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Drivers of macrofungal species composition in temperate forests, West Hungary: functional groups compared

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ABSTRACT

The most influential environmental drivers of macrofungal species composition were studied in managed, even-aged, mixed forests of Órség National Park, Hungary. Functional groups of macrofungi were analyzed separately by non-metric multidimensional scaling and redundancy analysis exploring their relations to tree species composition, stand structure, soil/litter conditions, microclimate, landscape, and management history. There was some evidence that macrofungi are related to drivers that are relatively easy to measure. Wood-inhabiting fungal species composition is driven primarily by the species composition of living trees, while substratum properties and microclimate play minor roles. The terricolous saprotrophic community was determined principally by a litter pH gradient involving tree species composition and soil/litter properties. Microclimate had no concordant effect. No obvious underlying gradients were detected on ectomycorrhizal fungal species composition; however, tree size and litter pH had significant effects. For each group, no clear responses to landscape or management history were detected.

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Introduction

Forest-dwelling macrofungal assemblages have been classified into three main functional groups: wood-inhabiting (including wood saprotrophs and necrotrophic parasites), ectomycorrhizal (EcM) and terricolous saprotrophic communities (Winterhoff 1992). In a global perspective, an enormous volume of research has been reported on the responses of macrofungal community composition to environmental variation. Wood-inhabiting fungal communities are driven principally by the amount and diameter (Heilmann-Clausen & Christensen 2004; Sippola et al. 2005; Ódor et al. 2006; Lonsdale et al. 2008), decay stage (Heilmann-Clausen & Christensen 2003b; Siller 2004; Heilmann-Clausen et al. 2014), age (Heilmann-Clausen 2001), species identity (Sippola et al. 2005; Küffer et al. 2008), complexity (Heilmann-Clausen & Christensen 2003a), and spatio-temporal availability (Siitonen 2001; Bässler et al. 2010; Halme et al. 2013) of dead wood. The microclimatic variation and pH within the wood (Boddy 1992, 2001; Salerni et al. 2002) or the interactions with other organisms (van der Wal et al. 2013) also have significant effects. EcM community composition is structured strongly by the N content (Toljander et al. 2006; Cox et al. 2010; Suz et al. 2014), pH (Baar & ter Braak 1996; Talbot et al. 2013) as well as temperature and moisture of soil (Claridge et al. 2000; Jones et al. 2003), species composition of host trees (Kernaghan et al. 2003; Smith & Read 2008; Morris et al. 2009), season (over the course of even a month) (Courty et al. 2008), fungal dispersal limitation among host trees (Peay et al. 2010), and timing of colonization and interspecific competition on the root surface (Kennedy et al. 2009; Kennedy 2010). In the same context, little is known about the determinants of terricolous saprotrophic communities, but the effects of litter quantity and pH (Tyler 1991; Ferris et al. 2000; Talbot et al. 2013), P content of the soil (Reverchon et al. 2010), tree species composition (O'Hanlon & Harrington 2012), and temperature (McMullan-Fisher et al. 2009) are documented to be highly important.

Many influential environmental drivers have been revealed, but are there drivers with consistent importance to macrofungal functional groups? When such drivers are sought, many difficulties are encountered. The relative importance of drivers varies across spatial scales (Claridge et al. 2000; Lilleskov & Parrent 2007; Büntgen et al. 2012) and along environmental gradients, such as elevation (Gómez-Hernández et al. 2012; Sundqvist et al. 2013) and rainfall (Lindblad 2001; Salerni et al. 2002). Also, the relative effects of drivers can be biased strongly by the edaphic heterogeneity of the studied habitats, and the factors (resources or environmental conditions) that are actually limiting in a habitat can have a disproportionately high influence on species composition (McMullan-Fisher 2008). In addition, community level responses are difficult to reveal, since great species diversity is found within fungal communities in which each species has slightly different environmental requirements (Boddy et al. 2008).

Based on the studies mentioned in the first paragraph, our knowledge of fungal community responses to environmental variation is biased by research history: (1) the majority of

studies have been conducted in Northern or Western Europe or in North America, thus, large regions are still under-represented; (2) the studies have rarely been focused on more than two functional groups (except e.g. Humphrey et al. 2000; Sato et al. 2012); (3) to obtain a clearer picture, many authors have used a limited pool of environmental factors and hence, several environmental impacts with probable significant effects remained unexplored on the sampling sites.

Given these complexities and research gaps, the present study has been designed in even-aged, managed forests with a restricted number of habitat types to try to reduce the effects of edaphic heterogeneity. By including several variables suggested by the literature, other factors that characterize the landscape and management history were also examined.

In accordance with the studies referenced in the first paragraph, it can be hypothesized that: (1) substratum properties, tree species composition, and microclimate have the strongest effects on macrofungal species composition at a stand scale, and (2) the relative influence of these factors differs among wood-inhabiting, EcM, and terricolous saprotrophic communities. The aims of this study are to find the most important environmental factors that best explain the macrofungal species composition of wood-inhabiting, EcM and terricolous saprotrophic communities, and provide information on the environmental requirements of fungal species.

Materials and methods

Study area

This study was carried out in Őrség National Park (ŐNP), West Hungary (46° 51'–55' North, 16° 06'–24' East (Fig 1A). In the ŐNP, the precipitation ranges between 700 and 800 mm yearly. Between 1901 and 2000, the mean minimum and maximum temperatures in winter were respectively –7.4 and 6.0 °C, while in summer 13.5 and 23.8 °C (measured in a nearby town, Szombathely, Hungarian Meteorological Service, OMSZ). The landscape is divided into hills and wide valleys at an elevation range of 250–350 m above sea level. The bedrock consists of alluvial gravel and clay. Nutrient-poor brown forest soils with pseudogley or lessivage (planosols or luvisols) are the most frequent soil types (Halász 2006; Dövényi 2010). The pH of the soil is acidic; it tends to range from 4.0 to 4.8 with a mean of 4.3 (Juhász et al. 2011).

Presently, forests cover 80 % of the ŐNP region, which has an area of ca. 350 km² (Dövényi 2010). Stands are dominated by beech (*Fagus sylvatica*), sessile and pedunculate oak [*Quercus petraea* and *Q. robur*, hornbeam (*Carpinus betulus*), and Scots pine (*Pinus sylvestris*). Forests are sometimes monodominant, but more often form mixed stands with great compositional diversity. The most frequent non-dominant tree species are *Betula pendula*, *Picea abies*, *Populus tremula*, *Castanea sativa*, *Prunus avium*, *Tilia* spp., and *Acer* spp. (Tímár et al. 2002). ŐNP is characterized by the highest proportion of private forest stands in Hungary where the dominant tree species usually varies from stand to stand. Therefore, the ŐNP is a suitable

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