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# Wood-inhabiting fungal communities: Opportunities for integration of empirical and theoretical community ecology

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## ABSTRACT

The interest in studying wood-inhabiting fungal communities has grown in recent years. This interest has mainly been motivated by the important roles of wood-inhabiting fungi in ecosystem functioning (e.g. nutrient cycling) and conservation biology (e.g. their sensitivity to forest management). In this paper, I argue that another important, but yet largely unexplored motivation for studying wood-inhabiting fungal communities, is their potential to advance fundamental community ecology. One major advantage of wood-inhabiting fungi as model systems is that they are organized as spatially well-defined metacommunities, thus conforming to the assumptions of many theoretical frameworks. Another major advantage is that they allow observations and manipulations over large numbers of local communities (habitat patches). After reviewing recent approaches in theoretical community ecology, I discuss how past empirical studies on wood-inhabiting fungal communities relate to community assembly processes, and provide future research directions on how the still unstudied assembly processes could be tackled using wood-inhabiting fungi as a model system.

## 1. Introduction

Much of the research in wood-inhabiting fungal communities has been motivated by their role in ecosystem functioning, or the need of identifying and conserving declining species and populations. Many wood-inhabiting fungal species are wood decomposers, with important functions of nutrient cycling (Boddy et al., 2008; Baldrian, 2016) and in the creation of new habitats for other wood-dwelling species in forest ecosystems (e.g. Fritz and Heilmann-Clausen, 2010; Cockle et al., 2012; Müller et al., 2014). As a result, many studies on wood-inhabiting fungal communities have focused on investigating how their diversity is linked to the decomposition process (e.g. Rajala et al., 2012; Valentín et al., 2014; Bradford et al., 2014; van der Wal et al., 2015; Purahong et al., 2016; Hoppe et al., 2016). Another reason why wood-inhabiting fungal communities have been the focus of much research relates to their high sensitivity to forest management. The reduction of the quantity, quality and continuity of deadwood caused by forest management has resulted in drastic declines of the wood-inhabiting fungal diversity and considerable changes in their community composition (e.g. Küffer and Senn-Irlet, 2005; Müller et al., 2007; Stokland and Larsson, 2011; Abrego and Salcedo, 2013; Nórdén et al., 2013; Juutilainen et al., 2014;

Saine et al., 2018). For these reasons, there is a great interest in designing conservation and sustainable forestry guidelines that preserve the wood-inhabiting fungal diversity (Lonsdale et al., 2008; Brunet et al., 2010; Junninen and Komonen, 2011).

In this article, I argue that fungal communities are highly interesting also for advancing fundamental community ecology, in particular to strengthen the two-directional interplay between theoretical and empirical community ecology. Wood-inhabiting fungal metacommunity systems can contribute greatly to advance ecological theory, by both providing data to test current theory, as well as bringing novel perspectives needed to develop new theory. Conversely, theoretical ecology can contribute greatly to advance empirical fungal ecology, by providing a conceptual framework in which to interpret results from different studies, and by suggesting new lines of research that may have thus far remained less explored. As I later explain in detail, the main advantages of using wood-inhabiting fungi as model systems in fundamental community ecology are twofold. First, wood-inhabiting fungi are organized in highly interactive, species-rich, temporally dynamic, and spatially well-defined metacommunities that conform to the assumptions of many theoretical frameworks. Second, wood-inhabiting fungi allow manipulation over large numbers of local communities inhabiting

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discrete habitat patches, i.e. the deadwood units. To develop my argument, I will first provide a brief summary of community ecology theory and provide an overview of how the current theory is connected to empirical data, with particular emphasis on those theoretical aspects which have been the least connected to empirical systems in any taxa. I will then describe how wood-inhabiting fungal metacommunities can be framed within the theoretical frameworks, and finally suggest new lines of research that would fill in the current gaps in the interplay between theory and empirical research in community ecology.

## 2. A brief summary of the prevailing theories in community ecology

Theoretical community ecology is undergoing a rapid conceptual transformation focusing on integrating previously competing theories into unifying frameworks (Weiher and Keddy, 1999; Morin, 2011; Vellend, 2016; Leibold and Chase, 2018). Influential unifying frameworks in community ecology are the Metacommunity Theory (Leibold et al., 2004; Leibold and Chase, 2018), the Assembly Rules Framework (Keddy, 1992) and Vellend's "Theory of Ecological Communities" (Vellend, 2010, 2016).

Metacommunity Theory (MT) explains how networks of local communities result from the interplay of stochastic and deterministic processes at both local and regional scales, where a metacommunity is defined as "a set of local communities that are linked by dispersal of multiple potentially interacting species" (Leibold et al., 2004; Holyoak et al., 2005). For explaining variation in species composition across habitat patches, MT synthesises four perspectives, also known as archetypes or paradigms. These four perspectives are the neutral, patch dynamics, species sorting, and mass effects perspectives. With its roots in Hubbell's Neutral Theory (Hubbell, 2001), the neutral perspective posits that all individuals are considered to be equal in competitive capabilities and niche preferences, irrespective of which species they belong to. Thus, in the neutral perspective, any variation in species composition emerges solely from stochastic ecological drift. The patch dynamics perspective assumes that species track ephemeral habitat patches through colonization-extinction dynamics, systematic variation in species composition being generated e.g. by the colonization-competition trade-off (Tilman, 1994). Related to the Niche Theory, the species sorting perspective focuses on the differences in the species niche preferences, which lead different species to inhabit different habitat patches (Chase and Leibold, 2003). The mass effects perspective differs from the species sorting perspective by assuming a much greater dispersal rate between the local communities within the metacommunity, so that the high dispersal rate influences variation in community composition. Three important assumptions of MT are that: (i) the four perspectives are not mutually exclusive (i.e. all can act simultaneously for a given metacommunity); (ii) the relative roles of each of the perspectives (and therefore processes) depend on the spatial scale; and (iii) the perspectives are just archetype examples along the broader spectrum of metacommunity dynamics (Brown et al., 2017).

Like MT, the Assembly Rules Framework (ARF) allows multiple processes to act simultaneously at multiple spatial scales. The assembly processes can be conceptually viewed as 'filters' acting at the scales ranging from the regional species pool to increasingly finer scales until the local community composition is determined (Zobel, 1997). Phylogeographic assembly processes, namely processes such as speciation and past large-scale migration, act at the largest spatial scales (Emerson et al., 2011). Ecological assembly processes refer to environmental filters, biotic filters, dispersal and stochastic processes. Environmental filters correspond to those abiotic factors which prevent or facilitate the establishment or persistence of species in local communities, and thus they may act from largest to smallest spatial scales (Kraft et al., 2015). Biotic filters refer to intraspecific (e.g. density dependence) and interspecific interactions (e.g. predation, mutualism, facilitation and competition) that determine the set of species that coexist in local

communities, and thus they act at smaller spatial scales (Araújo and Rozenfeld, 2014). Stochastic processes are those that generate divergence among communities occupying identical environments. These can involve demographic stochasticity (i.e. unpredictability in population size due to randomness of deaths and births), colonization-extinction stochasticity (i.e. unpredictability in species arrival and establishment), environmental stochasticity (i.e. unpredictability in population size caused by variation in environmental conditions) and genetic stochasticity (unpredictable changes in gene frequencies due to random genetic drift) (Ovaskainen and Meerson, 2010; Masel, 2011; Hanski and Ovaskainen, 2019). Dispersal refers to contemporary small-scale and large-scale migrations. An important assumption in ARF that the assembly processes do not act in isolation of each other. For example, environmental filters may modify the outcomes of the biotic interactions (Maron et al., 2014) and the importance of stochastic processes (Chase, 2007).

Recently, Vellend (2010; 2016) proposed a unifying framework that he called the "Theory of Ecological Communities" (TEC). Vellend brought a more synthetic perspective by integrating all processes of community dynamics into four fundamental or "high-level" processes: selection, ecological drift, dispersal, and speciation. Selection (*sensu* TEC) results from deterministic fitness differences between individuals of the same or different species, and is expected to change community composition to the extent that species vary in their average relative fitness. For instance, abiotic filtering and biotic filtering of the ARF are classified as selection processes of TEC, and the species sorting paradigm of MT considers these to play a major role. Ecological drift (*sensu* TEC) refers to the random component that drives community dynamics when demographic events occur at random with respect to species' identities, such as demographic stochasticity. Thus, ecological drift of TEC coincides with the stochastic processes of ARF, and the neutral paradigm of MT considers these to play a major role. Dispersal (*sensu* TEC) refers to the movement of species, either past large-scale migrations or contemporary smaller scale movements and large-scale migrations. Thus, dispersal of TEC coincides with the dispersal processes of ARF, and the mass effects and patch dynamics paradigms of MT consider dispersal to play a major role.

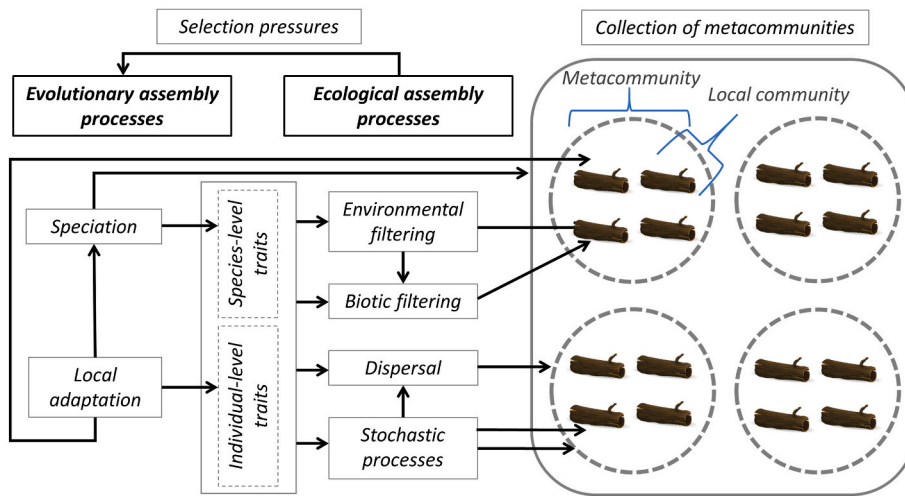
Rather than species' identities, it is their traits that determine how they respond to their environment and to each other (McGill et al., 2006; Cadotte et al., 2015). Both intra- and inter-specific trait variation are expected to be linked to environmental filtering (e.g. Kichenin et al., 2013), as well as biotic filtering (e.g. Carmona et al., 2019) and dispersal (e.g. Tamme et al., 2014) (Fig. 1). Thus, the identification of those traits that influence species' responses is crucial for gaining a predictive understanding of how ecological processes modulate community assembly.

## 3. How well is empirical research linked to theory in community ecology theory?

While much of the focus in empirical community ecology is on finding generalities in the processes structuring ecological communities across ecosystems and taxa (e.g. Hillebrand and Blenckner, 2002; Götzenberger et al., 2012; Belmaker and Jetz, 2012; Soininen, 2014; Müller et al., 2020), we still lack a clear quantitative synthesis of the relative contributions of the processes structuring ecological communities. I next summarize the key reasons why linking the above described theoretical frameworks to empirical studies has remained challenging in any taxa, not only in fungi.

*3.1. Challenge 1. Most empirical studies have focused on processes that are easy to study, providing a biased perspective on the prevailing assembly processes*

Most studies focusing on disentangling the relative effects of different assembly processes highlight the major role of environmental filtering in structuring ecological communities (e.g. Diaz et al., 1998;



**Fig. 1.** Conceptualization of how different ecological and evolutionary assembly processes interplay with each other to shape ecological communities at different scales. Ecological assembly processes refer to environmental filters (abiotic and habitat factors preventing or facilitating species colonization and persistence), biotic filters (intra- and interspecific interactions), dispersal (movement and migration) and stochastic processes (divergence among initially identical communities occupying identical environments). Ecological processes may exert selective pressures causing local adaptation in the early phase of the evolutionary timeline, and ultimately speciation. As a consequence of the evolutionary processes, individuals and species vary in their traits, which in turn affect ecological assembly processes. Ecological communities are conceptualized following the meta-community framework, which is illustrated using wood-inhabiting fungal metacommunity systems: deadwood units delimit local fungal communities which are linked to other local communities by dispersal, forming spatially well-defined meta-community systems. The arrows illustrate the spatial

scale (patch, metacommunity, or collection of metacommunities) at which the different assembly processes operate.

Lebrija-Trejos et al., 2010; Laliberté et al., 2014; Glassman et al., 2017). However, other processes such as biotic filtering, dispersal and stochastic processes may have equal or even bigger roles (Stegen et al., 2013; Fraaije et al., 2015; Powell et al., 2015) but they remain less studied, largely because environmental effects are easiest to statistically capture from observational data (Ovaskainen et al., 2019). In the same line, among the four perspectives in MT, species sorting and mass effects are the easiest ones to evaluate and thus there is bias towards studies testing and supporting these two perspectives (Logue et al., 2011). Furthermore, many empirical studies target ecological processes without considering evolutionary assembly processes. While the use of quantitative phylogenies in bringing an evolutionary perspective to community ecology is increasing (Webb et al., 2002; Kraft et al., 2007; Cavender-Bares et al., 2009), evolutionary processes such as local adaptation and speciation remain still poorly integrated into community ecology (Mittelbach and Schemske, 2015; Weber et al., 2017).

### 3.2. Challenge 2. Local communities usually lack discrete boundaries

Habitat patches are often more continuous than conceptualized in theory, or their boundaries are not even known. Thus, in many empirical studies the spatial scale at which local communities are bounded are arbitrarily defined. ARF allows definition of the local species communities as the set of species found at the finest scale considered, and can be conveniently adapted in empirical studies. However, because the relative effects of different assembly processes vary across spatial scales (McGill, 2010; Trisos et al., 2014; Hart et al., 2017; Mod et al., 2020), the flexibility for defining the spatial boundaries of local communities comes along with the limitation that the application of the ARF is highly study-specific, making it difficult to draw general conclusions across studies. In contrast, MT is built upon the theoretical scenario of well-defined habitat patches, where ecological communities are viewed as a set of spatially bounded local communities (Leibold et al., 2004; Leibold and Chase, 2018). Natural local communities with well-defined boundaries are for instance aquatic ecosystems such as riverine networks (Brown and Swan, 2010) and pond systems (Chase 2007; De Bie et al., 2012; Sakaeva et al., 2016). However, most local communities usually lack the discrete boundaries conceptualized in MT, for which reason it has proved difficult to directly link it to natural systems (Logue et al., 2011).

### 3.3. Challenge 3. Inferring the underlying processes from non-manipulative observational data is difficult

The vast majority of empirical studies in community ecology are based on non-manipulative observational data. However, non-manipulative observational data do not directly reveal the underlying processes, merely patterns that are generated by the underlying processes. Because multiple combinations of individual assembly processes can generate very similar or even identical patterns of community organization, inferring the underlying processes solely from data on patterns is challenging (Cale et al., 1989; Dormann et al., 2018; Ovaskainen et al., 2019). To address this challenge, much of the recent research in statistical ecology has focused on developing methods that enable connecting patterns in observational data more closely to the underlying mechanisms (Ovaskainen and Abrego, 2020). Yet, the only reliable way of gaining conclusive evidence about the underlying processes in empirical research is to conduct experimental (manipulative) approaches purposely designed to capture the focal processes (e.g. Kneitel and Miller, 2003; Chase 2007; Chase 2010; Howeth and Leibold, 2013). However, testing for the assembly processes is highly tedious or even unfeasible for many species-rich communities, while the reality is that the majority of life on Earth forms species-rich communities (e.g. fungi, plants, arthropods, bacteria).

## 4. How is empirical research on wood-inhabiting fungi linked to theory in community ecology?

A single deadwood unit contains from tens to hundreds of fungal species with various ecological roles such as wood decomposing (saprotrophic fungi), mycorrhizal, endophytic, parasitic and lichenized species (Ottosson et al., 2015). How such taxonomical and functional diversity is maintained in single deadwood units has long intrigued fungal ecologists. Even if this question is of a highly fundamental nature and tightly connected to ecological theory, research in fungal community ecology has seldom been motivated by the development or testing of general theory (but see e.g. Toljander et al., 2006; Fukami et al., 2010; Hiscox et al., 2015; O'Leary et al., 2018; Hagege et al., 2019a; O'Leary et al., 2021), more often by the key roles of fungi related to ecosystem functioning (e.g. Rajala et al., 2012; Valentín et al., 2014; Bradford et al., 2014; van der Wal et al., 2015; Purahong et al., 2016; Hoppe et al., 2016), or by conservation concerns (e.g. Küffer and Senn-Irlet, 2005; Müller et al., 2007; Stokland and Larsson, 2011; Abrego and Salcedo,

2013; Nordén et al., 2013; Juutilainen et al., 2014; Saine et al., 2018). However, as both the role of fungi in ecosystem functioning as well as the causes behind their declines ultimately link to the mechanisms underlying community assembly, the large body of literature on fungal community ecology already provides ample possibilities for linking to theory. As I will review below, processes related to environmental and biotic filtering have been long studied and are relatively well understood, whereas the roles of stochasticity, dispersal and especially evolutionary assembly processes are still less understood. Furthermore, the link from species traits to community assembly processes is currently a hot topic and new knowledge is being generated fast.

#### 4.1. Environmental filtering

Empirical studies on wood-inhabiting fungi have mostly proposed that the highly multidimensional variety of microhabitats that deadwood offers (e.g. wounds, rot holes, cavities, attached branches, roots, phloem, sapwood or heartwood) combined with the high specialization of wood-inhabiting fungi for such habitats is one of the main reasons behind the coexistence of the high diversity within deadwood units (Stokland et al., 2012). At the forest stand-level, the wood-inhabiting fungal diversity has been suggested to be maintained by the heterogeneity of deadwood in terms of variation in the sizes, decay stages and host tree species (Heilmann-Clausen and Christensen, 2004; Hottola et al., 2009; Bässler et al., 2010; Abrego and Salcedo, 2013; Olou et al., 2019). This is largely because deadwood of different sizes, decay stages and tree species provide different physical-chemical characteristics which determine the occurrences of different wood-inhabiting fungal species (Juutilainen et al., 2017; Krahe et al., 2018; Purahong et al., 2018; Leonhardt et al., 2019; Müller et al., 2020). Other local environmental factors that influence wood-inhabiting fungal communities are the microclimatic conditions (Bässler et al., 2010; Pouska et al., 2017) and deposited nitrogen levels (Allison et al., 2009; Andrew et al., 2018). At the larger scales, wood-inhabiting fungal communities strongly respond to environmental conditions such as macroclimate (Heilmann-Clausen et al., 2014; Abrego et al., 2017a; Thorn et al., 2018; Andrew et al., 2018; Olou et al., 2019), forest connectivity (Nordén et al., 2013, 2018; Abrego et al., 2015; Ruete et al., 2017) and macrohabitat structure such as vegetation type (Ordynets et al., 2018). In other words, abiotic environmental filtering has been considered the most important process creating variation in wood-inhabiting fungal communities both at the local and the larger scales, and many studies have (explicitly or implicitly) viewed fungal metacommunities from species sorting perspective.

#### 4.2. Biotic filtering

It is also relatively well established that variation in wood-inhabiting fungal communities is not only the result of environmental filtering, but also biotic filtering. Experimental studies have shown that competitive interactions for space and nutrients are the most common interaction types among wood-inhabiting fungi (Boddy, 2000; Hiscox et al., 2018). However, other interaction types such as mycoparasitism (Griffith and Barnett, 1967) or facilitation (growth stimulation through metabolite secretion, Heilmann-Clausen and Boddy, 2005) also occur among wood-inhabiting fungi. The interactive relationships among wood-inhabiting fungi strongly influence the colonization success of newly arriving species during deadwood's decomposition process, i.e. the assembly history or priority effects are important in determining wood-inhabiting fungal community dynamics (Fukami et al., 2010; Ottosson et al., 2014; Hiscox et al., 2015; Norberg et al., 2019). Furthermore, the outcome of the species interactions depends on abiotic environmental conditions such as temperature (Hiscox et al., 2016) or the spatial arrangement of the deadwood resources (O'Leary et al., 2018). The role of interspecific interactions has also been assessed by applying statistical methods that allow disentangling those species'

co-occurrences that can be explained by the environmental conditions, from those that cannot be explained by them (Ovaskainen et al., 2010, 2016). These kinds of analyses are increasingly used to understand the role of biotic interactions in wood-inhabiting fungal communities, as those co-occurrences that cannot be explained by environmental variation can be hypothesized to result from interactive relationships (e.g. Ottosson et al., 2014; Norberg et al., 2019; Saine et al., 2020). While only experimental approaches can provide conclusive evidence on the interactions (Dormann et al., 2018), these statistical approaches provide a useful tool for hypothesizing about species interactions from non-manipulative observational data.

#### 4.3. Stochasticity and dispersal

While the roles of environmental and biotic filtering have been much emphasized, at the same time it has remained difficult to predict which particular species are present in a particular deadwood unit (Abrego et al., 2017a,b; Norberg et al., 2019; Kolesidis et al., 2019). What is currently not very well understood is whether this is because it is difficult to accurately measure the relevant abiotic and biotic predictors, or whether other relevant underlying processes such as stochastic and dispersal processes have been unaccounted for. Several studies have indeed suggested that variation in wood-inhabiting fungal communities can relate also to dispersal (Norros et al., 2012, 2015; Abrego et al., 2015) and stochastic processes (Baldrian et al., 2016; Abrego et al., 2017b; Norberg et al., 2019; Hagge et al., 2019b). However, accurately quantifying the roles of stochastic and dispersal processes in community structure remains a challenge for any taxa, not only for fungi.

#### 4.4. Link from species traits to assembly processes

Because ecological assembly processes are ultimately influenced by species (response) traits (McGill et al., 2006; Cadotte et al., 2015), there has been an increasing interest in understanding the link between wood-inhabiting fungal traits and species responses to environmental variation. However, compared to other taxa such as animals or plants, trait-based approaches are only emerging in fungal community ecology (Crowther et al., 2014; Aguilar-Trigueros et al., 2015; Nguyen et al., 2016; Dawson et al., 2019; Zanne et al., 2020). Trait-based community ecology of wood-inhabiting fungi has mostly focused on traits measurable from the sexual structures (fruit bodies and spores) (Dawson et al., 2019), but some studies have also carried out measurements to the vegetative structures (mycelia) (Lustenhauer et al., 2020). Fruit body morphology has been found to be linked to the size (Bässler et al., 2014), decay stage (Abrego et al., 2017b) and species (Purhonen et al., 2020) of the deadwood resources. Generally, large deadwood units hold species with larger and more robust reproductive structures (i.e. species with perennial and pileate fruit bodies), which mostly occur in intermediately decayed deadwood (Bässler et al., 2014; Abrego et al., 2017b). Purhonen et al. (2020) found that species with perennial and pileate fruit bodies were also more often specialized to Norway spruce (*Picea abies*) than to other boreal host tree species. Dispersal traits characterizing the size and shape of sexual spores have also been linked to deadwood size: Species occurring on large deadwood units have large and spherical spores, whereas species occurring on small deadwood units have small and elongated spores (Purhonen et al., 2020). At larger spatial scales, wood-inhabiting fungi with perennial and pileate fruit bodies are especially vulnerable to forestry practices, likely due to their higher level of specialization to large deadwood units which have diminished due to forest land use (Nordén et al., 2013; Bässler et al., 2014; Abrego et al., 2017b). Smaller fungal spores can travel longer distances than larger spores (Norros et al., 2014), and thick-walled spores better survive under the harsh (UV-radiation and freezing) conditions characterizing open areas (Norros et al., 2015). However, empirical studies have not provided conclusive evidence of whether spore morphology is linked to landscape characteristics (Nordén et al., 2013; Bässler et al., 2014;

Abrego et al., 2017b). In a time-series analysis of fungal fruit body data which also included wood-inhabiting fungi, Andrew et al. (2016) found that the species fruiting in warmer conditions produce smaller spores. Nutritional mode (whether species are ectomycorrhizal or saprotrophic) is linked to deadwood decay stage, deadwood in advanced decay stages holding larger proportions of ectomycorrhizal wood-inhabiting fungal species (Abrego et al., 2017b; Mäkipää et al., 2017). These and other links from traits to species occurrence patterns have been reported mainly at the correlative level, experimental validations of their causal effects remaining scarce.

#### 4.5. Phylogeographic assembly processes

The historical processes influencing the current geographical distributions of species such as speciation and past large-scale dispersal remain poorly understood for wood-inhabiting fungi. In a large-scale study, Ordynets et al. (2018) observed that apyloporoid fungal community composition (composed mostly by wood-inhabiting species) poorly reflected the spatial configuration of post-glacial forest refugia, suggesting that historical dispersal barriers are not a strong determinant of the contemporary fungal distributions. Results from those trait-based studies that account for fungal phylogenetic constraints have observed high phylogenetic trait conservatism, namely that phylogenetically related species have similar traits and occur in similar environmental conditions (Bässler et al., 2014; Abrego et al., 2017b; Thorn et al., 2018; Hagge et al., 2019b).

### 5. Future research directions for advancing both theory and empirical research in wood-inhabiting fungi

As reviewed above, despite the great recent advances in research on wood-inhabiting fungal communities, the understanding on how their communities are assembled is still limited. In parallel, despite the great recent advances on the development of general and unifying conceptual frameworks for theoretical community ecology, the link between theoretical and empirical community ecology remains weak, largely because of many ecological communities not directly fitting to theoretical frameworks. I argue that wood-inhabiting fungal communities provide a yet largely unexplored model system that can greatly strengthen the link between theoretical and empirical community ecology:

An attractive feature of wood-inhabiting fungal communities is that they can be framed not only within the ARF but also within MT, as single deadwood units (e.g. stumps, fallen logs or branches) can be viewed as “habitat patches” (Fig. 1). From a metacommunity perspective (*sensu* Leibold et al., 2004), fungal species inhabiting deadwood units can thus be conceptualized to represent local communities that are linked to other deadwood units by dispersal. This perspective was originally adopted by Jönsson (2008), who used a habitat-tracking meta-population model to understand the colonization-extinction dynamics of wood-inhabiting fungi. Since then, the concept of patch-tracking meta-populations or -communities has been used to describe wood-inhabiting fungal communities in some studies (Halme et al., 2013; Moor et al., 2021), but this conceptualization has not yet become widely used. As I argued above, one of the main challenges for advancing empirical community ecology is that the spatial boundaries of the habitat patches (and consequently local communities) are unknown for most ecological communities. The fact that wood-inhabiting fungal communities are organized in spatially well-defined metacommunities allows separation of the effects of local assembly processes (i.e. those working at the deadwood unit level) from larger-scale assembly processes (e.g. Krah et al., 2018; Müller et al., 2020).

There are other spatially well-defined metacommunity systems as well (e.g. dendritic networks, ponds, and island systems) which have previously been used to test and develop theory in community ecology (e.g. Brown and Swan, 2010; De Bie et al., 2012; Sakaeva et al., 2016). However, compared to these, wood-inhabiting metacommunity systems

have the additional advantage that the habitat patches are movable and thus allow spatial manipulations (e.g. translocations of the entire local communities) over different environmental gradients. Furthermore, one may find a huge amount of deadwood units (habitat patches) varying in their characteristics of sizes and decay stages (e.g. Halme et al., 2019), allowing replication of the experiments for habitat patches of different spatial and also temporal characteristics (Fukuwasa and Matsukura, 2021). Importantly, this characteristic allows replication of the experiments as much as needed. Replicability is thus one of the most important characteristics of fungal metacommunities to conclusively test hypotheses in community ecology.

Wood-inhabiting fungal communities are species rich, allowing either selection of a small number of species for intensive experiments, or alternatively to investigate the dynamics of entire species-rich metacommunity systems. While all wood-inhabiting fungi do not necessarily fruit and hence comprehensively surveying them from fruit body observations is not possible (Boddy 2001; Ovaskainen et al., 2013), DNA-based approaches have revolutionized the possibility of surveying fungal communities (Lindahl et al., 2013). However, DNA-based fungal species identification may involve high levels of uncertainty (Nguyen et al., 2015; Abarenkov et al., 2018; Palmer et al., 2018; Nilsson et al., 2019). The species composition of local communities can be manipulated by inoculating fungal species into hosts (Abrego et al., 2016), which brings the possibility of *in situ* testing hypotheses about biotic interactions, such as colonization-extinction tradeoffs, competition-colonization tradeoffs, or priority effects. Recently, Lustenhouwer et al. (2020) isolated over 1500 wood-decaying fungal species to make measurements of their vegetative structures in the laboratory, further demonstrating the feasibility of bringing trait-based perspectives and measuring the growth rates of these species-rich metacommunities under (controlled) laboratory conditions. A still largely unexplored methodology that brings great promise to investigate fungal interactions and functional traits is given by the fast evolving omics approaches (Baldrian and López-Mondéjar, 2014; Silva 2016). Both laboratory experiments (Hussein et al., 2013; Norros et al., 2015) and aerial spore sampling (Abrego et al., 2018) can be used to bring mechanistic understanding of the role of dispersal in wood-inhabiting fungal communities. There are also other taxonomic groups inhabiting deadwood (e.g. saproxylic bacteria, arthropods, bryophytes and nematodes), which if investigated simultaneously with fungi, offer the opportunity of generalizing the results across taxa (e.g. Heilmann-Clausen et al., 2014; Hagge et al., 2019b; Müller et al., 2020) or investigating food-web dynamics (Odriozola et al., 2021). Lastly, as quantitative phylogenies (Naranjo-Ortiz and Gabaldón, 2019), trait databases (Pölme et al., 2020) and large-scale fungal distribution databases are becoming increasingly available (Větrovský et al., 2020), new horizons for investigating phylogeographic processes in wood-inhabiting fungal communities are also emerging.

### 6. Conclusions

I conclude that wood-inhabiting fungal metacommunity systems offer highly suitable models for addressing still unresolved topical questions in community ecology. The four main advantages of using wood-inhabiting fungi as a model system for community ecology are that: (1) they are organized in spatially well-defined metacommunity systems; (2) they form species-rich communities which can be comprehensively surveyed with DNA-based methods and which can be isolated for trait measurements in the laboratory; (3) they allow experimental setups including spatial manipulation and manipulation of the local communities; and (4) previous research on wood-inhabiting fungal communities has shown that different assembly processes influence their communities, providing an excellent baseline for the future research.

## Declaration of competing interest

I declare no conflict of interest.

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## References

- Abarenkov, K., Somervuo, P., Nilsson, R.H., Kirk, P.M., Huotari, T., Abrego, N., Ovaskainen, O., 2018. Protax-fungi: a web-based tool for probabilistic taxonomic placement of fungal internal transcribed spacer sequences. *New Phytol.* 220, 517–525.
- Abrego, N., Norros, V., Halme, P., Somervuo, P., Ali-Kovero, H., Ovaskainen, O., 2018. Give me a sample of air and I will tell which species are found from your region: molecular identification of fungi from airborne spore samples. *Mol. Ecol. Resour.* 18, 511–524.
- Abrego, N., Oivanen, P., Viner, I., Nordén, J., Penttilä, R., Dahlberg, A., Heilmann-Clausen, J., Somervuo, P., Ovaskainen, O., Schigel, D., 2016. Reintroduction of threatened fungal species via inoculation. *Biol. Conserv.* 203, 120–124.
- Abrego, N., Salcedo, I., 2013. Variety of woody debris as the factor influencing wood-inhabiting fungal richness and assemblages: is it a question of quantity or quality? *For. Ecol. Manag.* 291, 377–385.
- Abrego, N., Bässler, C., Christensen, M., Heilmann-Clausen, J., 2015. Implications of reserve size and forest connectivity for the conservation of wood-inhabiting fungi in Europe. *Biol. Conserv.* 191, 469–477.
- Abrego, N., Christensen, M., Bässler, C., Ainsworth, A.M., Heilmann-Clausen, J., 2017a. Understanding the distribution of wood-inhabiting fungi in European beech reserves from species-specific habitat models. *Fungal Ecol.* 27, 168–174.
- Abrego, N., Norberg, A., Ovaskainen, O., 2017b. Measuring and predicting the influence of traits on the assembly processes of wood-inhabiting fungi. *J. Ecol.* 105, 1070–1081.
- Aguiar-Trigueros, C.A., Hempel, S., Powell, J.R., Anderson, I.C., Antonovics, J., Bergmann, J., Cavagnaro, T.R., Chen, B., Hart, M.M., Klironomos, J., Petermann, J. S., Verbruggen, E., Veresoglou, S.D., Rillig, M.C., 2015. Branching out: towards a trait-based understanding of fungal ecology. *Fungal Biol. Rev.* 29, 34–41.
- Allison, S.D., LeBauer, D.S., Ofrecio, M.R., Reyes, R., Ta, A., Tran, T.M., 2009. Low levels of nitrogen addition stimulate decomposition by boreal forest fungi. *Soil Biol. Biochem.* 41, 293–302.
- Andrew, C., Halvorsen, R., Heegaard, E., Kuyper, T.W., Heilmann-Clausen, J., Krisai-Greilhuber, I., Bässler, C., Egli, S., Gange, A.C., Høiland, K., Kirk, P.M., Senn-Irlet, B., Boddy, L., Büntgen, U., Kausserud, H., 2018. Continental-scale macrofungal assemblage patterns correlate with climate, soil carbon and nitrogen deposition. *J. Biogeogr.* 45, 1942–1953.
- Andrew, C., Heegaard, E., Halvorsen, R., Martínez-Peña, F., Egli, S., Kirk, P.M., Bässler, C., Büntgen, U., Aldea, J., Høiland, K., Boddy, L., Kausserud, H., 2016. Climate impacts on fungal community and trait dynamics. *Fungal Ecol.* 22, 17–25.
- Araújo, M.B., Rozenfeld, A., 2014. The geographic scaling of biotic interactions. *Ecography* 37, 406–415.
- Baldrian, P., López-Mondéjar, R., 2014. Microbial genomics, transcriptomics and proteomics: new discoveries in decomposition research using complementary methods. *Appl. Microbiol. Biotechnol.* 98, 1531–1537.
- Baldrian, P., 2016. Forest microbiome: diversity, complexity and dynamics. *FEMS Microbiol. Rev.* 41, 109–130.
- Bässler, C., Müller, J., Dziock, F., Brandl, R., 2010. Effects of resource availability and climate on the diversity of wood-decaying fungi. *J. Ecol.* 98, 822–832.
- Baldrian, P., Zrůstová, P., Tláškal, V., Davidová, A., Merhautová, V., Vrška, T., 2016. Fungi associated with decomposing deadwood in a natural beech-dominated forest. *Fungal Ecol.* 23, 109–122.
- Bässler, C., Ernst, R., Cadotte, M., Heibl, C., Müller, J., 2014. Near-to-nature logging influences fungal community assembly processes in a temperate forest. *J. Appl. Ecol.* 51, 939–948.
- Belmaker, J., Jetz, W., 2012. Regional pools and environmental controls of vertebrate richness. *Am. Nat.* 179, 512–523.
- Boddy, L., 2000. Interspecific combative interactions between wood-decaying basidiomycetes. *FEMS Microbiol. Ecol.* 31, 185–194.
- Boddy, L., 2001. Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. *Ecol. Bull.* 49, 43–56.
- Boddy, L., Frankland, J.C., van West, P., 2008. *Ecology of Saprotrophic Basidiomycetes*. Elsevier Academic Press, London, United Kingdom.
- Bradford, M.A., Warren II, R.J., Baldrian, P., Crowther, T.W., Maynard, D.S., Oldfield, E. E., Wieder, W.R., Wood, S.A., King, J.R., 2014. Climate fails to predict wood decomposition at regional scales. *Nat. Clim. Change* 4, 625–630.
- Brown, B.L., Swan, C.M., 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. *J. Anim. Ecol.* 79, 571–580.
- Brown, B.L., Sokol, E.R., Skelton, J., Tornwall, B., 2017. Making sense of metacommunities: dispelling the mythology of a metacommunity typology. *Oecologia* 183, 643–652.
- Brunet, J., Fritz, Ö., Richnau, G., 2010. Biodiversity in European beech forests - a review with recommendations for sustainable forest management. *Ecol. Bull.* 53, 77–94.
- Cadotte, M.W., Arnillas, C.A., Livingstone, S.W., Yasui, S.E., 2015. Predicting communities from functional traits. *Trends Ecol. Evol.* 30, 510–511.
- Cale, W.G., Henebery, G.M., Yeakley, J.A., 1989. Inferring process from pattern in natural communities. *Bioscience* 39, 600–605.
- Carmona, C.P., de Bello, F., Azcárate, F.M., Mason, N.W.H., Peco, B., 2019. Trait hierarchies and intraspecific variability drive competitive interactions in Mediterranean annual plants. *J. Ecol.* 107, 2078–2089.
- Cavender-Bares, J., Kozak, K.H., Fine, P.V.A., Kembel, S.W., 2009. The merging of community ecology and phylogenetic biology. *Ecol. Lett.* 12, 693–715.
- Chase, J.M., Leibold, M.A., 2003. *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press, Chicago, Illinois, USA.
- Chase, J.M., 2007. Drought mediates the importance of stochastic community assembly. *Proc. Natl. Acad. Sci. Unit. States Am.* 104, 17430–17434.
- Chase, J.M., 2010. Stochastic community assembly causes higher biodiversity in more productive environments. *Science* 328, 1388.
- Cockle, K.L., Martin, K., Robledo, G., 2012. Linking fungi, trees, and hole-using birds in a Neotropical tree-cavity network: pathways of cavity production and implications for conservation. *For. Ecol. Manag.* 264, 210–219.
- Crowther, T.W., Maynard, D.S., Crowther, T.R., Peccia, J., Smith, J.R., Bradford, M.A., 2014. Untangling the fungal niche: the trait-based approach. *Front. Microbiol.* 5, 579.
- Dawson, S.K., Boddy, L., Halbwachs, H., Bässler, C., Andrew, C., Crowther, T.W., Heilmann-Clausen, J., Nordén, J., Ovaskainen, O., Jönsson, M., 2019. Handbook for the measurement of macrofungal functional traits: a start with basidiomycete wood fungi. *Funct. Ecol.* 33, 372–387.
- De Bie, T., De Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., Hampel, H., Denys, L., Vanhecke, L., Van der Gucht, K., Van Wichelen, J., Vyverman, W., Declercq, S.A.J., 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecol. Lett.* 15, 740–747.
- Diaz, S., Cabido, M., Casanoves, F., 1998. Plant functional traits and environmental filters at a regional scale. *J. Veg. Sci.* 9, 113–122.
- Dormann, C.F., Bobrowski, M., Dehling, D.M., Harris, D.J., Hartig, F., Lischke, H., Moretti, M.D., Pagel, J., Pinkert, S., Schleuning, M., Schmidt, S.I., Sheppard, C.S., Steinbauer, M.J., Zeuss, D., Kraan, C., 2018. Biotic interactions in species distribution modelling: 10 questions to guide interpretation and avoid false conclusions. *Global Ecol. Biogeogr.* 27, 1004–1016.
- Emerson, B.C., Cicconardi, F., Fanciulli, P.P., Shaw, P.J.A., 2011. Phylogeny, phylogeography, phylobetadiversity and the molecular analysis of biological communities. *Phil. Trans. Biol. Sci.* 366, 2391–2402.
- Fraaije, R.G.A., ter Braak, Cajo, J.F., Verduyn, B., Verhoeven, J.T.A., Soons, M.B., 2015. Dispersal versus environmental filtering in a dynamic system: drivers of vegetation patterns and diversity along stream riparian gradients. *J. Ecol.* 103, 1634–1646.
- Fritz, Ö., Heilmann-Clausen, J., 2010. Rot holes create key microhabitats for epiphytic lichens and bryophytes on beech (*Fagus sylvatica*). *Biol. Conserv.* 143, 1008–1016.
- Fukami, T., Dickie, I.A., Wilkie, J.P., Paulus, B.C., Park, D., Roberts, A., Buchanan, P.K., Allen, R.B., 2010. Assembly history dictates ecosystem functioning: evidence from wood decomposer communities. *Ecol. Lett.* 13, 675–684.
- Fukasawa, Y., Matsukura, K., 2021. Decay stages of wood and associated fungal communities characterise diversity–decomposition relationships. *Sci. Rep.* 11, 8972.
- Glassman, S.L., Wang, L.J., Bruns, T.D., 2017. Environmental filtering by pH and soil nutrients drives community assembly in fungi at fine spatial scales. *Mol. Ecol.* 26, 6960–6973.
- Götzenberger, L., de Bello, F., Bräthen, K.A., Davison, J., Dubuis, A., Guisan, A., Lepš, J., Lindborg, R., Moora, M., Pärtel, M., Pellissier, L., Pottier, J., Vittoz, P., Zobel, K., Zobel, M., 2012. Ecological assembly rules in plant communities—approaches, patterns and prospects. *Biol. Rev.* 87, 111–127.
- Griffith, N.T., Barnett, H.L., 1967. Mycoparasitism by basidiomycetes in culture. *Mycologia* 59, 149–154.
- Hagge, J., Abrego, N., Bässler, C., Bouget, C., Brin, A., Brustel, H., Christensen, M., Gossner, M.M., Heilmann-Clausen, J., Horák, J., Gruppe, A., Isacson, G., Köhler, F., Lachat, T., Larrieu, L., Schlaghamersky, J., Thorn, S., Zapponi, L., Müller, J., 2019b. Congruent patterns of functional diversity in saproxylic beetles and fungi across European beech forests. *J. Biogeogr.* 46, 1054–1065.
- Hagge, J., Bässler, C., Gruppe, A., Hoppe, B., Kellner, H., Krahe, F., Müller, J., Seibold, S., Stengel, E., Thorn, S., 2019a. Bark coverage shifts assembly processes of microbial decomposer communities in dead wood. *Proc. Biol. Sci.* 286, 20191744.
- Halme, P., Ódor, P., Christensen, M., Piltaver, A., Veerkamp, M., Walley, R., Siller, I., Heilmann-Clausen, J., 2013. The effects of habitat degradation on metacommunity structure of wood-inhabiting fungi in European beech forests. *Biol. Conserv.* 168, 24–30.
- Halme, P., Purhonen, J., Marjakangas, E., Komonen, A., Juutilainen, K., Abrego, N., 2019. Dead wood profile of a semi-natural boreal forest – implications for sampling. *Silva Fenn.* 53 (4), 10010.
- Hanski, I., Ovaskainen, O., 2019. *Metapopulation Models*. Encyclopedia of Ecology (Second Edition). Elsevier, Oxford, pp. 136–144.
- Hart, S.P., Usinowicz, J., Levine, J.M., 2017. The spatial scales of species coexistence. *Nat. Ecol. Evol.* 1, 1066–1073.
- Heilmann-Clausen, J., Boddy, L., 2005. Inhibition and stimulation effects in communities of wood decay fungi: exudates from colonized wood influence growth by other species. *Microb. Ecol.* 49, 399–406.
- Heilmann-Clausen, J., Christensen, M., 2004. Does size matter?: on the importance of various dead wood fractions for fungal diversity in Danish beech forests. *For. Ecol. Manag.* 201, 105–117.
- Heilmann-Clausen, J., Aude, E., van Dort, K., Christensen, M., Piltaver, A., Veerkamp, M., Walley, R., Siller, I., Standovář, T., Ódor, P., 2014. Communities of wood-

- inhabiting bryophytes and fungi on dead beech logs in Europe - reflecting substrate quality or shaped by climate and forest conditions? *J. Biogeogr.* 41, 2269–2282.
- Hillebrand, H., Blenckner, T., 2002. Regional and local impact on species diversity – from pattern to processes. *Oecologia* 132, 479–491.
- Hiscox, J., Clarkson, G., Savoury, M., Powell, G., Savva, I., Lloyd, M., Shipcott, J., Choimes, A., Amargant Cumbriu, X., Boddy, L., 2016. Effects of pre-colonisation and temperature on interspecific fungal interactions in wood. *Fungal Ecol.* 21, 32–42.
- Hiscox, J., O’Leary, J., Boddy, L., 2018. Fungus wars: basidiomycete battles in wood decay. *Stud. Mycol.* 89, 117–124.
- Hiscox, J., Savoury, M., Muller, C.T., Lindahl, B.D., Rogers, H.J., Boddy, L., 2015. Priority effects during fungal community establishment in beech wood. *ISME J.* 9, 2246–2260.
- Holyoak, M., Leibold, M.A., Holt, R.D., 2005. *Metacommunities: Spatial Dynamics and Ecological Communities*. The University of Chicago Press, Chicago.
- Hoppe, B., Purahong, W., Wubet, T., Kahl, T., Bauhus, J., Arnstadt, T., Hofrichter, M., Buscot, F., Krüger, D., 2016. Linking molecular deadwood-inhabiting fungal diversity and community dynamics to ecosystem functions and processes in Central European forests. *Fungal Divers.* 77, 367–379.
- Hottola, J., Ovaskainen, O., Hanski, I., 2009. A unified measure of the number, volume and diversity of dead trees and the response of fungal communities. *J. Ecol.* 97, 1320–1328.
- Howeth, J.G., Leibold, M.A., 2013. Predation inhibits the positive effect of dispersal on intraspecific and interspecific synchrony in pond metacommunities. *Ecology* 94, 2220–2228.
- Hubbell, S.P., 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.
- Hussein, T., Norros, V., Hakala, J., Petäjä, T., Aalto, P.P., Rannik, Ü., Vesala, T., Ovaskainen, O., 2013. Species traits and inertial deposition of fungal spores. *J. Aerosol Sci.* 61, 81–98.
- Jönsson, M.T., Edman, M., Jonsson, B.G., 2008. Colonization and extinction patterns of wood-decaying fungi in a boreal old-growth *Picea abies* forest. *J. Ecol.* 96, 1065–1075.
- Junninen, K., Komonen, A., 2011. Conservation ecology of boreal polypores: a review. *Biol. Conserv.* 144, 11–20.
- Juutilainen, K., Mönkkönen, M., Kotiranta, H., Halme, P., 2014. The effects of forest management on wood-inhabiting fungi occupying dead wood of different diameter fractions. *For. Ecol. Manage.* 313, 283–291.
- Juutilainen, K., Mönkkönen, M., Kotiranta, H., Halme, P., 2017. Resource use of wood-inhabiting fungi in different boreal forest types. *Fungal Ecol.* 27, 96–106.
- Keddy, P.A., 1992. Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.* 3, 157–164.
- Kichenin, E., Wardle, D.A., Peltzer, D.A., Morse, C.W., Freschet, G.T., 2013. Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. *Funct. Ecol.* 27, 1254–1261.
- Kneitel, J.M., Miller, T.E., 2003. Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. *Am. Nat.* 162, 165–171.
- Kraft, N.J.B., Cornwell, W.K., Webb, C.O., Ackerly, D.D., 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *Am. Nat.* 170, 271–283.
- Kolesidis, D.A., Boddy, L., Eastwood, D.C., Yuan, C., Fowler, M.S., 2019. Predicting fungal community dynamics driven by competition for space. *Fungal Ecol.* 41, 13–22.
- Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S., Levine, J.M., 2015. Community assembly, coexistence and the environmental filtering metaphor. *Funct. Ecol.* 29, 592–599.
- Krah, F., Seibold, S., Brandl, R., Baldrian, P., Müller, J., Bässler, C., 2018. Independent effects of host and environment on the diversity of wood-inhabiting fungi. *J. Ecol.* 106, 1428–1442.
- Küffer, N., Senn-Irlet, B., 2005. Influence of forest management on the species richness and composition of wood-inhabiting basidiomycetes in Swiss forests. *Biodivers. Conserv.* 14, 2419–2435.
- Laliberté, E., Zemanek, G., Turner, B.L., 2014. Environmental filtering explains variation in plant diversity along resource gradients. *Science* 345, 1602–1605.
- Lebrija-Trejos, E., Pérez-García, E.A., Meave, J.A., Bongers, F., Poorter, L., 2010. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology* 91, 386–398.
- Leibold, M.A., Chase, J.M., 2018. *Metacommunity Ecology*. Princeton University Press, Princeton, New Jersey, USA.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7, 601–613.
- Leonhardt, S., Hoppe, B., Stengel, E., Noll, L., Moll, J., Bässler, C., Dahl, A., Buscot, F., Hofrichter, M., Kellner, H., 2019. Molecular fungal community and its decomposition activity in sapwood and heartwood of 13 temperate European tree species. *PLoS One* 14, e0212120.
- Lindahl, B.D., Nilsson, R.H., Tedersoo, L., Abarenkov, K., Carlsen, T., Kjoller, R., Kõljalg, U., Pennanen, T., Rosendahl, S., Stenlid, J., Kuserud, H., 2013. Fungal community analysis by high-throughput sequencing of amplified markers – a user’s guide. *New Phytol.* 199, 288–299.
- Logue, J.B., Mouquet, N., Peter, H., Hillebrand, H., 2011. Empirical approaches to metacommunities: a review and comparison with theory. *Trends Ecol. Evol.* 26, 482–491.
- Lonsdale, D., Pautasso, M., Holdenrieder, O., 2008. Wood-decaying fungi in the forest: conservation needs and management options. *Eur. J. Forest. Res.* 127, 1–22.
- Lustenhauer, N., Maynard, D.S., Bradford, M.A., Lindner, D.L., Oberle, B., Zanne, A.E., Crowther, T.W., 2020. A trait-based understanding of wood decomposition by fungi. *Proc. Natl. Acad. Sci. U.S.A.* 117, 11551–11558.
- Mäkipää, R., Rajala, T., Schigel, D., Rinne, K.T., Pennanen, T., Abrego, N., Ovaskainen, O., 2017. Interactions between soil- and dead wood-inhabiting fungal communities during the decay of Norway spruce logs. *ISME J.* 11, 1964–1974.
- Maron, J.L., Baer, K.C., Angert, A.L., 2014. Disentangling the drivers of context-dependent plant–animal interactions. *J. Ecol.* 102, 1485–1496.
- Masel, J., 2011. Genetic drift. *Curr. Biol.* 21, R837–R838.
- McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* 21, 178–185.
- McGill, B.J., 2010. Matters of scale. *Science* 328, 575.
- Mittelbach, G.G., Schemske, D.W., 2015. Ecological and evolutionary perspectives on community assembly. *Trends Ecol. Evol.* 30, 241–247.
- Mod, H.K., Chevalier, M., Luoto, M., Guisan, A., 2020. Scale dependence of ecological assembly rules: insights from empirical datasets and joint species distribution modelling. *J. Ecol.* 108, 1967–1977.
- Moor, H., Nordén, J., Penttilä, R., Siitonen, J., Snäll, T., 2021. Long-term effects of colonization–extinction dynamics of generalist versus specialist wood-decaying fungi. *J. Ecol.* 109, 491–503.
- Morin, P.J., 2011. *Community Ecology*. John Wiley & Sons, Ltd.
- Müller, J., Engel, H., Blaschke, M., 2007. Assemblages of wood-inhabiting fungi related to silvicultural management intensity in beech forests in southern Germany. *Eur. J. Forest. Res.* 126, 513–527.
- Müller, J., Jarzabek-Müller, A., Bussler, H., Gossner, M.M., 2014. Hollow beech trees identified as keystone structures for saproxylic beetles by analyses of functional and phylogenetic diversity. *Anim. Conserv.* 17, 154–162.
- Müller, J., Ulyshen, M., Seibold, S., Cadotte, M., Chao, A., Bässler, C., Vogel, S., Hage, J., Weiß, I., Baldrian, P., Tláškal, V., Thorn, S., 2020. Primary determinants of communities in deadwood vary among taxa but are regionally consistent. *Oikos* 129, 1579–1588.
- Naranjo-Ortiz, M., Gabaldón, T., 2019. Fungal evolution: diversity, taxonomy and phylogeny of the Fungi. *Biol. Rev.* 94, 2101–2137.
- Nguyen, N.H., Smith, D., Peay, K., Kennedy, P., 2015. Parsing ecological signal from noise in next generation amplicon sequencing. *New Phytol.* 205, 1389–1393.
- Nguyen, N.H., Song, Z., Bates, S.T., Branco, S., Tedersoo, L., Menke, J., Schilling, J.S., Kennedy, P.G., 2016. FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecol.* 20, 241–248.
- Nilsson, R.H., Anslan, S., Bahram, M., Wurzbacher, C., Baldrian, P., Tedersoo, L., 2019. Mycobiome diversity: high-throughput sequencing and identification of fungi. *Nat. Rev. Microbiol.* 17, 95–109.
- Nordén, J., Åström, J., Josefsson, T., Blumentrath, S., Ovaskainen, O., Sverdrup-Thygesen, A., Nordén, B., 2018. At which spatial and temporal scales can fungi indicate habitat connectivity? *Ecol. Indic.* 91, 138–148.
- Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E., Ovaskainen, O., 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. *J. Ecol.* 101, 701–712.
- Norberg, A., Halme, P., Kotiaho, J.S., Toivanen, T., Ovaskainen, O., 2019. Experimentally induced community assembly of polypores reveals the importance of both environmental filtering and assembly history. *Fungal Ecol.* 41, 137–146.
- Norros, V., Rannik, Ü., Hussein, T., Petäjä, T., V. T., Ovaskainen, O., 2014. Do small spores disperse further than large spores? *Ecology* 95, 1612–1621.
- Norros, V., Karhu, E., Nordén, J., Vähätalo, A.V., Ovaskainen, O., 2015. Spore sensitivity to sunlight and freezing can restrict dispersal in wood-decay fungi. *Ecol. Evol.* 5, 3312–3326.
- Norros, V., Penttilä, R., Suominen, M., Ovaskainen, O., 2012. Dispersal may limit the occurrence of specialist wood decay fungi already at small spatial scales. *Oikos* 121, 961–974.
- Odrizola, I., Abrego, N., Tláškal, V., Zrústová, P., Morais, D., Větrovský, T., Ovaskainen, O., Baldrian, P., 2021. Fungal communities are important determinants of bacterial community composition in deadwood. *mSystems* 6 e01017–e01020.
- O’Leary, J., Eastwood, D., Müller, C., Boddy, L., 2018. Emergent properties arising from spatial heterogeneity influence fungal community dynamics. *Fungal Ecol.* 33, 32–39.
- O’Leary, J., Journeaux, K.L., Houthuijs, K., Engel, J., Sommer, U., Viant, M.R., Eastwood, D.C., Müller, C., Boddy, L., 2021. Space and patchiness affects diversity–function relationships in fungal decay communities. *ISME J.* 15, 720–731.
- Olou, B.A., Yorou, N.S., Striegel, M., Bässler, C., Krah, F., 2019. Effects of macroclimate and resource on the diversity of tropical wood-inhabiting fungi. *For. Ecol. Manage.* 436, 79–87.
- Ordynets, A., Heilmann-Clausen, J., Savchenko, A., Bässler, C., Volobuev, S., Akulov, O., Karadelev, M., Kotiranta, H., Saitta, A., Langer, E., Abrego, N., 2018. Do plant-based biogeographical regions shape aphylloroid fungal communities in Europe? *J. Biogeogr.* 45, 1182–1195.
- Ottosson, E., Kubartová, A., Edman, M., Jönsson, M., Lindhe, A., Stenlid, J., Dahlberg, A., 2015. Diverse ecological roles within fungal communities in decomposing logs of *Picea abies*. *FEMS Microbiol. Ecol.* 91, fiv012.
- Ottosson, E., Nordén, J., Dahlberg, A., Edman, M., Jönsson, M., Larsson, K., Olsson, J., Penttilä, R., Stenlid, J., Ovaskainen, O., 2014. Species associations during the succession of wood-inhabiting fungal communities. *Fungal Ecol.* 11, 17–28.
- Ovaskainen, O., Abrego, N., 2020. Typical statistical methods applied by community ecologists. In: *Joint species Distribution Modelling: with Applications in R*. Cambridge University Press, Cambridge, pp. 30–38.
- Ovaskainen, O., Rybicki, J., Abrego, N., 2019. What can observational data reveal about metacommunity processes? *Ecography* 42, 1877–1886.



- Ovaskainen, O., Abrego, N., Halme, P., Dunson, D., 2016. Using latent variable models to identify large networks of species-to-species associations at different spatial scales. *Methods Ecol. Evol.* 7, 549–555.
- Ovaskainen, O., Hottola, J., Siitonen, J., 2010. Modeling species co-occurrence by multivariate logistic regression generates new hypotheses on fungal interactions. *Ecology* 9, 2514–2521.
- Ovaskainen, O., Meerson, B., 2010. Stochastic models of population extinction. *Trends Ecol. Evol.* 25, 643–652.
- Ovaskainen, O., Schigel, D., Ali-Kovero, H., Auvinen, P., Paulin, L., Norden, B., Norden, J., 2013. Combining high-throughput sequencing with fruit body surveys reveals contrasting life-history strategies in fungi. *ISME J.* 7, 1696–1709.
- Palmer, J.M., Jusino, M.A., Banik, M.T., Lindner, D.L., 2018. Non-biological synthetic spike-in controls and the AMPtk software pipeline improve mycobiome data. *PeerJ* 6, e4925.
- Pöhlme, S., Abarenkov, K., Henrik Nilsson, R., Lindahl, B.D., Clemmensen, K.E., Kauterud, H., Nguyen, N., Kjoller, R., Bates, S.T., Baldrian, P., Frøslev, T.G., Adojaan, K., Vizzini, A., Suija, A., Pfister, D., Baral, H., Järvi, H., Madrid, H., Nordén, J., Liu, J., Pawłowska, J., Pöldmaa, K., Pärtel, K., Runnel, K., Hansen, K., Larsson, K., Hyde, K.D., Sandoval-Denis, M., Smith, M.E., Toome-Heller, M., Wijayawardene, N.N., Menolli, N., Reynolds, N.K., Drenkhan, R., Maharachchikumbura, S.S.N., Gibertoni, T.B., Læssøe, T., Davis, W., Tokarev, Y., Corrales, A., Soares, A.M., Agan, A., Machado, A.R., Argüelles-Moyao, A., Detheridge, A., de Meiras-Otoni, A., Verbeken, A., Dutta, A.K., Cui, B., Pradeep, C. K., Marin, C., Stanton, D., Gohar, D., Wanasinghe, D.N., Otsing, E., Aslani, F., Griffith, G.W., Lumbsch, T.H., Grossart, H., Masigol, H., Timling, L., Hiiesalu, I., Oja, J., Kupagme, J.Y., Geml, J., Alvarez-Manjarrez, J., Ilves, K., Loit, K., Adamson, K., Nara, K., Küngas, K., Rojas-Jimenez, K., Biteniaks, K., Irinyi, L., Nagy, L.G., Soonvald, L., Zhou, L., Wagner, L., Aime, M.C., Öpik, M., Mujica, M.I., Metsoja, M., Ryberg, M., Vasar, M., Murata, M., Nelsen, M.P., Cleary, M., Samarakoon, M.C., Doilom, M., Bahram, M., Hagh-Doust, N., Dulya, O., Johnston, P., Sepp, S., Mundry, S., Luo, Z., Bose, T., Vahter, T., Netherway, T., Yang, T., May, T., Varga, T., Li, W., Coimbra, V.R.M., de Oliveira, V., Rodrigo, Targino, de Lima, V.X., Mikryukov, V.S., Lu, Y., Matsuda, Y., Miyamoto, Y., Kõljalg, U., Tedersoo, L., 2020. FungalTraits: a user-friendly traits database of fungi and fungus-like stramenopiles. *Fungal Divers.* 105, 1–16.
- Pouska, V., Macek, P., Zibarová, L., Ostrov, H., 2017. How does the richness of wood-decaying fungi relate to wood microclimate? *Fungal Ecol.* 27, 178–181.
- Powell, J.R., Karunarathne, S., Campbell, C.D., Yao, H., Robinson, L., Singh, B.K., 2015. Deterministic processes vary during community assembly for ecologically dissimilar taxa. *Nat. Commun.* 6, 8444.
- Purahong, W., Arnstadt, T., Kahl, T., Bauhus, J., Kellner, H., Hofrichter, M., Krüger, D., Buscot, F., Hoppe, B., 2016. Are correlations between deadwood fungal community structure, wood physico-chemical properties and lignin-modifying enzymes stable across different geographical regions? *Fungal Ecol.* 22, 98–105.
- Purahong, W., Wubet, T., Lentendu, G., Hoppe, B., Jariyavidyanont, K., Arnstadt, T., Baber, K., Otto, P., Kellner, H., Hofrichter, M., Bauhus, J., Weisser, W.W., Krüger, D., Schulze, E., Kahl, T., Buscot, F., 2018. Determinants of deadwood-inhabiting fungal communities in temperate forests: molecular evidence from a large scale deadwood decomposition experiment. *Front. Microbiol.* 9, 2120.
- Purhonen, J., Ovaskainen, O., Halme, P., Komonen, A., Huhtinen, S., Kotiranta, H., Læssøe, T., Abrego, N., 2020. Morphological traits predict host-tree specialization in wood-inhabiting fungal communities. *Fungal Ecol.* 46, 100863.
- Rajala, T., Peltoniemi, M., Pennanen, T., Mäkipää, R., 2012. Fungal community dynamics in relation to substrate quality of decaying Norway spruce (*Picea abies* [L.] Karst.) logs in boreal forests. *FEMS Microbiol. Ecol.* 81, 494–505.
- Ruete, A., Snäll, T., Jonsson, B.G., Jönsson, M., 2017. Contrasting long-term effects of transient anthropogenic edges and forest fragment size on generalist and specialist deadwood-dwelling fungi. *J. Appl. Ecol.* 54, 1142–1151.
- Saine, S., Aakala, T., Purhonen, J., Launis, A., Tuovila, H., Kosonen, T., Halme, P., 2018. Effects of local forest continuity on the diversity of fungi on standing dead pines. *For. Ecol. Manage.* 409, 757–765.
- Saine, S., Ovaskainen, O., Somervuo, P., Abrego, N., 2020. Data collected by fruit body- and DNA-based survey methods yield consistent species-to-species association networks in wood-inhabiting fungal communities. *Oikos* 129, 1833–1843.
- Sakaeva, A., Sokol, E.R., Kohler, T.J., Stanish, L.F., Spaulding, S.A., Howkins, A., Welch, K.A., Lyons, W.B., Barrett, J.E., McKnight, D.M., 2016. Evidence for dispersal and habitat controls on pond diatom communities from the McMurdo Sound Region of Antarctica. *Polar Biol.* 39, 2441–2456.
- Silva, R.N., 2016. Perspectives in genomics the future of fungi in 'omics, era. *Curr. Genomics* 17, 82–84.
- Soininen, J., 2014. A quantitative analysis of species sorting across organisms and ecosystems. *Ecology* 95, 3284–3292.
- Stegen, J.C., Lin, X., Fredrickson, J.K., Chen, X., Kennedy, D.W., Murray, C.J., Rockhold, M.L., Konopka, A., 2013. Quantifying community assembly processes and identifying features that impose them. *ISME J.* 7, 2069–2079.
- Stokland, J.N., Larsson, K., 2011. Legacies from natural forest dynamics: different effects of forest management on wood-inhabiting fungi in pine and spruce forests. *For. Ecol. Manage.* 261, 1707–1721.
- Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in Dead Wood. Cambridge University Press, Cambridge.
- Tamme, R., Götzenberger, L., Zobel, M., Bullock, J.M., Hoofman, D.A.P., Kaasik, A., Pärtel, M., 2014. Predicting species' maximum dispersal distances from simple plant traits. *Ecology* 95, 505–513.
- Thorn, S., Förster, B., Heibl, C., Müller, J., Bässler, C., 2018. Influence of macroclimate and local conservation measures on taxonomic, functional, and phylogenetic diversities of saproxylic beetles and wood-inhabiting fungi. *Biodivers. Conserv.* 27, 3119–3135.
- Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75, 2–16.
- Toijander, Y.K., Lindahl, B.D., Holmer, L., Högberg, N.O.S., 2006. Environmental fluctuations facilitate species Co-existence and increase decomposition in communities of wood decay fungi. *Oecologia* 148, 625–631.
- Trisos, C.H., Petchey, O.L., Tobias, J.A., 2014. Unraveling the interplay of community assembly processes acting on multiple niche axes across spatial scales. *Am. Nat.* 184, 593–608.
- Valentín, L., Rajala, T., Peltoniemi, M., Heinonsalo, J., Pennanen, T., Mäkipää, R., 2014. Loss of diversity in wood-inhabiting fungal communities affects decomposition activity in Norway spruce wood. *Front. Microbiol.* 5, 230.
- van der Wal, A., Ottosson, E., de Boer, W., 2015. Neglected role of fungal community composition in explaining variation in wood decay rates. *Ecology* 96, 124–133.
- Vellend, M., 2010. Conceptual synthesis in community ecology. *Q. Rev. Biol.* 85, 183–206.
- Vellend, M., 2016. *The Theory of Ecological Communities*. Princeton University Press, Princeton, New Jersey, USA.
- Větrovský, T., Morais, D., Kohout, P., Lepinay, C., Algora, C., Awokunle Hollá, S., Bahnmann, B.D., Bříohnědá, K., Brabcová, V., D'Alò, F., Human, Z.R., Jomura, M., Kolařík, M., Kvasničková, J., Lladó, S., López-Mondejar, R., Martinović, T., Mašíňová, T., Meszárosová, L., Michalčíková, L., Michalová, T., Mundry, S., Navrátilová, D., Odriozola, I., Piché-Choquette, S., Štursová, M., Svec, K., Tláskal, V., Urbanová, M., Vlk, L., Vorišková, J., Žifčáková, L., Baldrian, P., 2020. GlobalFungi, a global database of fungal occurrences from high-throughput-sequencing metabarcoding studies. *Scientific Data* 7, 228.
- Webb, C.O., Ackerly, D.D., McPeck, M.A., Donoghue, M.J., 2002. Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.* 33, 475–505.
- Weber, M.G., et al., 2017. Evolution in a community context: on integrating ecological interactions and macroevolution. *Trends Ecol. Evol.* 32, 291–304.
- Weihner, E., Keddy, P., 1999. *Ecological Assembly Rules: Perspectives, Advances, Retreats*. Cambridge University Press, Cambridge, United Kingdom.
- Zanne, A.E., Abarenkov, K., Afkhami, M.E., Aguilar-Trigueros, C., Bates, S., Bhatnagar, J. M., Busby, P.E., Christian, N., Cornwell, W.K., Crowther, T.W., Flores-Moreno, H., Floudas, D., Gazis, R., Hibbett, D., Kennedy, P., Lindner, D.L., Maynard, D.S., Milo, A.M., Nilsson, R.H., Powell, J., Schildhauer, M., Schilling, J., Treseder, K.K., 2020. Fungal functional ecology: bringing a trait-based approach to plant-associated fungi. *Biol. Rev.* 95, 409–433.
- Zobel, M., 1997. The relative of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends Ecol. Evol.* 12, 266–269.