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Dead wood dependent organisms in one of the oldest protected forests of Europe: Investigating the contrasting effects of within-stand variation in a highly diversified environment

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ABSTRACT

Old-growth forests are dynamic systems characterized by high levels of fine-scale structural variability. This variability is thought to support biodiversity by providing a range of environmental conditions within stands, such as canopy openness and dead wood abundance and quality. However, the response of many taxa, including those dependent on dead wood, to fine-scale habitat variability within old-growth stands remains under-studied in many temperate forests. We used saproxylic fungi and beetles as model groups to test the influence of within-stand variation in canopy openness and dead wood quantity and quality in an old-growth beech-dominated woodland left unmanaged in the Czech Republic since at least 1838 (Zofinsky prales and Hojna Voda). Responses to habitat variability differed both between and within taxa. Species composition was most influenced by canopy openness, with the beetle community responding positively to openness but the fungal community responding negatively. Species richness of beetles was also most influenced by canopy openness, while the number of red-listed beetle species was more associated with dead wood quantity. Fungi were significantly associated with high amounts of dead wood, with a critical threshold exceeding 300 m^3 per hectare. Overall, fungal responses were more complex than for beetles, with the former more associated with undisturbed (closed-canopy) patches, and the latter with disturbed/gapped patches. These results demonstrate the role of fine-scale habitat variability within old-growth forests and provide a potential model for managed forests. Perpetuating a full range of structural variability, including disturbance-generated gaps and dead-wood pockets, will help sustain a broader range of late-successional biodiversity.

1. Introduction

Old-growth forests are often characterized as an equilibrial or climax condition, yet they are dynamic systems driven by disparate fine- to meso-scale disturbances, diverse developmental pathways, shifting microenvironments, and competitive interactions governing spatial patterns of mortality and recruitment (Donato et al., 2012; Svoboda et al., 2012; Lutz et al., 2014). These processes generate and maintain spatial heterogeneity, which in turn influences the spatiotemporal distribution of associated organisms – from large old trees to organisms not visible to the naked eye (Lindenmayer et al., 2004). In many temperate forest regions, protected reserves of old forest are small patches embedded within a large landscape of younger managed forest, resulting in an island-like distribution of areas with high amounts of certain habitat features such as dead wood and associated organisms (Schiegg, 2000; Muller et al., 2013, 2014). At a cursory glance, the small area of natural reserves in otherwise developed regions suggests they may be relatively spatially uniform in habitat structure and function – classified as either undisturbed and near the hypothetical climax or totally disturbed as one large gap (Horak and Pavlicek, 2013). However, these processes are not uniform throughout the continent (Muller et al., 2013, 2014) and substantial variation exists in habitat structure and quality between and

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even within reserved forests. In this study we explore fine-scale variability in habitat within an old-growth forest, one of the oldest in all of Europe, and how it influences the distribution of two key groups of organisms, saproxylic beetles and fungi.

A primary limitation in grouping protected forests into a bag called "old-growth" is that they can vary widely in management history and time since last major disturbance (Muller et al., 2014). Old-growth structure and function differ between relatively recently developed mature/old stands and very old stands (e.g. Franklin et al., 1986; Freund et al., 2015), and forest management models based on these dynamics vary correspondingly. In Europe, for example, inferences from forests that were abandoned relatively recently, or from coppice regimes, or old-growth lacking spatial continuity, do not necessarily encompass the whole relevant range of habitat associations (Sverdrup-Thygeson and Lindenmayer, 2003; Moning and Muller, 2009). Probably the oldest European protected areas date from the early 18th century, established in 1718 in Brocken (NP Harz) in central Germany (Welzholz and Johann, 2007). The remaining reserved tracts were protected nearly a hundred years later, dating from the beginning of the 19th century – 1802 in Punkaharju Esker in south-east Finland and 1803 in Theresienhain in German Bavaria (Welzholz and Johann, 2007). Probably the fourth oldest protected areas are our study sites, Zofinsky prales and Hojna Voda, which were established more than 170 years ago, in 1838, by nobility and contain trees over 400 years old (Vrska and Hort, 2008).

Thus far, research in protected forest reserves has been mostly single-taxon based. This statement is not a critique; however we suggest that with more eyes (in this case more taxa) we can see more (in this case habitat structure). Multi-taxon approaches provide a more synthetic perspective on habitat relations, but do contain their own inherent challenges (e.g. Fontaine and Kennedy, 2012; Winter et al., 2015). The data processing and analyses pose challenges associated with different quantification of different organisms (e.g., number of individuals is useful for animals but not fungi), different relevant environmental predictors, and different spatial scaling of both organisms and their environments (e.g., tree, patch, landscape). Results among different groups also may contrast, making an overall interpretation more difficult (Muller et al., 2007; Horak et al., 2014). Nevertheless, if results are to be incorporated into forest conservation practice, which must simultaneously address the needs of many groups of organisms, then some synthesis is necessary.

Obligate saproxylic organisms, whose development is virtually completely interconnected with dead wood habitats, are presently used as indicators of conditions in forests (Horak et al., 2014), and also for analyses of response to environmental gradients (Muller et al., 2007; Moning and Muller, 2009). Fungi and beetles are among the most studied saproxylic organisms in Europe and elsewhere, frequently used for assessment of forest biodiversity (Paillet et al., 2010). The forest management community is familiar with aspects of habitat for fungi and beetles. In addition, these organisms provide a critical link in temperate forest food webs, supporting higher trophic levels such as small mammals and birds associated with both young and old forests (e.g. Lehmkuhl et al., 2004). Thus, understanding variations in habitat relations of these groups is highly relevant to conservation science.

In this study, we investigated the effect of within-stand variation of dead wood (as a habitat feature) and canopy openness (as a microclimatic characteristic), which are thought to be the most important patch-scale parameters governing the distribution of saproxylic organisms (Norden and Paltto, 2001; Lindhe et al., 2005). Namely, we quantified the amount and quality of potentially suitable habitat (i.e. dead wood) and sun exposure as the microclimatic expression of light conditions, and how these vary over relatively fine scales within an old forest stand. We used saproxylic beetles (Coleoptera) and fungi (Fungi) as potential indicators of conditions in the reserved forest, and also assessed their red-listed representatives (Farkac et al., 2005; Holec and Beran, 2006), as they are good indicators of the conservation value of European forests. We evaluated the response of species richness, composition and abundance of individual species of dead wood dependent beetles and fungi to gradients in dead wood and canopy openness found within old-growth forests, and also for any apparent thresholds in richness or individual species with respect to key environmental predictors.

2. Methods

2.1. Study area

The protected forests of Novohradske hory (Czech Republic) – Zofinsky prales (48.6651N; 14.7056E; 102.71 ha) and Hojna Voda (48.7062N; 14.75264E; 8.56 ha) – have been unmanaged since at least 1838 (Vrska and Hort, 2008) and contain trees over four centuries old (Albrecht et al., 2003). The surrounding landscape is dominated by human-propagated Norway spruce (*Picea abies*) plantations (nearly 90% of total tree species composition), in contrast to our study forests which are broadleaved islands dominated by European beech (*Fagus sylvatica*) with admixed Norway spruce, and occasional presence of silver fir (*Abies alba*), Wych elm (*Ulmus glabra*) and Sycamore maple (*Acer pseudoplatanus*). Some parts of Zofinsky prales are thought to be in essentially virgin (never managed) condition (Albrecht et al., 2003; Vrska and Hort, 2008) – extremely rare for central Europe – and both areas are rated as having among the highest conservation values (i.e., concentration of threatened and rare species, long spatiotemporal continuity) in the Czech Republic. The successional stage of the forest is advanced late-successional, with an all-aged tree structure, strong representation of shade-tolerant under- and mid-stories, well-developed canopy gaps, and abundant large dead wood. Mean altitude of the study areas was approximately 845 m a.s.l., and the topography was relatively diversified with respect to slope and aspects. The approximate distance between Zofinsky prales and Hojna Voda is 5.7 km.

2.2. Sampling

We sampled saproxylic organisms within 32 stratified (24 in Zofinsky prales and 8 in Hojna Voda) patches of 314 m^2 (10-m radius plots) that captured a range of environmental conditions present within the forest reserve.

Saproxylic beetles sensu (Schmidl and Bußler, 2004) were trapped using trunk tree traps, as this trap type is highly successful in trapping dead wood associates including flightless fauna (Horak et al., 2013). The traps, filled with saturated saline solution and a small amount of detergent as a conservation medium, were fixed to a mature tree at the center of the study patch. Traps were regularly emptied from the end of March to the end of September 2010. Trapped individuals of beetles were identified to the species level with the help of Czech specialists on particular beetle families, mentioned in the acknowledgements.

Saproxylic fungi (sensu Hagara et al., 2005) were visually sampled in each 10-m radius (314 m^2) patch that surrounded the trap. We checked all dead wood pieces for visible fruiting bodies. We aimed at macromycetes but excluded species with corticioid fruitbodies, pyrenomycetes, and inoperculate discomycetes with apothecia smaller than 10 mm, except those well identified. Four visits were made – once in July, twice in September, and once in October 2010.