forest fungal diversity faces multiple potential threats such as habitat loss and fragmentation (Grilli et al., 2017), nitrogen deposition (Lilleskov et al., 2011, 2019), climate change (Dahlberg et al., 2010) or wildfires (Salo and Kouki, 2018). Declining area of old-growth forests and intensification of timber production have been also reported as disturbances for fungal diversity in forest ecosystems since they can cause a lack of ecological continuity (Dahlberg et al., 2010).

Indeed, since fungal diversity and community composition are strongly dependent on forest structural attributes, they are likely to be affected by forest management and silvicultural practices, which can entail considerable changes in the forest ecosystems, e.g., by removing and/or replacing tree species, altering the age class structure, altering biomass and carbon dynamics and modifying the proportion of deadwood (Paillet et al., 2010), as well as modifying microclimatic and soil conditions (Wiensczyk et al., 2002). Although forest management practices have been studied regarding their effect on sporocarp productivity (Tomao et al., 2017), there is even a higher need for understanding also the impact of forest management-related anthropogenic disturbances on fungal diversity and community composition, and how these community changes affect fungal functional attributes. However, there is still a significant lack of knowledge about this topic, which prevents the development of sound guidelines and best management practices to preserve fungal diversity (Bonet et al., 2010). Indeed, previous research has been scattered, based on localised studies and mostly focused on specific functional groups such as ectomycorrhizal or saprotrophic (mainly wood-inhabiting) fungi. Given the increasing interest in the conservation of fungi (Moore et al. 2001; Molina, 2008; Heilmann-Clausen et al., 2014), a compiling effort of the existing knowledge on the links between forest management and fungal diversity is therefore necessary, but currently missing in the scientific literature.

Bearing in mind these considerations, this study aims at reviewing the current knowledge on the effect of forest management on the diversity of saprotrophic fungi (including litter, soil and wood-inhabiting species) and ectomycorrhizal fungi. Following this introduction and a methodology section describing the literature selection procedure, we review the relationships between forest stand structure and fungal diversity and fungal communities (Section 3). Then, we review the effects on fungal diversity caused by (i) the absence of forest management (Section 4); (ii) the main silvicultural practices in even-aged forestry (Section 5) and in continuous cover forestry (Section 6); and (iii) other management practices and anthropogenic disturbances (i.e., mushroom picking, logging, prescribed burning, fertilization) (Section 7). In Section 8, we draw conclusions and guidelines about the preferable forest management practices for fungal diversity conservation. Lastly, Sections 9 and 10 summarize the main findings from the literature review, discuss knowledge gaps and recommend areas for further research.

2. Literature selection

We selected the scientific literature from a search performed in December 2018, in which we looked for studies reporting the effect of forest management activities on fungal diversity and fungal communities. Relevant publications were identified by searching the online database of ISI Web of Science using the following search words: "((forest management OR silviculture) AND (fungal diversity OR fungal richness OR fungal communit*))".

This search identified 1337 publications, which were initially filtered by title and abstract (67) before reading the full text. This list was supplemented by examining references of these articles for additional publications. We retained a paper in the literature when it was associated with one or more categories of interest (i.e. forest stand attributes, silvicultural or other management practices). We included in the literature only research papers or reviews published in peer reviewed journals, preferring papers published in English. The literature selection was updated on 17th September 2019.

Regarding the content, we have included papers dealing with different sampling strategies aimed at assessing fungal diversity and community composition. Traditionally, fruiting body samplings were the most reliable approach to sample fungal communities. Unfortunately, since a large part of the fungal life cycle occurs in microscopic stages and belowground, fruiting body samplings only target a small fraction of the whole community. During last years, an increasing body of the literature is progressively using DNA metabarcoding approaches to profile fungal communities occurring mostly during mycelia stages, which should give a more complete picture of the fungal community colonizing distinct substrates (i.e. wood, litter, soil). However, due to still large methodological pitfalls and biases of these new technologies (Nilsson et al., 2018), and to the fact that the both methods (fruiting body sampling and DNA metabarcoding) rely on distinct stages of the fungal community life-cycle, the sensitivity of each fungal life-stage to environmental drivers and disturbances may be different. When possible, here we try to illustrate literature findings based on both approaches and highlight potential discrepancies.

This process produced a list of papers (Table S1) that, nevertheless, is not meant to be a full representation of all papers ever published on this topic. Indeed, during the literature selection we ceased the search for literature on a specific item when there was enough agreement about the results.

3. Effect of forest structure on fungal diversity and fungal communities

3.1. Stand age and successional stage

Various studies have shown changes in fungal community composition of sporocarps along forest succession, both for fungi inhabiting the soil or litter (e.g. Dighton and Mason, 1985; Hintikka 1988; Senn-Irlet and Brieri, 1999; Twieg et al., 2007) and the wood (Junninen et al., 2006). Fungal community composition and its dynamics have been proved to be influenced by the age of the associated host trees (Bonet et al., 2004; Ágreda et al., 2014) or the wood decay successional stage (Rajala et al., 2011; Seibold et al., 2015). In addition to changes in composition, several studies found changes in fungal diversity across forest age gradients (e.g., Twieg et al., 2007). For example, while higher sporocarp production has been observed in young and open *Picea excelsa* stands, a greater species richness has occurred in mature closed-canopy forest (Senn-Irlet and Bieri, 1999). Fungal community changes observed along age gradients are potentially related to several changes of site conditions, including modification of tree growth patterns, of carbohydrates amount available from the root system and of microclimate (e.g., less light reaching to the forest floor). Kyaschenko et al. (2017) related such effect also to changes in soil chemistry. They observed shifts from early-stage fungal communities specialized in organic matter decomposition toward, at later stages, mycorrhizal communities related with mobilization of nutrients from organic matter.

3.2. Tree cover

Overall, there is a positive relationship between the diversity of sporocarps of mycorrhizal fungi and tree cover (Villeneuve et al., 1989; Laganà et al., 1999; Baral et al., 2015). In this regard, results from Santos Silva et al. (2011) showed that canopy cover strongly shaped macrofungal communities in cork and holm oak open ecosystems. These authors showed that part of these compositional changes were driven by changes in richness in mycorrhizal fungi, with canopy cover around 50% having higher richness of mycorrhizal fungi compared to stands with lower canopy cover (around 30%). Therefore, canopy cover seems to be positively related to fungal diversity, particularly for mycorrhizal species (Fig. 1). Twieg et al. (2007) observed the greatest increase of average alpha fungal diversity in *Pseudotsuga* and *Betula* mixed stands where tree canopy closure is reached. Only a slight increase was observed thereafter. This coincides with the observation made by Dighton and Mason (1985) that the greatest species diversity seems to occur when there is canopy closure. Spake et al. (2016) also demonstrated that species richness of sporocarps of ectomycorrhizal macrofungi was principally related to the basal area of the stand (correlating with canopy cover).

These positive relationships between tree cover and fruiting body production parallel with observations below-ground biomass, with production of ectomycorrhizal mycelium also observed to peak during canopy closure (Wallander et al., 2010). However, the relationships between the above and below ground fluxes in mycorrhizal biomass remains unknown.

Tree cover affects also diversity of wood inhabiting fungi (Bässler et al., 2010) due to a change of microclimate conditions. Indeed, openness of the canopy influences temperature, variations in temperature and water availability, which are critical for fungi-driven wood decay (Rayner and Boddy, 1988). Even though microclimate was demonstrated to influence wood-inhabiting fungal diversity less than other variables (e.g. host tree diversity) (Krah et al., 2018b), Bässler et al. (2010) demonstrated that changes in microclimate conditions are important for richness and community composition of fungi living on woody debris, especially in the case of fine debris. Variables such as "exposure to sunlight" clearly linked to tree cover were found to be negatively associated to fungal species richness. The authors explained this effect with the negative effect of fluctuating microclimate on ephemeral, soft and thin fruiting bodies of some wood-inhabiting species (e.g. corticoids), which are common on fine debris (Berglund et al., 2005). Krah et al. (2018b) demonstrated how differences in canopy openness in the same forest can lead to a greater abundance of host specialists under shady canopies that shift towards communities dominated by host opportunists or microclimate harshness specialists in sunny gaps, thus leading to a higher diversity at stand level.

3.3. Tree species composition

Forest fungi also show high sensitivity to vegetation shifts and dynamics (Lauber et al., 2008). Indeed, even though there are cosmopolitan fungi associating with several host species (Krah et al., 2018a), there is a significant relationship between forest fungal communities and vascular plant composition (Packham et al., 2002; Goldmann et al. 2015; Landi et al., 2015; Krah et al., 2018b). This is partly due to the preference for specific host trees in the case of ectomycorrhizal species, as well as to differences in the litter properties and tree debris (i.e., needles, cones, and leaves) in the case of saprotrophic fungi (Vašutová et al., 2016). Furthermore, trees are also known to impact soil properties according to exudation patterns and root architecture (Bakker et al., 2014).

Cavard et al. (2011) concluded that ectomycorrhizal species richness is positively related to diversity of host tree species. This result is consistent with those reported by Rumberger et al. (2004) who found that Scots pine-beech mixed forests showed higher ectomycorrhizal richness than monocultures. Observed higher fungal species richness in these stands has been attributed to the species accumulation effect resulting from each host tree. Spake et al. (2016) showed that richness of both ectomycorrhizae and sporocarps of ectomycorrhizal species are positively associated to tree species diversity. Krah et al. (2018b) observed that host tree species is a more important driver of the community composition and the diversity of wood-inhabiting fungi than the environmental conditions (i.e. microclimate) or the host size.

With regards to fungi inhabiting forest soils belowground, the association between tree diversity and fungal diversity is still debated. Some authors found that tree species richness positively affect alpha diversity of soil fungi (Chen et al., 2017) both directly and indirectly (e.g. through modifications of soil properties in the different soil layers) (Thoms et al., 2011), suggesting that impacts of tree diversity on fungal diversity is rather complex. In other cases, no differences in fungal alpha diversity were found between pure and more diverse mixed stands (Massicotte et al., 1999; Durall et al., 2006; Tedersoo et al., 2016). These inconsistent diversity patterns may be explained by the inherent functional complexity of fungal communities inhabiting soils, which is not only related to host trees, but also to other biota, substrate availability and physico-chemical soil conditions (Cairney, 2012) that could overshadow the effects of host tree on fungal diversity.

3.4. Deadwood

Deadwood is a substantial component of forest structure and plays a relevant role for biodiversity conservation since it provides habitats for a multitude of wood-dependent organisms (Fig. 1) (Parisi et al., 2018). Deadwood can be divided into stumps, standing (dead trees, snags) and lying deadwood (logs, branches and twigs). Deadwood type and diversity affect fungal diversity due to the different species requirements for their enzymatic activities (e.g., moisture, wood density, chemical composition of wood). Pouska et al. (2010) and Shorohova and Kapitsa (2014), report that snags host lower diversity of sporocarps if compared to logs and stumps since microclimatic conditions are less stable and habitat availability is lower. Further, stumps are reported to host a lower species diversity than lying logs (Lindhe et al., 2004; Blaser et al., 2013).

Lying deadwood is usually classified according to its size in coarse

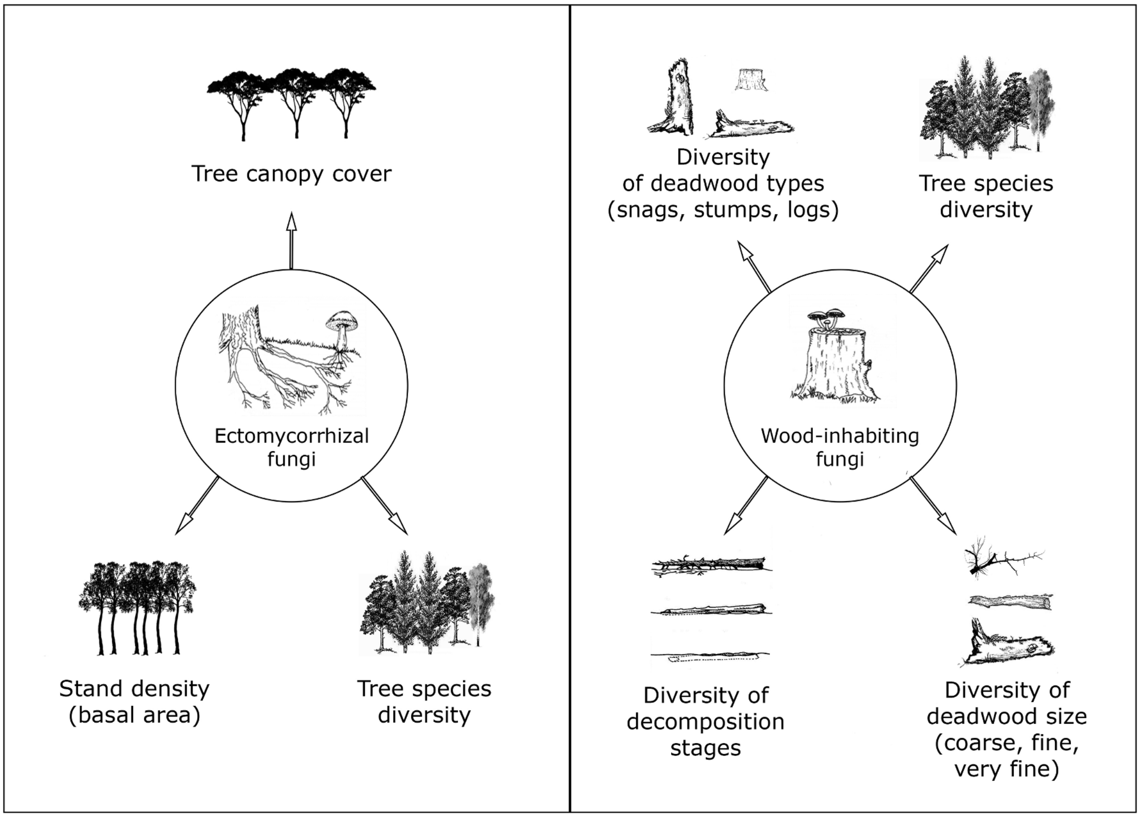

Fig. 1. Main forest stand structure attributes having a positive effect on diversity of ectomycorrhizal and wood-inhabiting fungi.

woody debris (mean diameter greater than 10 cm), fine woody debris (mean diameter between 5 and 10 cm) and very fine woody debris (mean diameter smaller than 5 cm) (Küffer and Senn-Irlet, 2006; Juutilainen et al., 2014). The size of deadwood has been proved to influence fungal diversity: a positive relationship between coarse woody debris size and wood-inhabiting macrofungal species richness has been reported by several authors (e.g. Heilmann-Clausen and Christensen, 2004; Blaser et al., 2013; Seibold et al., 2015). This is likely due to the longer persistence of deadwood with larger diameters on the forest floor because of a lower decomposition rate. Thus, the coexistence and the succession of a higher number of species with different ecological requirements can occur on larger logs (Grove and Forster, 2011; Parisi et al., 2018). Moreover, according to the species-area theory, habitats with a larger area are expected to support more species than smaller ones (MacArthur and Levins, 1967; Martínez de Aragón et al., 2007) and there is a limit to the number of competing species which can coexist (MacArthur and Levins, 1967; Seibold et al., 2015). However, the abundance of fine and very fine coarse debris also supports fungal diversity (Lindner et al., 2006). Juutilainen et al. (2011) demonstrated that species richness could be underestimated by at least 10% if fine deadwood is not considered.

Decay stage has been also reported as an important factor influencing wood-inhabiting fungal diversity (Abrego and Salcedo, 2011). Kubartová et al. (2012) attributed the changes in fungal mycelium diversity and composition to changes in fungal species according to their different ecological strategies. Similarly, Rajala et al. (2011) observed a shift from soft-rot fungi inhabiting early stages of decomposing wood, to white, brown-rot and ectomycorrhizal fungi in late wood decomposition stages. In this regard, based on both sporocarp surveys and fungal DNA metabarcoding of decaying logs, species richness increases in more advanced decomposition stages (Fischer et al., 2012; Kubartová et al., 2012; Rajala et al., 2011; Penttilä et al., 2013). Parisi et al. (2018) suggest that heterogeneous decomposition of highly decayed deadwood supports a more diverse fungal community since it hosts a greater variety of microhabitats. Moreover, logs characterized by an advanced decomposition are reported as relevant habitats for rare and threatened species (Berglund et al., 2011).

The positive effect of amount of deadwood, diversity of deadwood size and stage of wood decomposition on wood-inhabiting fungal richness and community composition has been also described for tropical ecosystems (Olou et al., 2019), suggesting a general pattern of the diversity drivers of wood-inhabiting fungi across ecosystems worldwide.

4. Managed *versus* unmanaged forests

If no management practices are performed for a long time, stands may gradually evolve into so-called “old-growth forests”. In the absence of anthropogenic disturbances, forests may slowly recover the natural disturbance dynamics (forest fires and windstorms, parasite outbreaks, fungal decay, gap creation due to insects) and develop those stand structural features (large living trees, large amount of deadwood, canopy gaps of various size, coexistence of senescent, mature and initial stages) typical of primary forests (Burrascano et al., 2013). In such unmanaged old-growth-like forests, the life cycle of trees is not interrupted by any silvicultural operation, and natural dynamics are not controlled by forest management (Heilmann-Clausen et al., 2017). Thus, total living biomass and richness, and the abundance of deadwood habitats, are different from those in managed mature forests (Hilmers et al., 2018).

Old-growth forests are recognized as an important reserve of fungal diversity for several fungal functional guilds. Indeed, a very large number of ectomycorrhizal species can be hosted in old growth stands (Richard et al., 2004; Zhang et al., 2017). In this regard, Kranabetter et al. (2018) found up to 238 ectomycorrhizal fungal species (detected by molecular analysis of root tips and sporocarps collection) in old-growth *Pseudotsuga menziesii* stands in British Columbia (Canada). According to the meta-analysis by Spake et al. (2015), 90 years was the

Table 1
Effect on fungal diversity and on change in fungal species composition caused by thinning and regeneration cuts in the selected experiments carried out in even-aged forests.

Silvicultural practice	Target group	Effect	Dominant tree species	Reference
Thinning	Ectomycorrhizal, saprotrophic and parasitic fungi	Change in macrofungal species composition after thinning even if there was no difference in plot-wise species richness	*Shorea robusta*	Baral et al. (2015)
	Ectomycorrhizal, soil-inhabiting saprotrophic, wood-inhabiting fungi	A decrease in macrofungal species richness in both medium and high intensity thinned stands	*Cryptomeria japonica*	Lin et al. (2015)
	Ectomycorrhizal fungi	Decrease of species diversity	*Quercus suber*	Maghnia et al., 2017
	Saprotrophic, macrofungi	Increase of species richness in light intensity thinned stands	*Chamaecyparis formosensis*	Lin et al. (2011)
	Wood-inhabiting fungi	Decrease of species richness Species with a significant preference for stumps are more frequent with increasing management intensity	*Fagus sylvatica*	Müller et al. (2007)
	Ectomycorrhizal and soil-inhabiting saprotrophic species	No significant effect on fungal species richness and diversity	*Pinus pinaster*	Castaño et al. (2018)
Clear-cut	Ectomycorrhizal species	Decrease of ectomycorrhizal species richness and diversity	*Pinus contorta; Abies lasiocarpa; Picea engelmannii;Pseudotsuga menziesii; Betula papyrifera; Pinus sylvestris*	Bradbury (1998), Hagerman et al. (1999), Jones et al. (2003), Twieg et al. (2007), Parladé et al. (2017, 2019)
Shelterwood methods/ retention forestry	Wood-inhabiting fungi	Decrease of species richness	*Picea abies*	Toivanen et al. (2012)
	Ectomycorrhizal species	Decrease of sporocarp producing species with decreasing tree retention	*Pseudotsuga menziesii*	Luoma et al. (2004)
		Almost all of the ectomycorrhizal species belowground are retained with retention of 30% of the trees	*Pinus sylvestris*	Sterkenburg et al. (2019)
		Retained trees preserve ectomycorrhizal communities locally but have no effect on the surrounding harvested areas	*Pseudotsuga menziesii; Tsuga heterophylla; Pinus sylvestris;*	Luoma et al. (2004, 2006b); Jones et al. (2008), Varenius et al. (2017)
		Timber harvest has a minor effect on ectomycorrhizal richness in a 30–50 year perspective even if a significant effect on fungal community composition lasts	*Pinus sylvestris*	Varenius et al. (2016, 2017)

average time for recovery to old-growth values of ectomycorrhizal fungal richness, which suggests that fungal diversity can be restored if stands are no longer managed for a long time.

A recent study about ectomycorrhizal sporocarp richness shows higher species richness in beech- and spruce-dominated managed forests in Czech Republic, compared to non-managed stands (Dvorak et al., 2017). Goicoechea et al. (2009) did not find any difference in the number of observed root ectomycorrhizal morphotypes between old-growth and clear-cut beech stands in Spain. These partially inconsistent results may be explained by the different investigated forest ecosystems and the different methods used for surveys. In this regard, Dvorak et al. (2017) suggest that looking only at sporocarps could lead to an underestimation of actual ectomycorrhizal diversity because the fructification of ectomycorrhizal fungi in unmanaged forests dominated, for example, by beech may be less frequent and patchier than in other forest types. This bias is particularly evident if the monitoring period is short (one or two years), which, opposite to long-term inventories, may prevent the proper detection of many rare species.

When looking at saprotrophic species, old-growth forests tend to have higher richness compared to managed stands (Dvorak et al., 2017), especially when wood-inhabiting fungi are considered. Since the total amount of deadwood is usually higher in unmanaged forests, many authors have argued that they are crucial for preserving diversity of wood-inhabiting fungi (Heilmann-Clausen et al., 2017). For instance, Juutilainen et al. (2014) found that fungal diversity found in coarse woody debris, and partially fine woody debris, was higher in unmanaged than in managed *Picea excelsa* dominated forests. Spruce forests –unmanaged since the beginning of 1900– also represented the habitat for most of the rare species detected in that study. Abrego and Salcedo (2013) reported similar results for beech stands in Northern Spain, i.e., lower diversity of wood-inhabiting fungi in managed forests due to the lack of the niche they require. Indeed, species present only in unmanaged forests were found on deadwood in advanced stages of decomposition or on coarse woody debris, which are usually the most reduced deadwood types in managed forests. Similarly, Halme et al. (2017) found that old-growth forests are very suitable habitats for rare species of wood-inhabiting fungi such as *Hericium herinaceus* (Kunca and Ciliak, 2017).

Blaser et al. (2013) compared unmanaged and managed forests in central Europe, finding lower sporocarp species richness of wood-inhabiting fungi in unmanaged forests than in managed forests. The authors explained this result because of the lack of natural tree death during the short time since management abandonment (10–30 years). Runnel and Lõhmus (2017), comparing wood-inhabiting sporocarp fungal communities of old-growth and managed forests in Estonia, found that managed forests can host most of old-growth associated polypores, with the only exceptions of some rare species (Saar et al., 2007). Spake et al. (2016) also reported that set-aside broadleaved plantations (around 180 years old) can attain the species richness of old-growth semi-natural forests (1000 years old). Similar results have been showed by Oria-de-Rueda et al. (2010) in the Mediterranean context. These evidences may be explained inasmuch as management represents a source or type of "disturbance", which can therefore provide new opportunities of colonization for diverse fungal communities.

5. Even-aged forest management

5.1. Thinning

Thinning is the removal of a fraction of trees within a stand in order to enhance the growth of the remaining trees by reducing the competition among them. It is a very common silvicultural operation in even-aged stands, where successive thinning cuts may be combined along the rotation period. As an anthropogenic disturbance, it may affect biodiversity and related forest ecosystem processes (Bengtsson et al., 2000), especially if the effects of these disturbances are then amplified by other environmental drivers such as drought or extreme rainfalls (Kauserud et al., 2008).

Regarding its effect on fungal communities, many authors have found a decrease of ectomycorrhizal species richness after thinning (Table 1). Baral et al. (2015) report that community-managed sal (*Shorea robusta*) forests in central Nepal experienced a change in macrofungal species composition after thinning even though there was no difference in plot-wise species richness. The authors explained it as the combined results of fungal succession (Frankland, 1998) and improvement in forest health. In particular, they found a slightly higher proportion of mycorrhizal fungi – an indicator of forest health according to Egli (2011) – in the stands managed for > 10 years (35%) than in those managed for < 10 years (30%). Lin et al. (2015) observed a decrease in species richness of saprotrophic macrofungi in both medium– (25% of trees) and high-intensity (50% of trees) thinned stands in arbuscular-associated *Cryptomeria japonica* plantations. Similarly, managed and thinned *Quercus suber* stands hosted lower ectomycorrhizal diversity as compared to unmanaged stands (Maghnia et al., 2017). This result can be explained by the effect of thinning on microclimatic conditions (more accelerated wetting and drying of the soil) (Pilz and Molina, 2002), which can lead to a change in the presence and abundance of fungal species based on their specific temperature and water requirements. At the same time, the removal of host trees can reduce the populations of mycorrhizal species in the soil even if mycorrhizal fungi associated to the remaining trees may thrive (Bonet et al., 2012) due to the increased allocation of carbohydrates to the mycorrhizal fungi from the enhanced-growing remaining trees (Savoie and Largetau, 2011). In any case, thinning effects on mycorrhizal communities depend on whether the remaining trees can host mycorrhiza of these communities (Rosenvald and Lohmus, 2008) and on the specific conditions of the forest site, on the impacts of harvesting operations and on intensity of forest thinning (Bonet et al., 2012). Indeed, Lin et al. (2011) found a higher species richness of saprotrophic macrofungi in lower intensity thinned stands (removal of around 30% of trees) of *Chamaecyparis formosensis* plantations compared to the heavily thinned (around 50% removal) or the unthinned stands. Even for wood-inhabiting fungi, species richness has been found to be lower in thinned stands, especially if intensive thinning is applied and most of the deadwood is removed (Müller et al., 2007). Species linked to coarse woody debris habitats are associated to low management intensity. In addition, lower fungal richness has been found in beech forests subjected to higher levels of wood extraction, in comparison with natural or semi-natural forests (Purahong et al., 2014a). However, a positive effect of thinning may be the increase of tree stumps, i.e. fungal species with a significant preference for them can be more frequent with increasing management intensity (Müller et al., 2007; Parisi et al., 2018).

When considering fungal communities belowground, forest management may also influence composition and diversity (Jones et al., 2003; Hartmann et al., 2012). In this regard, Castaño et al. (2018) report that thinning did not significantly affect fungal community composition nor fungal species diversity. Neither saprotrophic nor ectomycorrhizal species richness was reduced by thinning, regardless its intensity. The authors explain the results suggesting that (i) substrates of saprotrophic species were not affected by the thinning operations and that (ii) most ectomycorrhizal species can survive belowground supported by the remaining trees, seedlings or other ectomycorrhizal plants remaining in the plots by maintenance of the so-called fungal networks.

5.2. Regeneration methods

Regeneration methods are harvesting techniques that aim to successfully establish a new cohort of trees that contributes to the forest renovation. Regeneration methods in even-aged stands can be categorized into two main groups: clear-cutting and shelterwood methods. Clear-cutting is a silvicultural operation in which all the trees are removed at the same time. Conversely, shelterwood methods are a progression of high intensity thinnings in which some living trees are retained to produce and spread seeds to support regeneration. Such forest management practices produce a significant disturbance in forest stands and affect diversity in general. As demonstrated by Chaudhary et al. (2016), retention forestry and clear-cutting have a very different effect on species richness depending on the examined taxa (birds, arthropods, plants, mammals, fungi, etc.). Similarly, many ecosystem processes occurring in soils such as organic matter decomposition are also affected by clear-cutting (Kohout et al., 2018). In the particular case of fungi, both clear-cutting and shelterwood regeneration methods can cause a lowering of fungal diversity (see Table 1).

Fungal diversity is strongly affected by clear-cutting. This practice can lead to an important reduction of ectomycorrhizal species (Jones et al., 2003; Twieg et al., 2007; Parladé et al., 2017; 2019) and to a change in soil fungal community composition (Kyaschenko et al., 2017). These effects are particularly pronounced if recolonisation of new roots by mycorrhizal fungi is not supported by the presence of stumps (Toivanen et al., 2012) and living roots after the regeneration cut (Peter et al., 2013). In this regard, if retention trees are preserved from the clear-cut, the mycorrhizal fungal diversity has been proved to be higher than in stands where all the trees are removed (Rosenvald and Lohmus, 2008). Recent studies from Sterkenburg et al. (2019) show that tree retention enhance the maintenance of the most frequent ectomycorrhizal species belowground in boreal forests. The same authors showed that almost all the ectomycorrhizal species were retained with tree retention values of 30%, in contrast to clear-cuts, which resulted in the loss of 95% of the ectomycorrhizal species. Similar results have been found by Parladé et al. (2019) in Mediterranean forests. In addition, fungal communities have been shown to be resilient and resistant to variable-retention harvesting (Philpott et al., 2018). Indeed, remnant trees act as a fungal reservoir from which mycorrhizal fungi colonize tree regeneration roots (Dahlberg et al., 2001; Luoma et al., 2006b; Peter et al., 2013). Luoma et al. (2004) compared different levels and spatial patterns of tree retention (from 15 to 100% retention in stand basal area and comparing dispersed vs aggregated retention trees) and found that richness was reduced most in the plots were only 15% of trees were dispersedly retained, whereas 75% tree retention showed the lowest richness reduction. On the other hand, a more recent study by Varenius et al. (2017) reports that ectomycorrhizal fungal communities in managed boreal *Pinus sylvestris* stands are more influenced by environmental filtering, resulting from environmental changes induced by harvest, than by the continuity of trees. The authors suggest that ectomycorrhizal fungal species adapted to conditions in old natural stands could not cope with the overall new environmental conditions induced by the harvest, regardless of whether seed trees were retained or not. Permanently retained trees seemed to maintain ectomycorrhizal communities of old natural stands locally but had no effect on the surrounding harvested areas. This is in line with the study of Jones et al. (2008), who reported that ectomycorrhizal communities in retention patches of 5 m in diameter are very similar to those of the unharvested forests, whereas this “conservation” effect disappeared 10 m into the harvested area.

The effects of final cuts on fungal community composition inhabiting soils can last for several decades after harvest. For instance, in *Pinus sylvestris* boreal stands studied by Varenius et al. (2016, 2017), significant differences in diversity and community composition remained 30–60 years after harvest regardless of the regeneration method (using seed trees or through replanting of clear-cuts). However, species richness resulted similar to undisturbed stands after such period, suggesting that timber harvest has a negligible effect on ectomycorrhizal species richness in a 30–50 year perspective (Varenius et al., 2016). However, how these effects remain along time may depend on the intensity of the regeneration methods used and on the forest ecosystem itself. For example, Sterkenburg et al. (2019) have recently shown that most of the ectomycorrhizal taxa are preserved also in the short term when only 30% of the trees are retained in *Pinus sylvestris* stands. On the other hand, a long lasting effect was found by Kranabetter et al. (2005), who showed that large differences in species composition of epigeous macrofungi can last for up to 120 years in naturally regenerated western hemlock – lodgepole pine forests.

6. Uneven-aged forest management in continuous cover forestry

Uneven-aged forests, where tree cover is continuously maintained (Pukkala and von Gadow, 2012), are usually managed by selective cutting. This silvicultural practice is considered to constitute a close-to-nature forest management because it is based on natural regeneration and creates unevenly aged forest structures as found in unmanaged or pristine forests (Gossner et al., 2013). Indeed, continuous cover forestry is considered by several authors a promising silvicultural technique for maintaining forest biodiversity (Torras and Saura, 2008; Légaré et al., 2011). Purahong et al. (2014b) found that fungal richness after selection cutting is not significantly different from that of unmanaged forests with regards to wood-inhabiting fungi. They also compared it with diversity in even-aged stands, where richness of wood-inhabiting fungi resulted significantly lower. Similar results were found for leaf-litter fungal communities (Purahong et al., 2015).

Dove and Keeton (2015) found that neither single tree nor group selection significantly reduce fungal species richness in a mixed broadleaved-coniferous forest, particularly if management practices that minimize site impacts are undertaken: e.g., logging conducted on frozen ground to minimize soil compaction and releasing residual coarse wood debris.

However, since in selection cutting most large trees are harvested (Qiu et al., 2006), this management approach can be also considered to be intensive (Purahong et al., 2014b). Removing single big trees or small groups/patches of trees in order to facilitate regeneration results in forest gap creation. Opening of gaps in the canopy cover has been associated to a reduction of diversity of ectomycorrhizal mushrooms in the gaps in comparison with closed canopy stands (Grebenc et al., 2009), especially if larger gaps are opened and all the trees in the gap are removed (De Groot et al., 2016). These results are consistent with the findings of Bässler et al. (2014), who demonstrated that selective cutting alter natural fungal community assembly processes, since near-to-nature logging may act as a habitat filter in promoting species able to respond more flexibly to the disturbance. This effect is more sensible if management intensity increases by removing overmature trees and dead wood from the stand (Bader et al., 1995). The effect of the creation of canopy gaps over saprotrophic fungal diversity has been tested by Brazee et al. (2014). They did not find significant reduction in species abundance, but when coarse woody debris was created and retained in the stand, species abundance and diversity consistently improved.

7. Other forest management practices and disturbances

7.1. Mushroom picking

Since in the last decades picking mushrooms for recreational or market purposes have become a popular activity, overharvesting and possible damage to fungal resources have been studied. Even if there are only very few experiences about the potential consequences of mushroom picking on fungal dynamics (Egli et al., 1990; Egli et al., 2006; Luoma et al., 2006a), the studies conducted so far suggest that sporocarp richness is not affected by harvesting. In a long-term experiment (1975–2003) in Switzerland, Egli et al. (2006) tested the effect of mushroom harvesting technique on mushroom abundance and occurrence. They found that long-term and systematic harvesting did not reduce future yields of sporocarps nor species richness, regardless of the harvesting technique (picking or cutting). Similarly, no negative effects of intensive mushroom picking have been observed in the mycelium biomass of *Boletus edulis* along four productive seasons in Scots pine forests located in Northern Spain (Parladé et al., 2017).

7.2. Salvage logging

Timber harvesting after thinning or regeneration cuts has a great influence on mushroom occurrence. In particular, it may affect physical properties of the soil causing soil compaction and therefore reduction of water retention capacity (Picchio et al., 2012).

A recent experiment on the effect of tree harvesting after a natural disturbance (wind) in boreal ecosystems demonstrated that salvage harvesting can reduce macrofungal species richness and fruiting abundance (Ford et al., 2018): a higher species richness was found in the plots where all the falled trees were left on the soil. This evidence is explained by the combined effect of reduction in deadwood volume and alterations to the ectomycorrhizal-associating plant community due to the loss of host trees and to the damages to the soil.

7.3. Prescribed burning

An important and widely used silvicultural operation to reduce fire risk is prescribed burning. It aims at removing fuel loads by controlled fires. In order to determine the optimal fire regimes for prescribed burning, the multiple effects on ecosystem components should be considered to ensure ecosystem stability and sustainability in the long-term.

Martín-Pinto et al. (2006) found that total, mycorrhizal and saprotrophic species diversity in *Pinus pinaster* forests and scrublands dominated by *Cistus ladanifer* was significantly lower in burned areas. At the same time, fire significantly increased the abundance of the pyrophytic mycorrhizal species (e.g. *Leccinum corsicum*). In the same scrubland ecosystems, Hernández-Rodríguez et al. (2015a, 2015b) evaluated the effect of fire on fungal diversity by comparing the differences between total burning and total clearing of the vegetation and found opposite trends between mushroom diversity and mushroom yields. Authors found that diversity of mycorrhizal and saprotrophic species was slightly higher after burning than after clear-cutting, likely due to an increase of pyrophytic species after fire occurrence. With these findings, the authors suggest that prescribed burning may be a better alternative than total clearing if fungal diversity conservation is the main goal.

Oliver et al. (2015) found a significant fungal community shift resulting from frequent prescribed fires conducted every two or three years. However, the richness and diversity of the communities remained unchanged suggesting likely taxon reordering. In their experiment, fungal community composition where no burn treatments were undertaken in the last ten years differed only marginally from unburned plots, suggesting how return to community state preceding the fires takes at least a decade. It is worth noting that the intensity of fires implemented in prescribed fire management is usually lower than wildfires, which tend to have greater impacts and longer lasting effects (Carter and Foster, 2004). Oliver et al. (2015) also tested the effect of the burning season, finding no significant effects on fungal communities. These results partly contrast with those by Smith et al. (2004), who reported greater richness associated to spring fires as compared to other season burns.

In an experiment in central Oregon, Reazin et al. (2016) evaluated community responses to low- and high-intensity fires, finding a rapid community turnover attributable to a few fire-prone ascomycetes that dominate post-fire communities. This effect has been reported by several authors that describe a massive and positive response of fire-prone species such as some strains of *Morchella* spp. (Pilz et al., 2004; Winder and Keefer, 2008; Richard et al., 2015). Such a large contribution of a few dominant species caused a clear decline in fungal species evenness and richness, especially in highly intense burned plots. These results are in line with those reported by Dahlberg et al. (2001) who found that hard-burn treatments are able to eliminate all mycorrhizae in the soil

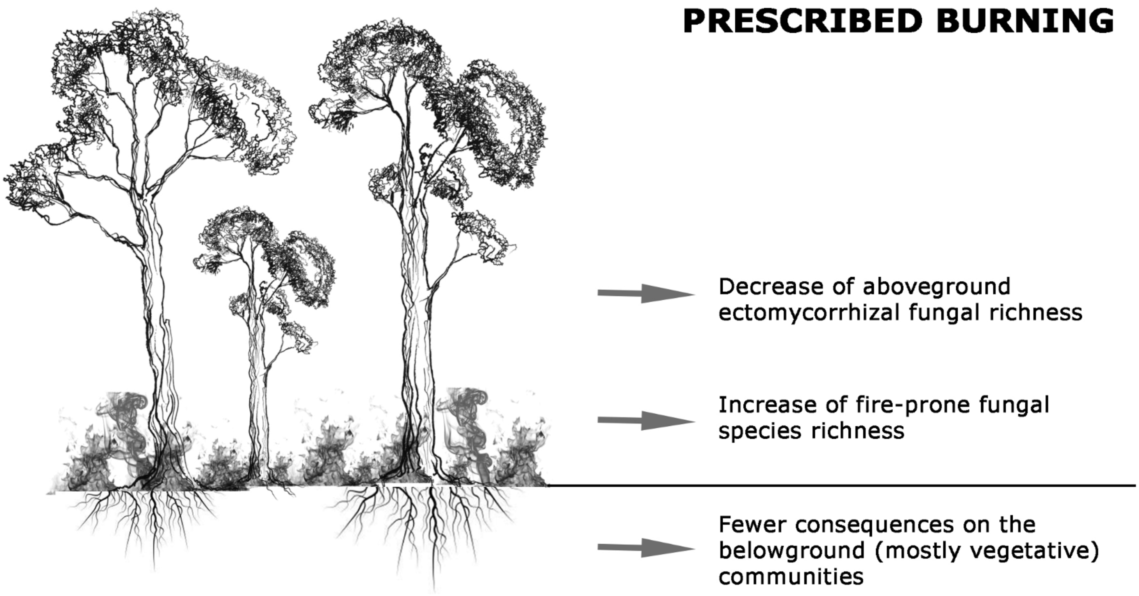

Fig. 2. Main effects of prescribed fire on fungal richness and diversity.

whereas slight-burn treatments leave part of the mycorrhizal flora alive (especially in mineral soil). In contrast to rapid colonization by the post-fire fungi, recovery of soil fungal communities to pre-fire condition may take more than ten years (Dooley and Treseder, 2012; Oliver et al., 2015; Hart et al., 2018).

Taudière et al. (2017) have reviewed the main studies on the effect of fire on ectomycorrhizal species and have concluded that prescribed burning has a negative effect on the aboveground ectomycorrhizal fungal richness (i.e. reproductive structures). However, fewer consequences are reported on the belowground (mostly vegetative) communities (Smith et al., 2004; Anderson et al., 2007) (Fig. 2).

7.4. *Fertilization*

In the last decades, nitrogen deposition has increased due to the combustion of fossil fuels and field fertilization for intensive agricultural (Reay et al., 2008) and forestry (e.g. short rotation coppices) activities (e.g. Fabio and Smart, 2018; Kern et al., 2018). Since 1980s, several authors have linked this phenomenon to the decline in the species richness of fungal fruit bodies in Europe, particularly of ectomycorrhizal species (Jansen and van Dobben, 1987; Rühling and Tyler, 1991)

The reduction of species diversity and mycelium growth of ectomycorrhizal fungi has been confirmed by several experiments in which inorganic nitrogen inputs are increased in forest ecosystems (Peter et al., 2001; Nilsson and Wallander, 2003; Trudell and Edmonds, 2004; Gillet et al., 2010; Lilleskov et al., 2011; Jones et al., 2012). Furthermore, Zheng et al. (2017) reported an increase of the ratio of both saprotrophic and parasitic fungi to total fungi in fertilized soils of *Eucalyptus*-dominated drylands in Australia. However, Zheng et al. (2017) found that fertilization altered fungal community composition, but not diversity. These results have been explained by the reduction of C allocation to the roots when N availability in the soil is high, so that trees would reduce the exchange of C with mycorrhizal fungi (Demoling et al., 2008). Indeed, ectomycorrhizal symbiosis is regarded as an adaptation to the nitrogen-limited soil conditions (Peter et al., 2013). It is worth highlighting that this effect is also species-specific, i.e., some ectomycorrhizal species (e.g., *Paxillus involutus* or *Lactarius rufus*) may be less affected, or are able to increase their production of sporocarps in nitrogen-enriched forest soils (Peter et al., 2001).

8. Best forest management practices for fungal diversity conservation

One of the main challenges for forest management is to find a sustainable way to balance the use of timber resources and the conservation of biodiversity. The review of the effect of the most common management activities on fungal communities and diversity enables to give some recommendations to support fungal diversity also in managed forests.

8.1. *Enhancing stand structural complexity*

Many authors suggest that undisturbed and unmanaged forests are preferable to support fungal diversity (Abrego and Salcedo, 2013; Heilmann-Clausen et al., 2017). However, it is possible to conserve and also to increase fungal diversity using forestry practices if stand structural complexity and late-successional forest characteristics are enhanced (Fig. 3). In this regard, Dove and Keeton (2015) proposed a silvicultural regime which promotes vertically differentiated canopy layers, elevated volumes and densities of snags and deadwood (enhanced by 140% on average over pre-harvest amount), variable horizontal density (including small canopy gaps), and reallocation of basal area to larger size classes (target basal area of 34 m^2 ha^{-1} and maximum diameter at breast height of 90 cm) (Keeton, 2006). They found that this silvicultural regime aimed at bringing to an old-growth-like stand structure promotes fungal species richness better than conventional selection systems. Plots managed using this “Structural Complexity Enhancement” treatment showed higher fungal species richness compared to controls and traditional selective cuts, since habitat conditions (e.g. high canopy closure, wood debris availability, etc.) was maintained enabling both ectomycorrhizal and saprotrophic fungi to persist and establish after disturbance. This has also been explained by the creation of new habitats, i.e. standing and lying deadwood, that may compensate for disturbances caused by forest management in group selection (Dickie et al., 2009) and single tree selection harvesting (Kranabetter and Kroger, 2001; Blaser et al., 2013). Thus, if residual deadwood is totally removed, fungal populations and diversity can be negatively affected (Bader et al., 1995).

Stand structural complexity should be also complemented with an increase of tree mixtures, preserving trees belonging to different species during silvicultural cuts. Indeed, tree species diversity has been demonstrated to be positively related to fungal diversity of ectomycorrhizal (Rumberger et al., 2004; Cavard et al., 2011) and wood-inhabiting fungi (Krah et al., 2018b).

8.2. Promoting the presence of deadwood

The importance of dying and dead trees for conservation of wood-inhabiting fungal species is well known: most of the fungal community of wood-inhabiting fungi may be sustained even in commercial forests by leaving higher amounts of coarse deadwood in the forests (Müller et al., 2007; Abrego and Salcedo, 2013; Parisi et al., 2018). However, leaving considerable amounts of deadwood in the harvested stands is not always implemented in forest management operations. Favoring the presence of deadwood in managed stands is compatible with timber harvesting (Parisi et al., 2018). An increase of deadwood can be obtained, for example, by keeping trees with lower economic value or retaining deadwood created by windstorms or pathogens. In protected forest reserves, intentional felling or girdling trees could be recommended because this would lead to a big deadwood input and disrupt age class characteristics of the forests at the same time (Blaser et al., 2013). Following the results of Abrego and Salcedo (2011, 2013), who demonstrated that diversification in size and decomposition stage of deadwood may enhance fungal diversity, forest management should promote the presence of natural decaying logs of different species, sizes and decomposition stages, better if exposed to different microclimatic conditions (Błońska et al., 2017, Krah et al., 2018b). Furthermore, since fungal diversity and composition in decaying wood is different between stumps and logs even for the same tree species, Van der Wal et al. (2017) and Suominen et al. (2019) suggested to combine the releasing of different wood sources after cuts in order to increase wood-inhabiting fungal species diversity (see Fig. 3). In this regard, Krah et al. (2018b) suggest enriching deadwood regardless of the availability and distribution of existing deadwood in the surroundings, which proved to not affect fungal diversity.

The results of studies conducted in tropical forests (e.g., Olou et al., 2019) suggest a general consistency of the pattern and potential drivers of the diversity of wood-inhabiting fungi in tropical and temperate or boreal forests. Therefore, existing knowledge from Northern hemisphere should be used for the conservation of wood-inhabiting fungal diversity also in tropical macroclimatic zones. Indeed, enhancing the presence of deadwood objects of diverse size, tree species and decomposition stage leads to an effective conservation and increase of species richness and community composition of wood-inhabiting fungi in macroclimatic zones.

8.3. Conducting reduced-impact logging

Even-aged management, bringing to more simplified stand structures, has been proven to reduce fungal diversity, at least in the short term. However, some silvicultural practices may mitigate the impacts on fungal diversity in even-aged stands. For instance, a pivotal recommendation for forest managers is to use as much as possible low impact logging operations (e.g., motor manual felling and extraction of whole trees by yarder rather than using heavy machinery to fell the trees). This results in minimal disturbance to soil since it reduces scarification and compaction (Bonet et al., 2012; Castaño et al., 2018) and, therefore, the impact on the richness and diversity of soil-inhabiting fungi.

8.4. Promoting tree retention forestry

Retaining trees in clear-cuts may support the conservation of fungal diversity, particularly of ectomycorrhizal species. In this regard, shelterwood methods –when applicable– are preferable to obtain regeneration. Some recommendations about the methods to spatially distribute retained trees can be also given to forest managers. Luoma et al. (2004) suggested combining the use of dispersed and aggregated green-tree retention. Such a mix would contribute to maintaining higher levels of mushroom diversity in the aggregates by ameliorating edge effects. Sterkenburg et al. (2019) suggest increasing current standard 5% value of retention trees in boreal forests, as 75% of species may be lost under the current forest certification standard value.

Another way to enhance ectomycorrhizal maintenance would be retaining intact forest patches. Accordingly, Kranabetter et al. (2013) suggested a patch size of at least 0.2 ha, since they found that the abundance of ectomycorrhizal species was reduced along the entire gradient of patch sizes (from single trees to 0.12 ha) ten years after forest harvesting. However, both methods could be complementary, as their effectiveness on preserving taxa may depend on the ecology and the traits of each fungal species. For example, dispersal limitation of several ectomycorrhizal species (Peay et al., 2012; Peay and Bruns, 2014) may determine patch size. In addition, how sensitive are these communities to forest fragmentation may determine the appropriateness of intact gaps vs randomly distributed retention trees and vice versa.

8.5. Improving landscape heterogeneity and connectivity

Another strategy to enhance fungal diversity is the increase of landscape heterogeneity. Diversity of silvicultural regimes in the same region may enable the coexistence of different habitats hosting different fungal communities and therefore increasing beta diversity. In this regard, the so-called “land sparing”, which consists of increasing timber yields in productive forests and reducing pressure on forests of high conservation value, may be also a suitable approach for holistic land management (Parisi et al., 2018). However, when enhancing landscape heterogeneity, improving the connectivity among forest patches to conserve fungal diversity also becomes a crucial landscape management strategy (Juutilainen et al., 2016). For instance, Abrego and Salcedo (2014) found that in small forest patches, tree densities and the variability of woody debris are lower, therefore causing decrease of wood-inhabiting fungal richness. In this regard, Spake et al. (2016) highlighted the important role of over-mature planted forest stands –particularly those composed by mixed stands with high basal area– as an effective way to connect and expand ecological networks of ancient old-growth forests.

Many fungal species rely on spore dispersal to colonize new habitats, but to what extent fungi are dispersal limited still deserves further research. For example, Galante et al. (2011) observed that most of the spores fell within the first few meters from the fruit bodies, but it has also been shown that still some of the spores may travel far distances if they reach the turbulent layer (Després et al., 2012). In addition to airborne dispersion, fungi can also disperse further through other organisms such as insects (Seibold et al., 2019). Dispersal limitation has been shown at least for several specific species (Peay et al., 2012; Norros et al., 2012; Peay and Bruns, 2014). Because of this dispersal limitation, a reduction of ectomycorrhizal species richness was observed in seedlings planted away from forest patches (Peay and Bruns, 2014). However, a recent review showed contradictory results depending on the approach used to measure dispersal limitation; direct studies and field experiments tend to show dispersal limitation in fungi, but population genetic analyses not (Komonen and Müller, 2018). Dispersal limitation, if any, together with low establishment success, may constrain fungal colonization to other habitats in fragmented landscapes (Norros et al., 2012). However, whether lack of connectivity may constrain spore dispersal and therefore fungal colonization and diversity still needs more empirical evidence.

9. Main gaps in knowledge and needs for further research

In this review we have examined and summarized the main effects that stand structure and silvicultural practices may have on fungal

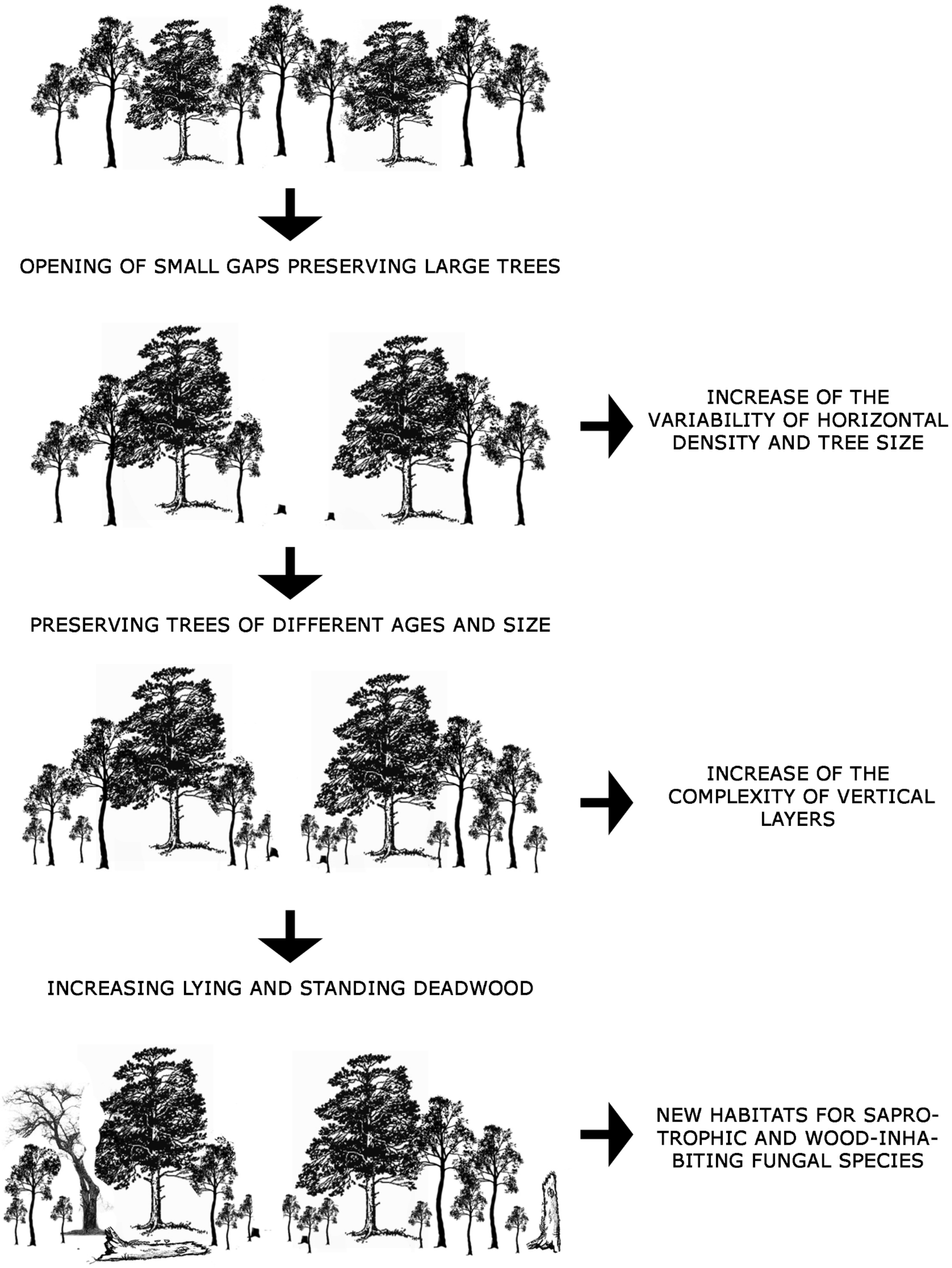

Fig. 3. Forestry practices contributing to the conservation of ectomycorrhizal and wood-inhabiting fungal diversity.

diversity and community composition. This work enabled us to identify the main gaps in knowledge requiring further research, which can be summarized in the following points:

i. Most studies conducted to date have been carried out in temperate and boreal ecosystems of Europe and North America. Our scientific understanding of the consequences of forest management in other forest ecosystems and biomes (e.g., tropical and subtropical forests subject to logging, forest degradation and transformation into plantations) and in other regions of the world is still very limited.
ii. The context of global change should also be considered in future research. In this regard, climate change is expected to cause changes in precipitation and temperature patterns influencing both, fungi and their hosts (e.g. tree species migration) with a still unknown effect on fungal diversity and community composition. Furthermore, global disturbances in the C and N cycles (increased CO_2 in the atmosphere; nitrogen deposition) are likely to affect fungal communities (Suz et al., 2014). In this context, a further effort should be devoted to evaluate the adaptive responses of fungal communities under different global change and forest management scenarios.
iii. Most of the studies dealing with wood-inhabiting fungi have focused on coarse woody debris. Only few papers have considered fine and very fine woody debris (e.g., Lindner et al., 2006;

Juutilainen et al., 2011, 2014). Since the latter are the portions of deadwood more commonly released in managed forests, the study of the diversity associated with them could help to delineate mitigation measures to support fungal diversity also in managed stands. In this regard, further research about richness and diversity of fungi living on the deadwood produced by forest management (e.g. stumps) is needed.

iv. The effect of forest management practices on soil-inhabiting fungi (including symbiotic and free-living soil fungi) has been mostly inferred based on sporocarp occurrence. However, in future research, this type of survey should be coupled with the evaluation of composition and abundance of mycelium in the soil using high-throughput DNA sequencing techniques to profile the fungal communities or qPCR to quantify the total and species-specific fungal biomass (Liu et al., 2016; Parladé et al., 2017; Castaño et al., 2018). In addition, new surveys should also profile the active fungal communities by, for example, sequencing the fungal RNA (Rajala et al., 2011). These methods can reduce the underestimation of fungal richness and diversity surveyed based on collecting only sporocarps. Indeed, the disappearance of fruiting bodies of some species after logging may not be definitive, but simply related to the new microclimatic conditions at soil level.

v. Many silvicultural practices have been proved to affect fungal communities and diversity. However, little is known about the duration of this effect since only few studies (e.g. Spake et al., 2015; Varenius et al., 2016, 2017) explored the long-term effects of such man-induced disturbances. In this regard, long-term experiments are still needed to understand how long the consequences of silvicultural practices might last on both aboveground and belowground communities. These long-term studies may also shed further light on the abundance and occurrence of rare and threatened fungi in managed forests because these categories are hardly detected in short-term experiments.

vi. Forest stand structure and silvicultural management affecting fungal diversity and community have been explored mainly in high forests. Little is known about diversity and composition in coppices even if this silvicultural regime is very common in broadleaved stands in boreal, temperate and Mediterranean ecosystems.

vii. Close-to-nature silvicultural practices like those proposed by Dove and Keeton (2015) are promising approaches to support fungal diversity in managed stands. It would be a relevant gain in knowledge to apply them and test their effects on fungal diversity in different ecosystems and climate regimes in order to provide more precise and evidence-based suggestions to forest managers.

viii. Most studies have shown if management practices or stand structure variables influence fungal communities. However, an organic overview of the relative contribution of all those factors linked to anthropogenic disturbances on fungal diversity is still missing. More experiments are therefore needed which disentangle such effects (Seibold et al., 2015). Understanding which are the major drivers affecting fungal dynamics would greatly help forest managers to define more efficient forest management practices oriented to increase fungal diversity.

ix. There is a need for a better understanding of the specific functions of the fungal taxa found in forest ecosystems. A better understanding of the functional attributes of the taxa should be helpful to predict resistance and resilience of forest ecosystems and associated processes to disturbances. The (meta)genomic approaches should help in providing potential functions to many taxa.

10. Conclusions

Literature addressing the influence of forest management on fungal diversity and community composition carried out over the last two decades confirmed the great interest in evaluating the impact of anthropogenic disturbances on forest ecosystems biodiversity conservation. Different stands structure attributes (age, tree cover, stand density, tree species composition), management history (managed vs unmanaged) and silvicultural treatments (thinning, clearcutting, shelterwood methods, selective cutting) were taken into account in these studies. Overall, the results of the examined studies highlighted that silvicultural practices, by modifying stand characteristics and microclimatic conditions, may have different effects on fungal communities according to the type of treatments, the methodological approaches and the target functional groups investigated.

The reviewed studies reported a positive relation between fungal diversity and stand structure variables such as canopy cover, basal area of the stand, particularly for mycorrhizal species. Furthermore, abundance and diversity (in size and decomposition stage) of deadwood are reported as features positively related to richness of wood-inhabiting fungi. Tree species diversity has been reported to be positively related to diversity of both mycorrhizal and wood-inhabiting fungi, being in the latter case even more important than the environmental factors or local amount of deadwood.

Concerning silvicultural cuts, although there seems to be a consensus on the fact that sporocarp diversity and community composition may be negatively affected by thinning, the fungal community as represented by the mycelia belowground may be very resistant and/or resilient to forest management-related anthropogenic disturbance in the case of low-impact harvesting operations. Clear-cutting negatively affects fungal diversity, mainly of mycorrhizal fungi. The negative effect of this treatment could be reduced if several mature trees are kept as

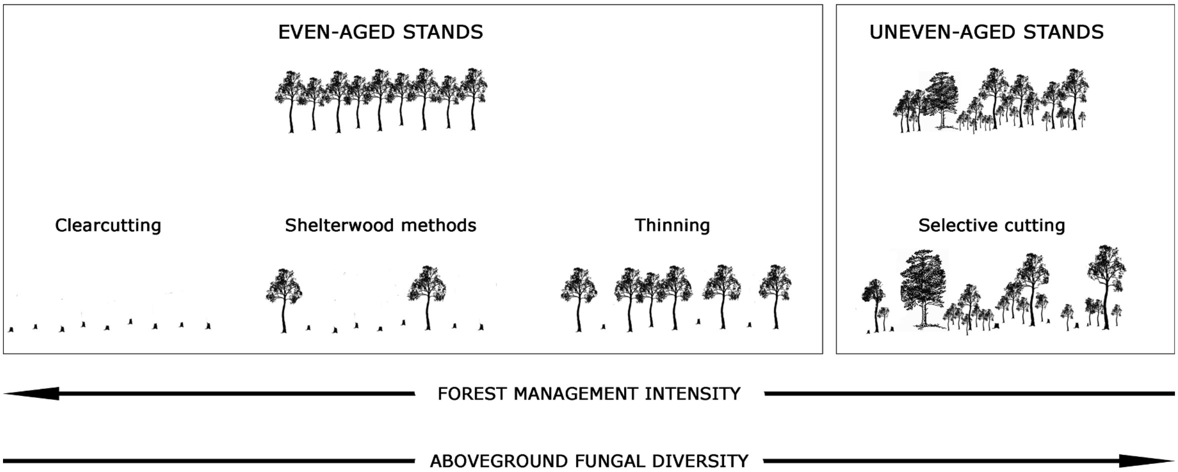

Fig. 4. Main silvicultural practices in even-aged and uneven-aged stands affecting aboveground fungal diversity.

retention trees. For this reason, in even-aged stands shelterwood methods may be preferable to support fungal diversity during the regeneration period (Fig. 4).

A controversial effect of selective cuts is reported in the literature since some authors found no effects on fungal richness while others reported a reduction of species diversity, especially if several overmature trees are removed. In any case, this silvicultural practice was the preferable method to manage stands since fungal diversity resulted more similar to that of undisturbed forests. Regardless of the silvicultural cut type, logging operations seem to be one of the major drivers negatively affecting fungal diversity due to their impact on soils. Therefore low-impact operations are preferable to support fungal diversity.

Other management practices such as prescribed burning showed a negative effect on aboveground ectomycorrhizal fungal richness with fewer consequences on the belowground communities. However, an increase of the richness of pyrophytic species (e.g., some strains of *Morchella* spp.) have been observed. On the other hand, some very common anthropogenic disturbances, like mushroom picking, proved to not affect fungal diversity.

In conclusion, a better understanding of the effect of silvicultural practices on fungal diversity and community dynamics can provide a basis for forest management plans which may reduce trade-offs between timber harvesting and biodiversity conservation. Indeed, fungal diversity can be conserved in managed forests if (i) low-impact logging operations are performed; (ii) stand structural complexity and late-successional forest characteristics are enhanced; (iii) tree species mixture is enhanced; (iv) deadwood amount and diversity is promoted, and (v) landscape heterogeneity and connectivity is improved or maintained.

Declaration of Competing Interest

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

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