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Canopy closure determines arthropod assemblages in microhabitats created by windstorms and salvage logging

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ABSTRACT

Conifer-dominated forests of the Northern Hemisphere are prone to natural disturbances, such as windstorms, which create canopy openings by downing single trees to complete stands. The size of a windthrow determines how strongly microclimatic conditions are changed. After windstorms, damaged trees are commonly logged to 'salvage' economic returns, but effects on biodiversity are often negative. One cause of these negative effects on biodiversity might be the alteration of storm-created microhabitats, for example, as branches are cut off and root plates are flipped back into their pits when trunks are removed. The effect of these alterations of microhabitats on biodiversity under open and closed canopies, which represent extremes of microclimatic conditions, remains unclear. To investigate the relative importance of canopy closure and microhabitats for arthropod assemblages, we created six artificial windthrows located under an open canopy and six under a closed canopy by uprooting three spruce trees per plot. We used permutational analysis of variance to test whether cutting branches off uprooted trees and allowing them to rot on the forest floor affects branch-dwelling saproxylic beetles and whether repositioning upright root plates in their pits affects assemblages of carabids, epigeal spiders and harvestmen. Our final data set comprised 7657 arthropod individuals belonging to 28 species of saproxylic beetles, 28 species of carabids, 85 species of epigeal spiders, and 8 species of harvestmen. Carabid abundance was higher under a closed canopy and the number of epigeal spider species was higher under an open canopy. Canopy closure also significantly affected the assemblage composition of saproxylic beetles, carabids and epigeal spiders, with a higher mean moisture affinity of these assemblages on plots under a closed canopy. Arthropod assemblages of root plates and root plate pits did not differ, but the composition of branch-dwelling saproxylic beetle assemblages on cut and uncut branches significantly differed. Overall, assemblages of saproxylic beetles, carabids, epigeal spiders and harvestmen were predominantly determined by canopy closure and not by alteration of storm-created microhabitats. Nevertheless, entire crowns of downed spruce trees should be retained in salvage-logged forests to provide this microhabitat for saproxylic beetle assemblages typical for naturally disturbed forests.

1. Introduction

Coniferous forests of the boreal and temperate zone are naturally prone to stand-replacing disturbances, such as wildfires, insect outbreaks and windstorms (Kurz et al., 2008; Seidl et al., 2014; Kulakowski et al., 2016). Norway Spruce (*Picea abies*) is one of the economically most important and most widespread tree species in Europe (Brus et al., 2011). However, mature spruce forests are prone to outbreaks of the European Spruce Bark Beetle (*Ips typographus*), which are often promoted by preceding wind storm damage (Schroeder, 2010). Storm-felled spruces provide a variety of microhabitats, such as coarse woody depris, downed tree crowns, snags, bare soils, and root plate pits and mounds (Peterson

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and Leach, 2008; Swanson et al., 2011). They thus provide a plenitude of ecological niches at relatively small spatial scales and promote forest biota, such as birds (Thorn et al., 2016c; Zmihorski, 2010) and arthropods (Bouget and Duelli, 2004; Gibb et al., 2006).

Despite the numerous positive effects of these microhabitats on biodiversity, the increasing demand for timber compels forest managers to intervene rapidly in naturally disturbed stands to 'salvage' valuable timber (Donato et al., 2006; Nappi et al., 2004; Stokstad, 2006). Numerous studies have shown negative impacts of stand-scale salvage logging on biodiversity of, e.g. birds (Castro et al., 2010; Hutto and Gallo, 2006), saproxylic beetles (Cobb et al., 2011; Thorn et al., 2014) and carabids (Buddle et al., 2006; Koivula and Spence, 2006). These effects of salvage logging on biodiversity on the stand scale are predominantly mediated by increased insolation and removal of dead wood (Thorn et al., 2016b). Salvage logging, however, alters also the remaining dead-wood habitats by changing the distribution of dead-wood diameter and decay stage classes (Priewasser et al., 2013). For instance, the cutting of sun-exposed branches when the main trunk is removed can decrease the number of branch-dwelling saproxylic beetle species (Thorn et al., 2014). Moreover, salvage logging reduces the density of root-plate pits and mounds (Waldron et al., 2013). These alterations of microhabitats might cause the impacts of salvage logging on arthropod assemblages that colonize these microhabitats.

The opening of the tree canopy when trees are downed by a windstorm leads to higher insolation. How strong canopy closure changes depends on the severity and size of the windthrow (Bouget and Duelli, 2004; Shorohova et al., 2009). Canopy closure is among the main drivers of forest-dwelling taxa (Lehnert et al., 2013; Seibold et al., 2016). As both differences in canopy closure and number of created microhabitats increase with windthrow size, these factors are naturally correlated. Survey studies of large windthrows are thus not able to untangle the effects of canopy closure and microhabitat on biodiversity or determine whether the effects are caused by the windthrow or salvage logging. Small windthrows, i.e. a few downed trees, are more suitable for studies aimed at untangling the relative importance of microhabitats and canopy closure for biodiversity. Such windthrows can be located at forest edges where the canopy is more open or inside stands under a closed canopy (Liu and Hytteborn, 1991).

To experimentally test the effects of canopy closure and alteration of storm-created microhabitats by salvage logging on biodiversity, we created six small artificial windthrow plots under an open canopy and six under a closed canopy, each consisting of three downed trees. Two of the three trees per plot were salvage logged, i.e. trunks were removed, branches were cut off and root plates were snapped back into root-plate pits. We surveyed saproxylic beetles (Coleoptera) associated with branches and epigeic arthropods, i.e. carabids (Carabidae), epigeal spiders (Araneae) and harvestmen (Opiliones) associated with root-plate pits and mounds. In particular, we compared species numbers and composition of arthropod communities between (i) branches that remained attached to the trunk (elevated branches) and branches that were cut off trunks and remained on the forest floor (cut branches) as well as between (ii) root plate pits (pit) and root plates that had snapped back to close the root plate pit when they were cut off the main trunk (root plate).

2. Methods

2.1. Study area and artificial windthrows

The study was carried out in the high montane forests of the Bavarian Forest National Park in south-eastern Germany, covering a total of 24,250 ha (Thorn et al., 2016b). Forest stands above 1000 m a.s.l. are naturally dominated by Norway Spruce (*Picea abies*), with low proportions of Mountain Ash (*Sorbus aucuparia*), European Beech (*Fagus sylvatica*) and Silver Fir (*Abies alba*). The average annual temperature ranges from 3.5 to 7 °C, and the average annual precipitation varies between 1200 and 1800 mm (Bässler et al., 2010). During the last decades, windstorms and outbreaks of the European Spruce Bark Beetle (*Ips typographus*) have led to changes in forest structures and canopy cover in the Bavarian Forest National Park (Thorn et al., 2016b). Naturally disturbed stands in the core zones of the national park remain unlogged, while affected stands in the management zones are salvage logged, with the aim of avoiding further spread of bark beetles to nearby private forests. During typical salvage logging, branches are cut off and remain on site, main trunks are removed to prevent pest infestation, and each root plate that is cut off the trunk snaps back and closes the root plate pit (Thorn et al., 2014).

We created 12 artificial windthrow plots across the northern part of the Bavarian Forest National Park in April 2013; six plots are located under a closed canopy and six are under an open canopy, i.e. at the edge of large forest gaps, to capture differences in canopy closure (Fig. 1). On each plot, natural storm disturbance, i.e. windthrow, was simulated by pulling down and uprooting three mature spruce trees of similar physical conditions with iron ropes and winches. Immediately after the trees were uprooted, two of the three trees per plot were cut above the root plate and branches were cut off and left on the forest floor. When each root plate was cut off, it snapped back and closed the root-plate pits, leaving only a vertical stump. The third uprooted tree with branches and root plate attached to the trunk was left as a control, leaving an open pit. This experiment was part of a larger experiment to investigate mechanical bark treatments on saproxylic insects and fungi developing in tree trunks. Thus, branches were cut off the trees (for details of experimental design, see Fig. 1 and Thorn et al., 2016a).

2.2. Arthropod sampling

For sampling branch-dwelling saproxylic beetles, we collected bundles of branches attached to the control trees ("elevated branches") and branches that had been cut from the two salvage-logged trees in April 2013 and left on the ground ("cut branches") (Fig. 1c). Each bundle consisted of four branches of 45 cm in length and 1.5 cm in diameter. Bundles were collected in August, September, October and November 2013, resulting in a total of 96 bundles of branches (2 bundles per plot $\times$ 12 plots $\times$ 4 months). The bundles were stored in cardboard boxes for nine months and emptied two months after the last beetle emerged to rear all beetles that colonized the branches. Emerging saproxylic beetles were trapped in a 99% alcohol solution within a transparent plastic vial mounted at the opening of the cardboard box.

To sample carabids, epigeal spiders and harvestmen, we used four pitfall traps per plot. Two traps were placed in the root-plate pit of the control tree, and two traps were placed on the repositioned root plate near the stump (Fig. 1d). The 48 traps of the entire experimental design operated during the entire growth season from the end of April to the beginning of October, in 2013–2015, resulting in three survey years. Traps consisted of a 500 ml white plastic cup sunk flush with ground level and covered about 10 cm above ground level by a PVC roof to shield the trap from rain. Coarse-meshed wire (3 cm $\times$ 4 cm) was placed in the upper third of the cups to reduce the by-catch of small mammals, reptiles and amphibians. Arthropods were trapped in a 3.0% copper-vitriol solution in 2013/14 and in a saturated saline solution in 2015 (Lassauce et al., 2012). Both pitfall traps and rearing boxes were emptied monthly.