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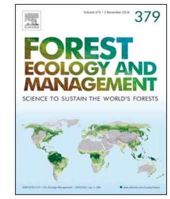

Experiments with dead wood reveal the importance of dead branches in the canopy for saproxylic beetle conservation

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ABSTRACT

Vertical gradients of habitats are a typical characteristic of forest ecosystems. Sun-exposed dead wood in the upper canopy, for instance, provides a habitat for saproxylic beetles distinct from that in the more shaded dead wood below the canopy. Canopy research, however, is challenging due to both the limited accessibility and potential confounding effects of temperature on trapping probability when activity traps are used. We studied saproxylic beetle assemblages along a complete vertical gradient without bias caused by temperature effects on activity. Using crane-like constructions attached to the top of large Silver Fir trees (*Abies alba*), we exposed bundles of freshly cut branches of European Beech (*Fagus sylvatica*), Silver Fir and Norway Spruce (*Picea abies*) in three different vertical strata (upper canopy, mid-canopy and near the ground). The bundles in the upper canopy were fully exposed to the sun and the bundles in the mid-canopy and near the ground were in the shade. We allowed beetles to colonize the bundles of branches for one growing period and then reared beetles from each bundle over three years. The species composition of saproxylic beetle assemblages differed between bundles in the upper canopy and near the ground; bundles in the mid-canopy had an intermediate assemblage composition. The abundance of saproxylic beetles was higher near the ground than in the upper canopy, whereas the number of species showed the opposite pattern. Overlapping confidence intervals of sample-based rarefaction and extrapolation curves for species diversity indicate that estimated gamma diversity per stratum is similar across the three strata. Our results support earlier studies that revealed the importance of habitat heterogeneity as a driver of the biodiversity of taxa associated with dead wood. As we controlled for wood diameter and tree species diversity, our study suggests that the microclimatic variability within dead wood – and thus habitat heterogeneity for saproxylic beetles – is higher in the upper canopy than near the ground. For biodiversity conservation in forests, our results support a strategy of enhancing the number of trees with microhabitats, particularly those with dead branches in the upper tree crown. Dead branches and standing dead trees should only be removed, e.g. for safety reasons, if no other option is available.

1. Introduction

A distinct feature of forest ecosystems is the pronounced vertical axis that creates gradients of several abiotic and biotic factors (Nakamura et al., 2017). For example, the higher sun exposure and wind in the upper canopy leads to stronger evaporation than in the lower canopy (Parker, 1995; Shaw, 2004). Leaves and branches in the upper canopy physiologically and structurally adapt to these abiotic conditions and differ from those in lower strata (Ulyshen, 2011, and references therein). Also fungi living on dead branches in the canopy have special strategies to cope with the strong tendency towards desiccation (Nunez, 1996). Many insect species have also adapted to life in the canopy (Basset et al., 2012, 2003), including a rich fauna of saproxylic, i.e. dead-wood-dependent, species (Schmidl and Bussler,

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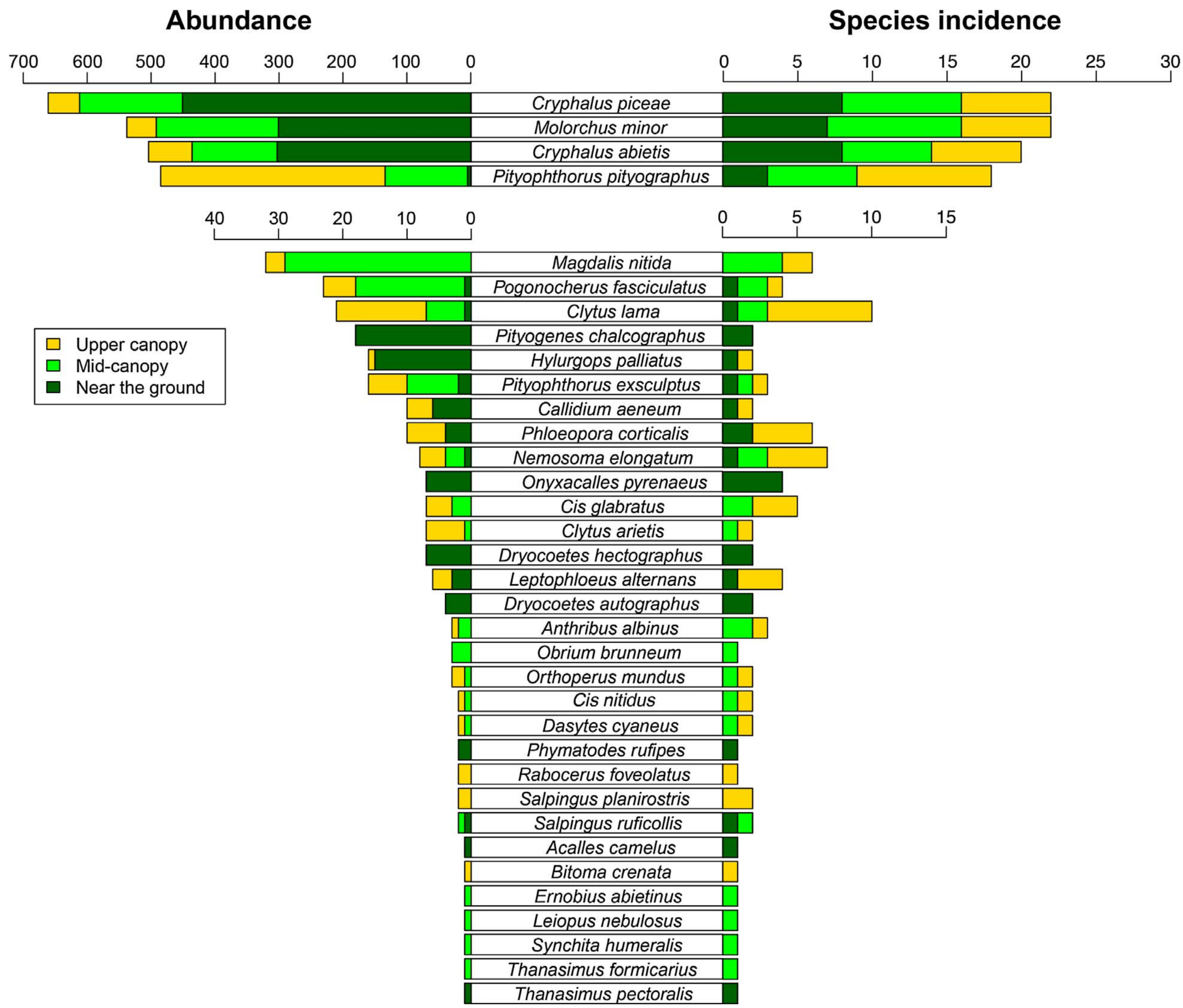

Fig. 1. Abundance and incidence of the 35 recorded saproxylic beetle species in bundles of dead branches placed in the upper canopy, mid-canopy and near the ground. For each bundle position, the incidence scale ranged from 0 to 10, with 10 indicating that the species was present in all 10 bundles at this position. Different strata are indicated by the bar colour. Note the different scale of the x-axes for the four most abundant species.

2008; Ulyshen, 2011).

For saproxylic insects, dead wood in the canopy provides a different type of habitat than dead wood on the forest floor, particularly when the forest floor is shaded; even within the canopy, different canopy layers can form a gradient of habitats (e.g. Weiss et al., 2016). Several factors that differ in the dead wood of different vertical strata could contribute to this gradient of habitats. First, many saproxylic insect species have a strong preference for particular microclimatic conditions, and thus, the species composition differs between sun-exposed and shaded dead wood (Seibold et al., 2016; Vodka et al., 2009). Second, many species differentiate between dead wood of different diameter classes, and the diameter distribution changes along the vertical axis, with dead wood of small diameter dominating the upper strata (Foit, 2010). Third, for insects associated with wood-decomposing fungi, differences in fungal species composition in different vertical strata (Unterseher et al., 2005; Unterseher and Tal, 2006) could influence assemblages of saproxylic beetles. Finally, colonization of new suitable substrate in the canopy might require airborne dispersal (Ulyshen 2011).

Most field studies comparing saproxylic beetle assemblages in different vertical strata have thus found differences in species composition (Foit, 2010; Maguire et al., 2014; Ulyshen and Hanula, 2007; Vodka et al., 2009; Weiss et al., 2016). Patterns of abundance, numbers of species and species richness along the vertical axis, however, have been less consistent. Some studies found abundances and numbers of species to be higher in strata near the ground than in the canopy above (Müller and Goβner, 2010; Vodka et al., 2009; Weiss et al., 2016), whereas others found no significant difference (Maguire et al., 2014; Ulyshen and Hanula, 2007) or even the opposite pattern (Normann et al., 2016; Plewa et al., 2017; Ulyshen and Sheehan, 2017). Moreover, diversity patterns of saproxylic beetles along the vertical axis can differ between tree species (Bouget et al., 2011) and among different beetle guilds or taxa (Plewa et al., 2017; Ulyshen and Sheehan, 2017; Wermelinger et al., 2007), and might depend on the diversity metric analysed (Floren et al., 2014).

Canopy arthropod research faces two methodological challenges that might contribute to the inconsistency in the results. First, insect activity increases with increasing temperature (Liu et al., 1995). Thus, if activity traps, such as flight-interception traps, are used, as in most studies, higher abundances in the sunny upper canopy compared to those in the shady lower canopy could be a consequence of insect activity. An alternative to activity traps is the rearing of insects from bait logs or natural dead wood because this method is less confounded by effects of temperature on trapping probability (Bouget et al., 2011; Müller et al., 2015; Vodka et al., 2009). Two studies in which insects were reared on oak dead wood found higher abundances and/or