



Dead-wood addition promotes non-saproxyllic epigeal arthropods but effects are mediated by canopy openness

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ABSTRACT

Restoring dead-wood amounts in forests is an increasingly and successfully applied conservation measure to counteract negative effects of intensive logging on biodiversity of saproxyllic taxa. By contrast, if and how dead-wood addition benefits the vast number of non-saproxyllic forest taxa, and how this varies with contextual factors like canopy openness, remains poorly understood. To enhance dead-wood addition strategies, it is thus important to understand how dead wood affects entire forests communities, not just saproxyllic taxa. To untangle effects of dead-wood addition and canopy openness on non-saproxyllic epigeal arthropods, we exposed different amounts of logs and branches on 190 0.1-ha plots located in sunny or shady mixed montane forests and sampled epigeal arthropods over three years. Canopy openness was a major driver of species assemblage composition and clearly mediated the effects of dead wood on epigeal beetles, spiders/harvestmen and springtails. Most species groups responded positively to the addition of dead wood. All groups decreased in number with increasing distance to dead wood. Dead wood affected taxa of both lower and higher trophic levels directly and taxa of higher trophic levels benefitted also indirectly owing to bottom-up effects. Our results indicate that increasing the amount of dead wood for conservation of saproxyllic taxa benefits also non-saproxyllic epigeal arthropods and thus, a larger number of forest species than commonly assumed. Because of the strong effects of canopy openness, similar to those found for saproxyllic taxa, dead wood in both sunny and shady forest stands is needed.

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1. Introduction

Dead wood is a keystone structure in forested ecosystems supporting a large fraction of forest biodiversity. An estimated 20–30% of all forest arthropod species are saproxyllic, for example, meaning they are directly or indirectly dependent on dying or dead wood (Stokland et al., 2012). Intensive forestry practices result in drastic reductions in the amount and variety of dead wood compared to

unmanaged forests (Lassauce et al., 2011, and references therein). Because of the loss of dead-wood habitats, many saproxyllic taxa have declined and are now threatened (e.g., Nieto and Alexander, 2010). To counteract loss of saproxyllic biodiversity, in many countries, particularly in Europe and North America, conservation strategies aim at increasing dead-wood volumes (e.g., Davies et al., 2007; Junninen and Komonen, 2011; Kilgo and Vukovich, 2014; Seibold et al., 2015). A worldwide meta-analysis has shown consistently positive effects of dead-wood addition on biodiversity of saproxyllic taxa, but a very heterogeneous response of non-saproxyllic taxa (Seibold et al., 2015). Saproxyllic populations benefit directly from increased habitat availability (Lassauce et al., 2011; Müller and Büttler, 2010) due to an increase in habitat heterogeneity (Seibold et al., 2016), but mechanisms behind the effects of dead wood on non-saproxyllic organisms remain poorly resolved.

Among non-saproxyllic taxa, epigeal arthropods are a species-rich group with a highly variable response to increased amounts of dead

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wood (Seibold et al., 2015), possibly due to various direct and indirect mechanisms by which species of different trophic levels are linked to dead wood. Added dead wood, for instance, increases structural complexity on the forest floor by increasing surface area that differs qualitatively from the surrounding leaf litter but also by trapping and accumulating leaf litter (Castro and Wise, 2010; Kappes et al., 2009). Decaying woody debris provides nutrients that benefits detritivores like springtails (Collembola) or, owing to bottom-up effects, predators such as carabid beetles (Coleoptera) and spiders (Araneae) (Chen and Wise, 1999). Dead wood, particularly large logs, represents a relatively stable source of moisture that might be beneficial for many taxa that are sensitive to strong fluctuations in moisture, particularly under sunny conditions (Ulyshen et al., 2011). Furthermore, crevices in dead wood and accumulated litter can provide shelter from extreme temperatures (Langlands et al., 2011) and from predators (Hoddle, 2003). In turn, predators might be attracted by dead wood because of increased prey abundance (Klecka and Boukal, 2014). These effects could differ among species groups depending on the diameter of the dead wood and the tree species (Castro and Wise, 2010; Castro and Wise, 2009). Therefore, not only the amount of dead wood but also the number of different types of dead wood, i.e. dead-wood diversity (Siitonen et al., 2000), might affect epigeal arthropod assemblages.

When dead wood is created intentionally during logging or restoration operations or by natural disturbances, openings in the forest are generated ranging from downed single trees to large forest clearings and thus, result in increased insolation and altered microclimatic conditions. This leads to higher mineralization rates and promotes higher densities of herbs and grasses, which in turn can affect epigeal taxa, as shown by numerous studies focusing on effects of logging on epigeal arthropods (e.g., Gunnarsson et al., 2004; Johansson et al., 2016; Koivula and Niemelä, 2003; Nittérus and Gunnarsson, 2006). Canopy openness has the potential to interact with effects of dead wood on epigeal arthropods (Thorn et al., 2016). Dead wood in open areas, for instance, might play a more important role in buffering against microclimatic extremes than dead wood beneath a closed canopy. To our knowledge, only one study has aimed at decoupling the effects of canopy opening and dead-wood addition on epigeal arthropods. By experimentally mimicking hurricane disturbance, Richardson et al. (2010) revealed that effects of canopy opening on litter-dwelling arthropods were stronger than effects of leaf and branch deposition in a tropical forest in Puerto Rico. However, the understanding of the mechanisms of how dead wood affects epigeal arthropods and how these effects interact with canopy openness remains limited.

We aimed at an understanding of the direct and indirect effects of dead wood and canopy openness on non-saproxyllic epigeal arthropod taxa of different trophic levels in temperate mixed forests. We experimentally added logs and branches on 190 plots to form gradients of dead-wood amount and dead-wood diversity. Half of these plots were located in sunny clearings and the other half were under a closed canopy. We sampled epigeal beetles, spiders, harvestmen and springtails on each plot during the early-successional phase at two distances from added dead wood. We tested the following hypotheses: i) epigeal arthropod abundance, richness and assemblage composition differ between sunny and shady forests; ii) the amount of dead wood per plot has direct positive effects on taxa of both lower and higher trophic levels and this pattern is stronger under sunny conditions than under shaded conditions; iii) the diversity of dead wood per plot positively affects species richness of taxa of both lower and higher trophic levels; iv) epigeal arthropod abundance and richness are higher when closer to dead wood and this pattern is stronger under sunny conditions than under shaded conditions; and v) taxa of higher trophic levels benefit from dead wood indirectly owing to increased densities of taxa of lower trophic levels (bottom-up effects).

2. Methods

2.1. Study area and experimental design

The experiment was conducted in the Bavarian Forest National Park in south eastern Germany. Overall, 190 0.1 ha plots were established in a randomized block design with five blocks across the management zone of the national park (Seibold et al., 2016; Seibold et al., 2014). Within each block, half of the plots (i.e. 19) were established in sunny clearings and the other half were established in mature forests under a closed canopy. Control plots had no dead wood. To the test plots, we added logs (diameter: 25–50 cm, length: 5 m) and/or branches (diameter: 3–5 cm, length: 2–3 m) that were cut less than eight weeks before. Each plot received dead wood either of European Beech *Fagus sylvatica* or Silver Fir *Abies alba* or of both tree species. These tree species are naturally dominant species in the montane zone of our study area. We varied the amount of added dead wood per plot by adding either a low or high amount of branches (8 branches, about $0.2 \text{ m}^3 \text{ ha}^{-1}$ or 80 branches, about $2 \text{ m}^3 \text{ ha}^{-1}$) or a low or high amount of logs (4 logs, about $10 \text{ m}^3 \text{ ha}^{-1}$ or 40 logs, about $100 \text{ m}^3 \text{ ha}^{-1}$) or a combination of logs and branches of low or high amounts. A gradient of dead-wood diversity was formed by varying the number of different dead-wood types per plot covering four levels: 0 – control plots; 1 – one of each of the four substrate types; 2 – either both diameter classes of the same tree species or only one diameter class of both tree species; 4 – all four dead-wood types. The surface area of all logs and branches was summed per plot to characterize precisely the amount of dead wood (Heilmann-Clausen and Christensen, 2004).

One of our objectives was to study the role of dead wood addition relative to sun exposure at plots with no and high tree canopy cover. Naturally downed trees in gaps provide long lasting sun exposed dead wood because considerable parts of the tree are located meters above ground. In our experiment, we tried to mimic this to some extent by placing half of the logs on top of other logs such that some were partly elevated and half of the logs had full soil contact. Due to differences in light availability, the herb layer (all vascular plants <1 m height; estimated on all plots in July 2012 (Londo, 1976)) differed strongly between sunny and shady plots (Fig. A1). Sunny plots were characterized by a dense herb layer of vascular plants and especially grasses, while most shady plots contained only single plant individuals in the herb layer and only rarely higher densities of low shrubs and young trees. In contrast to shady plots, sunny plots faced a fast succession and increasing cover of tall grasses, such as *Calamagrostis villosa*, and particularly young trees, mostly Silver Birch *Betula pendula*, Mountain-Ash *Sorbus aucuparia* and Norway Spruce *Picea abies*. To keep conditions of sun exposure constant over the whole study period and to avoid that added dead wood was covered by tall grasses leaning over logs and branches, the herb layer on each plot was trimmed once a year between late July and mid of August. By using brushcutters, all young trees and shrubs were trimmed to approx. 20 cm in height to keep the plots open. Furthermore, the herb layer, particularly tall grasses, was trimmed in the immediate surroundings of added dead wood and both pitfall traps. Thus, the herb layer in large portions of the 0.1-ha plots remained undisturbed, but dead wood and traps were not overgrown. Because of the low growth potential in the shady understorey, only single young trees had to be trimmed occasionally at shady plots.

2.2. Arthropod sampling and data processing

Epigeal arthropods were sampled using two pitfall traps per plot that were placed 5 m apart at a distance of 30 and 150 cm to the dead wood. Each trap consisted of a 400 ml polypropylene cup (95 mm diameter) sunk flush with ground level with a PVC roof placed over it about 5 cm above ground level to shield the trap from rain. A non-attracting 3% copper sulphate solution was used to kill and preserve trapped

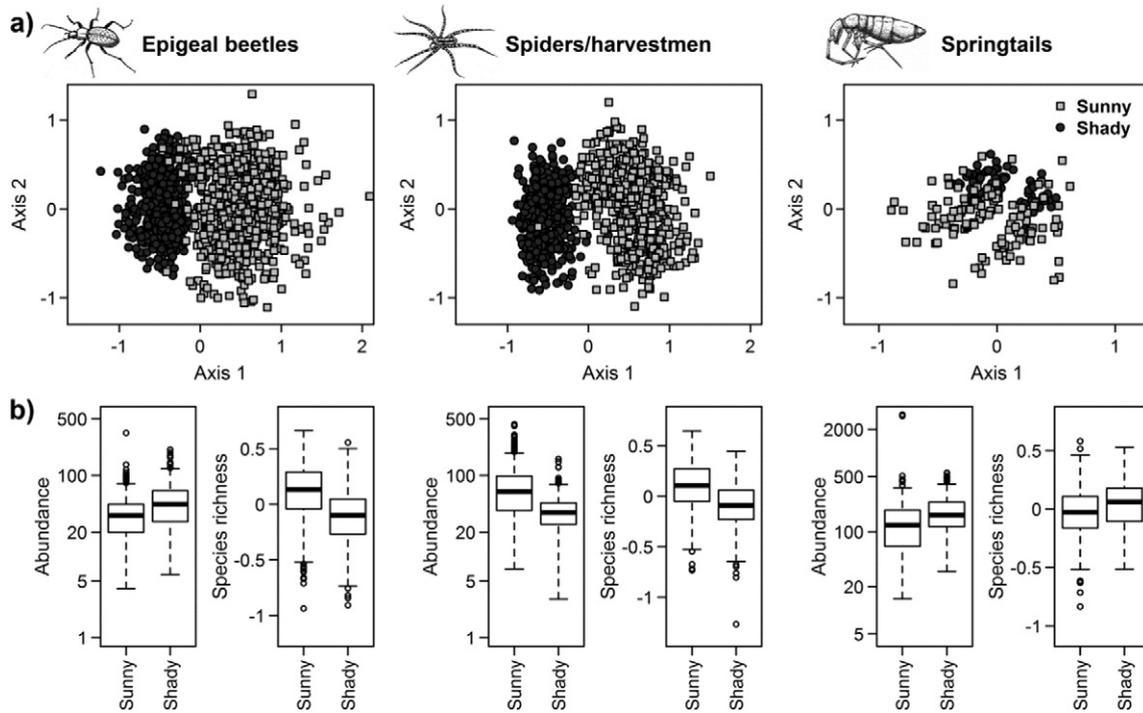


Fig. 1. a) Ordination of species composition of non-saproxyllic epigeal beetles, spiders/harvestmen and springtails on 190 experimental plots with added dead wood according to non-metric multidimensional scaling based on presence–absence data. b) Abundance and species richness (residuals of log-log relationship between observed species number and abundance) of all three species groups on shady and sunny plots. Note the log-scale of abundance on the y-axis.

arthropods (Stoeckle et al., 2010). Traps were operated during May (start of the growing season), July and September (end of the growing season) in 2012, 2013 and 2014 (i.e. beginning in spring after the experiment was set up) and emptied once a month. Two pitfall traps operated

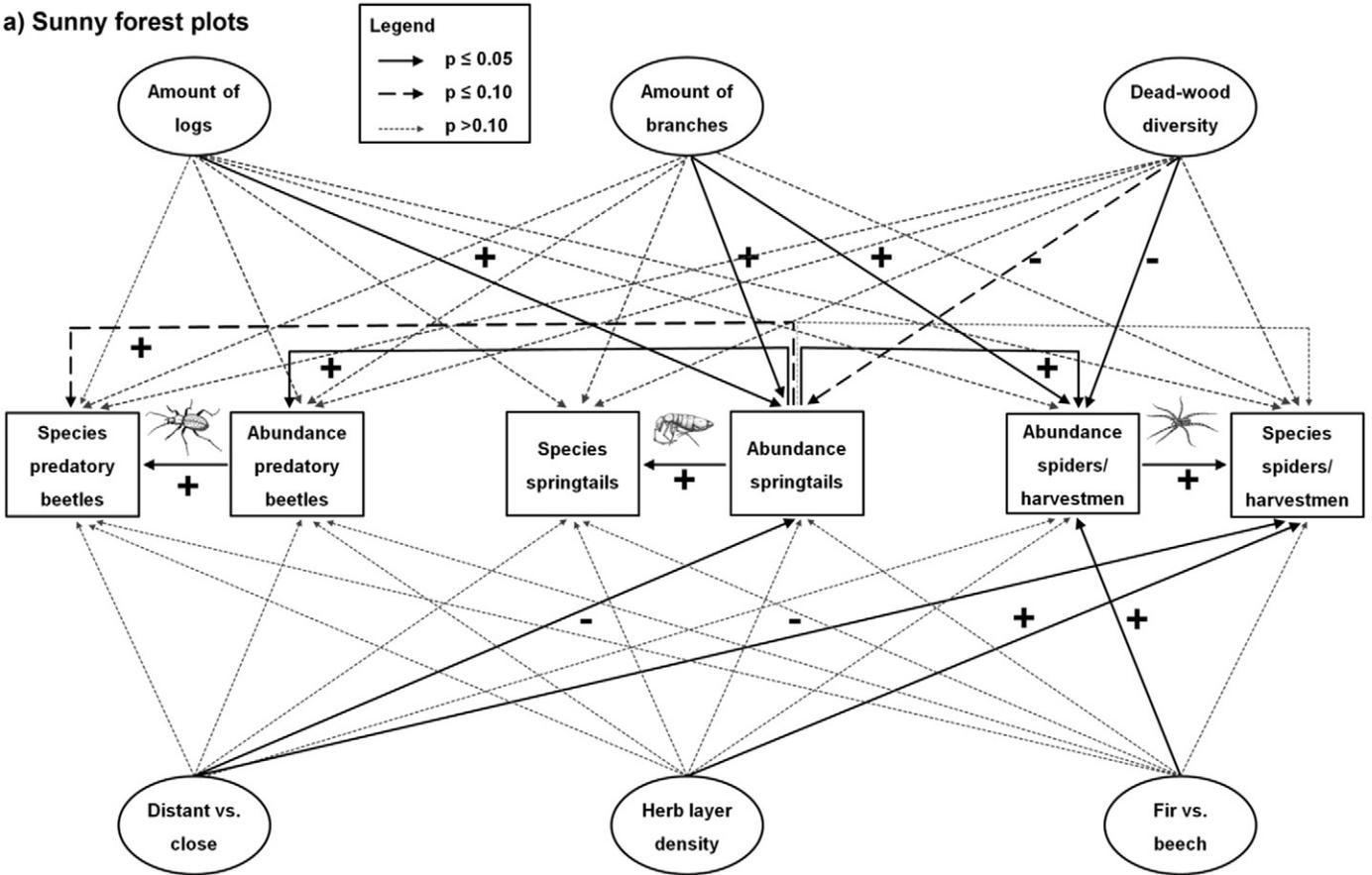
during these three months have proved to yield the sufficient number of specimens required to obtain good correlations of diversity measures with local habitat conditions (Müller and Brandl, 2009). From the material obtained, beetles, spiders, harvestmen and springtails were

Table 1

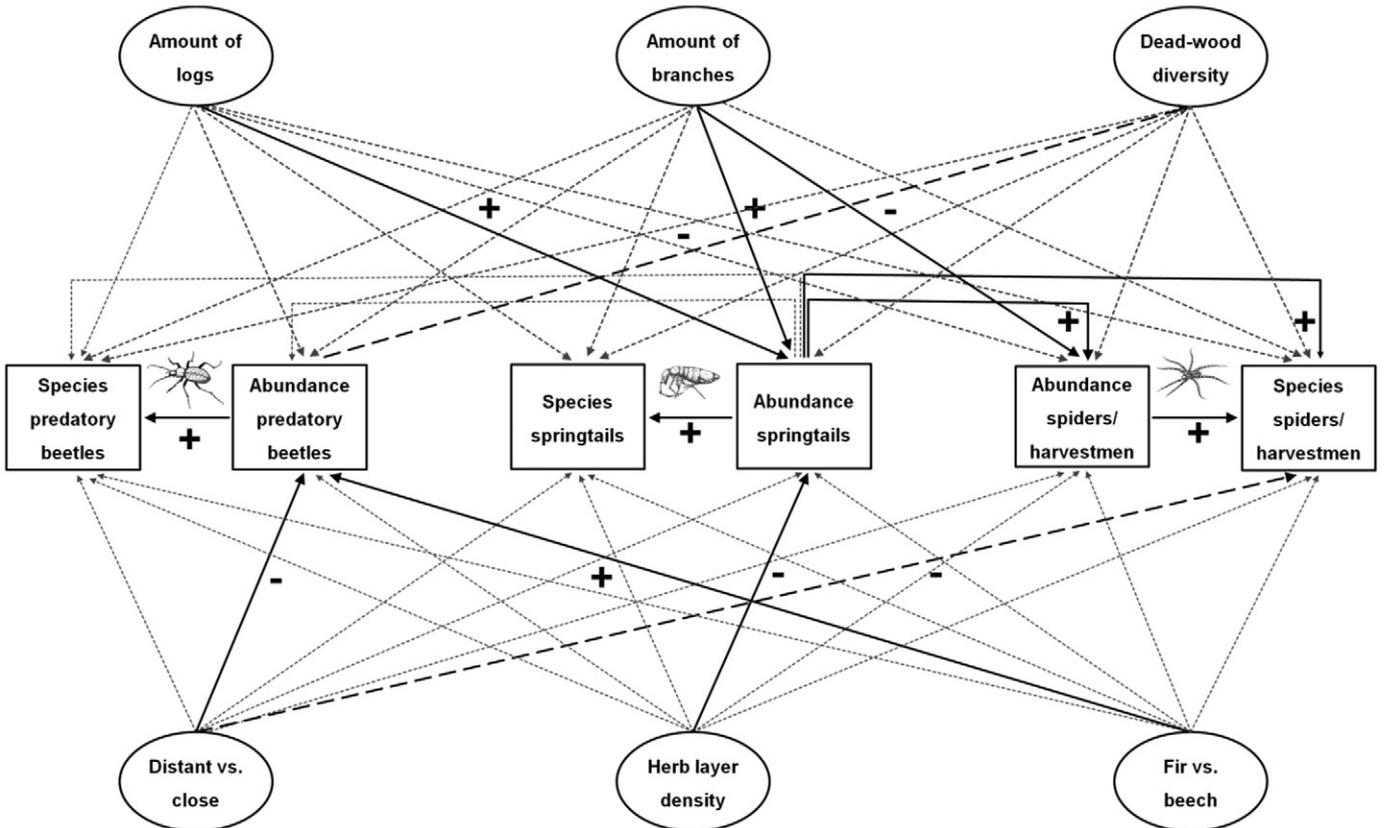
Results of linear mixed models for abundance (Poisson errors) and abundance-corrected species richness (Gaussian errors) of epigeal beetles, spiders/harvestmen and springtails from 190 experimental plots with study year, canopy openness (sunny vs. shady), amount of logs or branches, dead-wood diversity, tree species (fir vs. beech) and distance to dead wood as predictor variables. Effects of variables related to dead wood were estimated specifically for sunny and shady plots. All models contained plot nested in block to account for the nested design. Values in bold indicate significance ($p < 0.05$) or marginal significance ($p < 0.10$). Gray shading indicates a significant ($p < 0.10$) interaction between canopy openness and the respective variable related to dead wood as indicated by additional models.

Predictor variable	Epigeal beetles				Spiders/harvestmen				Springtails			
	Abundance		Species richness		Abundance		Species richness		Abundance		Species richness	
	z-Value	p-Value	z-Value	p-Value	z-Value	p-Value	z-Value	p-Value	z-Value	p-Value	z-Value	p-Value
Year	-2.77	0.006	-8.08	<0.001	-12.58	<0.001	5.94	<0.001				
Shady vs. sunny	2.36	0.018	-7.29	<0.001	-7.22	<0.001	-6.74	<0.001	1.72	0.085	1.42	0.350
Amount of logs												
on sunny plots	-1.71	0.086	-0.52	0.601	-1.54	0.123	0.75	0.453	3.84	<0.001	-0.48	0.631
on shady plots	-0.15	0.814	2.09	0.037	1.38	0.169	1.41	0.158	3.29	<0.001	0.03	0.974
Amount of branches												
on sunny plots	-0.97	0.333	-0.63	0.526	2.81	0.005	-1.56	0.120	3.09	0.002	-0.37	0.715
on shady plots	1.12	0.262	1.01	0.314	-1.03	0.302	-0.50	0.620	2.16	0.031	-0.57	0.570
Dead-wood diversity												
on sunny plots	0.74	0.459	-0.11	0.915	-1.27	0.204	0.54	0.458	-2.26	0.024	0.45	0.656
on shady plots	-2.02	0.043	-0.80	0.426	-0.08	0.935	-0.44	0.545	-0.91	0.363	0.00	0.997
Fir vs. beech												
on sunny plots	-0.15	0.884	-0.30	0.768	1.89	0.058	-1.67	0.095	0.28	0.779	-0.94	0.348
on shady plots	2.33	0.020	0.91	0.365	0.43	0.669	0.39	0.698	0.74	0.462	-0.59	0.559
Distant vs. close												
on sunny plots	-2.69	0.007	-1.87	0.061	-1.82	0.069	-3.43	<0.001	-1.93	0.053	0.13	0.897
on shady plots	-2.30	0.022	-0.00	0.997	-1.66	0.096	-2.36	0.018	-0.67	0.505	-0.20	0.838

a) Sunny forest plots



b) Shady forest plots



identified to the species level. However, due to their high abundances (~70,000 individuals per year), springtails were only identified in 2012. As we focused on non-saproxyllic beetle species, we identified saproxyllic species (Schmidl and Bußler, 2004) and excluded them from analyses. As necrophagous and coprophagous species might have been attracted by the smell of carrion in the traps, we also identified (Koch, 1989–1992) and excluded them from analyses. We pooled data on spiders and harvestmen because of the low number of harvestman individuals and their similar predatory lifestyles. For each of the three resulting species groups, data were then pooled per trap and year.

2.3. Statistical analyses

All statistical analyses were conducted in R 3.0.2 (www.r-project.org). We applied non-metric multidimensional scaling (NMDS) using the function *metaMDS* in the add-on package *vegan* (Oksanen et al., 2009) for presence–absence data of each of the three species groups to characterize the composition of species assemblages (obtained stress values after 20 runs = 0.18, 0.16 and 0.15 for beetles, spiders/harvestmen and springtails, respectively). The first, second and third axes of the NMDSs were further used as measures of species composition in our linear mixed models (see below). Before modeling, we calculated species richness independent from abundance (Gotelli and Colwell, 2001) as the residuals of linear models of the log–log relationship of the observed number of species and abundance. For springtails, the second NMDS axis was correlated to species richness ($r = 0.70$). All other axes as well as axes of spiders/harvestmen and epigeal beetles were independent from abundance and species richness (Table A1 Supporting information).

To test for effects of canopy openness and dead wood, we fitted generalized linear mixed models with Poisson errors for abundance and with Gaussian errors for species richness and NMDS scores separately for each species group. In all models, we estimated fixed effects of canopy openness (sunny vs. shady), the amount (log-transformed surface areas) of logs and branches, dead-wood diversity (ordered categories 0–4), tree species (fir vs. beech) and distance to dead wood (distant vs. close). Effects of the amount of logs and branches, dead-wood diversity, tree species and distance to dead wood were estimated specifically for sunny and shady plots. A second set of models included interaction terms between canopy openness and all five variables related to dead wood to test whether differences between their effects on sunny and shady plots were significant. The models for beetles and spiders/harvestmen also contained sampling year as a co-variable. All models included plot nested in block as a random effect to account for the nested design and temporal repetition on a plot. Poisson models included observation-specific random intercepts to account for overdispersion (Elston et al., 2001).

To test for differences in the response of taxa of different trophic levels and to separate direct effects of dead wood from indirect effects, we fitted structural equation models (SEM) separately for sunny and shady plots. This analysis considered only data from the first study year (2012) as data on springtails was available only for this year. For epigeal beetles, we only included predatory species (Koch, 1989–1992). Springtails then represented a lower trophic level and spiders/harvestmen and predatory beetles represented a higher trophic level. Response variables were the abundance and species density (i.e. the observed number of species per trap) of springtails, spiders/harvestmen and predatory beetles. Predictors were the amount of logs and branches, dead-wood diversity, tree species, distance to dead wood and herb layer density (arcsin transformed). Causal relationships included effects of abundance of taxa of lower trophic level on taxa of higher trophic level as well as effects of abundance on species density of the same

species group. We used the functions *sem.fit* and *sem.coefs* within the add-on package *piecewiseSEM*, which permits the creation of lists of Poisson models with random effects (Shipley, 2009). Single Poisson models were produced using the *glmer* function and included the plot nested in block as random factor.

3. Results

During the first three years after addition of dead wood to the plots, we recorded 525 epigeal beetle species (44,816 individuals), 249 spider species (69,092 individuals) and 11 harvestmen species (2194 individuals; see Table A2 for species lists). Springtails (one study year only) accounted for 36 species (68,018 individuals). Non-metric multidimensional scaling separated species assemblages of all three species groups clearly between sunny and shady plots (Fig. 1a).

Linear mixed models revealed strong effects of canopy openness on all three species groups (Tables 1 and A3). The abundance of epigeal beetles was higher on shady plots than on sunny plots and species richness of epigeal beetles as well as abundance and species richness of spiders/harvestmen were higher on sunny plots (Fig. 1b, Table 1). Canopy openness had strong effects on the composition of species assemblages of all three groups (Table A3). The addition of dead wood affected all three species groups, but for epigeal beetles and spiders/harvestmen, effects were mediated by canopy openness, as indicated by significant interaction terms (Table 1 and A3). On sunny plots, logs had a negative effect on abundance of epigeal beetles and branches affected the abundance of spiders/harvestmen positively. Epigeal beetle richness increased with increasing amount of logs on shady plots. Springtail abundance responded positively to both logs and branches on both shady and sunny plots. Logs (all three species groups) and branches (beetles; Table A3) affected the composition of species assemblages only on sunny plots. Dead-wood diversity negatively affected the abundance of epigeal beetles on shady plots and the abundance of springtails on sunny plots (Table 1). The assemblage composition of beetles was affected by dead-wood diversity on sunny plots (Table A3). Tree species did not affect the composition of species assemblages, but the abundance of both epigeal beetles and spiders/harvestmen was higher on plots containing fir dead wood than on plots containing beech dead wood (Table 1). The abundance of all three species groups as well as the species richness of both epigeal beetles and spiders/harvestmen were higher in pitfall traps located close to dead wood than in distant traps (Table 1); the assemblage composition of beetles and spiders/harvestmen differed according to the distance to dead wood (Table A3). Abundance and species richness of epigeal beetles and abundance of spiders/harvestmen decreased over the three study years, whereas species richness of spiders/harvestmen increased over this time (Table 1). Assemblage composition of epigeal beetles and spiders/harvestmen differed between study years (Table A3).

Structured equation modeling revealed that the amount of logs and branches had mostly positive direct effects on taxa of both lower and higher trophic levels (Fig. 2). Taxa of higher trophic levels increased in both abundance and species density with increasing abundance of taxa of lower trophic levels. Abundance and species density of taxa of both lower and higher trophic levels were higher in traps placed close to dead wood than in traps more distant to dead wood. Species density of spiders/harvestmen increased with herb layer density on sunny plots (Fig. 2a), but abundance of springtails decreased on shady plots (Fig. 2b). Plots containing fir dead wood had higher abundances of predatory beetles and spiders/harvestmen. Dead-wood diversity negatively affected the abundance of epigeal arthropods of both trophic levels.

Fig. 2. Results from structural equation modeling (SEM) for abundance and species density of taxa of lower trophic level (springtails) and higher trophic level (spiders/harvestmen and predatory epigeal beetles) on a) sunny plots and b) shady plots in the first year after dead-wood addition. All tested paths are shown.

4. Discussion

Overall, canopy openness was found to be a major driver of species assemblage composition of epigeal arthropods and quantitative differences were observed. Addition of dead wood affected species assemblage composition and had, with a few exceptions, positive effects on abundance or species richness or both of all epigeal arthropod groups. The effects of dead-wood logs and dead-wood branches differed and were clearly mediated by canopy openness and the species group. Dead-wood diversity negatively affected epigeal arthropods. Dead wood affected taxa of both lower and higher trophic levels directly and taxa of higher trophic levels indirectly via bottom-up effects. Traps located close to dead wood yielded different species assemblages and higher numbers of all three species groups than traps located farther away.

4.1. Effects of canopy openness

An opening of the forest canopy leads to increased insolation at the forest floor, higher temperature variation, increased soil moisture and reduced litter moisture (Richardson et al., 2010; Yi and Moldenke, 2008). Especially reduced litter moisture seems to have negative effects on the abundance of many litter arthropods (Richardson et al., 2010; Yi and Moldenke, 2008). In our study, litter moisture was lower on sunny plots than on shady plots (Fig. A2). This might also explain the lower abundance of springtails, which are particularly sensitive to drought (Pflug and Wolters, 2001) and possibly also the lower abundance of epigeal beetles (Fig. 1b). Increased available light led to higher densities of vascular plants and especially grasses on sunny plots (Fig. A1). Spider abundance and species richness is usually higher in forests with a dense herb layer, possibly because of increased abundance of phytophagous prey and the greater abundance and diversity of three-dimensional structures that allow different foraging strategies (Docherty and Leather, 1997 and references therein). In our study, herb layer density positively affected the species density of spiders/harvestmen on sunny plots (Fig. 2a). Thus, higher abundance and species richness of spiders/harvestmen on sunny plots might have also been caused by a richer herb layer (Docherty and Leather, 1997). Species richness of carabid beetles assemblages can be higher in forest gaps compared to adjacent closed forest as forest gaps host forest and open-habitat carabid species (Heliölä et al., 2001) and this might explain the higher species richness of epigeal beetles on sunny plots in our study.

Note that stronger growth of the herb layer at sunny plots required that young trees on the whole plot area and tall grasses close to added dead wood and pitfall traps had to be trimmed once a year at all sunny plots, while few shady plots needed such measures to keep levels of sun exposure constant over the three years of the study. Without this measure, the effects of canopy openness and of the interaction of canopy openness and dead wood on epigeal arthropods would have been confounded over time by ongoing plant succession and dead wood would have been increasingly overgrown at sunny plots. Trimming of the herb layer, however, may also affect epigeal arthropods and as all sunny plots but only few shady plots required this measure, our results regarding canopy openness and dead wood at sunny plots may have been affected by it. Because herb layer trimming (late July and August) took place after the vast majority of epigeal arthropods had been collected each year (May–July, see Table A4), however, we are not too concerned about this possibility. Moreover, the herb layer was not mowed but only trimmed to about 20 cm in height allowing quick recovery of the dominant species like the fast growing grass *C. villosa*. Furthermore, as trimming affected not the whole plot area, a considerable part of the herb layer of each plot remained undisturbed. The majority of epigeal arthropods may thus have been only weakly affected by herb layer treatment and thus, we are confident that the overall patterns of epigeal arthropod assemblages represent true responses to dead wood and

canopy openness. We acknowledge that some influences of herb layer trimming cannot be ruled out completely, however.

4.2. Effects of added dead wood

Dead wood can affect epigeal arthropods via several direct and indirect links. These different mechanisms and the heterogeneity among species groups subsumed as epigeal arthropods might explain the high heterogeneity of relationships between epigeal arthropods and dead wood (Castro and Wise, 2010; Seibold et al., 2015). Some studies have found positive effects of added dead wood on epigeal arthropods (Castro and Wise, 2009; Nittérus and Gunnarsson, 2006; Richardson et al., 2010), whereas others found no significant effects (Klepzig et al., 2012; Ulyshen and Hanula, 2009). In our study, all species groups responded mostly positive to the addition of dead wood (Table 1). Only the abundance of epigeal beetles decreased with increasing amounts of logs on sunny plots, possibly because more area is covered by dead wood and less by the herb layer, similar to the decline of phytophagous beetles captured in flight-interception traps on the same plots (Seibold et al., 2016). The relative importance of logs or branches was specific to the species group. Epigeal beetle assemblages were affected especially by logs, spiders/harvestmen by branches and springtails responded to logs and branches (Tables 1, A3). Fir dead wood was more beneficial than beech dead wood for beetles and spiders/harvestmen (Table 1). For web-building spiders, one possible explanation is that fir branches are more finely branched and more suitable for web building (McNett and Rypstra, 2000).

One mechanism by which dead wood could affect epigeal taxa of both lower and higher trophic levels directly is by providing a relatively stable source of moisture (Ulyshen et al., 2011). In our study, litter moisture close to dead wood was higher than further away (Fig. A2). Another direct mechanism by which dead wood could affect epigeal taxa is that added dead wood increases the volume and surface area of the habitat, i.e. the habitat amount, and also the structural complexity represented by, e.g., different surfaces types (Castro and Wise, 2010; Kappes et al., 2009). A higher habitat amount might promote larger populations (more individuals hypothesis; Clarke and Gaston, 2006) and higher structural complexity might provide habitat for epigeal species with different habitat preferences (habitat heterogeneity hypothesis; MacArthur and MacArthur, 1961). Consistent with the more individuals hypothesis, springtails increased in abundance but not in abundance-corrected species richness when dead wood was added (Table 1). Also in line with the more individuals hypothesis, spiders/harvestmen abundance but not species richness increased with increasing amount of branches at sunny plots (Table 1). By contrast, beetle abundance at shady plots did not respond to added dead wood, whereas abundance-corrected species richness increased with increasing amount of logs (Table 1). This pattern is consistent with the habitat heterogeneity hypothesis but not with the more individuals hypothesis. Hence, the driving mechanisms behind the response of non-saproxyllic epigeal taxa are group specific.

Increasing dead-wood diversity (e.g. tree species and diameter classes) promotes saproxyllic insect diversity (Seibold et al., 2016), but we did not see such a pattern for non-saproxyllic epigeal arthropods. In fact, the abundance of both springtails and beetles decreased with increasing dead-wood diversity in this study (Table 1). While it is not possible to explain these patterns based on available information, it should be noted that dead-wood diversity had no effect on species richness in this study.

An indirect way dead wood can affect epigeal arthropods of higher trophic levels is through bottom-up effects (Chen and Wise, 1999). Added dead wood increases the availability of food resources for detritivores, such as springtails (Marra and Edmonds, 1998), and thus leads to higher abundances (Table 1; Fig. 2). These organisms serve as prey for many larger predators, such as predatory beetles, spiders and harvestmen, and thus, addition of dead wood may indirectly promote

higher abundance and species richness of taxa of higher trophic levels (Fig. 2). Another indirect way dead wood might affect epigeal arthropods is by accumulating leaf litter (Kappes et al., 2007; Marra and Edmonds, 1998). In our study, leaf litter accumulated near dead wood and with increasing amounts of logs over the three years of the study (Table A5). Leaf litter depth did not affect any species group in the first study year when included in our structural equation models (Table A5); however, this might be attributed to the different time arthropod and litter data were recorded.

4.3. Effects of proximity to dead wood

On the dead-wood object level, a larger number of studies have found more epigeal beetle and spider individuals and/or species close to dead wood than distant from dead wood (reviewed by Ulyshen et al., 2011). Comparison of abundance data from pitfall traps close to and distant from dead wood might not necessarily mirror real differences in population densities, but might be confounded by a drift-fence effect of dead wood that leads to increased sampling numbers in traps close to dead wood (Melbourne, 1999). Although we placed pitfall traps 30 and 150 cm away from dead wood and thus left a corridor between a dead-wood object and the closer trap, the higher abundance of beetles and spiders/harvestmen in the trap close to dead wood (Table 1, Fig. 2) could be a result of the drift-fence effect. However, abundance-corrected species richness of beetles and spiders/harvestmen was also higher close to dead wood (Table 1) and the species composition these species groups differed according to distance to dead wood (Table A3). This suggested that differences in epigeal arthropod assemblages in close and distant traps were not just caused by methodological bias but instead resembled a response of these taxa to dead wood on small spatial scales.

The negative relationship between epigeal arthropod diversity and distance from dead wood found here and in previous studies raises questions about whether dead-wood objects result in an increase in arthropod abundance because of increasing populations, i.e. a demographic response, or are merely due to movements towards dead wood, i.e. an aggregational response (Solomon, 1949). It is unlikely that epigeal arthropod populations increase near dead wood because of reproduction to the same extent as they decrease through mortality further away from dead wood at the same time. Thus, similar (or lower) abundances on dead-wood plots and control plots, but abundances near dead wood higher than abundances distant from dead wood indicated that species respond by moving towards dead wood. Epigeal beetles in our study seem to have aggregated towards added logs; although abundance at the plot level decreased, abundances in traps close to dead wood were higher than in traps distant from dead wood (Table 1). By contrast, abundance of spiders/harvestmen and springtails was higher on dead-wood than control plots and higher in close than distant traps (Table 1). Thus, it is not possible to infer whether they showed a demographic or aggregational response or both.

4.4. Interacting effects of dead wood and canopy openness

It is thought that positive effects of dead wood on microclimatic conditions are especially beneficial for epigeal arthropods in sunny forests with low litter moisture (Ulyshen et al., 2011). But empirical studies to date have not found support for this hypothesis (Richardson et al., 2010; Ulyshen et al., 2011). Our study is therefore novel in finding effects of dead-wood amount on epigeal arthropods more pronounced in sunny forests than in shady forests. In particular, we found that the assemblage composition of epigeal beetles and spiders/harvestmen was more strongly affected by logs on sunny plots than on shady plots (Table A3) and that the abundance of spiders/harvestmen responded to the amount of branches more strongly on sunny plots than on shady plots (Table 1). However, logs affected beetle richness more strongly on shady plots than on sunny plots. Distance to dead wood

affected assemblage composition of spiders/harvestmen more strongly on sunny plots than on shady plots (Tables A3). One possible explanation is that the effect of microclimatic buffering of dead wood is more important in sunny forests than in shady forests.

4.5. Implications

Our findings support the idea that dead wood in general is a key-structure for forest biodiversity and that strategies of intentional dead-wood addition benefit not only saproxylic taxa, but also non-saproxylic epigeal arthropods. Therefore, the portion of forest species that benefit from increased dead-wood amounts certainly exceeds the 20–30% of species considered dependent on woody resources when considering the vast number of species that are not strictly dependent but favored by dead wood. Many of these species are involved in ecosystem processes, such as litter decomposition, nutrient cycling or pest control, and thus, promoting their populations by dead-wood addition may have important and so far underestimated positive effects also on these processes.

Canopy openness is a major driver of non-saproxylic epigeal arthropod assemblages, as has been shown also for saproxylic taxa. For both saproxylic and non-saproxylic invertebrates, dead wood should thus be enriched in both sunny and shady forest stands to maintain the full diversity of invertebrate assemblages. In regions where natural gap formation is anthropogenically limited, opening the canopy and adding woody debris by gap felling may be especially beneficial. While dead-wood diversity and dead-wood amount are similarly important for saproxylic beetles, the amount of dead wood seems to be more important for non-saproxylic epigeal arthropods. In particular, increasing the amount of branches in sunny forests and of large logs in shady forests positively affected all three non-saproxylic epigeal taxa.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2016.09.031>.

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