Understanding the distribution of wood-inhabiting fungi in European beech reserves from species-specific habitat models

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ABSTRACT

We assessed how environmental drivers influence the occurrences of wood-inhabiting macrofungi in European beech forests, using an extensive dataset of fruit body records collected in 53 reserves across twelve European countries. We found that the 105 species included in this study varied greatly in their responses to covariates related to resource quality, climate and forest connectivity, both in the strength and direction of the observed effects. Climate was the most important driver for some species, while others responded more to connectivity, or simply to the presence of high quality substrates within the reserves. Species occurrences varied also across geographical regions, especially between the UK and the rest of Europe. Our results show that wood-inhabiting fungi in European beech forests respond individualistically to habitat filters and differ in their biogeographical distribution patterns, and they thus provide a detailed perspective of how wood-inhabiting fungal communities are structured across Europe.

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1. Introduction

Communities of wood-inhabiting fungi are filtered by local factors related to dead wood quality and by regional factors related to climate, landscape history and forest naturalness (Heilmann-Clausen and Boddy, 2008; Junninen and Komonen, 2011; Heilmann-Clausen et al., 2014; Abrego et al., 2015). A broad body of literature has shown that wood-decay stage, associated tree species and size of the dead wood unit are the most important factors influencing fungal community composition at the finest spatial scale (i.e. the dead wood unit) (e.g. Küffer et al., 2008; Yamashita et al., 2010; Stokland, 2012; Rajala et al., 2015). At the

landscape scale, macroclimatic factors and factors related to forest naturalness, such as management history and connectivity, are of greater importance (e.g. Penttilä et al., 2006; Halme et al., 2013; Nordén et al., 2013; Heilmann-Clausen et al., 2014; Abrego et al., 2015; Fukasawa and Matsuoka, 2015).

Nevertheless, much of the variation seen in the wood-inhabiting fungal community composition has remained unexplained in most studies (e.g. Abrego et al., 2014, 2015; Heilmann-Clausen et al., 2014; Juutilainen et al., 2014). This might be due to a combination of stochastic community assembly processes and a failure to identify the relevant environmental constraints. Wood-inhabiting fungal communities are composed of many species, which differ in their individual responses to the environment. For instance, species show very individualistic optima in relation to the successional process of wood decay (e.g. Rajala et al., 2015), as well as for the size and type of inhabited dead wood unit (e.g. Küffer et al.,

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2008; Hottola et al., 2009). Likewise, although most wood-inhabiting fungal species respond negatively to forest management practices causing dead wood reduction and fragmentation (e.g. thinning and clear-cutting activities), human disturbance can be beneficial for some species (Müller et al., 2007; Nordén et al., 2013). Wood-inhabiting fungi can also respond differently to macroclimatic conditions, as some species are better adapted to continental climatic environments than others (Ódor et al., 2006; Bässler et al., 2010). In addition to showing interspecific variation in their responses to differing habitat conditions, wood-inhabiting fungi are subjected to other biogeographical forces such as historical speciation and extinction processes which also influence their current regional distribution. Thus far, the relative importance of these individual factors has mainly been studied at the community level, using species richness or community similarity as the response variable (e.g. Abrego et al., 2014; Heilmann-Clausen et al., 2014; Juutilainen et al., 2014; Fukasawa and Matsuoka, 2015). Thus, a species-specific assessment of the factors influencing the broad-scale distribution patterns of all species forming wood-inhabiting fungal communities can provide a more detailed insight into the spatial structure of these communities.

European beech (*Fagus sylvatica*) is a widespread tree species in Europe and constitutes one of the principal natural vegetation types on the continent (Pott, 2000; Brunet et al., 2010). Its distribution ranges from the mountains in the Mediterranean region in the South, to Southern Scandinavia in the North, and from the temperate region and mountains in the Iberian Peninsula in the West to the eastern foothills of the Carpathians and Crimean Peninsula in the East. Beech has been present in Europe since the early Holocene, and has since been subjected to several glaciations resulting in repeated retractions and expansions. It has reached its current distribution range by non-simultaneous expansions originating from several glacial refugia (Magri et al., 2006; Magri, 2008). The most recent major colonization event of beech in Europe was in the British Isles, where it arrived ca. 2000–3000 years BCE (Magri et al., 2006; Magri, 2008). Its distribution limits can be explained mainly by its sensitivity to dry summers and extremely cold winters (Fang and Lechowicz, 2006). As is the case for many other organisms, the North Atlantic Oscillation is an important factor delimiting the distribution of European beech, as it strongly influences the temperature and amount of precipitation in Europe (Ottersen et al., 2001).

The distribution range of European beech offers a suitable area for studying large scale distributions of wood-inhabiting species, not only because of the broad geographic range itself, but also because of the macroclimatic variation and differing degrees of habitat fragmentation across this area (Metzger et al., 2005; Parviainen, 2005; Heilmann-Clausen et al., 2014; Abrego et al., 2015). Climatically, although European beech is confined to the temperate zone, it experiences a Mediterranean influence towards its southern distribution limit, and an increasing continentality gradient towards the East (Metzger et al., 2005). The long history of land use in Europe has led to a highly fragmented beech forest landscape, especially in its northern and western distribution areas (Parviainen, 2005; Kaplan et al., 2009).

In this study, we analysed the species-specific responses of wood-inhabiting fungi to the main drivers known to explain community gradients in such organisms, using an extensive dataset collected in a standardized way in beech forest reserves across twelve European countries (Austria, Belgium, Bulgaria, Denmark, England, Germany, Hungary, Italy, the Netherlands, Slovakia, Slovenia, Sweden and the UK). The main objective was to explore the interspecific variation in species' responses to environmental factors, in order to get a more comprehensive understanding of their broad-scale distribution patterns. More specifically, we aimed

to: (1) measure the relative importance of connectivity, macroclimate, resource quality and regional effects in explaining the fruiting occurrences of wood-inhabiting fungal species within European reserves; (2) illustrate species-specific variation in the responses of wood-inhabiting fungi to the same covariates; (3) assess the factors influencing the distribution patterns of the indicator species proposed by Christensen et al. (2004).

2. Materials and methods

2.1. Study area and field data inventories

The dataset used in the present study was compiled from the 41 European beech forest reserves used in Abrego et al. (2015) and 12 additional reserves from three additional countries (see Supplementary Appendices 1 and 2 for the names and locations of sampled reserves). The criteria for site selection and survey design were the same as described in Abrego et al. (2015). Briefly, the main criteria for site selection were that sites should represent, as far as possible, the best examples of natural beech forests within each country and that, taken together, their locations should represent the distribution of European beech.

Fungal sampling was carried out between 2001 and 2014, during the main fruiting season in each European region (from late August to early November), surveying each dead wood unit (fallen beech trunks of at least 10 cm in diameter including their standing snag if present) one to three times. In each reserve, we attempted to cover all decay classes following the 1–5 classification system devised by Christensen et al. (2005), and to survey equal numbers of dead wood units per decay class. At the dead wood unit level, the fruiting presence of the following selected wood-inhabiting macrofungal species was recorded: polypores, agarics, pileate corticioids, thick resupinate corticioids (species from the genera, *Dentipellis, Phlebia, Steccherinum* and *Xylobolus*), larger discomycetes and stromatic pyrenomycetes. Most species were identified in the field, but when microscopic identification was necessary, specimens were collected and dried for further study in the laboratory.

2.2. Measured covariates

Our selection of environmental variables was based on those shown to significantly influence wood-inhabiting fungal species communities, based on results of our previous studies analyzing partly the same data (Ódor et al., 2006; Halme et al., 2013; Heilmann-Clausen et al., 2014; Abrego et al., 2015). The environmental variables included in this study are described in Table 1 and detailed in Supplementary Appendix 2. At the dead wood unit level, diameter at breast height and decay stage were recorded in the field. At the reserve level, annual precipitation, mean annual temperature, annual temperature range, connectivity at the 10 km spatial scale, area of the reserve and number of surveyed dead wood units were recorded. For characterizing respectively the mean annual temperature, annual temperature range and precipitation in the reserves, we used the climatic GIS layers BIO1, BIO 7 and BIO12 of Hijmans et al. (2005). Connectivity at the 10 km scale was computed for each reserve following the same procedure as described in Abrego et al. (2015), using Zonation Conservation Planning Software (Lehtomäki and Moilanen, 2013) and maps produced by Brus et al. (2012). To control for the effect of the sampling effort, we also included the number of sampled dead wood units as a reserve level covariate. The reserves were grouped in eight regional categories (henceforth called regions), according to their geographical location (see Supplementary Appendices 1 and 2).