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Review

Experimental studies of dead-wood biodiversity — A review identifying global gaps in knowledge

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ABSTRACT

The importance of dead wood for biodiversity is widely recognized but strategies for conservation exist only in some regions worldwide. Most strategies combine knowledge from observational and experimental studies but remain preliminary as many facets of the complex relationships are unstudied. In this first global review of 79 experimental studies addressing biodiversity patterns in dead wood, we identify major knowledge gaps and aim to foster collaboration among researchers by providing a map of previous and ongoing experiments. We show that research has focused primarily on temperate and boreal forests, where results have helped in developing evidence-based conservation strategies, whereas comparatively few such efforts have been made in subtropical or tropical zones. Most studies have been limited to early stages of wood decomposition and many diverse and functionally important saproxylic taxa, e.g., fungi, flies and termites, remain under-represented. Our meta-analysis confirms the benefits of dead-wood addition for biodiversity, particularly for saproxylic taxa, but shows that responses of non-saproxylic taxa are heterogeneous. Our analysis indicates that global conservation of organisms associated with dead wood would benefit most by prioritizing research in the tropics and other neglected regions, focusing on advanced stages of wood decomposition and assessing a wider range of taxa. By using existing experimental set-ups to study advanced decay stages and additional taxa, results could be obtained more quickly and with less effort compared to initiating new experiments.

Contents

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1. Introduction

1.1. Biodiversity in dead wood

Accumulations of dead wood in forest ecosystems provide important resources for a wide range of organisms, including both saproxylic species, i.e., directly or indirectly dependent on dying or dead wood, and non-saproxylic species. Saproxylic species include a wide variety of wood-decaying fungi, which are one of the most diverse but least understood groups among saproxylic taxa (Boddy et al., 2008; Stokland et al., 2012); a large proportion of all forest arthropod species (Grove, 2002a; Speight, 1989) and cavity-nesting birds (McComb and Lindenmayer, 1999 and references therein). Non-saproxylic species include many small-bodied litter-dwelling invertebrates and vertebrates that use woody debris for shelter and nesting (Fauteux et al., 2012; Mac Nally et al., 2001) or that benefit from dead wood as a relatively stable source of moisture and a buffer against extreme temperatures (Ulyshen et al., 2011). Additionally, many epixylic lichens and bryophytes use dead wood as their habitat (Andersson and Hytteborn, 1991; Spribille et al., 2008) and tree seedlings on decayed logs and plants growing near dead wood benefit from recycled nutrients and microclimatic conditions (Szewczyk and Szwagrzyk, 1996).

1.2. Dead wood — patterns and determinants of resource availability

Species associated with dead wood are sensitive to the amount, variety and distribution of woody debris, which collectively determine the availability of accessible resources (Sverdrup-Thygeson et al., 2014b). Various abiotic and biotic factors, e.g., climate, soil type and diversity of woody plant species, interact across a wide range of scales, e.g., biome, landscape and forest stand to determine the abundance and variety of resources available to saproxylic organisms (Fig. 1; Müller et al., 2015; Stokland et al., 2012). Anthropogenic forces, such as extraction of fuel wood and timber, and conservation management represent the extremes of a gradient of forest-use intensity and also play important and sometimes dominant roles in influencing the amount, variety and distribution of woody debris across the landscape (e.g., Gossner et al., 2013b). The nature of wood removal varies around the world, ranging from large-scale industrial harvests to the informal collection of woody material by local populations for domestic use (Grainger, 1999; Ribot, 1999). These activities determine the amount of dead wood within forest stands as well as the type of dead wood, e.g., stumps in managed forests and snags in unmanaged forests (Christensen et al., 2005; Grainger, 1999). Moreover, dead wood features created by natural disturbances are, to an increasing degree, consciously influenced by human decision makers who decide whether to salvage harvest or not (Lindenmayer et al., 2004). Without human impact, natural disturbances strongly affect the temporal and spatial dynamics of forests and dead wood (Radeloff et al., 2000; Seidl et al., 2014) and create specific resource types, such as charred wood after fire or uprooted trees after windthrows, both of which host specialized saproxylic species (e.g., Hyvärinen et al., 2006; Menzel et al., 2003). To compensate for the lack of trees affected by wild fire in managed landscapes, prescribed burning is now regularly applied in many regions (Similä and Junninen, 2012).

An additional group of factors act not on areal units, but on individual trees or dead-wood objects (Fig. 1). Sun exposure, for instance, affects microclimatic conditions and might strongly influence, in turn, the composition of saproxylic species assemblages (Bässler et al., 2010; Vodka et al., 2008). The composition of saproxylic assemblages is strongly determined by the type of dead wood as many species specialize on certain diameter classes, decay stages, vertical positions or tree species (Grove, 2002a; Heilmann-Clausen, 2001; Müller et al., 2015). Furthermore, many saproxylic species depend on the presence of other species as a resource or vector or for creating specific conditions in dead wood (Fukami et al., 2010; Strid et al., 2014). When dead wood develops naturally, the cause of death can be important. For example, a slow process of senescence creates different dead-wood substrates than a fast die-off and the different substrates thus host different saproxylic species assemblages (Ranius et al., 2009). Dead-wood snags created artificially, e.g., by using explosives, can be distinguished by some species from snags created naturally (Jonsell et al., 2004).

1.3. Dead-wood ecology in the context of ecological theories

Biodiversity patterns related to dead wood can be discussed in the context of a number of ecological theories. Patterns of species richness in relation to dead-wood amount, for instance, may follow mechanisms described by the *species-energy hypothesis* (Stokland et al., 2012; Wright, 1983) and effects of dead-wood diversity could be explained by the *habitat-heterogeneity hypothesis* (MacArthur and MacArthur, 1961). Habitat heterogeneity seems particularly important as effects of habitat heterogeneity peak at certain taxa-dependent spatial scales linked to keystone structures and dead wood represents such a keystone structure for saproxylic species (Tews et al., 2004). On larger spatial scales, habitat heterogeneity may be negatively perceived as fragmentation (Tews et al., 2004) and may become important when evaluating the spatial distribution of dead-wood substrates. The recently proposed *habitat-amount hypothesis* provides a synthesis of habitat size and isolation under the term “habitat amount”, which has to be experimentally determined for saproxylic organisms (Fahrig, 2013). Dead wood is an ephemeral resource and particularly in fragmented landscapes, spatial and temporal population dynamics of saproxylic species can be linked to the *theory of metapopulations* (Levins, 1969; Ranius et al., 2014). Following the *assembly theory* (Weiher and Keddy, 1995), environmental factors as well as the time of arrival of individual species during successive colonization of dead wood has strong effects on the composition of saproxylic assemblages (e.g. Bässler et al., 2014; Fukami et al., 2010). Furthermore, the *metabolic theory of ecology* (Allen et al., 2002) is a potentially important concept for dead-wood ecology and considers the effects of climate that have been shown to interact with dead-wood amount (Müller et al., 2014).

1.4. Acknowledging the importance of a resource under threat

Humans and organisms dependent on dead wood have competed for wood resources for thousands of years (Speight, 1989). Widespread forest clearance and the loss of old trees coupled with demands placed on remaining forest patches have dramatically reduced the amount and diversity of dead wood at a wide range of scales and throughout much of the world (Grove, 2002a; Lindenmayer et al., 2012; Siitonen, 2001). Over the past 20–30 years, hundreds of papers describing saproxylic communities in relation to the environment have been