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Beyond a minimum substrate supply: Sustaining saproxylic beetles in semi-natural forest management

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ABSTRACT

Woody debris provides substrate for a large part of forest biodiversity. Many saproxylic species are threatened by deadwood removal from commercial forests. However, deadwood availability alone may be insufficient to sustain those specialist species, given that naturally they inhabit diverse and dynamic forest ecosystems. We analysed the occurrence of saproxylic beetles under the conditions of semi-natural forestry in Estonia where managed stands are relatively rich in deadwood. We had two aims: (i) to estimate the role of deadwood amount taking into account other habitat factors for the beetles, and (ii) to contribute to the assessment of ecological sustainability of the silvicultural approaches used. The 128 studied stands represented four management stages: clear-cuts, retention cuts with solitary trees, mature commercial forests, and (as reference) old growth across a gradient of forest site-types. Using flight-intercept traps and rearing from wood samples, we captured 105 pre-defined habitat specialist species, of which 41% were of regional conservation concern. Site-scale occurrence of 34 species modelled for habitat factors depended mostly on management stage and forest type. Harvested sites (particularly retention cuts) were primarily preferred, and dry pine sites had a distinct fauna. Thirteen percent of target species favoured old growth, but in general, the beetle assemblages in old growth resembled those in mature commercial forest. Statistical significance of any stand characteristics (site type; stand structure) was established in only 62% of species, which indicates that there can be additional important factors, such as habitat connectivity, patch size or landscape history. These results highlight the importance of diverse forest management and protection approaches for deadwood-dwellers, which should aim for habitat heterogeneity along with substrate diversity. For beetle diversity, retention cutting performs much better than clear-cutting, but even deadwood-rich mature stands cannot fully substitute old growth. We conclude that deadwood abundance serves only as a starting consideration for reconciling timber production and the conservation of deadwood dependent biodiversity.

1. Introduction

Intensive forest management reduces dramatically the amount and diversity of woody debris, which is crucial in forest nutrient cycling and serves as a keystone structure for biodiversity (Harmon et al., 1986). This management-caused reduction is an amalgam of silvicultural and timber harvesting impacts and of the suppression of natural disturbances, such as fire, pests and pathogens (Jonsson and Siitonen, 2012). In many European forest regions, deadwood amounts are already an order of magnitude smaller than in natural forest. Such impoverishment is having profound impact on thousands of wood-inhabiting (saproxylic) species among invertebrates, fungi and bryophytes (Stokland and Siitonen, 2012; Seibold et al., 2015).

Deadwood ecology in natural-regeneration based and close-to-nature forestry systems is far less studied than in intensive systems. In this paper, we analyse such a system using saproxylic beetles as model organisms. Saproxylic beetles constitute one of the most species-rich groups vulnerable to the loss and fragmentation of deadwood rich habitats (Speight, 1989; Schiegg, 2000; Ehnström, 2001; Müller and Bütler, 2010; Stenbacka et al., 2010). In many countries, a high proportion of species in this ecologically diverse group has already become nationally rare and threatened (Grove, 2002; Komonen et al., 2008; Nieto and Alexander, 2010). Many saproxylic beetles act as bioengineers, facilitating decomposition through mutualism with fungi and microorganisms (Gossner

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et al., 2013). Differently from most wood-inhabiting fungi and bryophytes (Jonsson et al., 2005), many saproxylic beetle species prefer to live in sun exposed wood of intermediate decay (Jonsell et al., 1998; Dahlberg and Stokland, 2004). Such substrates are dynamic and transient, being naturally created by severe disturbances. One could thus expect saproxylic beetles to find appropriate habitats also in those managed forests where their substrates are provided in appropriate conditions. Beetle diversity and habitat relationships in contemporary landscapes could thus inform us on the functioning of deadwood pools under various forest management regimes, notably on multiple-use approaches. So far, however, the beetle research has mostly concentrated on comparing natural and intensively managed forests (but see Martikainen et al., 2000; Gossner et al., 2013; Sitzia et al., 2015).

Biodiversity response to habitat reduction is a sum of population-level processes, which are manifested as site-scale occurrences of species. The basic relationship between species occurrence and habitat availability (hereafter: 'habitat effect') may take various shapes, being inevitably complex, species-specific, and often poorly detectable in nature (Ranius and Jonsson, 2007). An important theoretical concept is that a critical threshold exists in habitat availability below which populations cannot persist; this has attracted much debate for its potential implications for cost-effective management of biodiversity (Johnson, 2013). According to the classic Levins' metapopulation model, the occupancy of a habitat patch depends on species' dispersal and colonization, as well as on within-patch demographic processes. This, together with habitat characteristics and dynamics, determines whether, and at which scale, a threshold effect appears (Ovaskainen and Hanski, 2003). Regarding deadwood habitat, thresholds have been again mostly derived from contrasts between natural and intensive forestry systems (e.g. Müller and Bütler, 2010; Junninen and Komonen, 2011) and it is unknown how the concept applies to more sustainable forestry systems.

The quality of habitat effects description depends on the accuracy and representativeness of field measurements. Problems can arise when habitat measurements describe only a part of true habitats suitable for target group; for example, based on research in impoverished landscapes where an incomplete set of habitats has been available. Another problem arises when there is covariation among habitat components, as forest management tends to affect simultaneously the total amount, diversity, and continuity of substrates, so that their contributions on biodiversity are difficult to distinguish (Siitonen, 2001; Liira and Kohv, 2010). Most saproxylic beetles seem to have moderately broad substrate preferences, i.e., main and alternative substrates (e.g. Milberg et al., 2014), but few quantitative niche assessments have been made at the species scale (e.g., Ranius et al., 2015; Sitzia et al., 2015). Around 5–10% of saproxylic insect, bryophyte or fungal species are considered to be at least regionally specific to tree species, size, decay stage, microclimate and other wood qualities (Jonsell et al., 1998; Dahlberg and Stokland, 2004).

In this paper, we describe habitat relationships of saproxylic beetles under semi-natural forest management regime, i.e., in forest landscapes that are predominantly managed using natural regeneration with native tree species (FAO, 2006). The study was performed in Estonia, where the forests are much less intensively managed than those in the well-studied neighbouring Nordic Countries. Thus, typical amounts of downed coarse deadwood in Estonia (Lõhmus and Kraut, 2010; Lõhmus et al., 2013; Sellis, 2014) are at or above the tentative critical thresholds for biodiversity conservation in European lowlands (Müller and Bütler, 2010). Our paper has two broad aims. From the beetle perspective, we complement the habitat studies performed (reviewed by Müller and Bütler, 2010) by exploring the role of deadwood amount in relation to other forestry-affected factors in these relatively favourable environments (cf. Ranius et al., 2015, for a study in an intensive system). We specify the association between beetle occurrence and volumes of different deadwood fractions and we also test for a threshold response. Our second aim is to provide, based on the habitat responses, a sustainability assessment of semi-natural forest management (as practiced in Estonia). Specifically, we investigate whether such forest management can create quality habitats not only in mature closed-canopy stands but also in open timber harvesting areas. To address these aims, we analyse the occurrence of a set of saproxylic beetles in relation to deadwood and other stand characteristics in a broad study setup, which comprises four management stages across five site-types.

2. Materials and methods

2.1. Study sites

The research was carried out in mainland Estonia (Fig. 1). The region belongs to the non-oceanic section of the European hemiboreal zone, between coniferous boreal and deciduous north-temperate forest zones (Ahti et al., 1968). Estonian forest lands (51% of the country) do not contain intensive plantations and >90% have been naturally regenerated. However, 20% of the forest area is drained, and owing to a long history of clear-cutting, old stands are rare (3% exceed 110 years of age). Ten percent of all forest area is now strictly protected and 15% is managed for environmental values (Keskkonnaagentuur, 2014); additionally, the commercial state forests (23%) maintain many features of structural diversity at near-natural levels (Liira et al., 2007; Lõhmus and Kraut, 2010; Lõhmus et al., 2013).

Our total sample of 128 sites comprised 116 sites surveyed during a large biodiversity project comparing forest management options (e.g. Lõhmus and Lõhmus, 2011) and 12 sites sampled for a study on slash extraction for a better representation of early responses to harvesting (Lõhmus et al., 2013). Each site encompassed a relatively homogeneous forest stand or a harvested area. The sites were selected for a factorial design of five forest site-types × four management stages. Only two sites were situated >50 m above sea level. All except two sites were state-owned and managed by the Estonian State Forest Management Centre, which holds a Forest Stewardship Certificate of sustainable forestry since 2002.

Four sampled site-types ranged over natural gradients of soil nutrient and moisture levels, and the fifth was an artificial, drained type (for detailed descriptions, see Lõhmus and Kraut, 2010; Remm et al., 2013). The site-types were: (i) dry boreal forests (mostly *Vaccinium* types) where the tree layer is dominated by Scots pine (*Pinus sylvestris*); (ii) meso-eutrophic mixed forests (*Oxalis* type), dominated either by Norway spruce (*Picea abies*) or Scots pine; (iii) eutrophic boreo-nemoral forests (mostly *Aegopodium* type) that were either diverse deciduous or spruce-deciduous mixtures, notably with silver birch (*Betula pendula*) and hard-wooded deciduous trees; (iv) mobile-water swamp forests, dominated by downy birch (*Betula pubescens*), black alder (*Alnus glutinosa*) and spruce; (v) artificially drained swamp forests (*Oxalis* type), which represent the second post-drainage generation of natural swamp forests (type iv above) and are developing towards meso-eutrophic forests (type ii).

In the basic sample of 116 sites, four management stages (an old-growth stand, a mature managed stand, a retention cut, and a clear-cut) were sampled as replicates of four sites close to each other on a landscape. These 29 clusters (six of each site-type, except for five clusters in mobile-water swamps) were supplemented with 12 retention cuts for a better representation of early responses to harvesting (two pairs in site-types i–iii) (Fig. 1). The