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Small-scale positive response of terrestrial gastropods to dead-wood addition is mediated by canopy openness

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ABSTRACT

Terrestrial gastropods can benefit from coarse woody debris, even though they are not saproxylic because dead wood maintains suitable microclimatic conditions and provides food resources and essential nutrients, e.g. calcium. Effects of dead wood on terrestrial gastropods have been studied mostly for coarse woody debris at intermediate and advanced stages of decomposition. However, it remains unclear whether dead wood at an early stage of decomposition and of small diameter has similar positive effects on terrestrial gastropods and how effects of dead wood are mediated by canopy openness. We experimentally exposed different amounts of fresh coarse and fine woody debris on 190 temperate forest plots with either high or low canopy openness and studied terrestrial gastropod activity three years after. Plots with high canopy openness had dense herb layers. Feeding activity of gastropods was higher close than distant to dead wood. This effect was stronger on shady plots. The amount of both fine and coarse woody debris positively affected the feeding activity of gastropods, but only on shady plots. The effect of coarse woody debris amount might be partly due to increased leaf litter accumulation. Our results indicated that dead wood plays a stronger role for terrestrial gastropods in shady than in sunny forests with a dense herb layer and that terrestrial gastropods benefit from both coarse and fine woody debris already at an early stage of decomposition. Thus, conservation strategies that aim at maintaining biodiversity of saproxylic assemblages by retaining or adding dead wood are also beneficial for gastropods, especially in shady forests.

1. Introduction

Many forest taxa worldwide are saproxylic, i.e., they depend on dead wood or other wood-inhabiting taxa (Speight, 1989), and thus benefit from increased amounts of dead wood (Andersson and Hytteborn, 1991; Bader et al., 1995; Caruso et al., 2010; Lassauce et al., 2011; Seibold et al., 2015). Dead wood, however, also affects non-saproxylic taxa, particularly many litter-dwelling invertebrates (Castro and Wise, 2010; Czeszczewik et al., 2013; Kappes et al., 2009; Mac Nally et al., 2001; Müller et al., 2005; Seibold et al., 2016a; Ulyshen and Hanula, 2009). One taxonomic group that is not considered saproxylic but seems to respond to dead wood is represented by terrestrial forest gastropods. Gastropods respond, for instance, positively to inputs of woody debris in tropical forests (Willig et al., 2014), and snail density decreases with increasing distance to dead wood (Kappes, 2005; Strätz et al., 2009). Terrestrial gastropods in general are a rather neglected taxonomic group in biodiversity studies (e.g. Paillet et al., 2010) despite their functional importance, for example for seed dispersal (Türke et al., 2012), and particularly their relation to dead wood has rarely been studied experimentally (for a review see Seibold et al., 2015).

Association of gastropods as well as other non-saproxylic invertebrates with dead wood might be caused by several ecological

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mechanisms. For example, dead wood increases structural habitat complexity directly and also indirectly through the accumulation of leaf litter (Marra and Edmonds, 1998; Topp et al., 2006), by trapping it like in a basket, which provides shelter and breeding space for litter-dwelling organisms, such as spiders, ground beetles, and potentially gastropods (Castro and Wise, 2010; Harmon et al., 1986; Kappes et al., 2009; Ulyshen and Hanula, 2009). Decaying dead wood and accumulated leaf litter represent an important source of carbon and nutrients for detrital food webs that include gastropods (Kappes, 2005; Locasciulli and Boag, 1987). In particular, calcium is crucial for snail reproduction and shell formation and is thus an important driver of snail diversity and density (Fournié and Chétail, 1984; Hotopp, 2002; Rieger et al., 2010; Schilthuizen et al., 2003). In regions with acidic soils, the calcium supply under and adjacent to strongly decayed coarse woody debris (CWD) is in a range favorable for land snails, and snail densities hence increase with increasing amount of CWD in advanced stages of decomposition (Müller et al., 2005). However, it remains unclear whether fine woody debris (FWD) has similar positive effects on terrestrial gastropods, and whether gastropods benefit from CWD also during earlier stages of decay.

Many gastropod species are sensitive to desiccation (Barker, 2001; Hylander et al., 2004; Martin and Sommer, 2004). Gastropods could suffer from increased temperatures and reduced litter moisture when canopy openness is increased by natural disturbances, harvesting, or thinning operations (Hylander et al., 2004). Even during dry periods, dead wood is a relatively stable source of moisture, which could positively affect gastropods (Hylander et al., 2004; Martin and Sommer, 2004; Ulyshen et al., 2011). Therefore, dead wood might be particularly important for gastropods in sunny forests with open canopies. However, it has also been reported that when canopy openness is increased, gastropods increase in abundance, possibly because of an increased herb layer density (Willig et al., 2014) or higher diversity of plants (Getz and Uetz, 1994; Müller et al., 2009). Overall, the relationship between dead wood, canopy openness, and terrestrial gastropods is still not well understood in temperate forest ecosystems.

To evaluate the effect of the amount of dead wood of two different diameter classes and canopy openness, as well as their interactions, on terrestrial gastropods, we experimentally exposed 800 m^3 of CWD and 5000 branches (FWD) on 190 plots in temperate montane forests. Half of the plots were located in sunny clearings, and the other half were in shady stands with a closed canopy. We sampled terrestrial gastropods and assessed their feeding activity as a proxy for density during the early decomposition stage, three years after dead wood was added. We tested the following hypotheses: (H1) feeding activity of terrestrial gastropods is higher near dead wood, (H2) feeding activity of terrestrial gastropods increases with the amount of dead wood, (H3) CWD has a greater effect on the feeding activity of terrestrial gastropods than FWD, and (H4) effects of dead wood are stronger on sunny plots than on shady plots.

2. Material and methods

2.1. Study area and experimental design

The experiment was conducted in the temperate montane mixed forests (*Luzulo-Fagetum*) of the Bavarian Forest National Park in southeastern Germany at elevations between 715 and 1200 m a.s.l. The dominant tree species are European beech *Fagus sylvatica* L., silver fir *Abies alba* (Mill.) and Norway spruce *Picea abies* (Karst.). Annual precipitation in the study area ranges between 1200 and 1800 mm, and the mean annual temperature varies between 3.8 and 5.8 °C depending on altitude (Bässler et al., 2010). Acidic sand and loam soils (brown earth and podsol) developed on hillsides essentially from granite and gneiss, which resulted in soil with low pH and productivity (Bässler et al., 2010; Bauer et al., 1988). The forests in the national park are mostly of anthropogenic origin but have been unmanaged for several decades, except from salvage logging of dead spruce in the management zone after bark beetle infestation. Natural disturbance due to bark beetle infestation and wind throw produced high variability of dead-wood amounts across the study area (Müller et al., 2010). Study plots were, however, located in gaps and beech dominated stand which were not subject to disturbance by wind throw or bark beetles over the course of the study.

In fall 2011, we removed natural dead wood and added freshly cut dead wood to 190 plots of 0.1 ha size, arranged in a randomized block design with five replicates, in the management zone of the national park (Seibold et al., 2016a, 2016b, 2014). Half of the plots were located in several year old sunny forest clearings originating from salvage logging after bark beetle induced tree dieback. The other half were in mature forest stands with almost completely closed canopies (shady). Canopy cover was estimated at the beginning of the experiment (mean canopy cover ± SD of sunny plots: 0.17 ± 1.54%; mean canopy cover ± SD of shady plots: 96.72 ± 5.39%). Litter moisture was lower on sunny plots than on shady plots and litter moisture close to dead wood was higher than further away (Seibold et al., 2016a). Added dead wood included logs (CWD; mean diameter ± SD: 32.5 ± 6.5 cm, length: 5 m) of European beech and/or silver fir and/or branches (FWD; mean diameter ± SD: 3.2 ± 1.2 cm, mean length: 2.7 ± 0.88 m) of one or both tree species. These tree species are two of the naturally dominant species in montane forests of the region. Control plots received no added wood and all other plots received either a low or high amount of FWD (8 branches, mean amount ± SD 0.14 ± 0.10 m^3 ha^{-1} or 80 branches, mean amount ± SD 2.2 ± 1.2 4 m^3 ha^{-1}) or CWD (4 logs, mean amount ± SD 15.85 ± 3.5 5 m^3 ha^{-1} or 40 logs, mean amount ± SD 114.96 ± 17.21 m^3 ha^{-1}) or low or high amounts of both CWD and FWD (mean amount ± SD 16.15 ± 2.73 m^3 ha^{-1} or 118.69 ± 22.36 m^3 ha^{-1}) together. This represents a gradient of dead-wood amount from the low amounts typical for European production forests to the extraordinarily high amounts created by forest disturbances (Müller et al., 2010). Dead wood was distributed in a way that distances between the single dead-wood objects were similar, i.e., on plots with high amounts of dead wood a larger area was covered. Half of the logs on a plot had full soil contact while the other half was partly elevated onto other logs to mimic natural conditions of fallen trees.

Sunny plots faced a fast succession and increasing cover particularly of young trees (mostly Silver Birch *Betula pendula* Roth, Mountain-Ash *Sorbus aucuparia* L. and Norway Spruce *P. abies*) and tall grasses, such as *Calamagrostis villosa* (Chaix ex Vill.) J.F. Gmel. To keep conditions of sun exposure constant, all young trees and shrubs were trimmed using brushcutters to approx. 20 cm in height once a year between late July and mid of August. At the same time, the herb layer, particularly tall grasses, was trimmed in the immediate surroundings of added dead wood and both cardboards to avoid that added dead wood was covered by tall grasses leaning over logs and branches. Thus, the herb layer in large portions of the 0.1-ha plots remained undisturbed, but dead wood and cardboards were not overgrown. Because of the low growth potential in the shady understory, only single young trees had to be trimmed occasionally at shady plots.

2.2. Gastropod sampling

Terrestrial gastropod assemblages can be sampled in a standardized way by collecting individuals from underneath cardboards that have been exposed on the forest floor (Hawkins