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The dying legacy of green-tree retention: Different habitat values for polypores and wood-inhabiting lichens

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ABSTRACT

The expanding practice of live-tree retention on clear-cuts represents a model case for conservation planning, because the high mortality of those trees requires balancing conflicting management goals in unpredictable conditions over long time frames. We explored the habitat provisioning function of dying retention trees for polypore and epixylic lichen assemblages. We sampled fallen trunks and snags created by known retention-tree deaths during the first post-harvest decade on 46 cut areas in Estonia, hemiboreal Europe. Those trees (particularly large fallen aspens) hosted a species-rich polypore assemblage that included several species of conservation concern. Lichen colonization of wood was slower and most species were found on pine snags. At the tree scale, the total species richness was highest on the trees that had died by trunk breakage creating both a snag and a log. To represent all species at the cutover scale, equal retention of different tree species and dead-wood types was sufficient for common species, but selective retention appeared necessary for species of conservation concern. The most frequent polypore species of conservation concern were either characteristic of specific substrates (notably aspen trunks) or early-successional stand conditions. We conclude that (i) dying retention trees are unlikely to provide dead-wood continuity at the stand scale and this function should be assessed at the landscape scale; (ii) effective habitat provisioning should include predicting and affecting the causes of tree death and linked management decisions based on the diversity, size, and longevity of the trees in specific landscape contexts.

1. Introduction

One of the greatest challenges of biodiversity conservation is how to integrate its goals effectively with production-oriented land use, which is expanding worldwide at the expense of natural ecosystems (Ehrlich and Pringle, 2008). This challenge includes an understanding of how to spend limited resources best for competing goals, also considering that some conservation goals can only be achieved in nature reserves. The relevant economic questions are related to the optimal use of thinly stretched money of conservation funds (James et al., 1999; Feng et al., 2006), while ecological knowledge is required to balance long-term and short-term benefits (e.g., Landres et al., 1999) and to distinguish and select among conflicting management goals (e.g., Curtis et al., 2007; Ahn et al., 2007; Kreutzweiser et al., 2012). Another layer of complexity is added by stakeholder communities: ownership and jurisdiction boundaries rarely match the domain of ecosystem processes (Christensen et al., 1996) and the system of decision making is fragmented.

Retention forestry is an important model case representing the complexities listed above – it is a globally prominent approach to address multiple ecological goals in forest management by long-term retention of key structures, such as live and dead trees, at the time of harvest on cut areas (Gustafsson et al., 2012). Such structures are analogues of the biological legacies that remain in the forest after natural disturbance and are crucial for providing habitats both for old-forest species and early-successional species (Franklin et al., 1997; Kaila et al., 1997). The fundamental challenge in retention forestry is that timber harvesting and biodiversity goals compete for the same trees, and biodiversity benefits become clear only at considerable amounts of retention (Rosenvald and Lõhmus, 2008), particularly when natural stand-replacing disturbances are considered a template (e.g., Hutto, 2006). Hence, there is an urgent need for ecological insights in operational terms – (minimum) amounts, characteristics and spatial pattern of retention objects – which could be analyzed for the costs and benefits of both single structures and complexes of them (e.g., Koskela et al., 2007). Additional practical challenges of retention forestry are set by information availability, time limits for the planning process, and the education and motivation of harvest operators who perform the retention in the field. Despite such complexity, the

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success of the retention approach is extensively documented for various biodiversity goals (Lindenmayer et al., 2012). What is lacking, however, is an explicit understanding of conflicting goals, and how they should be optimized.

This paper examines the problematic situation where foresters accept the direct reduction in timber harvest by retaining live trees (see Rosenvald and Lõhmus, 2008, for a review on their benefits) – only to see many trees dying soon on the cutover sites (e.g., Busby et al., 2006; Rosenvald et al., 2008). This raises three issues. (i) After their death, retention trees rapidly become unsuitable for epiphytes, herbivores and other live-tree inhabiting organisms (e.g., Lõhmus and Lõhmus, 2010) and may even create ecological traps for some birds (Robertson and Hutto, 2007). Hence, tree deaths may be undesirable for some conservation goals and longevity of the trees is an important management consideration. (ii) Unfortunately, when, and how a particular tree dies, is difficult to predict at retention. Combined with timber-value considerations, this has lead to suggestions of secondary harvesting after the death of the trees (e.g., Bergeron et al., 2002), which, however, conflicts with other conservation goals – importance of the dying trees for sustaining dead-wood habitats in the regeneration phase (Vanha-Majamaa and Jalonen, 2001; Sahlin and Ranius, 2009). (iii) Live tree retention that incorporates future dead-wood values becomes increasingly complex when the diverse requirements of wood-inhabiting organisms and stochasticity of their microhabitat formation and dispersal are considered (e.g., Jonsson et al., 2005), especially in the case of rare species. Solid empirical research is needed to understand which dead-wood habitats are most valuable in early successional forests – a focus that has gained only modest attention, with most studies on beetles (e.g., Kaila et al., 1997; Sippola et al., 2001) and a few on fungi (Lindhe et al., 2004; Junninen et al., 2007). However, no analysis has integrated multiple organism groups for tree retention recommendations.

We explore two ecologically different fungal groups (polypores and epixylic lichens) that contain many species depending on coarse dead-wood substrates. For such species, habitat continuity in cutovers can only be assured by the death of live trees over many decades (Sahlin and Ranius, 2009; Lõhmus et al., in press). Polypores (polyporoid basidiomycetes) form a taxonomically polyphyletic group, and they are traditionally delimited based on morphology. Most polypores are wood-decayers and prefer downed dead-wood (Heilmann-Clausen and Christensen, 2004; Lindhe et al., 2004). 'Epixylic lichens' are here distinguished according to their growth on exposed wood surfaces; they comprise morphologically and phylogenetically diverse lichenized and allied lichenicolous ascomycetes (typically crusts or calicioids, with sexual reproduction mode only; Spiribille et al., 2008). Epixylic assemblages are distinctly species rich on decorticate snags and include potential focal taxa for informing the management of these structures (Lõhmus and Lõhmus, 2001, 2011).

Based on those fungi, we address three gaps of knowledge. (i) How should their substrate requirements (in terms of dead-wood type, tree species, and size) be combined to maximize potential habitat value of retained live trees in terms of species richness? We analyze potentially conflicting requirements of different taxa at the tree-scale and solve set covering problems to represent full assemblages at a larger scale. (ii) What are the lengths of 'time-windows' (including colonization delay and species turnover during succession) for early assemblages of wood-dwelling fungi on cutovers? This is important for understanding tree mortality rates necessary for dead-wood habitat continuity at the cutover scale – notably for the distinct ephemeral assemblages of early decay stages in early-successional forests (Junninen et al., 2006; Lõhmus, 2011a) and for obligate epixylics whose habitat only forms along with the bark loss after tree death (Lõhmus et al., in press). (iii) Which species of conservation concern can inhabit dead retention trees (and which kind of trees), and do they include old-forest species 'lifeboated' from earlier forest? Such polypores have been reported from large retention trees in Fennoscandia but these studies (Lindhe et al., 2004; Junninen et al., 2007) were conducted in areas of generally high habitat value for fungi. We address those questions in a well-documented Estonian study system, where live retention trees have been surveyed throughout a decade for their survival (Rosenvald et al., 2008) and for the dynamics of epiphyte assemblages that are vulnerable to tree death (Lõhmus et al., 2006; Lõhmus and Lõhmus, 2010). We now analyze the fungal assemblages that have colonized snags and fallen trunks created by death of the retention trees at varying times and representing three tree species.

2. Methods

2.1. Study areas and study design

The study system comprised a post-harvest total of 3255 retention trees in all the 102 forest stands that had been retention harvested during 2001–2002 in four Estonian state forest districts (between 58°–59°N and 25°–27°E; see Rosenvald et al., 2008, for details and a map). Estonia is a well-forested (50% forest cover) flat lowland country situated in the European hemiboreal vegetation zone. The mean air temperature is ca. 17 °C in July and −6.5 °C in January; the average precipitation is 600–700 mm per year. All the districts sampled comprised large forest areas below 75 m a.s.l. and were subjected to even-aged management at rotations of 60–120 years (depending on tree species and site productivity). The dominant site types (sensu Paal, 1997) were dry boreal (mainly *Vaccinium myrtillus* type) and mesoeutrophic forests (*Oxalis* and *Hepatica* types) in the central Estonian districts and eutrophic boreonemoral and paludifying forests (mainly *Aegopodium* and *Filipendula* types) in the eastern districts.

Based on yearly data on retention-tree mortality during ten post-harvest years we sampled fallen trees and snags (standing dead trees or trunks with minimum height of 2 m) created by the tree deaths. We included the three most commonly retained tree species: European aspen (*Populus tremula* L.; hereafter 'aspen'), birch (*Betula* spp.) and Scots pine (*Pinus sylvestris* L.; hereafter 'pine'). We attempted to balance the sample to equal representation of times of death (0–10 years), but there was a shortage of recently dead pines and aspens because the mortality rates declined over time (Rosenvald et al., 2008). Our final sample consisted of 94 snags and 128 fallen trunks (Table 1), including 73 snags and trunks that originated from a single retention tree (died by stem breakage). Additionally, we sampled 15 snags that had remained from the pre-cut forest and were still standing after the ten years ('retained snags'; no such data were available for fallen trees). The sample trees were distributed in 48 cutover sites, which had a mean area of 2.9 ha (range 0.5–6.9 ha) and mean retention level of 12.9 trees (range 3–46) per ha. Besides birches (38%), pines (18%) and aspens (18%) the retained trees in the cutovers included 9% European ash (*Fraxinus excelsior* L.), 7% little-leaf linden (*Tilia cordata* Mill.) and 10% other tree species.

In addition to tree species and time since death, five tree characteristics were measured for each tree in 2010: diameter at 1.3 m from root neck (in broken, downed trunks – at the widest end); decay stage (sensu Renvall, 1995, with class 1 being the least decayed and class 5 most decayed); bark cover (%); distance from the nearest forest (m); and sun exposure. The sun exposure of snags was estimated by analyzing hemispherical photo images, taken during the first weeks of September 2010 using Nikon Fisheye Converter FC E8 attached to Nikon Coolpix 4500 digital camera. The photos were taken strictly upwards at 1.3 m height at the northern and