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Hydnoid fungi of the family Bankeraceae – their assemblages and vegetation ecology in Central Europe, Czech Republic

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ABSTRACT

The diversity of stipitate hydnoid fungi of the genera *Bankera*, *Hydnellum*, *Phellodon* and *Sarcodon* was studied at 92 microlocalities in the Czech Republic in 2010–2014. Their vegetation was documented by means of phytosociological relevés. In total, 26 hydnoid species were found. Individual microlocalities hosted 1–6 hydnoid species. Frequent co-occurrence of certain species pairs or groups was revealed. Multivariate analyses were used to test community patterns between hydnoids and vegetation, divided into layers and plant functional groups. We confirmed the hypothesis that vegetation layers and functional groups have different effects on the individual hydnoid species. The occurrence of hydnoids is conditional especially on the dominant tree species. The main vegetation gradient of hydnoid sites is represented by the proportion of deciduous versus coniferous trees. Smaller trees in shrub and herb layers do not play a significant role except for spruce. Some hydnoids occur at sites with a species-rich herb layer, whereas others occur at sites with ericoid heaths and lichens, wet sites covered with hygrophilous mosses, or bare soils only covered by litter. Possible factors favouring hydnoids and causing their accumulation at small sites are outlined, e.g. facilitation, phylogenetic conservatism and alteration of tree dominants during succession. Habitat conditions creating "hydnoid site quality" are summarized including the character of the Czech hydnoid-richest sites.

1. Introduction

Stipitate hydnoid fungi (Maas Geesteranus, 1975) of the family Bankeraceae, i.e. genera *Bankera*, *Hydnellum*, *Phellodon* and *Sarcodon*, are ectomycorrhizal symbionts of trees in a broad spectrum of forests, especially boreal and temperate ones (Smith and Read, 2008). The group includes fungi with conspicuous basidiomata, often growing in clusters (Maas Geesteranus, 1975; Breitenbach and Kränzlin, 1986; Ryman and Holmåsen, 1992; Pegler et al., 1997; Krieglsteiner, 2000; Nitare and Högberg, 2012). In Europe and some regions of North America, most species have decreased during the second half of the 20th century (Otto, 1990; Gulden and Hanssen, 1992; Hrouda, 2005a,b; Baird et al., 2013), probably due to sulphur and nitrogen depositions (Arnolds, 1989, 2010), although little experimental or gradient-based data are available directly for hydnoid fungi (Lilleskov et al., 2011). Due to this threat most species have been included in national Red Books and Red Lists (e.g. Benkert et al., 1992; Gärdenfors, 2005; Evans et al., 2006; Senn-Irlet et al., 2007; Smith et al., 2016). However, partial recovery is being seen in the 21th century (Arnolds, 2010).

Interesting phenomena have been documented in stipitate hydnoid fungi of the family Bankeraceae (termed hydnoids in agreement with the aforementioned literature) in the past two decades. Most species prefer soils covered with a thin layer of litter and humus (Hrouda, 1999). Moreover, a detailed study from the Olympic National Park, USA (Trudell and Edmonds, 2004) showed that *Hydnellum* and *Sarcodon* species prefer drier, nitrogen-poor soils. Studies using sequence data (ITS) helped to understand the delimitation of critical or new taxa and revealed cryptic species in some groups (Parfitt et al., 2007; Ainsworth et al., 2010; Baird et al., 2013; Loizides et al., 2016). Bridge and Panchal (2004) analysed the population structure of selected *Hydnellum* and *Phellodon* species showing that smaller sites are inhabited by homogeneous populations whereas the larger ones host heterogeneous or distinct populations. Van Der Linde et al. (2010) stated that establishment of new colonies of *Hydnellum peckii* and *Phellodon tomentosus* in a pine forest via

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transfer of soil with inoculum was unpredictable. This study was preceded by works on PCR-based detection of hydnoid mycelia in soil (Van Der Linde et al., 2008, 2009). Another study by Van Der Linde et al. (2012) showed that mycelia of hydnoids remain belowground and viable for at least 4 years without producing basidiomata.

Due to the narrow ecological requirements of some species, hydnoids have been selected as habitat indicators (e.g. Petersen, 2012; Bonsdorff et al., 2014). Reversely, Feest and Smith (2015) proposed that standardised biodiversity assessment using fungal indicators can predict occurrence of hydnoids in studied plots.

Field mycologists are well aware of the fact that several hydnoid species often grow together (e.g. Marren, 2002; Newton et al., 2002; Peiger, 2015) at very small sites. Such microlocalities are usually grouped into larger localities concentrated in specific areas, in Central Europe e.g. on northern slopes and foothills of the Alps, in southern Bohemia, and in the Carpathians (Hrouda, 1999; Papoušek, 2004). On the other hand, hydnoids are almost completely absent in other regions (Krieglsteiner, 1991), mostly those affected by air pollution. Some authors enumerate species recorded at larger localities (Marren, 2000) and present exact spatiotemporal data on individual hydnoid records (Van Der Linde et al., 2012). However, there is almost no detailed data on species number and composition at microlocalities shared by several hydnoid species. The only exceptions are the detailed works by Newton et al. (2002) and Peiger (2015).

We decided to study the phenomenon of common occurrence of several hydnoid fungi at particular microsites in a model area, the Czech Republic, a country with temperate forests located between the northern boreal and southern thermophilous forests and in the middle of the suboceanic/subcontinental gradient (Ellenberg, 1988). There is a good basis for such a study, as all data on the past occurrence of particular hydnoid species have been summarized by Hrouda (1992, 1999). His papers clearly show a rapid decline of some species during 1960–1990, leading to inclusion of most hydnoids into the Czech Red List (Holec and Beran, 2006). However, recent data document a reappearance of hydnoids in certain regions of the Czech landscape (Papoušek, 2004; Dvořák and Hrouda, 2005; Hrouda, 2016; vouchers in PRM, BRNM, BRNU, CB, HK; for acronyms, see Thiers, 2016). This is probably connected with an improvement in air quality in the past 25 years caused by legislation changes and technical measures such as desulfurisation and introduction of clean technologies (Czech Hydrometeorological Institute 2014a). This trend has been confirmed by the discovery of previously unknown and species-rich localities during 2000–2015 (Tejklová and Kramoliš, 2011; Holec et al., 2016; vouchers in aforementioned herbaria).

Our study analyses species richness and vegetation characteristics of hydnoid assemblages occurring at small sites. Hydnoid diversity is compared with vegetation variables recorded in phytosociological relevés. Using cluster and multivariate statistical methods we ask the following questions:

1. What is the diversity and composition of hydnoid assemblages?
2. To what extent is the composition of such assemblages related to different levels of vegetation (vegetation layers and/or plant functional groups)?
3. What is the relation of individual hydnoid species to vegetation dominants, composition, and structure?

2. Materials and methods

2.1. Sampling of field data

During 2010–2014, a total of 92 hydnoid sites (microlocalities) discovered at 26 localities in 4 regions of the Czech Republic (Bohemian Forest, southern Bohemia, Bohemian-Moravian Highlands, eastern Bohemia) were studied (Fig. 1). Altitudinally, the localities represent a gradient from the uplands to the mountains (420–930 m). Almost all microlocalities (Supplementary Material A1) are situated on acidic bedrock (granite, gneiss, sandstone), locality L1 on neutral to slightly alkaline bedrock, and those on fishpond dikes (localities NAD and VYŠ) basically acidic but with an unnatural higher pH caused by liming.

Our sampling covers ca. 80% of all hydnum-rich localities known in the country since the year 2000 as well as a high number of hydnum-poor ones. This preferential sampling design reflects both the spatial rarity of hydnoids and their distributional pattern in the real landscape (see Introduction). The selection of localities was carried out based on data published after 2000 (Holec 2004; Papoušek, 2004; Kučera et al., 2006; Hrouda, 2016), unpublished records of the first author (documented by vouchers in the PRM herbarium) and advice by local mycologists (see below). In total, we registered 208 records of hydnoid fungi.

The localities were represented by discrete, non-fragmented, more or less diversified forest complexes containing one to several hydnoid microlocalities, and surrounded by different landscapes (mostly treeless). They were about 2 × 2 to 5 × 5 km in size. All localities were searched for discrete hydnoid sites termed microlocalities (= microsites *sensu* Newton et al., 2002 or hotspots *sensu* Taylor et al., 2014). The purpose of using microlocalities as the basic study unit was to register exact data on the hydnoid species in relation to the neighbouring trees, shrubs, herbs, mosses and lichens recorded by means of standard phytosociological relevés (see below). Microlocalities were understood as small plots of homogeneous vegetation where basidiomata of one to several hydnoid species were grouped together. The distance of hydnoid basidiomata varied from about 0.5 to 2 m. The shape of each microlocality was influenced by its geomorphology and vegetation. Squares had sizes of 225 m^2, which fits the ideal square of 15 × 15 m, representing the area of a standard phytosociological relevé for forest communities. Patches and rectangles were smaller depending on the area of tree vegetation (i.e. on dikes surrounded by water and road). Neighbouring hydnoid sites with different vegetation (e.g. a young forest stand close to an old one) were studied as separate microlocalities. Boundaries of two neighbouring microlocalities were always more than 10 m apart (zone with no hydnoid basidiomata) but mostly much more. For basic data on microlocalities, see Supplementary Material A1. It is important to emphasize that

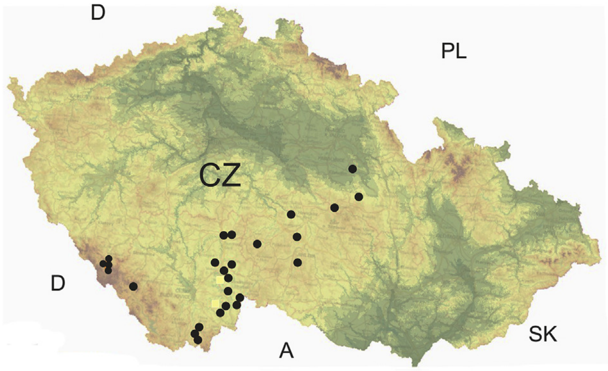

Fig. 1. Distribution of 26 studied localities in the Czech Republic. Microlocalities are not shown as their number (92) is too high for this resolution. For coordinates of microlocalities see Supplementary Material A1. Abbreviations: A – Austria, CZ – Czech Republic, D – Germany, PL – Poland, SK – Slovakia. Colours: green – lowlands, yellow to ochre – highlands and submontane areas, brown – mountains.