

Importance of dead wood for soil mite (Acarina) communities in boreal old-growth forests

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Abstract

We studied the importance of dead wood (coarse woody debris; CWD) for the mite (Oribatida and Mesostigmata) communities by comparing samples from CWD, soil under/beside CWD, forest floor outside CWD, and from living trunks of the same species (*Picea abies*, *Betula pubescens*, *Populus tremula*). Four spruce-dominated sites in old-growth forests in southern Finland were sampled. Our hypotheses were that (1) presence of CWD increases the diversity of the community, (2) the communities are influenced by state and kind of CWD, and (3) species assemblage in CWD is distinct from that on living trunks. Total numbers of Oribatida under/beside CWD were twofold as compared both with CWD and forest floor outside CWD, while the numbers of Mesostigmata close to and apart from CWD did not differ but were higher than in CWD itself. Community structure differed between trunks and stumps, and even more between CWD and forest floor, while it did not differ between soil under and away from CWD. No differences in community structure were found between the tree species in Oribatida, but in Mesostigmata the communities in birch and aspen stumps differed from those in spruce stumps and trunks of all species. The results indicate that CWD supports the diversity of the mite community of forest floor, the state (trunk/stump) and vicinity of CWD are more important than its origin (tree species), and the species assemblage on living trunks is distinct from that of dead wood.

Keywords: Coarse woody debris, CWD, dead wood, forest floor, soil mites, Oribatida, Mesostigmata

1. Introduction

The amount of coarse woody debris (CWD) in managed boreal forests is scanty due to intensive silvicultural practices (Finnish Forest Research Institute 2006). The situation is getting even worse by the increasing use of stumps and felling residues for energy production. In particular, CWD originating from deciduous trees is getting scant, since all hardwood was systematically removed from managed forests during the 1960's–1980's. Aspen was also removed because it is the host of a pathogenic microfungus (Heliövaara & Väisänen 1984). Old aspen, both living and dead, are known to be important for the species diversity in coniferous and mixed forests, since they provide living for specialized insects, fungi and epiphytic flora (Siitonen & Martikainen 1994, Andersson & Hytteborn 1991).

Amount and quality of CWD directly affect the saproxylic species feeding on dead wood, such as many Coleoptera and Diptera (Siitonen 1994a, Tikkanen et al. 2006). Decaying wood may also indirectly influence the decomposer community by providing source of energy and nutrients as well as distinct and unique microhabitats for many microbes and invertebrates, thus contributing to the species richness (Andersson & Hytteborn 1991, Lindblad 1998). It also increases moisture and nutrient solubility in the forest floor, and decreases the soil acidity (Kayahara et al. 1996). Thick trunks can decay for 150–200 years in the northern taiga zone (Hofgaard 1993).

Oribatid and mesostigmatid mites are important components in the decomposer community of forest floor. They are abundant in soil and litter, but occur also frequently in aboveground habitats such as field layer vegetation, canopies and trunks (Krantz & Walter 2009). The oribatids feed on fungal hyphae and dead plant material, to some extent also on lichens, mosses and algae (Luxton 1972, Siepel & de Ruiter-Dijkman 1993, Erdmann et al. 2007). Mesostigmata are generalist predators feeding mainly on nematodes, collembolans and eggs/larvae of Diptera (Karg 1989, 1993).

Oribatid communities overlap very little between forest floor and trunks (bark) of living trees (Gjelstrup 1979, Proctor et al. 2002, Beaulieu et al. 2006). Reports on the mite communities in dead wood are contradictory. Some evidence supports the assumption that true CWD specialists are rare; according to Seastedt et al. (1989), and Skubała & Sokołowska (2006) most species inhabiting decaying wood also live in forest floor or originate from living trees. However, the observations of Lindo & Winchester (2006), Siira-Pietikäinen et al. (2008) and Déchéne & Buddle (2010) indicate that the oribatid assemblage in CWD is distinct and differs from that in soil outside CWD.

It is unclear, whether CWD of different tree species provides species-specific microsites or resources, resulting in dissimilar communities. Some knowledge is available concerning mite communities on living trunks and foliage of certain tree species, while data on microarthropod associations in CWD of different trees is scant (Gjelstrup 1979, Behan-Pelletier & Walter 2000). Differences could be expected, because tree species differ from each other in many ways, such as chemical composition, microbial communities, epiphytic cover and bark structure, which are critical factors affecting food resources and microclimate (Laiho & Prescott 2004).

In the present study we examined the communities of Oribatida and Mesostigmata in and close to different kinds of CWD, to find out whether the state, origin or vicinity of CWD contribute to their diversity. We compared the mite communities in decaying trunks and stumps of three tree species, living trunks (bark) of the same species, soil under/beside CWD, and forest floor outside CWD, testing the following hypotheses: 1) presence and/or vicinity of CWD support the diversity of the mite communities of forest floor, 2) the communities are influenced by state and kind of CWD, and 3) the species assemblage in CWD is distinct from that on living trunks (corticolous fauna).

2. Material and methods

Four study sites were selected in Southern Finland (southern boreal vegetation zone) in old spruce-dominated mixed forests: Sipoo, Rörstrand (60° 27' N, 25° 12' E), Sipoo, Gillerberg (60° 21' N, 25° 10' E), Lammi, Papinmetsä (61° 03' N, 25° 02' E), Lammi, Kotinen (61° 14' N, 25° 04' E). At each site, one decaying spruce, birch and aspen trunk (diameter 30 to 50 cm), and one spruce, birch and aspen stump (30–50 cm) were chosen for sampling. From each,

three 100 cm³ samples were taken using a knife, including bark, phloem and rotten wood to a depth of 2–3 cm. In addition, three soil cores (25 cm² × 4 cm), including humus, litter and mosses, were taken immediately under/beside each trunk or stump, and six similar soil cores at each site apart from CWD. This sampling was done in September 2007. The studied logs and stumps were moderately decayed: the wood under the bark was still relatively hard and structurally sound; the knife was able to dig into 3 cm depth from the surface, and the bark was still mostly intact. In September 2011, living trees at the same study sites were sampled: 100 cm³ of bark of three old trees of each species (spruce, birch, aspen) at each site was collected from the height of 20–100 cm, using a knife.

Microarthropods were extracted from the samples using the ‘high-gradient’ canister extractor. After extraction, each set of three identical subsamples were pooled. Adult oribatid and mesostigmatid mites, and if possible, also Mesostigmata deutonymphs were identified and counted; unidentified juveniles were omitted. Identification and nomenclature are according to Giljarov (1975), Niedbała (1992), Weigmann (2006) (Oribatida) and Karg (1989, 1993) (Mesostigmata).

Differences in community structure were examined using the non-metric multidimensional scaling (NMS) ordination method (PC-ORD software, McCune & Mefford 1999). This was carried out twice: at first on the data without live trunks, excluding rare species (present in less than five samples) and transforming the original data by square root, and then on total data, including live trunks and all species, using $\ln(x+1)$ transformation.

In addition, Indicator Species Analysis was carried out (Dufrêne and Legendre’s method) using the same software. Indicator values were tested for statistical significance with a randomization technique (Monte Carlo).

3. Results

3.1. Oribatida

The oribatid material comprises 9932 specimens belonging to 96 identified species. Total numbers did not differ between trunks and stumps, between tree species, or between CWD and forest floor apart from CWD, but were approximately twofold under/beside CWD, compared with CWD itself or the forest floor outside CWD (ANOVA: $t_{22} = 2.20$, $p < 0.05$; $t_{22} = 5.43$, $p < 0.001$, respectively). The numbers on live trunks were very low in comparison with all other microhabitats (Appendix 1).

NMS (excluding live trunks) classified the communities into three main groups (3-dimensional solution, final stress = 17.249): 1. communities in forest floor and microhabitats under/beside CWD, 2. communities in trunks, and 3. communities in stumps (Fig. 1). The communities of forest floor habitats (1) had higher values than those in decaying wood (2–3) along the axis 1, (forest floor vs. CWD: $t_{40} = -6.52$, $P < 0.01$; under CWD vs. CWD: $t_{40} = 9.79$, $P < 0.01$), while the communities in trunks and stumps went apart on axis 2 ($t_{36} = 5.26$, $P < 0.01$) and axis 3 ($t_{32} = -2.95$, $P < 0.01$). The stumps had higher values along axis 2 and the trunks had higher values along axis 3. The communities under/beside decaying stumps differed slightly from those of forest floor along axis 2 ($t_{24} = 2.86$, $P < 0.01$). Communities in CWD originating from different tree species did not show significant differences.

The NMS analysis on the total data reveals that the community on living trunks is totally different from that on CWD and forest floor (Fig. 3). The tree species also differ significantly from each other ($T_{32} = -5.31$, $P < 0.01$), the community on spruce trunks coming closer to the forest floor and CWD communities (Fig. 3).

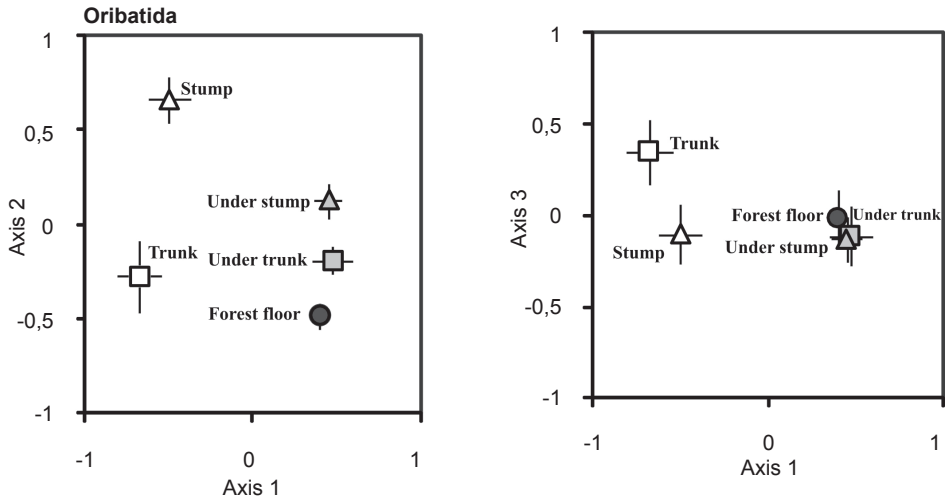


Fig. 1 Community structure of Oribatida in different forest floor microhabitats according to the NMS analysis (3-dimensional solution, data excluding live trunks).

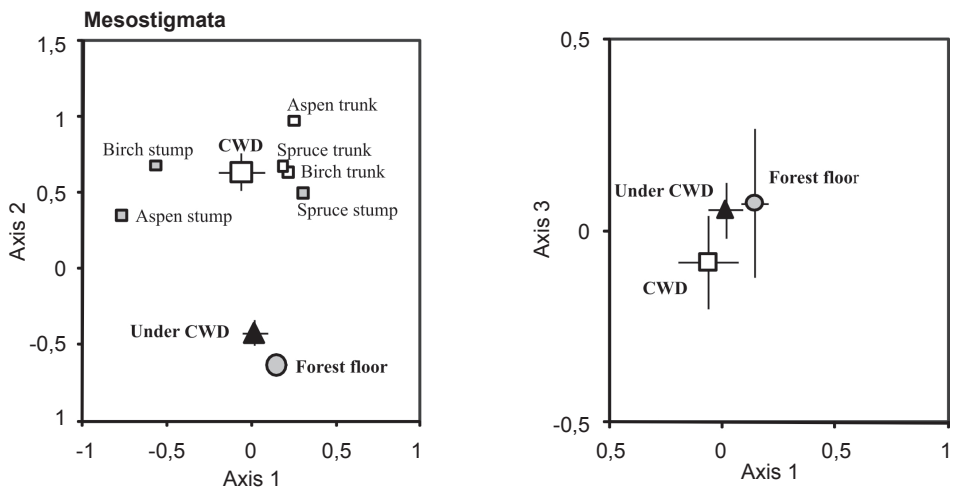


Fig. 2 Community structure of Mesostigmata in different microhabitats according to the NMS analysis (3-dimensional solution, data excluding live trunks).

The average number of species per sample was lowest on live trunks and highest under/beside CWD (Appendix 1). According to the indicator species analysis, six species were linked to dead wood; of these *Carabodes labyrinthicus* was the only one receiving a significant indicator value on trunks, all others occurring mainly or exclusively on stumps (*Euphthiracarus cribrarius*, *Furcoribula furcillata*, *Licneremaeus lignophorus*, *Scheloribates pallidulus*, *Oppia* sp.). Three species (*Phauloppia nemoralis*, *Zygoribatula exilis* and *Kunstdamaeus tecticola*) showed significant indicator values for live trunks. *Zygoribatula exilis* and also *Chamobates cuspidatus* were very abundant on aspen, but the variation was high, ranging from zero to 300 per litre.

Several species were linked to forest floor and/or soil under CWD (Appendix 1).

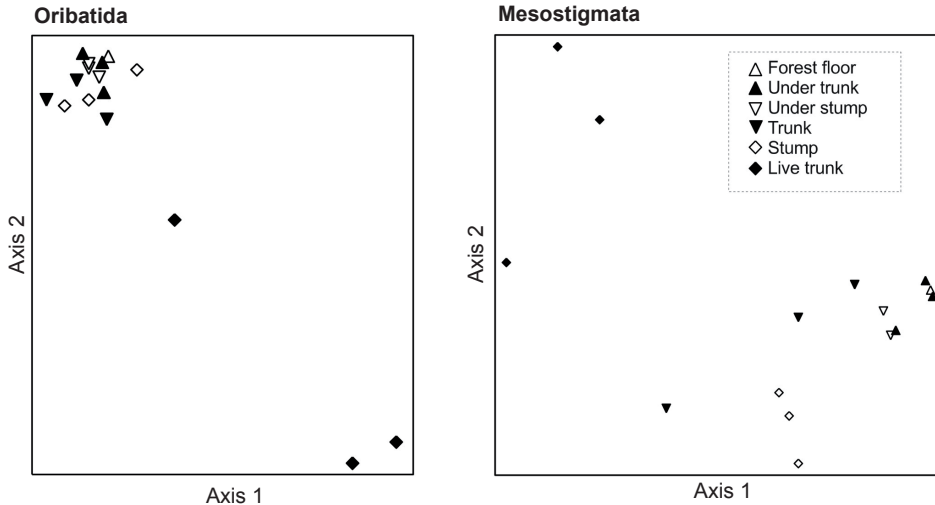


Fig. 3 Community structure of Oribatida and Mesostigmata according to the NMS analysis; average ages over sampling sites, data including live trunks (2-dimensional solution, dots with the same symbol indicate the tree species spruce, birch and aspen).

3.2. Mesostigmata

The total numbers of Mesostigmata (1602) were only one fifth of those of Oribatida, but the number of species was 75 vs. 96, indicating high species diversity. Mesostigmatid mites were more abundant in forest floor and under/beside CWD, when compared to CWD itself (ANOVA: forest floor vs. CWD: $t_{40} = 2.55$, $p < 0.05$; under CWD vs. CWD $t_{40} = 4.09$, $p < 0.01$). Total numbers did not differ between forest floor and under/beside CWD, between trunks and stumps, or between different tree species. Numbers on live trunks were very low (Appendix 2).

Differences in community structure were revealed by the NMS analysis (three-dimensional solution, final stress = 15.9) (Fig. 2). In the ordination graph (excluding live trees), the communities of CWD strongly differ from those of forest floor and soil under CWD along axis 2 (CWD vs. forest floor: $t_{26} = 6.26$, $p < 0.0001$; CWD vs. under CWD $t_{22} = -7.46$, $p < 0.001$). Within CWD, the communities in stumps of birch and aspen go clearly apart from those in spruce stumps and trunks of all tree species along axis 1 (birch: $t_{40} = -2.66$, $p < 0.05$; aspen: $t_{40} = -3.45$, $p < 0.01$). Along axis 2, CWD had higher values than forest floor, and along axis 1 birch and aspen trunks had higher values than stumps. The third dimension did not show dissimilarities between the variables (Fig. 2). Similarly to Oribatida, the NMS on the total data of Mesostigmata revealed a clear distinction between communities on live trunks and those in CWD or forest floor (Fig. 3), and also a significant difference between the tree species ($t_{32} = 5.31$, $P < 0.05$).

The number of species per sample was highest in forest floor under and outside CWD, moderate in CWD, and low on live trunks (Appendix 2). Eight mesostigmatid species showed significant indicator values for CWD, and two for live trunks. Of the latter, *Amblyseius fennicus* was found exclusively on live trees, but *Holoparasitus calcaratus* also on dead trunks of each species. Among the 'CWD specialists', *Microgynium rectangulatum* and *Microseius truncicola* occurred on stumps, *Cornodendrolaelaps cornutululus* on birch and aspen stumps, *Dinychus woelkei* in aspen CWD, *D. carinatus* on aspen stumps, and *D. septentrionalis*, *Sejus*

togatus and *Zercon curiosus* in all CWD, no one of them being more abundant on trunks. Aspen trunks and stumps showed an unexpected difference in species diversity: 27 species were found on stumps and only 11 on trunks (Appendix 2).

4. Discussion

Supporting our first hypothesis, the mite communities differed greatly between CWD and forest floor, but differences were also observed between the different CWD microhabitats. The most diverse communities were found under/beside CWD. The community structure in Oribatida differed between the state of CWD (trunks vs. stumps), but the origin (tree species) of CWD had hardly any influence on their communities. In Mesostigmata, both the state and the origin of CWD had significant effects on the communities. In both mite groups, several species showed a clear association with dead wood, stumps in particular, independently of its origin. (The communities of the four study sites also differed significantly from each other, but this was considered to be outside the scope of the present study.)

Total numbers of oribatids in CWD differed only slightly from those of forest floor apart from CWD. This result is in line with the observations of Skubała & Sokołowska (2006), who observed only slightly lower numbers in young decaying logs compared to forest floor. As shown by Seastedt et al. (1989) and Skubała & Sokołowska (2006) the abundance of mites in CWD depends on the time lapsed after the death of the tree. Peak values occurred in the decay classes II–IV, where also moisture and nutrient content as well as microbial biomass are high. The abundance of Oribatida in the soil under CWD indicates that this microhabitat offers more resources and/or favorable microclimate, though the community composition does not differ much from that in forest floor.

The strong difference in community structure between CWD and forest floor supports our earlier observations (Siira-Pietikäinen et al. 2008), revealing several species with significant indicator values for CWD. The latter study also indicated that the community in CWD is little affected by surrounding forest type or by latitude. Recently, Déchéne & Buddle (2010) showed that decaying aspen logs (at more advanced state of decay than in our study) harbor a distinct and more diverse oribatid community compared with soil away from the logs.

The relatively strong dissimilarity in the species assemblages between trunks and stumps is worthy of notice, since it could be expected that trunks and stumps differ less in terms of resource quality than do tree species. This observation can not be explained by easier access of stumps by soil mites, because the communities of stumps were less similar to those in forest floor, when compared to communities in trunks. More probable is that the microclimate stays more stable in stumps than in trunks, the latter being more exposed to weather.

Our study indicates that the origin (tree species) of CWD has hardly any effect on the oribatid community. This result is unexpected, because oribatids are considered to be, at least to some extent, selective in their feeding habits (Maraun et al. 1998), and the food items such as wood-decomposing fungi are known to differ considerably depending on the substrate. Tree species had some influence on the assemblage of Mesostigmata in CWD, and even more on both mite groups on living trunks. According to Beaulieu et al. (2006), tree species or bark structure do not affect the corticolous mite assemblage in Australian subtropical rain forests.

The study reveals that the origin of the mite community in CWD is not in the corticolous fauna on living trees: few species were in common. This is in accordance with André (1986), who observed that the mesostigmatid fauna on trunks is dominated by species that typically inhabit leaves and stems (family Phytoseiidae). Gjelstrup (1979) showed that the oribatid

community of living trunks varied along the distance from the ground in association with the epiphytic flora, and a clear gradient remained after death and overturning of the trunk. According to Proctor et al. (2002) the oribatid communities on live trunks and soil are almost 100% distinct (*Araucaria* forest, Australia). Lindo & Winchester (2007) reported that the lowest 4 m of trunks contain ground-dwelling species, above which level the 'arboreal' community prevails (redcedar temperate rain forest, Canada). Our data also support the suggestion of Proctor et al. (2002) that tree trunks represent habitat islands whose colonization is stochastic (high dissimilarity between individual trunks).

In line with the assumption that the soil under CWD contains more available nutrients and microbial biomass, compared to forest floor apart from CWD, it was understandable that some microphytophagous mites (*Oppiella nova*, Suctobelbidae spp.) (see Luxton 1972, Schatz 1983) occurred more abundantly under CWD (especially under stumps). The same trend was also noticed in macrophytophages: the numbers of species and specimens of Phthiracaridae and Steganacaridae was notable under CWD. However, the box mite *E. cribrarius* was more abundant in dead wood. According to Skubala & Duras (2008) the latter species favors dead wood and sapwood of beech logs over soil and litter. It is known as a macrophytophage, able to consume cellulose (Luxton 1972, Siepel & Ruiter-Dijkman 1993). Several species of the family Carabodidae occurred in CWD and under/beside stumps and trunks. The *Carabodes* species are known to favor CWD habitats, where fungal food is their main food source (Luxton 1972, Siepel & Ruiter-Dijkman 1993).

The Mesostigmata, which are generally regarded as generalist predators (Karg 1989, 1993), could be expected to be less dependent on the origin of CWD. However, some species showed a clear preference for aspen, either stumps or both stumps and trunks. It is well known that many species of Mesostigmata commonly inhabit CWD, such as *Microseius truncicola*, *Microgynium rectangulatum*, *Sejus togatus* according to Giljarov & Bregetova (1977), and *Dendrolaelaps* (*s. lat.*) spp. according to Hirschmann & Wisniewski (1983). Several *Dendrolaelaps* species are also commonly found phoretically on bark beetles and collected in their galleries. Their preferences for certain species of trees or beetles remain to be investigated (Hirschmann & Wisniewski 1983), but some specialization might be expected, since many CWD-inhabiting insects are known to be species-specific (Siitonen 1994 a,b).

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6. References

- Andersson, L. I. & H. Hytteborn (1991): Bryophytes and decaying wood: A comparison between managed and natural forest. – *Holarctic Ecology* **14**: 121–130.
- André, H. M. (1986): Notes on the ecology of corticolous epiphyte dwellers. 4. Actinedida (especially Tydaeiidae) and Gamasida (especially Phytoseiidae). – *Acarologia* **27**: 107–115.
- Beaulieu, F., D. E. Walter, H. C. Proctor, R. L. Kitching & F. Menzel (2006): Mesostigmatid mites (Acari: Mesostigmata) on rainforest tree trunks: arboreal specialists, but substrate generalists? – *Experimental and Applied Acarology* **39**: 25–40.

- Behan-Pelletier, V. M. & D. E. Walter (2000): Biodiversity of oribatid mites (Acari: Oribatida) in tree canopies and litter. – In: Coleman, D. C. & P. F. Hendrix (eds), *Invertebrates as webmasters of ecosystems*. – CABI Publishing, New York: 187–202.
- Déchêne, A. D. & C. M. Buddle (2010): Decomposing logs increase oribatid mite assemblage diversity in mixedwood boreal forest. – *Biodiversity and Conservation* **19**: 237–256.
- Erdmann, G., V. Otte, R. Langel, S. Scheu & M. Maraun (2007): The trophic structure of bark-living oribatid mite communities analysed with stable isotopes (^{15}N , ^{13}C) indicates strong niche differentiation. – *Experimental and Applied Acarology* **41**: 1–10.
- Finnish Forest Research Institute (2006): *Finnish Statistical Yearbook of Forestry*. – Vantaa, Finland.
- Giljarov, M. S. (ed.) (1975): A key to soil-inhabiting mites. Sarcopitiformes (in Russian). – “Nauka”, Moscow: 491 pp.
- Giljarov, M. S. & N. G. Bregetova (eds) (1977): A key to soil-inhabiting mites. Mesostigmata (in Russian). – “Nauka”, Moscow: 718 pp.
- Gjelstrup, P. (1979): Epiphytic cryptostigmatid mites on some beech- and birch-trees in Denmark. – *Pedobiologia* **19**: 1–9.
- Heliövaara, K. & R. Väisänen (1984): Effects of modern forestry on northwestern European forest invertebrates: a synthesis. – *Acta Forestalia Fennica* **189**: 1–32.
- Hirschmann, W. & J. Wisniewski (1983): Lebensräume der *Dendrolaelaps*- und *Longoseius*-Arten. – *Acarologie, Schriftenreihe für vergleichende Milbenkunde, Folge* **30**: 21–33.
- Hofgaard, A. (1993): 50 years of change in a Swedish boreal old-growth *Picea abies* forest. – *Journal of Vegetation Science* **4**: 773–782.
- Karg, W. (1989): Acari (Acarina) Milben, Unterordnung Parasitiformes (Anactinochaeta), Uropodina Kramer, Schildkrötenmilben. – In: Senglaub, K., H.-J. Hannemann & H. Schumann (eds): *Dahl, F. (Begr.), Die Tierwelt Deutschlands und der angrenzenden Meeresteile*. 67. Teil. – Gustav Fischer Verlag, Jena: 1–203.
- Karg, W. (1993): Acari (Acarina) Milben, Parasitiformes (Anactinochaeta) Cohors Gamasina Leach: Raubmilben. – In: Zoologisches Museum Berlin (eds): *Dahl, F. (Begr.), Die Tierwelt Deutschlands und der angrenzenden Meeresteile*. 59. Teil. – Gustav Fischer Verlag, Jena: 1–523.
- Kayahara, G. J., K. Klinka & L. M. Lavkulich (1996): Effects of decaying wood on eluviation, podzolization, acidification and nutrient status in soils with different moisture regimes. – *Environmental Monitoring and Assessment* **39**: 485–492.
- Krantz, G. W. & D. E. Walter (eds) (2009): *A manual of acarology*, 3rd ed. – Texas Technical University Press: 807 pp.
- Laiho, R. & C. E. Prescott (2004): Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. – *Canadian Journal of Forest Research* **32**: 763–777.
- Lindblad, I. (1998): Wood-inhabiting fungi on fallen logs of Norway spruce: relations to forest management and substrate quality. – *Nordic Journal of Botany* **18**: 243–255.
- Lindo, Z. & N. N. Winchester (2006): A comparison of microarthropod assemblages with emphasis on oribatid mites in canopy suspended soil and forest floors associated with ancient western red cedar trees. – *Pedobiologia* **50**: 31–41.
- Lindo, Z. & N. N. Winchester (2007): Resident corticolous oribatid mites (Acari: Oribatida): Decay in community similarity with vertical distance from the ground. – *Ecoscience* **14**: 223–229.
- Luxton, M. (1972): Studies of the oribatid mites of a Danish beech wood soil I. Nutritional biology. – *Pedobiologia* **12**: 434–463.
- Maraun, M., S. Migge, M. Schaefer & S. Scheu (1998): Selection of microfungus food by six oribatid mite species (Oribatida, Acari) from two different beech forests. – *Pedobiologia* **42**: 232–240.
- McCune, B. & M. J. Mefford (1999): *PC-ORD: Multivariate Analysis of Ecological Data*, Version 4. – MjM Software Design, Gleneden Beach, Oregon.
- Niedbala, W. (1992): *Phthiracaroida (Acari, Oribatida)*. Systematic Studies. – Elsevier: 612 pp.
- Proctor, H. C., K. M. Montgomery, K. E. Rosen & R. L. Kitching (2002): Are tree trunks habitats or highways? A comparison of oribatid mite assemblages from hoop-pine bark and litter. – *Australian Journal of Entomology* **41**: 294–299.
- Schatz, H. (1983): *Catalogus Faunae Austriae*. Teil IX. Oribatei, Hormmilben. – Österreichische Akademie der Wissenschaft, Vienna: 118 pp.

- Seastedt, T. R., M. V. Reddy & S. P. Cline (1989): Microarthropods in decaying wood from temperate coniferous and deciduous forests. – *Pedobiologia* **33**: 69–77.
- Siepel, H. & E. M. de Ruiter-Dijkman (1993): Feeding guilds of oribatid mites based on their carbohydrase activities. – *Soil Biology and Biochemistry* **25**: 1491–1498.
- Siira-Pietikäinen, A., R. Penttinen & V. Huhta (2008): Oribatid mites (Acari: Oribatida) in boreal forest floor and decaying wood. – *Pedobiologia* **52**: 111–118.
- Siitonen, J. (1994a): Decaying wood and saproxylic Coleoptera in two old spruce forests: A comparison based on two sampling methods. – *Annales Zoologici Fennici* **31**: 89–95.
- Siitonen, J. (1994b): Lahopuu ja lahottajasienet kovakuoriaisten elinympäristönä (Dead wood and decomposer fungi as environments of beetles; in Finnish). – *Luonnon Tutkija* **98**: 180–185.
- Siitonen, J. & P. Martikainen (1994): Occurrence of rare and threatened insects living on decaying *Populus tremula*: a comparison between Finnish and Russian Karelia. – *Scandinavian Journal of Forest Research* **9**: 185–191.
- Skubała, P. & M. Sokołowska (2006): Oribatida fauna (Acari, Oribatida) in fallen spruce trees in the Babia Góra National Park. – *Biological Letters* **43**: 243–248.
- Skubała, P. & M. Duras (2008): Do decaying logs represent habitat islands? Oribatid mite communities in dead wood. – *Annales Zoologici* **58**: 453–466.
- Tikkanen, O-P., P. Martikainen, E. Hyvärinen, K. Junninen & J. Kouki (2006) Red-listed boreal forest species of Finland: associations with forest structure, tree species and decaying wood. – *Annales Zoologici Fennici* **43**: 373–383.
- Weigmann, G. (2006): Acari, Actinochaetida. Hornmilben (Oribatida). (Unter Mitarbeit von L. Miko). – In: Dahl, F. (Begr.), *Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen u. nach ihrer Lebensweise*. 76. Teil. – Goecke & Evers, Kelttern: 1–520.

Appendix 1 Average numbers of Oribatida in different microhabitats (indiv. per litre; < 1 = 1). Asterisks denote species with significant indicator values for one or more microhabitats (NMS, Monte Carlo test; * = $P < 0.05$, ** = $P < 0.01$).

	Forest floor (n=8)	Under trunk (12)	Under stump (12)	Trunk (12)	Stump (12)	Live trunk(12)
Achipteriidae spp	19	49	21	19	23	23
<i>Acrogalumna longipluma</i> (Berlese 1904)		3	7	1	2	
<i>Adoristes ovatus</i> (C. L. Koch 1839)	5	2	3	2	1	1
<i>Atropacarus striculus</i> (C. L. Koch 1836)*	5	7	15			
<i>Autogneta longilamellata</i> (Michael 1885)				4	2	
<i>Autogneta parva</i> Forsslund 1947				1		
<i>Autogneta traegardhi</i> Forsslund 1947*	5	35	33	4	1	
<i>Banksinoma lanceolata</i> (Michael 1885)				3	2	
Brachytoniidae spp.	1	1	9		1	
<i>Caleremaeus monilipes</i> (Michael 1882)			2		3	
<i>Camisia biurus</i> (C. L. Koch 1839)						1
<i>Camisia spinifer</i> (C. L. Koch 1835)		1				
<i>Carabodes areolatus</i> Berlese, 1916		1		1		
<i>Carabodes coriaceus</i> C. L. Koch 1835		3		1		
<i>Carabodes femoralis</i> (Nicolet 1855)	3	56	44	76	19	
<i>Carabodes forsslundi</i> Sellnick 1953	1	5	3	1	35	
<i>Carabodes labyrinthicus</i> (Michael 1879)*	2		2	8	5	1
<i>Carabodes marginatus</i> (Michael 1884)				1	3	
<i>Carabodes subarcticus</i> Trägårdh 1902	1	13	30	23	77	1
<i>Carabodes tenuis</i> Forsslund, 1953					1	
<i>Cepheus cepheiformis</i> (Nicolet 1855)		1	1	1	2	
<i>Ceratoppia bibilis</i> (Hermann 1804)		1				1
<i>Ceratozetella thienemanni</i> Willmann 1943	2	2		1		
<i>Ceratozetes gracilis</i> (Michael 1884)*	1	3	5			
<i>Ceratozetes sellnicki</i> Rajska 1958	1		3			
<i>Chamobates borealis</i> (Trägårdh 1902)**	31	16	8	5	2	1
<i>Chamobates cuspidatus</i> (Michael 1884)	3	5	4	6	6	16
<i>Chamobates spinosus</i> Sellnick 1928		1	5			1
<i>Cultoribula berolina</i> Weigmann 2006						1
<i>Diapterobates humeralis</i> (Hermann 1804)						1

<i>Dissorhina ornata</i> (Oudemans 1900)	1	38	10	14	15	2
<i>Eniochthonius minutissima</i> (Berlese 1903)						1
<i>Epidamaeus kamaensis</i> (Sellnick 1926)	1					
<i>Epidamaeus bituberculatus</i> (Kulczynski 1902)					1	
<i>Eueremaes silvestris</i> (Forsslund 1957)	1	2	4		1	1
<i>Eupelops torulosus</i> (C. L. Koch 1839)	2	4	2	1	1	
<i>Euphthiracarus cribrarius</i> (Berlese 1904)*	1	2		2	11	
<i>Euphthiracarus monodactylus</i> (Willmann 1919)	6	17	37	3	3	
<i>Euzetes globulus</i> (Nicolet 1855)	3	3				
<i>Furcoribula furcillata</i> (Nordenskiöld 1901)*			2		5	1
<i>Galumna lanceata</i> (Oudemans 1900)			1			
<i>Gustavia microcephala</i> (Nicolet 1855)		1				
<i>Hafenrefferia gilvipes</i> (C. L. Koch 1839)		9	4	2	2	
<i>Hemileius initialis</i> (Berlese 1908)**	15	14	8	5	2	1
<i>Heminothrus longisetosus</i> Willmann 1925	11	4	13	1	1	
<i>Hermanniella dolosa</i> Grandjean 1931		1				
<i>Hypochtoniella minutissimus</i> (Berlese 1904)					1	
<i>Hypochtonius rufulus</i> C. L. Koch 1835*	6	9	6	1	1	
<i>Kunstdamaeus tecticola</i> (Michael 1888)**						2
<i>Liacarus coracinus</i> (C. L. Koch 1841)*	1	12	10	1	2	
<i>Liacarus subterraneus</i> (C. L. Koch 1844)	1	1	1			
<i>Licneremaes licnophorus</i> (Michael 1882)*			1		3	
<i>Medioppia subpectinata</i> (Oudemans 1900)**	31	58	62	8	1	
<i>Melanozetes mollicomus</i> (C. L. Koch 1839)		2	2	4	2	
<i>Mesotritia nuda</i> (Berlese 1887)	2	10	8	10	1	
<i>Metabelba pulverulenta</i> (C. L. Koch 1840)*	2	6	2			
<i>Microppia minutissima</i> (Paoli 1908)			1		1	
<i>Multioppia glabra</i> (Mihelçiq 1955)	5	5	1		5	
<i>Nanhermannia nana</i> (Nicolet 1855)	5	2	4		1	
<i>Nanhermannia sellnicki</i> Forsslund 1958	6		3			
<i>Neoribates aurantiacus</i> (Oudemans 1914)					1	1
<i>Nothrus palustris</i> C. L. Koch 1839		1	2			
<i>Nothrus silvestris</i> Nicolet 1855**	10	13	19	10	1	
<i>Ophidiotrichus tectus</i> (Michael 1884)					1	
<i>Oppia</i> sp.**		1			7	
<i>Oppiella nova</i> (Oudemans 1902)**	35	30	92	3	5	
<i>Oribatella calcarata</i> (C. L. Koch 1835)		2			1	2

<i>Oribatella</i> sp.			1	2	1	
<i>Oribatella sexdentata</i> Berlese 1916				3	1	
<i>Oribatula tibialis</i> (Nicolet 1855)	1	1	1	8	9	
<i>Paradamaeus clavipes</i> (Hermann 1804)	1	1			1	1
<i>Pergalumna altera</i> (Oudemans 1915)	1					
<i>Pergalumna nervosa</i> (Berlese 1914)	1	1	1	1	1	
<i>Phauloppia lucorum</i> (C. L. Koch 1841)				1	1	1
<i>Phauloppia nemoralis</i> (Berlese 1916)**						12
<i>Phthiracarus boresetosus</i> Jacot 1930**	15	21	13	1	1	
<i>Phthiracarus bryobius</i> Jacot 1930	2	21	2	7	3	1
<i>Phthiracarus crinitus</i> (C.L.Koch 1841)			1	1	1	
<i>Phthiracarus globosus</i> (C. L. Koch 1841)**	2	15	9		1	
<i>Phthiracarus longulus</i> (C. L. Koch 1841)**	11	35	38	3	2	
<i>Phthiracarus nitens</i> Nicolet 1855*	2	5	4	1	1	1
<i>Platyliodes</i> sp. juv.					2	
<i>Platynothrus peltifer</i> (C. L. Koch 1839)	14	3	1	4	1	
<i>Porobelba spinosa</i> (Sellnick 1920)	1	1			1	
<i>Poroliodes farinosus</i> (C. L. Koch 1840)						3
<i>Poroliodes</i> sp. juv.		1				
<i>Protoribates lagenula</i> (Berlese 1904)				2		
<i>Quadroppia quadricarinata</i> (Michael 1885)	1	22	5		5	
<i>Rhysotritia ardua</i> (C. L. Koch 1841)		2	1			
<i>Scheloribates laevigatus</i> (C. L. Koch 1836)		2	2	12		1
<i>Scheloribates latipes</i> (C. L. Koch 1844)	9	3		7	1	
<i>Scheloribates pallidulus</i> (C. L. Koch 1840)*		3	7	6	35	
<i>Spatiodamaeus boreus</i> (Bulanova-Zachvatkina 1957)	1					
<i>Steganacarus applicatus</i> (Sellnick 1920)**	32	52	24	2	1	
<i>Steganacarus carinatus</i> (C. L. Koch 1841)**	103	192	117	3	5	
<i>Subiasella quadrimaculata</i> (Evans 1952)		1	5	9	13	
Suctobelbidae spp*	20	36	45	4	8	
<i>Tectocephus velatus</i> (Michael 1880)	15	37	12	2	11	1
<i>Tritegeus bisulcatus</i> Grandjean 1953		1	1	1		
<i>Xenillus tegeocranus</i> (Hermann 1804)	1					
<i>Zygoribatula propingua</i> (Oudemans 1900)					1	
<i>Zygoribatula exilis</i> (Nicolet 1855)**				1	2	28
Total	458	908	780	304	370	99
Average species/sample	14	16	19	10	14	4.5

Appendix 2 Average numbers of Mesostigmata in different microhabitats (indiv./ litre; < 1 = 1). Asterisks denote species with significant indicator values for one or more microhabitats (NMS, Monte Carlo test; ** = P < 0.01, * = P < 0.05).

	Forest floor (n = 8)	Under CWD (24)	Spruce trunk (4)	Birch trunk (4)	Aspen trunk (4)	Spruce stump (4)	Birch stump (4)	Aspen stump (4)	Live bark (12)
<i>Amblyseius tавasticus</i> Karg & Huhta 2009						1			
<i>Amblyseius fennicus</i> Karg & Huhta 2012**									3
<i>Ameroseius longitrachus</i> Hirschmann 1963								2	
<i>Anthoseius richteri</i> (Karg 1970)									1
<i>Arctoseius insularis</i> (Willmann 1952)						1			
<i>Asca aphidioides</i> (Linné 1758)			3						
<i>Celaenopsis badius</i> Berlese 1836		1				2			1
<i>Cornodendrolaelaps cornutus</i> * (Hirschmann 1960)		1		1		12	14		
<i>Dendrolaelaps oudemansi</i> Halbert 1915	1	1	2		12		1		
<i>Dinychus arcuatus</i> (Trägårdh 1943)		2	1	7			2	3	
<i>Dinychus carinatus</i> * Berlese 1903		3						14	
<i>Dinychus perforatus</i> Kramer 1882	2	1	3	1					
<i>Dinychus septentrionalis</i> ** (Trägårdh 1943)		1		2	2	4	5	4	
<i>Dinychus sublaevis</i> (Trägårdh 1943)								2	
<i>Dinychus woelkei</i> * Hirschm. & Z.-Nicol 1969					7			7	
<i>Epicrius resinae</i> * Karg 1971	4	1		1					
<i>Eviphis ostrinus</i> ** (C.L.Koch 1836)	6	4	1	1					
<i>Gamasellodes bicolor</i> (Berlese 1918)				2					
<i>Geholaspis longispinosus</i> (Kramer 1876)		1			3				
<i>Holoparasitus calcaratus</i> * (C.L.Koch 1839)			1	1	1				3
<i>Holoparasitus tirolensis</i> Sellnick 1968		1						1	
<i>Hypoaspis oblonga</i> (Halbert 1915)		1							
<i>Hypoaspis vacua</i> (Michael 1891)	2	1							
<i>Hypoaspis aculeifer</i> * (Canestrini 1883)	7	2	1	2					
<i>Hypoaspis brevipilis</i> Bernhard 1955							1		
<i>Hypoaspis curtipilis</i> Hirschmann 1969							2		
<i>Hypoaspis giffordi</i> Evans & Till 1966						2			1
<i>Hypoaspis lubricoides</i> Karg 1971		1							
<i>Iphidosoma physogastris</i> Karg 1971	1								
<i>Iphidonopsis dendrophilus</i> (Karg 1969)						1		1	
<i>Iphidozercon gibbus</i> (Berl.ese 1903)		1							
<i>Lasioseius lawrencei</i> Evans 1958	1	1					1		
<i>Lasioseius ometes</i> (Oudemans 1903)			2					1	

<i>Leptogamasus suecicus</i> (Trägårdh 1936)	2	2			2	2	2		
<i>Macrocheles tardus</i> (C.L.Koch 1841)	1								
<i>Microgynium rectangulatum</i> * Trägårdh 1942					7	2	11		
<i>Microseius truncicola</i> * Trägårdh 1942	1					4	2		
<i>Multidendrolaelaps euepistomus</i> (Hirschmann 1960)							1		
<i>Multidendrolaelaps putte</i> Huhta & Karg 2010					4				
<i>Multidendrolaelaps tetraspinosus</i> (Hirschmann 1960)				1					
<i>Pachydellus problematicus</i> Mašán 2007	1								
<i>Pachydellus furcifer</i> (Oudemans 1903)		1							
<i>Pachyseius wideventris</i> Afifi & Nasr 1984	1								
<i>Paragamasus lapponicus</i> * (Trägårdh 1910)	5	7	1	1		2		2	1
<i>Paragamasus parrunciger</i> (Bhattacharyya 1963)		2		4			2		
<i>Paragamasus runcatellus</i> (Berlese 1903)	1	4		1	3	4			
<i>Paragamasus truncus</i> (Schweizer 1961)	1	2				6			
<i>Paragamasus vagabundus</i> (Karg 1968)	5	3					4	1	
<i>Parasitus lunulatus</i> (J. Müller 1859)	1								
<i>Parazercon radiatus</i> * (Berlese 1914)	18	8	9	2					1
<i>Pergamasus brevicornis</i> Berlese 1903	2	2	3	1	2		2	1	
<i>Proctolaelaps xyloteri</i> (Samšičák 1960)									1
<i>Prozercon kochi</i> * Sellnick 1943	5	4	1	2			1	1	
<i>Pseudoparasitus placentulus</i> (Berlese 1887)		1							
<i>Punctodendrolaelaps arvicolus</i> (Hirschmann 1960)			2	7				1	
<i>Punctodendrolaelaps fallax</i> (Leitner 1949)								1	
<i>Punctodendrolaelaps rotundus</i> (Hirschmann 1960)		1							
<i>Punctodendrolaelaps trapezoids</i> (Hirschmann 1960)		1	2						
<i>Sejus togatus</i> * C.L.Koch 1836		1	4	2		2	2	4	
<i>Trachytes aegrotata</i> (C.L.Koch 1841)	9	12	4			5		1	
<i>Trachytes pauperior</i> (Berlese 1914)	7	8	22	2					
<i>Trichouropoda ovalis</i> (C.L.Koch 1839)	1	5		2	1	2	10	2	
<i>Urodiaspis tecta</i> (Kramer 1876)	1	1	2						
<i>Uroobovella pulchella</i> (Berlese 1904)		1							
<i>Uroobovella vinicolora</i> (Vitzthum 1926)		1				3		2	
<i>Uropoda cassidea</i> (Hermann 1804)		1							
<i>Veigaia cerva</i> (Kramer 1876)		1							
<i>Veigaia exigua</i> (Berlese 1917)		1							
<i>Veigaia kochi</i> * (Trägårdh 1901)	2	2		1				2	
<i>Veigaia nemorensis</i> ** (C.L.Koch 1839)	18	19	11	5	1	3	1		
<i>Veigaia transisalae</i> Oudemans 1902								1	
<i>Vulgarogamasus kraepelini</i> * (Berlese 1905)	1	3	1	1				1	
<i>Zercon curiosus</i> * Trägårdh 1910		1	10	13	6	12	4	5	1
<i>Zercon triangularis</i> C.L.Koch 1836		1						1	
Total	103	115	87	63	42	75	60	73	10
Average species/sample	9.1	10.7	6.5	7.0	4.0	6.7	6.2	8.2	2.1