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Species associations during the succession of wood-inhabiting fungal communities

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A B S T R A C T

We studied fungal succession in decaying wood by compiling time-series data of fruit body observations. We tested the hypothesis that the presence of a primary species affects the probability of a succeeding species occurring later on the same log. Significant associations were detected for 15 species pairs; these were consistent with earlier findings on co-occurrence patterns in single time surveys. We used enrichment analysis to test if species with particular life-history attributes were more often associated with the occurrence of a succeeding species, or *vice versa*. White rot fungi and fungi abundant as mycelia were more often associated with the occurrence of succeeding species, compared to brown rot fungi and species with low mycelial abundance. Our results indicate that certain primary species cause priority effects and non-random co-occurrence patterns in the field. These successional patterns are likely to be connected both with substrate modification and species interactions.

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Introduction

Theories of succession have been central to ecological research for more than a century. Since Clements' (1916) climax concept and Gleason's (1926) individualistic model, a large body of research on succession has emerged, mainly focussing on plant communities. Today bacteria and fungi are also becoming incorporated into ecological models of succession (Peay et al., 2008). Even so, to understand how species communities are formed and how species interactions affect community structure remains a challenge. A prevailing view among empirical ecologists is that interspecific interactions play a significant role in determining the community composition and structure during community assembly, so that a resident species may affect the establishment success and subsequent growth of a colonizing species (Connell and Slatyer, 1977; Drake, 1991; Chase, 2003). In contrast, neutral theory assumes that species at the same trophic level are identical in their competitive abilities, and views community assembly as a purely random process (Hubbell, 2005).

Wood-inhabiting fungi are the main decomposers of dead wood in boreal forest ecosystems (Stokland et al., 2012). The decomposition of a dead tree depends on abiotic factors such as moisture and temperature, but also on the fungal decomposers themselves as fungal decay alters the chemical and physical properties of the wood (Stokland et al., 2012). Colonizing secondary species may be either facilitated, inhibited or neutral to these modifications by the primary species (Niemelä et al., 1995). An effect of a resident species on the establishment probability of subsequent colonizers is often referred to as a priority effect (Fukami et al., 2010). In wood-inhabiting fungal communities, single time point data showing non-random co-occurrence patterns in the field as well as laboratory studies suggest that the effects of primary species are important and may influence community structure in decomposer fungal communities (Niemelä et al., 1995; Heilmann-Clausen and Boddy, 2005; Fukami et al., 2010; Lindner et al., 2011; Dickie et al., 2012), and indirectly also affect nutrient and carbon dynamics in forest ecosystem (van der Wal et al., 2013).

Established fungi can be territorial, monopolize captured resources and defend the occupied wood patch against competing mycelia (Rayner and Boddy, 1988). Laboratory studies have shown that wood-inhabiting fungi differ in their competitive abilities (Holmer and Stenlid, 1997). The competitive outcome largely depends on the relative sizes of the competing mycelia (Holmer and Stenlid, 1993), the type and amount of resources the interacting fungi have access to and climatic environment (Boddy, 2000). Fungi are able to translocate nutrients and energy between different parts of their mycelium, hence fungal individuals with a large interconnected mycelium may have better competitive abilities compared to species with a small-sized mycelium (Boddy, 2001; Stenlid et al., 2008). Antagonistic interactions involve the production of antifungal compounds, mycoparasitism and morphological changes (Woodward and Boddy, 2008). Consequently, interspecific interactions between resident and colonizing fungi may result in changes to many aspects of community structure over time (Woodward and Boddy, 2008).

Based upon the observation of fruit bodies, Renvall (1995) put forward the idea that the presence of certain pioneer species may influence the following community development of wood-inhabiting fungi. Since then, a number of fruit body surveys have surveyed fungal colonization of Norway spruce (*Picea abies*) logs (Edman et al., 2004; Lindhe et al., 2004; Berglund et al., 2005; Edman et al., 2007; Jönsson et al., 2008; Olsson et al., 2011; Pouska et al., 2011; Halme and Kotiaho, 2012), although these studies did not focus on succession but e.g. compared colonization patterns in managed and natural forests. Two exceptions are Lindner et al. (2011) and Pouska et al. (2013) in which successional patterns in naturally colonized logs of Norway spruce were studied. By using molecular data, it was concluded that logs that had initially been inoculated with or naturally colonized by the early successional brown rot fungus *Fomitopsis pinicola* later differed in both species richness and community structure and had lost more mass compared to other logs (Lindner et al., 2011). Similarly, a difference in community structure in logs decayed by *F. pinicola* was found based upon fruit body observations (Pouska et al., 2013). Other fruit body studies have documented non-random patterns of co-occurrence based on snapshot data (Edman and Jonsson, 2001; Ylisirniö et al., 2009; Ovaskainen et al., 2010a), yet these studies lack the temporal dimension and are thus not conclusive in the importance of species associations during community assembly. Hence, the overall importance of species interactions during succession of wood-inhabiting fungal communities remains largely an open question.

Despite strong evidence of differential species' responses to primary species from laboratory studies (Holmer et al., 1997; Heilmann-Clausen and Boddy, 2005; Fukami et al., 2010), it has remained difficult to quantify the overall importance of successional dynamics in natural systems for three main reasons. First, experimental studies of succession are by necessity focused on a selected and restricted subset of species, while natural communities are often highly species rich, complex and vary in time and space. Second, long-term data with documented species immigration history on individual sites or substrata are scarce, making successional studies difficult (but see e.g. Weslien et al., 2011; Penttilä et al., 2013). Third, in systems with high species richness, the analysis of species-to-species associations leads to the problem of multiple non-independent statistical tests, making it challenging to interpret the results. Accordingly, most studies of fungal community assembly have been manipulative, or successional patterns have been indirectly inferred from single-time observations of fruit bodies in chronosequence studies. One major drawback with using presence and absence of fruit bodies is that it is not possible to account for the fact that some fungi are present as mycelia inside the wood without producing fruit bodies. Further, the influence of fungal life-history attributes on community assembly has seldom been addressed. Hence, it is not clear if successional trends in fungal communities follow those of macroorganisms, where communities in early succession are dominated by fast-growing opportunists with r-selected life-history traits, which are later replaced by more competitive k-selected species (Rayner and Boddy, 1988). In the present study, we compensate for