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Editorial

State of the art and future directions for mycological research in old-growth forests

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Without human impact, forests would cover more than half of the terrestrial surface of the planet. Millions of square kilometers of forests have been lost through expansion of husbandry grazing, agriculture and urbanization through the last millennia (Foley et al., 2005). Of the remaining forests roughly half are primarily used for timber production (Woodcock et al., 2015). Human influence on forest ecosystems has been especially severe in Europe where only a minor fraction of the original forest area remains in close to natural condition (Wallenius et al., 2010). These remaining old-growth forests (often also called natural, virgin, relict, pristine or primeval forests, although some authors distinguish between these notions, e.g. Buchwald 2005) attract the attention of many scientists including mycologists, because they offer the possibility to study uninterrupted natural processes. As reviewed by Burrascano et al. (2013), old-growth forests differ from mature managed forests not only in dead wood amounts and number of large trees, but also in living biomass. Both dead and live biomass has a buffering effect on the forest microclimate, which is considerably cooler, moister and less fluctuating than in managed forests (Frey et al., 2016). Considering processes, unmanaged old-growth forests differ from managed stands in many ways, most obviously in their non-interrupted life cycle of individual trees, but also in the presence of natural hydrology, soil formation processes (e.g. Šamonil et al., 2010), and disturbance dynamics that are normally under tight control in managed forests. Natural disturbance includes large scale dynamics related to parasite outbreaks, forest fires and heavy windstorms, and small scale dynamics related to gap creation due to insects, fungal decay and windstorms acting in interplay with grazers. These dynamics affect habitat conditions, and create natural gradients in time and space, that differ markedly from those found in managed forests, and explain why old-growth forest have crucial value for conservation of biodiversity (Wirth, 2009).

This special issue of *Fungal Ecology* is devoted to mycological research related to old-growth forests, and is based on contributions presented during the international symposium Fungi of Central European Old-Growth Forests (http://www.conferencepartners.cz/FCEOF2015/) which was held in Český Krumlov, Czech Republic, 14–17 September 2015. The symposium was organized on occasion of the 50th anniversary of the autonomous Mycological Department, National Museum, Prague, the staff of which has often been involved in old-growth forests research (e.g. Pilát, 1940; Svrček and Kubička, 1971; Pouzar, 1986). The symposium was attended by 47 scientists from 15 European countries. Abstracts of all contributions are available online (http://www.czechmycology.org/_cmo/CM67110.pdf).

From a mycological perspective, the most striking feature that makes old-growth forests special is the richness and abundance of dead wood habitats. In Europe, unmanaged old-growth forests, mostly protected as nature reserves, typically contain 10-30 times more dead wood than their managed counterparts (e.g. Christensen et al., 2005). Since fungi are the main wood decomposers in temperate ecosystems, this alone can explain the marked species richness difference commonly found between managed and unmanaged forests. It is no surprise that the early stage of mycological research in old-growth forest focused on 'flagship' localities like Muddus National Park in Sweden (Eriksson, 1958) and Białowieża in Poland (Karasiński et al., 2009). However, comprehensive and critical fungal oriented studies of particular old-growth forests (e.g. Holec et al., 2015a; Karasiński and Wołkowycki, 2015; Langer et al., 2015; Adamčík et al., 2016) are still rare (or unpublished), even if they are important both for science and practical site protection.

A rich body of field studies, mainly in Fennoscandia, has shown that the loss of old-growth forests has not only diminished species richness, but also affected the composition of wood decomposing fungal communities, with specialized species being unable to maintain populations in managed and fragmented forest landscapes, often to the benefit of generalists (Junninen and Komonen, 2011; Nordén et al., 2013). The overall value of old-growth forests for protecting wood-inhabiting fungi is broadly accepted, but it is less clear which conservation means are most cost effective to hinder further biodiversity loss. Should the protection of old-growth forest reserves be the main target? And if this is the case, should many smaller reserves be prioritized over fewer but larger ones? Or is it more important to support the development of close-to-nature forestry principles that allow sufficient habitat thresholds for wood-inhabiting fungi, also in the managed stands? These questions are classics in conservation biology, and

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are typically referred to as the SLOSS (Single Large reserve Or Several Small) issue (e.g. Higgs and Usher, 1980) and the land sparing versus land sharing issue (e.g. Edwards et al., 2014) respectively. They are easy to ask, and richly covered in the conservation literature, but complex to answer as they involve landscape history, socioeconomic aspects as well as the biology of the species concerned. Habitat preferences, niche width, dispersal ability, sensitivity to climatic conditions and interactions with other species all affect the survival probability of specific target species under various conservation scenarios.

So far the importance of old-growth forest habitats has mainly been focused on the fungal community level, addressing how species richness and composition respond to various drivers. In the present issue, Dvořák et al. (2017) complements this line of research with a comprehensive broad scale study that included all groups of macrofungi, and explored their general response to forest management and tree species composition in four forest landscapes in the Czech Republic. In a much more detailed study, Pouska et al. (2017) explore the effects of microclimatic conditions on fungal richness in decomposing spruce logs. While community studies are crucial for understanding overall drivers in species richness and composition, they do not provide exact understanding of habitat requirements of specific species of conservation concern. Unlike the case with charismatic animals and plants, there is however no tradition of studying the conservation needs at the species level in fungi, but this seems now to be changing. We welcome the increasing number of studies that address the ecology of single species or limited species group (e.g. Boddy et al., 2011; Runnel et al., 2014; Holec et al., 2015b). In this issue, Kunca and Čiliak (2017) continues this trend by exploring the autecology of the rare *Hericium erinaceus* in Slovakia, while Vogel et al. (2017) provide a detailed investigation of the substrate use and fruiting dynamics in the very common and often dominating brown rotter *Fomitopsis pinicola*.

The strong preference of some wood-inhabiting fungi for old-growth forest patches has repeatedly lead to the suggestion that these fungi could be used as indicators of a forest's conservation value. This aspect is reviewed by Halme et al. (2017), who thoroughly discuss the value of fungi as old-growth indicators, including whether they point to local forest continuity, habitat quality or landscape context. Early concepts were often unclear and did not explicitly specify what suggested indicators were supposed to indicate, except for vague concepts, e.g. conservation value. There is now a clear need to document the relevance of fungal indicators in conservation biology based on empirical evidence. Both Abrego et al. (2017) and Runnel and Lõhmus (2017) explore this aspect, based on extensive datasets from European beech forests, and Estonian mixed forests, respectively. They show that some suggested indicators are not obviously related to the habitat factors they were originally supposed to indicate. Both studies can be considered hybrids between community studies as described above and the more recent trend of exploring habitat requirements of single species. They combine broad scale collection of field data for numerous species across several sites with single species models to explore the role of habitat filters, but due to the project design many of the most demanding species are too sparsely represented to be properly analyzed.

While the ecology and habitat needs of wood-inhabiting fungi have been explored for decades, less is known about soil fungi and their relation to old-growth habitats. Based on fruit body inventories, Dvořák et al. (2017 in this issue) found the highest species richness of ectomycorrhizal fungi in managed forests, while terrestrial saprotrophs showed a tendency for higher richness in old-growth forests. It is unknown if these differences in fruiting patterns reflect underground diversity, but some recent studies based on environmental DNA samples have indicated that old-growth forests support different communities of both litter decomposers and ectomycorrhizal fungi than their managed counterparts (Goldmann et al., 2015; Purahong et al., 2015). In boreal forests, long-term successional processes (500 years) have been documented to change fungal communities in the humus layer with a shift from ectomycorrhizal to greater ericoid mycorrhizal dominance (Clemmensen et al., 2015). The presence of shorter term successional processes in ectomycorrhizal communities in new or reestablished forest stands is well known (e.g. Twieg et al., 2007), but how these processes affect species composition and beta-diversity gradients in old-growth forests under natural disturbance dynamics is poorly explored.

In this context, the approach of Simmel et al. (2017), in this issue, applying Ellenberg indicator values to fungi, is a very welcome step, which has the potential to increase our understanding of fungal ecology considerably in the coming decades. In plant ecology, Ellenberg indicator values are well known and often used as a tool to understand ecological gradients or time trends in plant communities when detailed measurements of habitat factors are missing or scarce (e.g. Diekmann, 2003). Ellenberg values have been developed for habitat factors that have direct implications for plant growth, including nitrogen, soil reaction (pH), continentality and temperature. These factors are highly relevant also for fungi, but as heterotrophs, they are, unlike plants, also highly dependent on available carbon pools (e.g. Clemmensen et al., 2015). Hence the suggestion by Simmel et al. (2017) to include openness, relating to soil development, is an interesting and relevant addition to the Ellenberg indicator system enhancing its relevance in a fungal context.

1. Future directions

A substantial number of studies in old-growth forests, including those reported in this issue of *Fungal Ecology*, have contributed to increase our knowledge of fungal ecology and conservation needs. So far, most studies have had a correlative approach, studying species richness patterns and community composition at landscape or stand scale. This is true, both for classical studies based on fruit bodies and for more recent approaches utilizing next generation sequencing of environmental DNA or RNA (e.g. Rajala et al., 2011; Kubartová et al., 2012; Purahong et al., 2015). Studies aiming to understand mechanisms structuring community assembly and species richness, have been conducted in the laboratory (e.g., Holmer and Stenlid, 1997; Wald et al., 2004) or have focused only on common species (Dickie et al., 2012; Hiscox et al., 2015). Hence processes important for the establishment and successful reproduction of rare species remain poorly understood. Investigations of dispersal dynamics of fungi have yielded conflicting insights into the role of dispersal limitation as a factor influencing species assembly in fragmented landscapes (e.g. Peay et al., 2010; Norros et al., 2012; Kivlin et al., 2014), and it is largely unknown how dispersal success translates into successful establishment of sexual reproductive individuals (but see Jönsson et al., 2008). Similarly, basic information on the life-histories of most fungi is missing, and evaluation of generation times and population sizes, e.g. for assessing threat levels for fungal red-listing, are based on qualified guesses in the best case (Dahlberg and Mueller, 2011).

To increase knowledge of fungal community ecology, we recommend a shift from descriptive, explorative and correlative approaches towards a more mechanistic understanding of species assembly by carefully designed studies based on clear hypotheses. Such studies would increase our understanding of why and how