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Decadal effects of emulating natural disturbances in forest management on saproxylic beetle assemblages

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ABSTRACT

Prescribed burning and retention forestry are used to bring the biological legacies of forest harvesting closer to those of natural disturbances. Although widely used, the effects of these methods on species assemblages in the longer term are still relatively unknown. In 2000, we established a large-scale replicated field experiment to explore the effects of prescribed burning and tree retention (four levels: 0, ten and 50 m^3 ha^{-1} and unharvested control) on saproxylic beetles. Assemblages were monitored over 10 post-treatment years. Our results showed that species richness of predators was increased by burning of the forest stand. Early- and late-stage xylophagous species increased in the first post-harvest year. Increased logging intensity led to a decrease in mycetophagous, early-stage xylophagous and predator species richness over the ten year period. In the burned unharvested stands, the total species richness remained high after ten years, but decreased to the pre-treatment level in the stands with retention trees, and to even lower levels in the clear-cuts. Furthermore, the saproxylic beetle assemblages in the burned unharvested stands differed from the assemblages in any of the harvested stands. Burning increased pyrophilous and rare and red-listed (RRL) species richness. Over the ten year period, the richness of those species collapsed in the harvested stands, but increased in the burned unharvested stands. Our results emphasize the difference in tree stand legacies between logging and natural disturbance, but also indicates that prescribed burning and retention forestry have the potential to alleviate the negative effects of forest management on biodiversity in the longer term.

1. Introduction

Intensive forest management and the effective prevention of natural disturbances have caused fragmentation and loss of natural forest habitats and, consequently, are a severe threat to many forest-dwelling species (Butchart et al., 2010; Kouki et al., 2001; Olsson et al., 2012). Natural early-successional forest biotopes that originate after severe disturbances, such as fire, insect outbreak and windstorm have decreased dramatically (Kouki et al., 2001; Swanson et al., 2011). These types of biotopes contain a high volume of dead wood, are highly heterogeneous and, thus, are highly important habitats for numerous species (e.g. Rubene et al., 2015; Stein et al., 2014; Winter et al., 2015).

Forest fires have been a characteristic feature of the boreal forest region for centuries. However, there is a large variation in fire frequency and severity depending, for example, on vegetation composition and the humidity of the forests (Wallenius et al., 2005). Variability in the intensity of fire and other natural disturbances, both spatially and temporally, has led to large heterogeneity in natural forests (Kuuluvainen, 2002, 2009; Pitkänen and Huttunen, 1999). Fire affects species assemblages directly by killing individuals but also indirectly by altering the characteristics of the habitat and the availability of resources (McCullough et al., 1998; Schowalter, 2012). Fire creates competition-free substrates, increased diversity in the type of available dead wood substrates and, as such, many species have evolved with fire-related disturbances (Boulanger and Sirois, 2007; McCullough et al., 1998; Wikars, 1997). Although the immediate impact of fire is often destructive for plants, polypore fungi and epiphytes (Baker et al., 2013a; Hämäläinen et al., 2014; Johnson et al., 2014; Junninen et al., 2008), the effect can turn positive in the longer-term (Baker et al., 2013a; Penttilä et al., 2013). Fire has been shown to have rapid, positive effects not only on various taxa, particularly beetles (e.g. Hyvärinen et al., 2005; Saint-Germain et al., 2004), but also other taxa such as flat bugs (Johansson et al., 2010) and woodpeckers (Hutto, 2008). However, very little is known as to how long these effects might persist.

In the managed forests of the boreal region, particularly in Fennoscandia, the occurrence of wildfires have declined considerably as a result of effective fire suppression methods, and clear-cut has become the main stand-replacing disturbance type. The biological legacies of clear-cuts, however, differ from natural disturbances in a number of fundamental ways (Junninen et al., 2006; Kouki et al., 2001). Natural large-scale disturbances, such as fire, wind, pathogens or insect outbreaks, typically leave in their wake a diverse amount of injured, dying and dead wood, but also living trees, whereas in clear-cuts nearly all

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trees are removed and the residual dead wood consists mostly of stumps and logging residues (Franklin et al., 2000; Jonsson et al., 2005; Junninen et al., 2006; Swanson et al., 2011). Changes in post-disturbance legacies have caused biodiversity loss in boreal forests with many species now classed as threatened (Berg et al., 1994; Gärdenfors, 2010; Rassi et al., 2010; Tikkanen et al., 2006).

Prescribed burning and retention forestry are methods developed to alleviate the negative effects of intensive forestry on biodiversity, by bringing the biological legacies of harvesting closer to the legacies of natural disturbances (Gustafsson et al., 2010; Similä and Junninen, 2012). Retention forestry aims to maintain some of the pre-harvest structures and functioning and, thus, help species to survive and recolonize post-harvest forests (Baker et al., 2013b; Gustafsson et al., 2010; Lindenmayer et al., 2012). Retention forestry is currently considered to be essential in achieving ecological sustainability globally (Lindenmayer et al., 2012; Mori and Kitagawa, 2014).

Previous studies have shown the variable impacts of retention forestry on different taxa. Pre-harvest ground vegetation, for example, cannot be preserved by low retention levels but the change of species assemblages is very high (Halpern et al., 2012; Johnson et al., 2014), whereas for epiphytic lichens and mosses, retention trees may function as “life-boat” substrates and stepping stones for colonization even in the long-term (Hedenås and Hedström, 2007; Hämäläinen et al., 2014; Olden et al., 2014). On the other hand, the immediate and/or delayed death of retention trees can help the survival of saproxylic species, such as polypores and beetles (Hyvärinen et al., 2009; Runnel et al., 2013; Suominen et al., 2015; Toivanen and Kotiaho, 2007), by maintaining dead wood continuity in post-harvest forests. However, a relatively high level of retention is needed for long-term benefits (Heikkala et al., 2014). Very few studies have addressed the impacts of retention forestry and prescribed burning simultaneously. As noted above, the long-term consequences of fire may differ sharply from the short-term effects, and there is an obvious need for long-term impact studies before the applicability of retention forestry and fire-related forest management, such as prescribed burning can be reliably assessed.

Beetles (Coleoptera) are the most species-rich taxon in the world (Foottit and Adler, 2009), and include a high and ecologically diverse number of forest-dwelling species. As a result of their diverse and species specific adaptation in different ecological conditions and habitats, beetles are a highly suitable group to study the effects of habitat changes on biodiversity. Furthermore, beetles have been shown to be adversely affected by intensive forestry (e.g. Martikainen et al., 2000; Paillet et al., 2010; Rassi et al., 2010). Several previous studies have reported remarkable shifts in beetle species composition in the short-term after fire (Hyvärinen et al., 2005, 2009; Johansson et al., 2011; Saint-Germain et al., 2004; Toivanen and Kotiaho, 2007). However, no experimental studies to date have shown the effects on the highly diverse group of saproxylic beetles over the long-term. Since these species are strictly dependent on dead wood and also include a high number of rare and threatened species, evaluation of their response to fire is appropriate in order to evaluate the overall biodiversity benefit that may accrue from retention forestry and prescribed burning.

The succession-cycle of a forest is very long. Under natural conditions, trees can live for hundreds of years and the decaying process of dead trees can last for many decades, depending on tree species and environmental conditions. The amount of coarse dead wood is very high after a stand-replacing disturbance, but it takes decades before new tree-generation can provide a renewed input of dead wood (Passovoy and Fule, 2006; Siitonen, 2001). Short-term monitoring is not able to show the overall effects of natural or anthropogenic disturbances on forest biodiversity. Thus, long-term data is essential when the effectiveness of conservation interventions for saproxylic species is assessed (Davies et al., 2008; Seibold et al., 2015b; Sverdrup-Thygeson et al., 2014). It is likely that the short-term and long-term effects may be different because of the inherent dynamics of tree mortality and dead wood dynamics in forest ecosystems.

In this study, we explored these effects over 10 post-harvest years. In 2000, we established a large-scale replicated field experiment based on the BACI-principle (Green, 1979), and followed the beetle assemblages with temporally repeated samplings. The aim was to explore (1) whether the pre-harvest saproxylic beetle assemblages were maintained, and (2) if natural post-fire assemblages, represented by burned unharvested forests in this study, are achieved by retention forestry and prescribed burning. We investigated species richness in different functional groups and also in pyrophilous and rare and red-listed (RRL) species and species assemblages over a 10 year post-harvest period. To our knowledge, this is the first study that has explored these effects over longer time scales with a particular focus on a high-diverse forest taxa; saproxylic beetles.

2. Material and methods

2.1. Study area and experimental design

The study area was located in eastern Finland, on the middle boreal vegetation zone (ca. 63°10'N, 30°40'E). A total of 24 stands, each ca 3–5 ha in area, were selected as experimental study sites within an approximate 30 km × 20 km area. The stands were originally ca. 150 year old pine-dominated forests, which were no longer intensively forested, but showed signs of old selective cuttings. The average initial volume of living trees in the stands was 288 m^3 ha^{-1} (SD = 71.1) and the average volume of dead wood was 41 m^3 ha^{-1} (SD = 17.5). The average proportions of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) in the stands were 72% and 22% respectively. Other tree species in the study stands were birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.), aspen (*Populus tremula* L.), gray alder (*Alnus incana* (L.)), goat willow (*Salix caprea* L.) and rowan (*Sorbus aucuparia* L.) There was no difference in the pre-harvest volumes of living and dead trees between the experimental treatment categories.

The study focused on two factors: retention harvests and prescribed burning. Harvesting treatments consisted of four different levels of retention: 0 (i.e. no retention trees), 10 and 50 m^3 ha^{-1} and an unharvested control. The retained trees were mostly left in small groups, each group approximately 200–300 m^2 in area at the lower retention level and 300–500 m^2 at the higher level. Each harvesting treatment was replicated six times and in half of those the stand was burned. The stands were harvested in the winter 2000–2001, and burning was carried out in summer 2001. The treatment combinations were randomly allocated to the study sites. Consequently, the experiment consisted of eight treatment combinations with three replicates of each. The implementation of the treatments has been described in detail in Hyvärinen et al. (2005).

Fire intensity on the study stands was evaluated by measuring the changes in the thickness of the humus layer. The layer was, on average, 27% thinner in the harvested burned stands and 8% thinner at the unharvested burned stands (Laamanen, 2002). Spatial heterogeneity in fire intensity was remarkable, especially in the unharvested stands. High fire intensity in the harvested stands resulted from a high volume of logging residues, which led to high immediate mortality rates in retention trees, especially at the lower retention level (Heikkala et al., 2014). In the burned stands, almost all trees died at the lower retention level and about 80% died at the higher retention level over the ten year period. In the unburned stands, mortality rates of the retention trees were lower: approximately two third of the trees at the higher retention level and more than half of the trees at the lower retention level were still alive ten years after the treatments (Heikkala et al., 2014). In the unharvested stands, immediate fire-caused mortality of the trees was relatively low: only 2.9% of the initial living volume of pines and 14.5% of spruces died in the first month after burning, and fire increased the volume of dead wood by 9.6 m^3 ha^{-1} on average (Sidoroff, 2001). However, delayed mortality over subsequent years maintained a continuous supply of fresh dead wood (based on our unpublished data).