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How does the richness of wood-decaying fungi relate to wood microclimate?



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1. Introduction

Species composition of fungi growing in and fruiting on dead wood is related to a range of trunk properties, e.g. size, decay stage, bark cover, trunk type (snag/log), contact with the ground, and the way the tree died (e.g. Lindblad, 1998; Pouska et al., 2011, 2016). Moreover, microclimatic conditions such as moisture and temperature inside trunks and in their vicinity considerably influence fungal community assembly (Heilmann-Clausen, 2001; Fukasawa et al., 2009; Pouska et al., 2016).

Species richness is related to several properties of logs (e.g. Høiland and Bendiksen, 1997; Schmit, 2005; Gates et al., 2011; Stokland and Larsson, 2011), and some of them, such as size, decay stage, cover by bryophytes and vegetation, mirror or even influence microclimate in wood (Heilmann-Clausen and Christensen, 2005; Pouska et al., 2016). Nevertheless, some properties may have different importance for red-listed and non-red-listed species, as indicated by Heilmann-Clausen and Christensen (2005).

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ABSTRACT

Microclimatic conditions in dead wood influence fungal growth and hence also species composition, but it remains unclear how they influence species richness in nature. We analysed fungal species richness based on the occurrence of fruit bodies on 2 m long segments of both standing and lying trunks of Norway spruce (*Picea abies*). The number of non-red-listed species was related positively to moisture, and negatively to both temperature extremes and fluctuations. The numbers of both red-listed and non-red-listed species were further differently influenced by trunk diameter and by trunk properties related to the progression in wood decay. These results indicate that the richness of fungal communities in dead wood is shaped by an interaction of wood decay, moisture and temperature fluctuations.

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More stable conditions are found in large and more decayed trunks (Stokland et al., 2012; Pouska et al., 2016), which are, however, rather rare in managed forests. As species rarity may reflect habitat rarity, there is a question whether the richness of red-listed species does increase with microclimatic stability. We considered red-listed species as rare, although the current Red Lists (Holec and Beran, 2006; Karasch and Hahn, 2010) contain some species that have been overlooked and may not be as rare or threatened as indicated, and some rare species are missing from the Red Lists.

We included two types of trunks in this study, snags (standing dead trunks) and logs, which differ in several aspects such as vertical/horizontal position, connection with the soil and different opportunities for colonisation by fungi. Unlike logs, standing snags cannot reach a final stage of decay (since when they are well decayed they fall), and they differ in both temperature and moisture conditions (Pouska et al., 2016). Besides, snags have rarely been included in similar studies.

Since microclimate influences fungal species assembly in trunks, it probably also influences species richness. To our knowledge, no study has examined whether there is a relationship of species richness of fruiting fungi and temperature in wood; only



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Allen et al. (2000) included wood moisture. We aim to investigate relations of microclimate (along with other properties of spruce trunks) to species richness of wood-decaying fungi. We attempted to answer these questions: is there a relationship between temperature and/or moisture conditions in trunks and fungal species richness? Are the numbers of red-listed and non-red-listed species influenced by the same characteristics in a similar way?

2. Materials and methods

The study was conducted in a natural spruce forest on Troimezná Mt. in the Bohemian Forest, Czech Republic (48°46′19″N, 13°49′37″E). The design of this study was the same as in Pouska et al. (2016), with one main difference: sporocarp surveys were conducted from July 2013 to May 2015 (nine visits) on the segments of 30 snags and 70 logs. The characteristics of the 2 m long segments of *Picea abies* trunks (Supplementary data) are the same as in Pouska et al. (2016), and they did not undergo any major changes during this period. The following characteristics were recorded: elevation; trunk type (snag/log); diameter; decay stage; surface disintegration; bark cover; branches; ground contact; lichen, bryophyte, spruce sapling and vegetation cover; contacting wood (number of other decaying trunks or stumps touching the segment); openness (fraction of open sky unobstructed by vegetation or any other objects); water content in the surface of wood measured on the basis of electric resistance. Temperatures were measured in the sub-surface layer of wood in 15 min intervals from 14th June to 21st October 2013.

Data processing. Temperature measurements underwent a process of smoothing and pruning for each combination (matrix) of two parameters: magnitude (M; range 0.1-5.0 °C) and velocity (V; range 0.0001-0.4 °C min⁻¹). This resulted in a number of truncated sections (three time-steps long events) of uniform temperature changes for selected pair of M and V, distinguished into night temperature decreases or day temperature increases. A matrix of event counts was then fitted by the following function:

 $\sqrt{N} = f - b \times M - c \times V$

where f is the frequency of events; the coefficient b represents the speed of decrease in event frequency with increasing M; and coefficient c represents the speed of decrease in event frequency with increasing V. In other words, the greater is a value (b or c), the smaller is the frequency (or probability) of more drastic (long or fast) temperature changes. Details on data processing are in Pouska et al. (2016).

The following temperature characteristics were used: Tmin (minimal recorded temperature); Tmax (maximal recorded temperature); f_ND (frequency of night temperature decreases); b*M_ND (rate of change of the frequency of night temperature decreases with the change of their magnitude); c*V_ND (rate of change of the frequency of night temperature decreases with the change of their velocity); c*V_DI (rate of change of the frequency of day temperature increases with the change of their velocity); see Supplementary data for details.

Statistical analyses. Regressions were used to evaluate the dependence of species richness, divided into the numbers of redlisted and non-red-listed species, on characteristics of trunk segments, either for all trunks together or separately for logs only; snags were not included separately because only five of the 30 snags hosted some red-listed species. We tested marginal effects of characteristics because some characteristics were correlated and might thus be excluded if using a method of stepwise selection, although they can be biologically interesting. Parametric transformations (log transformation, square-root transformation and square transformation) were considered to maximise the linearity of relations of predictors with species numbers, or second-power polynomials were included if relations were unimodal. All statistical analyses except ordination analyses were done using R, version 3.1.1 (R core team, 2014).

Redundancy analysis (RDA) with the numbers of red-listed and non-red-listed species as explanatory variables and the trunk characteristics as response variables was used to visualise their relationships. We preferred reverse analysis because we included all the characteristics with significant marginal effects. Due to strong unimodal relation of the number of non-red-listed species to decay stage, we combined trunk type with decay stages and displayed them as five categories. RDA was performed in Canoco 5 (ter Braak and Šmilauer, 2012).

3. Results and discussion

In total, 85 species were found on the studied trunk segments, out of which 27 non-red-listed species and three red-listed species on snags and 61 non-red-listed species and 14 red-listed species on logs (Supplementary data). The average numbers of non-red-listed/red-listed species per snag segment were 2.2/0.2 (maximum 6/1), and per log segment 3.1/0.8 (maximum 7/3). Characteristics with significant relations to species numbers on all trunks are in Fig. 1.

Microclimatic characteristics were related to non-red-listed species as well as to red-listed species, however, in a different way (Fig. 1, Table 1). The number of non-red-listed species was negatively related to night temperature decreases, i.e. f_ND and b*M_ND. The number of red-listed species was negatively related to day temperature increases in all trunks only, i.e. c*V_DI (greater value expresses fewer fast changes). Snags had greater c*V_DI than logs (Pouska et al., 2016), i.e. snags experienced fewer fast temperature increases than logs, likely due to their vertical position reaching above the vegetation; snags were thus warmed more continuously during mornings or evenings, but received less direct

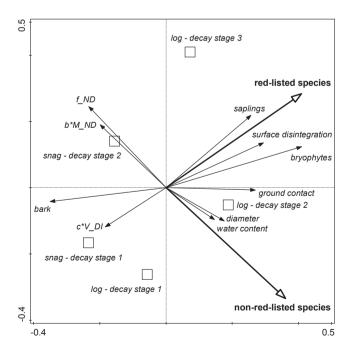


Fig. 1. RDA ordination diagram showing the relations of trunk segment characteristics to species richness. More non-red-listed species were on weakly and moderately decayed logs with greater water content and with fewer night temperature decreases (f_ND); more red-listed species were on moderately and strongly decayed logs with greater frequency of fast temperature increases (c*V_DI).

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