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Influence of deadwood on density of soil macro-arthropods in a managed oak–beech forest

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Abstract

In a 2-year study we investigated soil macro-arthropods (Opilionida, Araneida, Pseudoscorpionida, Isopoda, Diplopoda, Chilopoda, Coleoptera) in a forest where forestry management is nature oriented and includes the accumulation of about 10 m^3 deadwood per ha. We focused on soil arthropod density close to (c-CWD) or distant from coarse woody debris (d-CWD) in different locations of the forest stand (interior location versus edge zone) and in different seasons (summer versus winter). We found twice as many individuals of almost all taxa at c-CWD sites compared to d-CWD sites. The influence of CWD on most taxa of soil arthropods was more pronounced in the edge zone than in the interior location. In the edge zone c-CWD sites yielded significantly higher numbers of all taxa in both seasons. In the interior location seasonal effects occurred. For example, Pseudoscorpionida and Coleoptera-Larvae preferred c-CWD sites only in summer, whereas Araneida preferred c-CWD sites only in winter. A three-way ANOVA, regarding site, location and season as the main factors, emphasised the dominant influence of CWD on the density of all taxa. Consequently, CWD is an important structural component that serves as a habitat for many saprophagous species and thus locally improves the nutritional situation of a forest stand. CWD also may reduce the pest species problem because it harbours many zoophagous soil macro-arthropods as well.

Keywords: Edge zone; Leaf litter; Season; Soil arthropoda; Temperate deciduous forest; Woody debris

1. Introduction

Soil invertebrates improve soil fertility and productivity of forest ecosystems (Kautz and Topp, 1998; Gonzales and Seastedt, 2001; Cárcamo et al., 2001) and are important links in detritus-based food chains (Ponsard et al., 2000). Structural heterogeneity increases biodiversity in forest ecosystems for numerous taxa including arthropods (Sulkava and Huhta, 1998; McGee et al., 1999). Emerging philosophies of forest ecosystem management stress the increase of biological diversity and ecological functions by increasing structural complexity within managed stands. Structural diversity of the forest floor can be provided by downed coarse woody debris (CWD) (Harmon et al., 1986). However, only a low amount of deadwood is present in most managed Central European forests (1–3 m^3/ha, Ammer, 1991). In Central Europe only 0.2% of the deciduous forests are in a relatively natural state (Hannah et al., 1995), which includes a high amount of deadwood (50–200 m^3/ha, Korpel, 1995).

In some managed broad leaved forests CWD is left as a contribution to biodiversity and sustainability.

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Many saproxylic arthropods are known to depend on CWD (Speight, 1989; Jonsell et al., 1998; Sippola et al., 2002), and some of them are involved in nutrient cycling (Ausmus, 1977). However, the influence of CWD on arthropods living on the forest floor has only rarely been studied (e.g. Marra and Edmonds, 1998). For example, spiders of all developmental stages are known to utilise the different microhabitats offered by CWD (Buddle, 2001).

In a forest, physical and chemical conditions may be different between the edge zone and interior locations (Foggo et al., 2001). Wind approaching forest edges creates a jet of elevated wind speed which may extend into parts of the forest (Raynor, 1971). This elevated wind speed not only alters physical conditions occurring on the forest floor but also blows away a substantial part of the leaf litter which otherwise serves as a habitat for numerous arthropods. Exposed to such environmental extremes CWD may locally improve conditions for soil invertebrates (McMinn and Crossley, 1996) for at least some time of the year. Lloyd (1963) observed that centipedes and isopods migrated to CWD during warmer weather but lived in the litter layer during colder weather.

We studied some taxa of soil macro-arthropods living on the forest floor of a managed oak–beech forest in which nature oriented forestry is practised. The objective of this research was to study the impact of downed CWD in two different locations of the forest during different seasons. We addressed the following hypotheses:

1. Population densities increase in sites close to CWD.
2. The effect of CWD on the abundance of soil macro-arthropods is stronger in the edge zone than in the interior of the forest stand.
3. The aggregation of soil macro-arthropods close to CWD is more pronounced during summer than during winter months.

2. Materials and methods

2.1. Study site description

The oak–beech forest is 14.1 ha in size and situated in the Westerwald (50°26′N, 7°50′E) near the city Montabaur on a plateau of Devonian sediments covered by about 10,000-year-old ash-size pumice. The soil is a well-aerated brown earth with a moder form of humus. The elevation of the study sites ranges from 300 to 325 m. A shallow slope of 2–4° is facing to southwest.

The oak–beech forest is 120 years old, some 200-year-old oak trees are interspersed. The dominant tree species are *Fagus sylvatica* (50%) and *Quercus petraea* (45%). The remaining 5% consists of sycamore maple (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*), pine (*Pinus sylvestris*), spruce (*Picea abies*) and larch (*Larix decidua*). The dense crown layer covers about 80–90%. A shrub layer is not developed, though in some gaps there is a dense growth of young *A. pseudoplatanus* trees. The dominant spring geophyte is *Anemone nemorosa*.

The standing crop is about 850 m^3/ha, an increase of 3% per year (ca. 26 m^3/ha) is calculated. In 1991 and 1995 some of the trees were felled. About 1% of the standing crop (ca. 10 m^3/ha) including coarse woody debris was left on the forest floor.

2.2. Field sampling

Our investigations were carried out in 2000 and 2001. We distinguished between two locations, one situated in the interior of the forest stand and the other within the forest edge zone. The edge zone comprised the outermost 50 m of the forest stand. The distance between locations is 500 m. The edge zone faces to southwest, which is the main wind direction. Southwest of the oak–beech forest, there are extended arable fields and meadows. Thus, wind currents approaching the forest edge create a jet of increasing wind speed and powerful turbulences.

For testing the influence of downed CWD at both locations we further distinguished between sample sites close to coarse woody debris (c-CWD: mean distance from CWD < 10 cm) and samples distant from coarse woody debris (d-CWD: mean distance from CWD > 500 cm). The CWD regarded in this study were moderately decayed logs ($Z^0 2$ according to Albrecht (1991)) with a diameter of 20–40 cm and a minimum length of 200 cm. The average amount of this size class of deadwood was 7 m^3/ha.

We sampled the litter layer (L and O horizon). Each leaf litter sample covered an area of 300 cm^2.

Extraction of soil arthropods was carried out using Tullgren funnels.

2.3. Data analysis and experimental design

The analyses in this paper are based upon data collected in two subsequent years and 6 months per year. Eight replicates were taken per site and month. For a sample a certain log was chosen only once to avoid pseudoreplication (Hurlbert, 1984). Data obtained within the same months of the 2 years were pooled to minimise climatic effects between years. Thus, the number of samples per site was reduced to $n = 48$. The collections made during the warm season (May, June, July) and during the cold season (November, December, April) were separated to test the influence of the time of the year (summer versus winter).

We used data on higher taxonomic levels as densities were too low for statistical analysis on the species level. Most of our data were not normally distributed. Consequently, data are represented as median $\pm$ median absolute deviation ($\mathrm{m} \pm \mathrm{MAD}$) and we used the non-parametric Mann–Whitney U-test for pair-wise comparison of data sets. Two factors, i.e. site (c-CWD versus d-CWD) and location (interior location versus edge zone), were used to explain the variance of arthropod abundance. In a three-way ANOVA we additionally tested the influence of season (summer versus winter). Data were transformed to $\log(x + 1)$ to minimise violations of parametric statistics. When variances were heterogenous (Levene, $P < 0.2$) only those factors with $P \leq 0.001$ were regarded as significant (Sachs, 1992). We found no interactions between main factors unless otherwise stated.

3. Results

3.1. Effect of coarse woody debris and location

All higher taxa of the soil macrofauna occurred in higher numbers at c-CWD sites than at d-CWD sites (Table 1). The differences between c-CWD and d-CWD sites were highly significant for the mean abundances of most taxa at the interior location and the edge zone as well ($P < 0.001$, Fig. 1). Differences were most evident for the zoophagous Chilopoda and Araneida, the saprophagous Isopoda, and Coleoptera-Adults and Coleoptera-Larvae. The Coleoptera of the forest floor included both nutritional groups.

In a first step we tested the influence of site (c-CWD versus d-CWD) and location (interior location versus edge zone) by a two-way ANOVA. For Chilopoda ($R^2 = 0.31$) we found an influence of the site (Levene: n.s., $F = 66.8, P < 0.001$) and of the location ($F = 10.0, P = 0.002$). However, a slight interaction between both main factors occurred ($F = 5.8$, $P = 0.019$). The dominant species were *Lithobius crassipes* (L. Koch), *L. curtipes* (C.L. Koch) and *L. mutabilis* (L. Koch). Geophilomorpha were represented only by *Strigamia acuminata* (Leach).

The density of Araneida was only affected by site (Levene: $P < 0.2, F = 55.0, P < 0.001, R^2 = 0.25$) with highest numbers occurring at c-CWD sites (Fig. 1). One conspicuous species was the agelenid spider *Coelotes terrestris* (Wider). The most abundant

Table 1
Number of individuals collected and density of soil macro-arthropods (individuals per m^2) in a managed oak–beech forest of the Westerwald

	c-CWD		d-CWD	
	Individuals	Individuals per m^2	Individuals	Individuals per m^2
Opilionida	123	21	53	9
Araneida	1726	299	998	173
Pseudoscorpionida	616	106	289	50
Isopoda	1926	334	269	46
Chilopoda	1114	193	486	84
Diplopoda	181	31	66	11
Coleoptera-Adults	1407	244	555	96
Coleoptera-Larvae	2566	445	1217	211

Densities are given for the sites close to CWD (c-CWD) and distant from CWD (d-CWD).

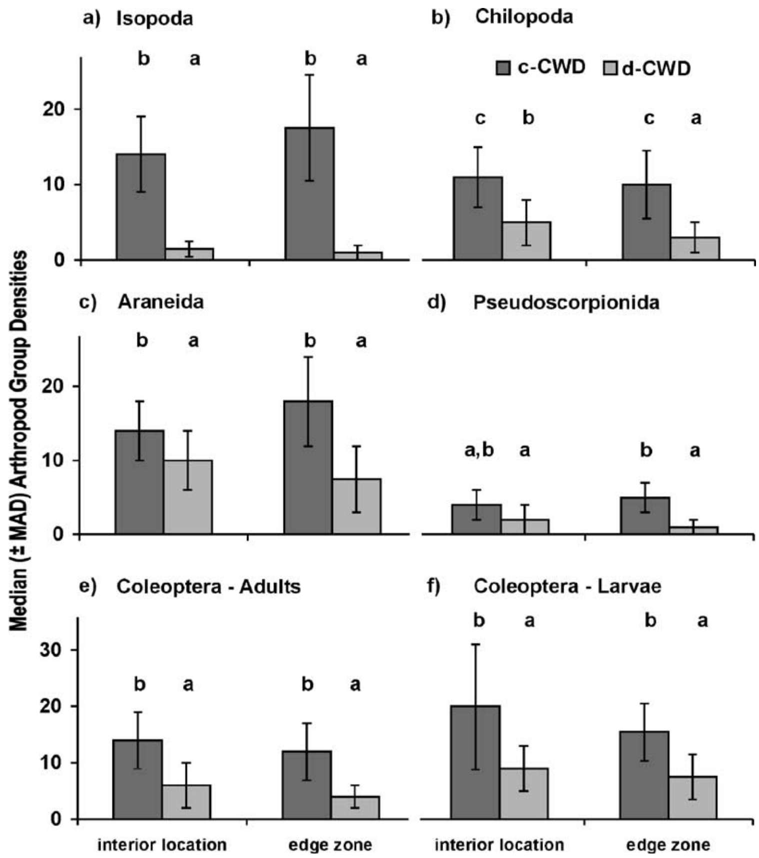

Fig. 1. Median (±MAD) per 600 cm^2 ($n = 48$) of the densities of the six most common groups of soil macro-arthropods in four different sites of a managed oak–beech forest. We compared sites close to (c-CWD) or distant from coarse woody debris (d-CWD) for the interior location of the forest and the edge zone as well. For each group, significant differences ($P < 0.001$) between the sites are marked with different letters.

species belonged to Linyphiidae, of which *Drapetisca socialis* (Sundevall) was common.

The Isopoda were most strongly influenced by site (Levene: $P < 0.2, F = 266.7, P < 0.001, R^2 = 0.60$), and showed highest densities at c-CWD sites independent of location (Fig. 1). The most abundant species were *Trichoniscus pusillus* Brandt, *Ligidium hypnorum* (Cuv.), *Oniscus asellus* L. and *Porcellio scaber* Latr.

Coleoptera-Adults also aggregated at the c-CWD sites (Fig. 1). The two-way ANOVA revealed a significant influence of site only (Levene: $P < 0.2$, $F = 94.7, P < 0.001, R^2 = 0.34$). Most predatory beetles belonged to Staphylinidae. The staphylinids revealed highest numbers at c-CWD sites (Table 2). A preference to either c-CWD or d-CWD sites was not detectable on the species level ($P > 0.05$) although we observed a certain preference of *Habrocerus capillaricornis* (Grav.) and *Lathrobium brunnipes* (F.) for c-CWD sites. The dominant staphylinids were *Geostiba circellaris* (Grav.), *Oxypoda annularis* Mannh., and *Othius myrmecophilus* (Grav.). Characteristic, but less common species of both sites were *Othius punctulatus* (Goeze), *Philonthus decorus* (Grav.), *Atheta crassicornis* (F.) and *Atheta fungi* (Grav.).

The predatory Pselaphidae—of which *Biploporus bicolor* (Denny) was most abundant—also were more common at c-CWD sites (Table 2). Characteristic representatives of the sporadically occurring Carabidae were *Cychrus attenuatus* F., *Trechus obtusus* Er., *Pterostichus oblongopunctatus* (F.) and *Abax parallelepipedus* (Pill. Mitt.).

The most common mycetophagous species of Coleoptera belonged to the families Ptiliidae and

Table 2
Two-factorial ANOVA on the effects of site (close to CWD, distant from CWD) and of the locations within the forest (edge zone, interior location) on the number of different Coleoptera taxa living on the forest floor

Taxonomic group	Factor	Levene	F	P	R^2
Adults					
Staphylinidae	Site	n.s.	8.3	0.007	0.33
Pselaphidae	Site	n.s.	12.8	0.001	0.36
Ptiliidae	Site	$P < 0.2$	35.8	<0.001	0.55
Larvae					
Cantharidae	Site	n.s.	27.1	<0.001	0.55
	Location	n.s.	7.1	0.011	
Zoophagous l.	site	$P < 0.2$	19.4	<0.001	0.46
Non-zoophagous l.	Site	$P < 0.2$	29.4	<0.001	0.55

Only factors which revealed a significant influence are mentioned when there was no interaction between factors.

Lathridiidae. Among Ptiliidae we collected several *Acrotrichis* spp. including the dominant *A. intermedia* (Gillm.). This species accounted for more than 80% of the Ptiliidae. We collected most Ptiliidae at c-CWD sites (Table 2). Also, Lathridiidae showed a strong aggregation pattern at c-CWD sites. The dominant species were *Aridius nodifer* (Westw.), *Enicmus rugosus* (Hbst.) and *Dienerella elongata* (Curt.). *Nargus wilkini* (Spence) (Cholevidae) was the most common saprophagous beetle.

Coleoptera-Larvae also revealed higher numbers at the c-CWD sites (Fig. 1). For the Coleoptera-Larvae we distinguished between two feeding types, i.e. zoophagous and non-zoophagous. The latter group included individuals of mycetophagous, saprophagous and phytophagous species. For the zoophagous larvae we found a significant influence of c-CWD sites (Table 2). The most common representatives of the zoophagous larvae belonged to the Cantharidae, which were influenced both by site and location (Table 2). Larvae of Cantharidae were most common at c-CWD sites of the interior locations of the forest stand. The non-zoophagous larvae were most abundant at c-CWD sites of the forest edge (Table 2). We also found several saprophagous larvae of *Cryptocephalus* spp. (Chrysomelidae) exclusively at c-CWD sites of the forest edge.

Pseudoscorpionida (Fig. 1) and Opilionida were significantly influenced by site exclusively in the edge zone ($P < 0.001$). The two-way ANOVA confirmed an aggregation at c-CWD sites for Pseudoscorpionida (Levene: $P < 0.2, F = 50.8, P < 0.001, R^2 = 0.23$). The dominant species was *Neobisium muscorum* (Leach), which accounted for more than 90% of all Pseudoscorpionida in both locations. The Opilionida, which were mainly represented by *Lophopilio palpinalis* (Hbst.), occurred too sporadically to perform a two-way ANOVA. The abundance of Diplopoda was even too low to reveal any significant influence of site or location. *Glomeris marginata* (Vill.) and *G. conspersa* C.L. Koch were characteristic species, which occurred in both locations.

3.2. Effect of season

In some soil animal groups we found a seasonal effect on densities (summer versus winter). For example, Pseudoscorpionida revealed higher densities during winter ($P < 0.001$). We further compared the densities within sites for summer and winter months (Fig. 2). In the edge zone, two taxa occurred in higher numbers during summer, i.e. woodlice at the d-CWD site ($P < 0.05$, Fig. 2a) and centipedes at the c-CWD site ($P < 0.05$, Fig. 2b). In the interior location, Araneida (Fig. 2c) revealed higher densities at d-CWD sites during summer. Irrespective of site Pseudoscorpionida usually occurred in significantly higher numbers during winter ($P < 0.05$, Fig. 2d). Coleoptera-Adults were significantly more abundant at d-CWD sites of the interior locations in winter (Fig. 2e), whereas Coleoptera-Larvae did not show any seasonality (Fig. 2f).

For a given location we tested site differences for the two seasons. In the edge zone, all taxa occurred in significantly higher number at c-CWD sites irrespectively of season ($P < 0.05$). In the interior location we

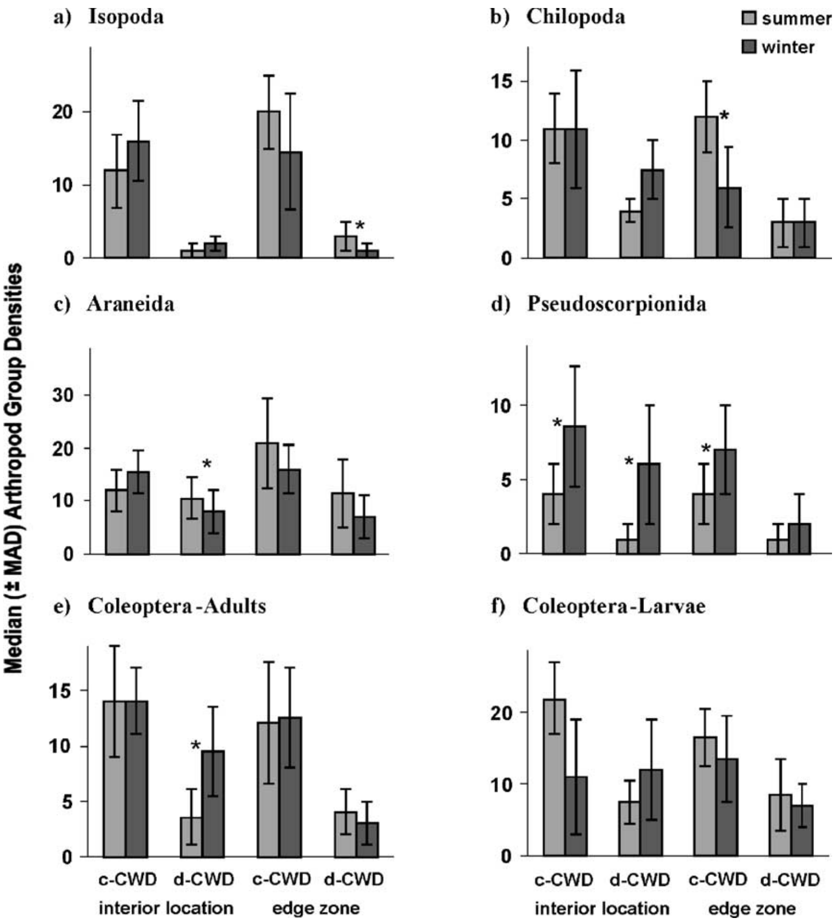

Fig. 2. Median (±MAD) per 600 cm^2 ($n = 48$) of the densities of the six most common groups of soil macro-arthropods. The arthropods, (a) Isopoda, (b) Chilopoda, (c) Araneida, (d) Pseudoscorpionida, (e) Coleoptera-Adults and (f) Coleoptera-Larvae, were sampled in four different sites of a managed oak–beech forest. We separated between the interior location of the forest and the edge zone. Both locations included sites close to (c-CWD) or distant from coarse woody debris (d-CWD). We compared densities from summer- and winter-months. $^*P < 0.05$.

found significantly higher densities for Isopoda, Chilopoda, Diplopoda and Coleoptera-Adults at c-CWD sites irrespective of season. Araneida was the group which was significantly more abundant ($P < 0.001$) at c-CWD sites only during winter months. In contrast, Pseudoscorpionida and Coleoptera-Larvae revealed significantly higher densities ($P < 0.001$) only during summer months. The density of Opilionida and Diplopoda was not affected by deadwood in both seasons.

3.3. Simultaneous effect of all factors

In a further step we tested the simultaneous influence of site (c-CWD and d-CWD), of season (summer and winter) and of location (edge zone and interior location) on the density of all taxa in a three-way ANOVA. The explanation of variances was highest for the saprophagous isopods ($R^2 = 0.61$, Table 3). We found a significant effect of site, but no influence of location and season. The distribution pattern of the predatory chilopods also was significantly influenced by CWD, whereas location only marginally affected the occurrence and season had no effect (Table 3). For further taxa, the influence of site was also significant and contributed most to the explanation of variance (Table 3). Only for Pseudoscorpionida, season contributed significantly to the variance. For none of the taxa investigated the location significantly influenced the density.

Table 3
Three-factorial ANOVA on the effects of site (close to CWD, distant from CWD), of the locations within the forest (edge zone, interior location) and season (summer, winter) on the density of different arthropod taxa living on the forest floor

Taxonomic group	Main factors		
	Site	Location	Season
Isopoda (model: $R^2 = 0.61$)			
F	276.1	5.5	0.0
P	0.000	0.02	0.87
Chilopoda (model: $R^2 = 0.33$)			
F	67.8	10.1	1.7
P	0.000	0.002	0.19
Araneida (model: $R^2 = 0.30$)			
F	57.6	0.9	6.8
P	0.000	0.34	0.01
Pseudoscorpionida (model: $R^2 = 0.36$)			
F	59.1	2.5	31.83
P	0.000	0.11	0.000
Coleoptera-Adults (model: $R^2 = 0.36$)			
F	95.6	3.0	1.2
P	0.000	0.09	0.26
Coleoptera-Larvae (model: $R^2 = 0.17$)			
F	29.3	1.5	0.3
P	0.000	0.22	0.61

Levene: $P < 0.2$. *P*-values of all models were significant ($P < 0.001$), no significant interactions between main factors occurred.

4. Discussion

Structural diversity enhances the abundance and diversity of biota. The accumulation of coarse woody debris is an important structural component in forest ecosystems (McMinn and Crossley, 1996). The minimum accumulation of CWD in managed Central European broad leaved forests was calculated at 40–60 m^3/ha to attain natural levels (Korpel, 1997; Haase et al., 1998). CWD offers sheltered microhabitats and may serve for food and as a site for breeding (Harmon et al., 1986). One or more of these beneficial effects may have caused the high densities of arthropods at c-CWD sites.

Especially isopods were extremely aggregated at c-CWD sites. The isopod species found need moist habitats to prevent a net loss of water (Lindquist, 1972; Mayes and Holdich, 1975; Hadley and Quinlan, 1984). Sheltered habitats may improve reproduction, survival of juveniles and nutritional requirements (Warburg et al., 1984). The higher density of saprophagous Diplopoda (Table 1) also may be caused by the beneficial nutritional situation at c-CWD sites. Constantly moist conditions enhance growth and abundance of bacteria and mycelia on deadwood (Fog, 1977). This also explains the aggregation of *Acrotrichis intermedia* and other mycetophagous Ptiliidae at c-CWD sites. All these groups are involved in comminution of the deadwood and thus in nutrient cycling (Ausmus, 1977; Swift, 1977).

The larval stages of many Coleoptera living on the forest floor are susceptible to desiccation and show highest survival rates at saturated humidity (Topp, 1994). The moist conditions at c-CWD sites give one explanation for the local high abundance of Coleoptera-Larvae irrespective of feeding type. Also, some Araneida (Baehr and Eisenbeis, 1985) and Chilopoda (Littlewood, 1991) are sensitive to desiccation. These predators of the forest floor may have profited both from microclimatic conditions and the aggregation of potential food items at c-CWD sites.

Edge habitats are often recognised as incompatible with the requirements of many forest species, and the proliferation of forest edges has threatened the diversity of many forest communities (Yahner, 1988; Paton, 1994). To a large extent, the physical environment determines species distribution at forest edges and underpins many of the characteristic biological properties of edges. Edge zones are typically warmer, drier, windier, and receive more sunlight than undisturbed sites in the interior of forest stands (Matlack and Litvaitis, 1999; Foggo et al., 2001). Closed forest edges are often built up by a dense mass of shrubs and saplings. The investigated forest edge was not closed and vegetation of shrubs was poorly developed. As a result, air movements had a strong drying effect on the leaf litter and CWD. We expected that animal densities would decline at these adverse climatic conditions. However, Chilopoda was the only group which was significantly less common in the edge zone than in the forest interior. There was no further group in which the abundance significantly differed between the edge zone and the interior of the forest stand, although a few species were restricted to the edge zone. However, the adverse climatic condition in the edge zone led to a stronger association of soil arthropods to c-CWD sites than in the interior location. In the edge zone, all taxa significantly preferred c-CWD sites in both seasons. We assume that the soil arthropods avoid the drought during summer and the cold during winter. In the edge zone, both climatic extremes are intensified by the wind currents. The adverse microclimatic conditions were less pronounced in the forest interior. This may for some groups have led to a distribution pattern, which was independent of CWD in one season.

5. Conclusion

Downed CWD is an important structural component on the forest floor, which enhances densities of many macro-arthropods, including zoophagous, saprophagous and mycetophagous species. Thus, CWD not only increases species diversity but also functional diversity. One important aspect of soil macro-arthropods is the comminution of organic matter and the regulation of mineralisation processes. Another aspect is the regulation of potential pest species by predators which prefer c-CWD sites. Consequently, forest stands should both directly and indirectly benefit from the accumulation of CWD. We assume the beneficial effects of CWD will be enhanced if a large variety of stages of decomposition and sizes is left on the forest floor. These aspects warrant further studies. The current trend to enhance the amount of CWD should be continued in managed broad leaved forests of the temperate region.

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