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Growth sites of polypores from quantitative expert evaluation: Late-stage decayers and saprotrophs fruit closer to ground

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ABSTRACT

Life history traits are key to why species occur when and where they do and how their populations will respond to environmental changes. However, dispersal-related traits of fungi are generally poorly known. We studied how spore release height from the ground, an important determinant of airborne dispersal, is connected to other traits in polypores. We collected expert evaluations of fruit body growth sites for 140 species and found that experts generally provided consistent estimates of height above the ground. Height was correlated with other traits: species fruiting on living trees, earlier decay stages and deciduous hosts tend to fruit higher above the ground. While our data do not allow mechanistic explanations, our study demonstrates the potential of expert knowledge and identifies fruit body height above the ground as one consistent trait relevant to species' life history strategies. We recommend a more comprehensive expert survey as one cost-efficient way towards a more trait-based fungal ecology.

1. Introduction

The functional characteristics, or traits, of organisms are central to the big questions in ecology, such as why there is such a variety of species, why they occur where they do, and how they give rise to ecosystem-level properties and processes. While this is by no means a new insight, conceptual advances have only relatively recently provided a common framework for the ecological approaches that explicitly take traits into account (McGill et al., 2006; Webb et al., 2010). The emergence of the field of trait-based ecology has been accompanied by increasing efforts to systematically gather trait information for a large number of species, most famously exemplified by the TRY database of global plant traits (Kattge et al., 2011). The first comprehensive analyses of the TRY data are now reshaping our understanding of plant diversity (Díaz et al., 2016). Initiatives of similar scale are so far absent for the Fungal Kingdom, but the momentum is growing: for instance, Aguilar-Trigueros et al. (2015) recently reviewed and called for trait-based approaches in fungal ecology.

The obvious hurdle obstructing the way towards a more trait-based fungal ecology is the scarcity of trait data – understandably, given the remaining gaps in the knowledge of basic ecology and taxonomy of fungal species that are prerequisites to the identification and robust definition of relevant traits. While carefully measured trait data is unquestionably pivotal, its accumulation is slow especially given the urgent nature of many of the applied questions we are facing, such as predicting and preventing the further decline of threatened species. We argue that in relatively well-known groups such as the polyporoid wood-inhabiting fungi, the active body of professional and non-professional experts presents a large reservoir of qualitative but also semi-quantitative information on species traits that could be tapped to complement traditional scientific measurements.

Dispersal is one of the key life history processes that shape population dynamics and hence is at least indirectly relevant for most, if not all, ecological phenomena. Dispersal-related traits are thus highly valuable for any trait-based approaches. Following the movement ecology framework of Nathan (2008), dispersal-related traits include those affecting movement capacity and those

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affecting navigation capacity. In passive airborne dispersers such as many fungi, the main dispersal-related traits are the characteristics of the diaspores that determine their aerodynamic behaviour and longevity in the atmosphere, the reproductive organs that determine the manner in which they are released, as well as the site and timing of diaspore release (Gregory, 1973; Soons et al., 2004; Damschen et al., 2008; Nathan et al., 2011; Norros, 2013). These traits are involved in both making movement possible (movement capacity) and determining where the diaspores are likely to land (navigation capacity).

In airborne dispersal, the site of diaspore release is important primarily due to the different exposure of different sites to turbulent airflows. In general, both average wind speed and turbulence increase with height from the ground (Stull, 1988; Seinfeld and Pandis, 2006). This vertical turbulence gradient is prominent also within plant canopies such as forests (Massman and Weil, 1999). Thus, fruit body height from the ground is the most obvious indicator of the dispersal potential provided by different sites of diaspore release. Indeed, greater release height has been shown to enable longer dispersal distances in plants (Soons et al., 2004; Gomez, 2007) and has become a standard parameter included in mechanistic models of airborne dispersal (Nathan et al., 2011). For forest fungi, mechanistic model simulations predict that spores do reach longer dispersal distances when released higher in the canopy, even though their dispersal is less sensitive to release height than that of larger propagules such as plant seeds (Norros et al., 2014).

Dispersal-related traits are particularly relevant when trying to understand and predict the responses of different species to habitat loss and fragmentation. Habitat fragmentation affects the balance of the costs and benefits of dispersal (Comins et al., 1980; Gilpin and Soulé, 1986; Bonte et al., 2012), and the optimal dispersal strategy in a fragmented landscape depends on the specific conditions (Travis et al., 2010; North et al., 2011; Poethke et al., 2011). Thus, it is plausible to hypothesize that the populations of different dispersers respond differently to fragmentation over ecological timescales, although it is not easy to predict whether high dispersal capacity should make species more or less vulnerable to fragmentation. There is some empirical evidence for a link – either positive or negative – between dispersal capacity and vulnerability to fragmentation from plants and animals (e.g. Henle et al., 2004; Pereira et al., 2004; Ockinger et al., 2010), but the question has very rarely been addressed in fungi.

By occupying a spatially limited and ephemeral, ever changing substratum, wood-inhabiting fungi are confronted with a need to be efficient colonisers, reproducers and recolonisers (Jönsson et al., 2008; Lonsdale et al., 2008). The need for efficient colonisation is even more evident taking into account that wood in different decay stages host clearly different fungal assemblages (Heilmann-Clausen, 2001), and thus the window of opportunity for an individual species is likely to be short. Moreover, in most human-dominated areas of the world, forest habitats have been dramatically altered by forestry and fragmented by other land use practices (Foley et al., 2005; Woodcock et al., 2015). Wood-inhabiting fungi have shown an inevitable response to the changes: for example in Finland and Sweden almost half of all polypore species are currently red-listed (Gärdenfors, 2010; Rassi et al., 2010) and, for a number of species, there is evidence for a negative effect of fragmentation beyond the linear effect of decreasing resources (Nordén et al., 2013). On the other hand, some species have not been affected and others even seem to benefit from fragmentation (Nordén et al., 2013). Attempts to relate the different fragmentation responses of wood-inhabiting fungi to species traits have so far revealed that fragmentation vulnerability is higher in specialist than generalist species, in species that decay primarily spruce, in species in which fruit bodies appear at intermediate to late stages of decay, in species preferring large, naturally fallen trunks, in annual species, in rare species, and in species with small spores (Berglund and Jonsson, 2008; Berglund et al., 2011; Stokland and Larsson, 2011; Nordén et al., 2013). Although there is some evidence suggesting that rare wood-inhabiting fungi are limited by dispersal (Norros et al., 2012), a direct link between dispersal capacity and vulnerability to habitat fragmentation has so far been elusive (Norros, 2013).

Here, we present and analyse expert-based data on the sites of spore release in polyporoid wood-inhabiting fungi. Using a quantitatively formulated query form, we collected evaluations from Finnish experts of the typical heights at which 140 polypore species produce their fruit bodies in Finland. Based on the expert evaluations, we assessed (1) how consistent and species-specific the growth heights of different polypore species are. Further, we studied (2) how the preference for different growth heights is related to species-specific spore morphology, fruit body longevity, substratum preferences, commonness in Finland and vulnerability to habitat fragmentation.

2. Material & methods

2.1. Fruiting height estimates

To obtain fruit body height estimates for polypore species we utilised the extensive knowledge of Finnish polypore specialists. Finland is globally probably the leading country considering ecological research activity focusing on polypores (Junninen and Komonen, 2011), using polypores as conservation tools (Halme et al., 2009) and hence also the number of experienced field mycologists specialised on polypores. We prepared a questionnaire and gave these experts an opportunity to answer to it by contacting them through an email list that is targeted to and followed by more or less all Finnish polypore experts. All volunteering experts were included in the study, i.e. there was no further selection or screening. Experts answered the questionnaire independently in their own time without knowing the other respondents' identities or answers.

The personal profile section of the questionnaire was used to evaluate the experience each expert has in observing polypores in the field. We asked the number of years during which the expert has conducted polypore surveys, the average number of survey days in each year, and the proportion of experience spent in different vegetation zones and biotopes (see the profile summaries in Supplementary Appendix 1). Ten experts with a combined experience of 3545 fieldwork days filled in the query. The raw data from the questionnaires is included as Supplementary Appendix 1.

The fruiting height section of the questionnaire included the list of polypore species that commonly occur in Fennoscandian boreal forests, have been taxonomically stable units in recent years (Niemelä, 2005; Kotiranta et al., 2009) and were accompanied with good knowledge of their traits, such as spore measurements and fragmentation responses (Niemelä, 2005; Nordén et al., 2013). This list included altogether 140 species. The experts were asked to estimate the number of personal field observations they had of each of the species. In addition, they were asked to evaluate the percentage of observations situated in six different growth height categories, which were clarified with a diagram (Fig. 1) and category descriptions: I. within a decaying log (for example inside a hollow log); II. on the lower surface of a log, in a place where the log is attached to the ground; III. on the lower surface of a log, in a place where the log is slightly detached but no more than 20 cm from the ground; IV. on any other surface of a decaying log or on any other surfaces (on stumps etc.) but below 1 m height; V. on any surface, between 1 and 5 m height; VI. on any surface, more than 5 m