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

Tobias Kirchenbaur[a,*], Thomas Fartmann[b,c], Claus Bässler[a,d], Franz Löffler[b,c], Jörg Müller[a,d], Christian Strätz[e], Sebastian Seibold[a,f]

[a] Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany
[b] Department of Biodiversity and Landscape Ecology, Faculty of Biology/Chemistry, University of Osnabrück, Barbarastraße 13, 49076 Osnabrück, Germany
[c] Institute of Biodiversity and Landscape Ecology (IBL), Hafenweg 31, 48155 Münster, Germany
[d] Field Station Fabrikschleichach, Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Glashüttenstraße 5, 96181 Rauhenebrach, Germany
[e] Büro für ökologische Studien, Oberkonnersreuther Str. 6a, 95448 Bayreuth, Germany
[f] Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, Center for Food and Life Sciences Weihenstephan, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

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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

* Corresponding author.
E-mail addresses: tobiekb@gmail.com (T. Kirchenbaur), t.fartmann@uos.de (T. Fartmann), claus.baessler@npv-bw.bayern.de (C. Bässler), franz.loeffler@uos.de (F. Löffler), joerg.mueller@npv-bw.bayern.de (J. Müller), christian.straetz@bfoes.de (C. Strätz), sebastian-seibold@gmx.de (S. Seibold).

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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 ± 1.24 m^3 ha^{-1}) or CWD (4 logs, mean amount ± SD 15.85 ± 3.55 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 et al., 1998; Ovaska and Sopuck, 2003; Prezio et al., 1999). Similarly, the feeding activity of terrestrial gastropods can be estimated by measuring the surface area of exposed cardboard that shows signs of gastropod feeding activity (Strätz et al., 2009) (see Appendix). We exposed two pieces of corrugated cardboard (900 cm^2; 30 cm × 30 cm) on each of the 190 plots for the complete growing season (May to September) in 2014. On each plot, a cardboard was placed close to the added dead wood (approx. 15 cm) and a second cardboard was placed ~1.7 m distant from the first cardboard and any dead wood on the plot. The leaf litter layer was not disturbed.

Before transferring the cardboard pieces to the lab in plastic bags, all gastropods found on or below the cardboard were collected for further determination. Cardboard pieces were dried in an oven at 60 °C for about 2 days to allow removal of attached litter before the estimation of feeding activity. Following Strätz et al. (2009), we estimated gastropod feeding activity by placing a wooden framed grid (5 cm × 5 cm grid) on top of both sides of a cardboard and counted the number grid squares showing signs of gastropod feeding activity (see Appendix). This means maximally 72 grid squares per cardboard could show signs, as there were 36 squares on the upper and 36 on the lower side of each cardboard. Signs of feeding activity included holes and rasping marks (Fig. A2). As parts of the cardboard were sometimes missing, we also used the framed grid to record the number of squares without feeding marks.

To obtain information on species assemblages, all gastropods found during cardboard collection or in dried and sieved (18 mm and 4 mm mesh size) litter previously attached to the cardboard were identified to species level according to Wiese (2014). Only the slug species *Arion fuscus* (Müller, 1774) and *Arion brunneus* (Lehmann, 1862) could not be classified without dissection and were therefore assigned to one group. After drying of the litter, shelled gastropods could still be identified, but slugs were not classifiable. However, because of their larger size, slugs were frequently found when the cardboard pieces were collected. Species assemblages recorded with this method do not represent complete forest gastropod assemblages (Coppolino, 2010), but represent gastropod assemblages living on the surface of the forest floor (Hawkins et al., 1998).

2.3. Statistical analyses

All collected data were statistically analyzed using R 3.0.3 (R Development Core Team, 2014). Abundance and species numbers per plot were too low to allow detailed statistical analyses and focus was therefore put on gastropod feeding activity. To evaluate how dead wood affects the feeding activity of gastropods and how effects are mediated by canopy openness, we calculated a binomial generalized linear mixed model (GLMM; function *glmer* in package *lme4*). The response, feeding activity, was modeled as the number of squares with signs of feeding relative to the total number of squares per cardboard at the end of the study using the function *cbind*. In the model, we estimated fixed effects of canopy openness (sunny vs. shady) and – specifically for shady and sunny plots – of distance to dead wood (distant vs. adjacent), tree species (fir vs. beech), number of tree species (0, 1 or 2), amount of FWD, amount of CWD (both ordinal variables with three levels: 0, 1, 2) as well as the interaction between FWD and CWD amount. The model included random effects of plot nested in block to account for the nested study design. A second model included interactions between canopy openness and all predictors related to dead wood to test whether differences between their effects on sunny and shady plots were significant. For both models, Nagelkerke's Pseudo R2 was calculated (Nagelkerke, 1991).

3. Results

3.1. Gastropod abundance and richness

We recorded 638 individuals of 22 different gastropod species, and 49 individuals of the *Arion fuscus/Arion brunneus* group (Table A1). The most frequently found species was *Euconulus fulvus* (Müller, 1774) (300 individuals), a widespread generalist, but we also recorded red-listed species such as *Semilimax kotulae* (Westerlund, 1883) (46), *Discus ruderatus* (Férussac, 1821) (6), *Vitrea subrimata* (Reinhardt, 1871) (1), *Arion rufus* (Linnaeus, 1758) (6), and *Arion alpinus* (Pollonera, 1887) (3). Total species numbers on sunny and shady plots were similar, but sunny plots hosted more individuals (Table A1).

3.2. Feeding activity

Feeding activity was positively correlated to the number of gastropod individuals and species ($p < 0.001$), but the relationships were weak ($r_{pearson} = 0.21$ and 0.23, respectively; Fig. A1). Our linear mixed model revealed feeding activity to be similar on sunny and shady plots (Table 1 and Fig. 1). Feeding activity was higher near dead wood than at a distance of ~1.7 m. Increasing the amount of FWD and CWD positively affected feeding activity, but only on shady plots and the effect of CWD was only marginally significant. The interaction of FWD and CWD amount was negative and marginally significant, indicating weaker positive effects when both diameter classes were present. Feeding activity was higher when fir dead-wood was present on shady plots; number of tree species had no significant effect. Significant interactions between canopy openness and distance to dead wood ($p < 0.001$) and marginally significant interactions between canopy openness and amount of CWD ($p = 0.07$) and amount of FWD ($p = 0.10$) indicated stronger effects of these three variables on shady than on sunny plots. Nagelkerke's Pseudo R2 was 0.212 for both models.

Table 1
Results of a linear mixed effects model of gastropod feeding activity relative to canopy openness and added dead wood tested specifically for sunny and shady plots. All models contained plot nested in block as random factor to account for the nested design. Bold values indicate significant results ($p \leq 0.1$) and gray shading indicates a significant interaction ($p \leq 0.1$) between canopy openness and the respective variable as tested in a separate model.

Variable	*z*-Value	*p*-Value
Sunny vs. shady	−1.365	0.172
Distant vs. close		
on sunny plots	**−2.286**	**0.022***
on shady plots	**−9.179**	**<0.001*****
Amount of FWD		
on sunny plots	−0.400	0.689
on shady plots	**1.986**	**0.047***
Amount of CWD		
on sunny plots	−0.845	0.398
on shady plots	**1.713**	**0.087**$^{\cdot}$
Interaction between amount of CWD and amount of FWD		
on sunny plots	−0.306	0.759
on shady plots	**−1.861**	**0.063**$^{\cdot}$
Number of tree species		
on sunny plots	0.228	0.820
on shady plots	−1.429	0.153
Fir vs. beech		
on sunny plots	0.084	0.933
on shady plots	**2.173**	**0.030***

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; $^{\cdot}$ $p < 0.1$.

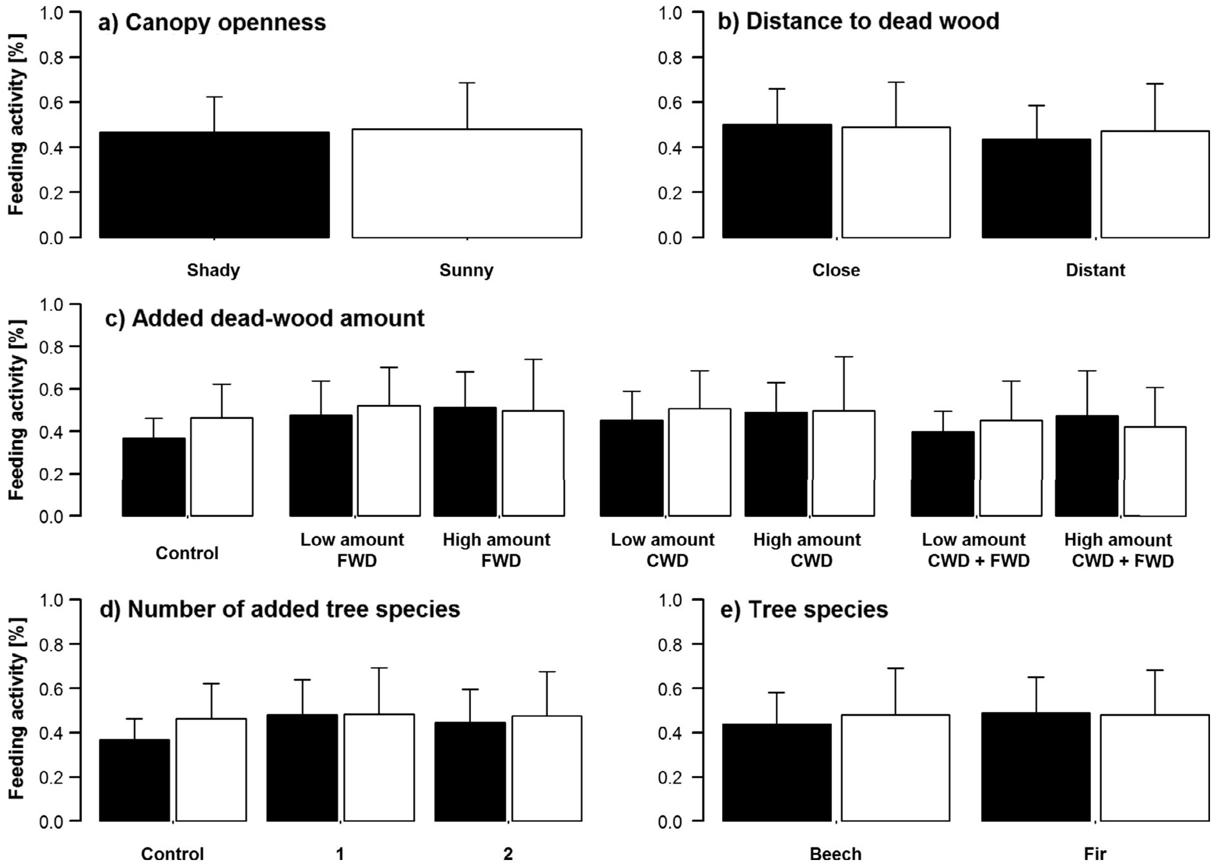

Fig. 1. Barplots showing the gastropod feeding activity [%] relative to (a) canopy openness, (b) distance to dead wood and (c – e) dead wood variables tested in GLMMs (Table 1), together with the corresponding standard deviation as error bar. For (b – e) feeding activity [%] is shown for shady (black) and sunny (white) plots, respectively.

4. Discussion

Overall, our results indicated that terrestrial gastropods show higher activity close to woody debris and that increasing the amount of CWD or FWD positively affected gastropods already three years after dead-wood addition. The response of terrestrial gastropods to dead wood was, however, mediated strongly by canopy openness as effects of distance to dead wood, amount of CWD and amount of FWD were stronger in shady than in sunny forests.

Dead wood is crucial for many forest taxa (Müller and Bütler, 2010; Stokland et al., 2012) and adding dead wood promotes species numbers of saproxylic and many non-saproxylic taxa (Seibold et al., 2015). In shady forests, dead wood positively affects terrestrial gastropod density, diversity (e.g., Kappes, 2005; Kappes et al., 2009, 2006; Mac Nally et al., 2001) and activity within a distance of up to 20 m (Strätz et al., 2009). The threshold for amounts of CWD that separate closed canopy stands with low snail density from those with high snail density is 57 m^3 ha^{-1} in temperate forests with acidic soils (Müller et al., 2005). The positive effects of dead wood can be caused by favorable microclimatic conditions near dead wood which is a stable source of moisture (Kappes, 2005; Kappes et al., 2006; Ulyshen et al., 2011) or by the high amounts of nutrients stored in dead wood and particularly in bark tissue (Möller, 2009) that might promote especially shell-forming snails in forests with acidic soils (Müller et al., 2005). Our results confirmed higher gastropod activity near dead wood in shady forest habitats and showed that the same pattern occurs also in sunny forest habitats. Adding CWD or FWD to the plots increased snail activity on shady, but not on sunny plots.

Canopy openness is a major driver of species composition of forest communities (Fartmann et al., 2013; Helbing et al., 2014; Horak et al., 2014; Seibold et al., 2016a, 2016b; Stokland et al., 2012) but whether increasing canopy openness promotes species numbers or not differs between taxonomic groups (Nascimbene et al., 2013; Seibold et al., 2015). Increasing canopy openness leads to increased insolation at the forest floor, higher temperature variation and reduced litter moisture (Richardson et al., 2010; Yi and Moldenke, 2008). Particularly reduced litter moisture seems to have negative effects on the abundance of many litter invertebrates (Richardson et al., 2010; Seibold et al., 2016a; Yi and Moldenke, 2008) including gastropods (Hylander et al., 2004). However, increased light availability leads to higher density of ground vegetation in forests with high canopy openness, which was also true in our study (Seibold et al., 2016a) and which may positively affect gastropod assemblages (Getz and Uetz, 1994). Potentially harsher microclimatic conditions and reduced ground moisture on sunny plots could have been buffered by dense ground vegetation which may explain why we found no difference in feeding activity between sunny and shady plots. This is supported by Hylander et al. (2004) who found that clear cutting negatively affects gastropod density and richness owing to reduced litter moisture levels, but that clear cutting has no effect on wet sites with high plant and moss cover.

Climate and canopy openness can mediate effects of dead wood on invertebrates (Müller et al., 2015; Seibold et al., 2016a, 2016b). It is often assumed that epigeal arthropods benefit more strongly from positive effects of dead wood on microclimatic conditions in sunny forests with low litter moisture (Ulyshen et al., 2011). Moisture is especially crucial for land snails, due to their high water loss, caused by their permeable skin and mucous secretion (Barker, 2001). By contrast, our results indicate that effects of dead wood on terrestrial gastropods were stronger in shady than in sunny forests. This may also be explained by lower importance of dead wood as source of moisture when dense ground vegetation buffers potentially negative microclimatic effects of high canopy openness. Furthermore, gastropod assemblages in shady forests without a dense herb layer might comprise more detritivorous and mycetophagous species than phytophagous species, and thus, dead wood and accumulated litter might be more attractive for gastropod assemblages in shady forests.

Owing to its higher volume, CWD stores more nutrients than FWD and affects microclimatic conditions more strongly (Harmon et al., 1986). This may explain why the amount of CWD in rather advanced stages of decomposition – when nutrients are released – is generally an important factor for snails (Müller et al., 2005). However, FWD decomposes faster and releases nutrients earlier than CWD (Graham and Cromack, 1982; Harmon et al., 1986). Dead wood in our study was 2–3 years old. While FWD was already quite strongly deteriorated, CWD was in a relatively early stage of decomposition. This may explain why we found slightly stronger effects of FWD on gastropod activity than of CWD indicating that also increasing amounts of FWD promote terrestrial gastropods. Nevertheless, our results indicate that terrestrial gastropods benefit from increased amounts of CWD not only at a later stage of decomposition but already 2–3 years after its creation.

Fir dead wood increased gastropod activity more strongly than beech dead wood. Possible explanations are differences in nutrient content, decomposition rate and structural differences between these tree species. Saproxylic insect diversity is promoted by increasing dead-wood diversity (e.g. number of tree species and diameter classes; Seibold et al., 2016b). However, we found no effect of number of tree species and a negative interaction between amount of FWD and CWD indicating that positive effects of dead-wood addition are weaker when both diameter classes are added. It is not possible to explain these patterns based on available information.

A possible indirect mechanism how dead wood can affect gastropods and other epigeal invertebrates is the accumulation of leave litter (Kappes et al., 2006, 2009). Litter accumulated near dead wood can enhance positive microclimatic effects of dead wood (Kappes, 2005; Kappes et al., 2009; Locasciulli and Boag, 1987) and also serve as a direct (Horsák et al., 2013; Juřičková et al., 2008) and indirect source of nutrients owing to bacteria and fungi growing on litter (Kappes, 2005). In our study, the litter layer was deeper near dead wood and increased with the volume of CWD (see Appendix). Therefore, some parts of the positive effect of the amount of CWD on gastropod activity might be due to the accumulated leaf litter.

5. Conclusions

Although terrestrial gastropods are clearly not considered saproxylic, our study confirms positive effects of dead wood on gastropod activity in temperate montane forests within a few years after dead-wood addition. This corroborates that dead wood is a crucial habitat feature for forest biodiversity in general, not just for saproxylic species. Effects of dead wood on terrestrial gastropod activity, however, were strongly mediated by canopy openness indicating that dead wood is more important for terrestrial gastropods in shady forests. While gastropod activity was higher near dead wood in both sunny and shady forests, increasing the amount of CWD or FWD increased terrestrial gastropod activity only in shady forests. This indicates that both CWD and FWD are important for terrestrial gastropods and that CWD promotes gastropods already at an early stage of decomposition, maybe partly by accumulating leaf litter. Thus, conservation of saproxylic taxa by retaining or supplementing dead wood promotes also terrestrial gastropod assemblages in temperate montane forests, particularly in shady forests.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.03.034.

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