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A comparison of microarthropod assemblages with emphasis on oribatid mites in canopy suspended soils and forest floors associated with ancient western redcedar trees

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Summary

Microarthropod abundance, oribatid mite species richness and community composition were assessed in the high canopy (ca. 35 m) of an ancient temperate rainforest and compared with microarthropod communities of the forest floor. Microarthropods were extracted from 72 core samples of suspended soils and 72 core samples from forest floors associated with six western redcedar trees in the Walbran Valley on the southwest coast of Vancouver Island, Canada. Total microarthropod abundances, mesostigmatid and astigmatid mites, Collembola and other microarthropod abundances were significantly greater in forest floors compared to canopy habitats. Oribatid and prostigmatid mite abundance were not significantly different between habitats. The relative abundances of all microarthropod groups considered in this study differed significantly between habitats. Eighty-eight species of oribatid mites were identified from the study area. Eighteen of the 53 species observed in suspended soils were unique to the canopy. Cluster analysis indicates that the arboreal oribatid mite community is distinct and not a taxonomic subset of the forest floor assemblage, however, canopy oribatid mite communities are more heterogeneous in species composition than in the forest floor. © 2005 Elsevier GmbH. All rights reserved.

Introduction

Oribatid mites (Acari: Oribatida) are typically the dominant component of the microarthropod fauna in most forest floor systems (Petersen and Luxton 1982). Oribatid mites are also species rich and numerically dominant in temperate and tropical

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forest canopies (Behan-Pelletier and Walter 2000). Oribatid mites are observed in many arboreal habitats, including bark and trunks of trees (Nicolai 1993; Prinzing 2001; Proctor et al. 2002), leaf domatia and stems (Spain and Harrison 1968; Walter and O'Dowd 1995), moss, lichen and other corticolous epiphytic cover (Sevd and Seaward 1984; André 1985), and in accumulations of organic matter known as suspended soils (Paoletti et al. 1991; Wunderle 1992; Behan-Pelletier et al. 1993; Winchester et al. 1999). Factors affecting the diversity and abundance of arboreal oribatid mite communities include tree species, elevation and size of suspended soil patches (Fagan and Winchester 1999; Wardle et al. 2003), as well as random dispersal events of individual species (Behan-Pelletier and Winchester 1998).

Canopy oribatid mite communities contribute significantly to overall forest biodiversity and are functionally important components of forest systems. In canopy/ground comparison studies, the number of oribatid mite species in common between the two habitats is typically 40%. For example, Wunderle (1992) found 40% of oribatid mite species in a tropical forest in Peru were common to both canopy and forest floor habitats, Behan-Pelletier et al. (1993) revealed 41% of oribatid mite species in a Venezuelan forest were common to both canopy and forest floor samples, and Winchester et al. (1999) found 43% of 71 oribatid mite species collected from Sitka spruce canopy and forest floor habitats were shared in common.

In this paper, we compare the abundance of microarthropods and the species richness and composition of oribatid mite communities in suspended soils of the high canopy and forest floors associated with ancient western redcedar trees in the Walbran Valley on Vancouver Island, British Columbia, Canada. This study complements other studies of soil fauna in temperate Canadian forest systems, and specifically other canopy systems on Vancouver Island such as the Carmanah Valley (Winchester et al. 1999), Mt. Cain (Fagan and Winchester 1999) and the Montane Alternative Silviculture Systems (MASS) project (Behan-Pelletier et al. 2002).

Materials and methods

Site description

The Walbran Valley is located on the southwest coast of Vancouver Island, British Columbia, Canada

between the towns of Port Renfrew and Bamfield. This watershed is 13 147 ha, largely intact, and lies entirely in the Coastal Western Hemlock biogeoclimatic zone (Meidinger and Pojar 1991). The climate is characterized by wet, humid, cool summers and mild winters, and a mean annual precipitation of 2990.5 mm is typical for this area (http://climate.weatheroffice.ec.gc.ca/climate_normals/in-

dex_e.html [cited 4 April 2005]). The dominant conifers in this valley are western hemlock (*Tsuga heterophylla* (Rafn.) Sarg.), Sitka spruce (*Picea sitchensis* (Bong) Carr.), silver fir (*Abies amabilis* (Dougl.) Forb.), and western redcedar (*Thuja plicata* D. Don).

The study area within this valley (48°39'N, 124°35'W) is approximately 8 km from the Pacific coast at an elevation of 200 m above sea level and is characterized by a high abundance of ancient (>800 years old) western redcedar. These ancient western redcedars have a multi-furcated main trunk, a unique morphology referred to as a candelabra structure, which allows for the accumulation of organic matter and the formation of many discrete, isolated patches of suspended soil of varying depth.

Sample collection and experimental design

Single rope climbing methods (Perry 1978; Barker and Standridge 2002) and techniques that have been devised over 10 years for canopy research in association with the University of Victoria were used to access the suspended soils within the crowns of six western redcedar trees. Sampling was conducted September 10-14, 2004. Individual PVC corers (160 series, 3.175 cm diameter, 25 cm length) were used to collect three replicate core samples from each of four large suspended soils within each tree. Three replicate core samples were also collected at cardinal directions on the forest floor at 1.5 m from the trunk of each tree for a total of 144 core samples collected (72 from the canopy and 72 from the forest floor). Core samples were left in the corers to minimize disturbance during transport from the field to the laboratory.

In the laboratory, each intact core sample was extruded from the plastic corer and measured for depth and wet weight before extraction of microarthropods. Microarthropods were extracted into 75% EtOH using Berlese funnels for 48 h. Following extraction core dry weights were measured and the percent moisture content (expressed as percent dry weight (dwt)) was calculated gravimetrically by recording the change in mass. This study incorporates a nested randomized block design with six trees serving as replicate blocks and having suspended soils nested within the canopy habitat of each tree. Forest floor aspects (N, S, E, W) were nested within the forest floor habitat associated with each tree.

Specimen identification and data analyses

Extracted microarthropods were sorted into the following taxonomic groups: mites (Acari), springtails (Collembola) and other microarthropods, which included pseudoscorpions (Pseudoscorpiones), beetles (Coleoptera), ants (Hymenoptera), millipedes and centipedes (Myriapoda), and spiders (Araneae). The Acari were further identified to suborder (Mesostigmata, Prostigmata, Astigmata and Oribatida) and adult oribatid mites were identified to species. Representative specimens were slide mounted using Hoyer's medium (Krantz 1978) and a reference collection is in preparation for deposition at the Canadian National Collection, Ottawa, Canada, and for the Pacific Forestry Centre, Victoria, British Columbia, Canada.

Microarthropod abundance, expressed as number of individuals per gram dry weight of substrate, was used to estimate population abundances. The relative abundance of Acari suborders, Collembola and other microarthropods is expressed as the percent of total abundance of microarthropods.

An *F*-test was used to test for differences between pooled samples from the canopy and forest floor habitats for abundance of major microarthropod groups, relative abundance of major microarthropod groups, moisture content and depth of core measurements. We used the general linear model for randomized block designs (SPSS for Windows 2001) to test the effect of tree and nested sample (suspended soil, aspect). A significance level of 0.05 was used for all analyses.

Theoretical total species richness for canopy and forest floor habitats was calculated using first- and second-order Jackknife, Chao 1 and 2 estimators. All estimates were performed using EstimateS (Colwell 2005). The Chao 1 and 2, like the Jackknife estimate, are non-parametric methods for estimating species richness (Chao 1987). The Chao 1 is based on the number of rare species (singletons and doubletons), while the Chao 2 is based on presence/absence data. The Jackknife and Chao estimates become independent of sample size after half the theoretical total fauna is observed (Jackknife) or when the observed number of species is greater than the square root of two times the theoretical total fauna (Chao) (Colwell and Coddington 1994). Coleman rarefaction curves are used to plot the theoretical species accumulation and supplement the observed species accumulation curves. Values for these curves were also calculated using EstimateS at 50 randomized permutation tests without sample replacement. Similarity among sites (trees) within the canopy and forest floor habitats was compared using the Bray–Curtis similarity index using Primer 5 for Windows (2001), and the top oribatid mite species driving dissimilarity between habitats were identified using SIMPER analysis. All similarity measures were performed on standardized species abundance data (# individuals/100 g dwt).

Results

Physical measurements

The average moisture content of the forest floor was significantly greater than the average for suspended soils (df = 1, f = 139.6, P = 0.000). Average suspended soil moisture content was 135% (SD+65.5) and on the forest floor moisture content was 265% (SD \pm 84.9). Average suspended soil moisture content within a tree was highly variable and all trees were significantly different from at least one other tree (LSD post hoc test). The moisture content of the forest floor was not significantly different between trees. The average depth of suspended soils was significantly greater than the depth of the forest floor (df = 1,f = 292.6, P = 0.000). Average suspended soil depth was 7.6 cm (SD ± 2.4) versus 4.3 cm(SD+1.8) on the forest floor. Suspended soils sampled in this study were at an average height of 35 m from the ground (min. 21 m, max. 45 m) and had an average surface area of $0.85 \,\mathrm{m^2}$ (min. $0.30 \,\mathrm{m^2}$, max. $2.76 \,\mathrm{m^2}$). Neither the average height nor the average surface area of the suspended soils was significantly different among the six trees.

Microarthropod abundances

Average abundance of total microarthropods was significantly greater on the forest floor than in the canopy (Fig. 1a), as were the average abundance of mesostigmatid and astigmatid mites, Collembola, and other microarthropods. The average abundance of oribatid and prostigmatid mites in suspended soils was not significantly different from the average abundance on the forest floor.

Relative abundances of all groups were significantly different between canopy and forest floor





Figure 1. Major microarthropod taxa extracted from core samples taken from suspended soils of the crowns (35 m) and forest floors associated with six western redcedar trees in the Walbran Valley of Vancouver Island, Canada, (a) absolute abundance (# individuals/g dwt), (b) relative abundance (% of total) of individuals enumerated within each habitat. Values are means \pm SE. Significance is **P*<0.05, ***P*<0.01.

habitats (Fig. 1b). Oribatid and prostigmatid mites were significantly greater in relative abundance in the canopy than on the forest floor, while all other groups had significantly lower relative abundance in the canopy (Fig. 1b).

Oribatid mite diversity

A total of 88 species representing 66 genera and 46 families were identified from 9966 adult oribatid mites (5273 from canopy, 4693 from forest floor) collected from Berlese extractions (Appendix A). Observed and theoretical species richness using first- and second-order Jackknife, Chao 1 and 2 estimates are 1.5–2.0 times higher in the forest floor habitat compared with the canopy (Table 1).

Table 1.Observed and theoretical total oribatid mitespecies richness for canopy and forest floor habitatsassociated with western redcedar trees in the WalbranValley on Vancouver Island, British Columbia, Canada

	Canopy	Forest floor
Observed Jackknife 1st order Jackknife 2nd order Chao 1 (bias corrected) Chao 2 (bias corrected) Chao 1 (classic calculation) Chao 2 (classic	53 64.84 (\pm 3.34) 67.87 58.0 (\pm 3.66) 60.02 (\pm 4.57) 59.33 (\pm 4.92) 61.56 (\pm 5.95)	70 87.73 (\pm 4.21) 103.33 99.6 (\pm 16.10) 111.15 (\pm 21.32) 109.50 (\pm 28.54) 129.16 (\pm 45.05)
calculation)		

Values are mean estimates $(\pm SD)$ based on 50 randomized permutation tests without sample replacement.



Figure 2. Observed and estimated oribatid mite species richness based on species accumulation curves and rarefaction methods (average of 50 randomizations without sample replacement $(\pm SD)$) for 144 core samples taken from canopy and forest floor habitats associated with western redcedar trees in the Walbran Valley of Vancouver Island, Canada.



Figure 3. Similarity dendrogram of suspended soils (SS) within the high canopy (35 m) and the forest floor (FF) for six western redcedar trees sampled in the Walbran Valley, Vancouver Island, Canada. Values are based on Bray–Curtis similarity indices of 88 oribatid mite species abundances.

Species accumulation and rarefaction curves for canopy and forest floor habitats also demonstrate that oribatid mite species richness is greater on the forest floor (Fig. 2).

Fifty-three species of oribatid mites were observed from canopy habitats, of which 18 species (20.45% of total species richness) were unique to the canopy and not found on the forest floor. Seventy species of oribatid mites were observed in the forest floor habitat associated with western redcedar, of which 36 species (40.91% of total) were not found in the canopy, and the remaining 34 species of oribatid mites (38.63% of total) shared in common between canopy and forest floor habitats. Rare species are included in these species richness values.

Canopy sites were more similar to each other, as were forest floor sites, with overall similarity between canopy and forest floor habitats being low (35%) (Fig. 3). The abundances of six species of oribatid mites accounted for 50% of the dissimilarity between canopy and forest floor habitats (Table 2). 36

Table 2. Top oribatid mite species drivers of Bray---Curtis dissimilarity between canopy and forest floor habitats associated with western redcedar trees in the Walbran Valley on Vancouver Island, British Columbia, Canada

Species	% Contribution	Abundance trend
Archiphthiracarus sp. 1	12.96	High general abundance
Epilohmannia sp.	11.81	High general abundance
Oppiella nova	7.16	High general abundance
Moritzoppia sp.	6.76	High canopy abundance
Scheloribates sp.	6.72	High canopy abundance
Nanhermannia elegantula	4.44	High forest floor abundance
Cumulative contribution	49.85	

The abundance trend of the species that allows for high contribution to dissimilarity is also listed.

Discussion

Microarthropod abundances

Oribatid mites dominated the microarthropod fauna in both forest floor and canopy habitats associated with western redcedar trees in the Walbran Valley. Oribatid mite abundance (#/g dwt) was not significantly different between forest floor and canopy habitats, suggesting that suspended soils of this system provide a comparable habitat for oribatid mites. However, total microarthropod abundance was significantly greater in forest floor habitats associated with western redcedar trees compared to suspended soils of canopy habitats due to significantly greater abundances of mesostigmatid and astigmatid mites, Collembola, and other microarthropods. Oribatid mite dominance within the canopy is well documented for both temperate (Schowalter 1989; Winchester et al. 1999) and tropical (Nadkarni and Longino 1990; Behan-Pelletier et al. 1993) forests as well as in forest floor systems (Wallwork 1983), with dominance of oribatid mites in forest canopies being attributed to tree architecture and the accumulation of organic matter within the canopy system (Winchester and Behan-Pelletier 2003).

Paoletti et al. (1991) found that oribatid mites dominated the microarthropod fauna in a tropical Venezuelan rainforest in both forest floor and arboreal soils, but total microarthropod abundances were up to 10 times greater in the soil associated with epiphytes versus the forest floor. Paoletti et al. (1991) attributed the lower abundance of oribatid mites on the forest floor to greater predation pressure than in arboreal habitats. In the present study proportions of predator groups such as Mesostigmata and other microarthropods were significantly lower in suspended soils of western redcedar compared to forest floors, but abundances of oribatid mites did not differ significantly between canopy and ground habitats.

Nadkarni and Longino (1990) found relative abundances of major arthropod taxa were the same in organic matter sampled from tropical canopy and forest floor systems in Costa Rica, however absolute abundances of all groups were significantly lower in the canopy. Lower arthropod abundance was attributed to differences in microclimate conditions, dispersal capabilities of the organisms and the quality of the organic matter associated with these two habitats. Canopy climatic conditions are more extreme than forest floors, with greater exposure to wind, insolation and more frequent wet/drv cvcles, however suspended soil deposits that accumulate within the canopy are high in organic matter and provide habitat for oribatid mites (Nadkarni 1994). Drought extremes influence the abundance and number of oribatid mite species (Siepel 1996) but stability of soil microclimates increases with depth (Wallwork 1983) and thus oribatid mites and small prostigmatid mites may be able to resist desiccation without having to relocate during dry periods by compensatory redistributing to depth in the suspended soils (Prinzing 2005). With significantly lower moisture content and significantly greater depth in suspended soils compared to the forest floor, such a mechanism for preventing desiccation in arboreal mites may exist in this system.

Oribatid mite species richness

There are 110 genera from 51 families of oribatid mites previously recorded from arboreal habitats worldwide (Behan-Pelletier and Walter 2000), with the highest canopy species richness (127 species) recorded from suspended soils in a tropical forest in Peru (Wunderle 1992). Other species-rich canopy studies include Behan-Pelletier et al. (1993) who recorded 69 species from bromeliads and suspended soils in a Venezuelan forest canopy, and Winchester et al. (1999) who recorded 43 oribatid mite species from moss mats on Sitka spruce branches of a Canadian temperate rainforest. With 53 oribatid mite species observed in the canopy habitat of western redcedar, the present study is the highest number of oribatid mite species recorded for a temperate canopy study, and is the third highest species rich recording in canopies worldwide. High species richness in all the aforementioned studies is consistent with the presence of complex and heterogeneous habitat of welldeveloped suspended soils associated with epiphytes and moss mats.

In this canopy ecosystem, while the observed species accumulation curve approaches an asymptote, the initial incline of the rarefaction curve is steeper than the initial curve of the observed species accumulation suggesting that in this habitat species heterogeneity is greater than can be expected from sampling error alone (Colwell and Coddington 1994). The species accumulation curve for the forest floor habitat show that five new species were added to the list in the last three samples taken from the forest floor, however, despite this, the rarefaction curve follows the observed species accumulation curve closely. Buddle et al. (2005) warn that rarefaction curves can give biased results in sample-based data, if there is inequality in sampling effort (i.e. number of samples collected or individuals caught), but the present study enumerated a high and nearly equal amount of individuals in 144 samples from suspended soils (5272 adult individuals) and forest floors (4693 adult individuals), preventing this bias.

First- and second-order Jackknife estimates of species richness give conservative theoretical values of species richness in the forest floor habitat compared to higher estimates from Chao 1 and 2 calculations. Estimates of species richness using classic-calculated Chao 1 and 2 estimators suggest that in the 72 samples taken for this study on the forest floor, only a little over half the theoretical species potentially present were observed. Therefore, additional sampling of both canopy and forest floor habitats is warranted.

Similarity between canopy and forest floor habitats

The amount of unique canopy species (20%) suggests that the canopy oribatid mite community associated with ancient western redcedar in the Walbran Valley is distinctly different from the forest floor and not just a random subset of the forest floor assemblage. The number of species shared between forest floor and canopy habitats, 40%, is similar to Wunderle (1992) who found 22% of oribatid mite species were strictly arboreal, 38% were found only on the forest floor and 40% were common to both canopy and forest floor habitats in a tropical forest

in Peru. The 40% shared oribatid species value appears to be common for canopy/ground overlap, and has previously been attributed to the dispersal capabilities of the shared species. Aoki (1973) called these the "wandering forms" which moved between ground and canopy systems, however, Proctor et al. (2002) found distinct trunk and ground mite communities and that the trunks were habitats in and of themselves, not acting as highways for ground fauna to migrate into the canopy. Some Acari have been shown to form part of the aerial plankton, or alternately, they may be passengers on organic matter, moss and lichen thalli redistributed within the canopy during wind events (Nadkarni and Matelson 1991), which may also lead to the presence of arboreal mites on the ground.

Species found in the canopy that are not typically recorded as arboreal and were not found in forest floor samples include: Moritzoppia sp., Eueremaeus marshalli, Oribatula sp., Eniochthonius minutissimus, and many species of the family Brachychthoniidae. While this study shows a dominance of higher (Brachypylina) oribatid mites in the canopy, it is the first study to show lower (Macropylina) oribatids as both species-rich and abundant in a canopy system. In a review of oribatid mites in arboreal habitats, Behan-Pelletier and Walter (2000) found over 90% of recorded arboreal oribatids were brachypyline versus an average of 74% brachypyline oribatids in litter and soil systems. The proportion of brachypyline oribatid mites in this study was similar in canopy (61%) and forest floor (59%) habitats, and are both lower than proportions of Brachypylina in forest floor samples from White spruce (64%) and Aspen (64%) stands of the mixed-wood boreal forest in northern Alberta (Lindo and Visser 2004).

Winchester et al. (1999) attributed the dominance of the Brachypylina in the canopy to feeding habits and niche specialization due to morphological and physiological modifications such as resistance to desiccation. We attribute the abundance and diversity of the lower oribatid mites in the present study to the extent of development and depth of the suspended soils in ancient western redcedar that provide an increased and more complex habitat template than other tree species.

Bray–Curtis indices for all 12 sampling sites (6 trees \times 2 habitats) show low (35%) overall similarity between canopy and forest floor, but within each of these habitats, similarity is high among the different sampling sites (trees). These results reflect similar studies by Aoki (1973), Wunderle (1992), and Karasawa and Hijii (2004) who found high similarity within arboreal or ground habitats and low similarity between the different habitats. Within the forest floor habitat, different trees

group together with a high amount of similarity (60–80%). The close grouping of the forest floor habitat is expected since, although heterogeneous, the forest floor is a continuous habitat.

Within the canopy, trees group together with moderate to high (45–65%) similarity, showing that there is greater variability in oribatid mite community composition among trees within the canopy versus among trees within the forest floor habitat. The groupings of canopy sites, based on the Bray–Curtis index values do not appear to be related to the proximity of trees to one another, as trees 5, 6 and 7 are in the closest proximity to one another (<20 m base to base) yet do not show the greatest similarity among trees in their oribatid mite communities.

We are still unsure of the mechanism for colonization of oribatid mites in suspended soils and other canopy habitats, and how colonization is related to the dispersal capabilities of different oribatid mite species. Since most soil fauna distribute based on microhabitat associations, the main factor influencing distributions is the availability of suitable habitat (Anderson 1977). Increased habitat heterogeneity with increasing size of suspended soil islands may be a determining factor in shaping the oribatid mite communities of western redcedar canopies. Wardle et al. (2003) showed experimentally and in an observational study of epiphytic soil islands, that diversity of microarthropod orders and densities of Acari and Collembola were greater in larger islands. In neither the observational or experimental study did height of epiphyte from the forest floor or proximity to other epiphytes have an effect on microarthropod diversity or density. A similar relationship was documented by Simberloff (1976) in mangrove forests in Florida, where the number of arthropod species decreased as island size decreased.

Habitat heterogeneity and complexity, one explanation of the observed species/area relationship, has been shown to be important in shaping arboreal mite communities. Spain and Harrison (1968) collected 17 species of oribatid mites from *Olearia colensoi* leaves of a temperate New

Zealand forest canopy, and showed that older leaves had an increased abundance of oribatid mites which they attributed to increased organic matter and available food resources. Walter and O'Dowd (1995) showed that as structural complexity of leaves and the presence of domatia increased the diversity and abundance of canopy mites in an Australian tropical forest increased. In soil systems, increasing mite diversity with increasing soil microhabitat complexity is well known (Anderson 1977). In neotropical epiphytic mats similar in structure to the suspended soils of this study, Yanoviak et al. (2004) found arthropod communities were stratified in vegetative and humic regions of the mat, suggesting that both areas are important sources of biodiversity.

Well-developed suspended soils in the canopy of ancient western redcedar are a complex habitat and support rich, diverse oribatid mite communities as this study shows. Suspended soils and forest floors may be more similar to one another than either is to bark or other corticolous substrates due to the complexity of the suspended soil habitat (Prinzing and Woas 2003). As development stage of suspended soils is important in sustaining and supporting large, diverse communities of arthropods in forest canopies, and ancient forests are more structurally complex and heterogeneous compared with young, even-aged stands (Franklin and Van Pelt 2004), the preservation of ancient forests is important to preserving arboreal biodiversity.

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Appendix A

Oribatid mite species (Acari: Oribatida) from canopy and forest floor habitats associated with western redcedar trees in the Walbran Valley, Vancouver Island, British Columbia, Canada. Numbers following each taxon are number of specimens collected and relative abundance (% of total) within each habitat

Family	Species	Canopy	Forest floor
Palaeacaridae	Palaeacarus hystricinus Trägårdh, 1932	1 (0.0%)	37 (0.8%)
Eniochthoniidae	Eniochthonius minutissimus (Berlese, 1904)	28 (0.5%)	0

Atopochthoniidae Pterochthoniidae	Atopochthonius artiodactylus Grandjean, 1948 Pterochthonius angelus (Berlese, 1910)	23 (0.4%) 0	43 (0.9%) 7 (0.1%)
Brachychthoniidae	Synchthonius crenulatus (Jacot, 1938)	5 (0.1%)	24 (0.5%)
	Synchthonius sp.	13 (0.2%)	0
	Fobrachychthonius sp	3 (0 1%)	0
	Brachychthonius sp.	0	28 (0.6%)
	Sellnickochthonius sp. 1 pr. zelawaiensis (Sellnick	105 (2.0%)	28 (0.6%)
	1978)	105 (2.0%)	20 (0.0/0)
	Sellnickochthonius sp. 2	304 (5.8%)	6 (0.1%)
	Liochthonius sp. 1	47 (0.9%)	47 (1 0%)
	Liochthonius sp. 7	96 (1.8%)	28 (0.6%)
	Liochthonius sp. 2	122 (2.3%)	317 (6.8%)
	Liochthonius sp. 4	72 (0 4%)	1 (0.0%)
Parbypochthoniidae	Parhypochthonius aphidinus sp. pr. octofilamentis	10 (0.2%)	10 (0.2%)
ramypoentionindae	lacot 1938	10 (0.2%)	10 (0.2%)
Cohypochthoniidao	Gabupachthanius sp	0	2 (0 0%)
Phthiracaridao	Archiphthiracarus sp. 1	0 566 (10 7%)	(0.0%)
Fittillacalidae	Archiphthiracarus sp. 7	0	1122 (23.7%)
Oribotritiidaa	Archiphenideurus sp. 2 Oribatritia sp	0	ZI (0.4%)
Onbountildae	Under (Portoso, 1997)		4 (0.1%)
	Mesolifila fluda (Deflese, 1007)	2 (0.0%)	3(0.1%)
Fruch the increase of the s	Function of the second se		14 (U.3%)
Euphtniracaridae	Euphtniracarus monyx walker, 1965	6(0.1%)	55 (1.2%)
Epilonmanniidae	Epilonmannia sp.	604 (11.5%)	639 (13.6%)
Nothridae	Nothrus sp. nr. silvestris Nicolet, 1855	0	1 (0.0%)
Camisiidae	Camisia sp. 1	0	1 (0.0%)
	Camisia sp. 2 nr. abdosensilla Olszanowski et al.	0	1 (0.0%)
	2002	•	
	Platynothrus sp. nr. peltifer (C.L. Koch, 1839)	0	101 (2.2%)
Trhypochthoniidae	Trhypochthonius tectorum (Berlese, 1896)	48 (0.9%)	0
Malaconothridae	Malaconothrus sp.	2 (0.0%)	56 (1.2%)
Nanhermanniidae	Nanhermannia elegantula Berlese, 1913	2 (0.0%)	295 (6.3%)
	Nanhermannia sp. nr. comitalis Berlese, 1916	0	84 (1.8%)
Hermanniidae	Hermannia gibba (C.L. Koch, 1840)	1 (0.0%)	35 (0.7%)
Hermanniellidae	Hermanniella sp. nr. occidentalis Ewing, 1918	0	4 (0.1%)
Neoliodidae	Teleliodes sp.	0	1 (0.0%)
Hungarobelbidae	Hungarobelba sp.	0	1 (0.0%)
Damaeidae	Damaeidae sp. nr. <i>Epidamaeus</i> sp. 1	0	2 (0.0%)
	Epidamaeus sp. 2 nr. floccosus Behan-Pelletier and	7 (0.1%)	0
	Norton, 1985		
	Epidamaeus sp. 3	0	6 (0.1%)
	Belba (Belba) sp.	9 (0.2%)	0
	Belba (Protobelba) californica (Banks, 1904)	0	2 (0.0%)
Cepheidae	<i>Eupterotegaeus rhamphosus</i> Higgins and Woolley, 1963	188 (3.6%)	0
	<i>Eupterotegaeus</i> sp. nr. <i>rostratus</i> Higgins and Woolley, 1963	1 (0.0%)	2 (0.0%)
Damaeolidae	Damaeolus sp.	0	8 (0.2%)
Eremaeidae	Eueremaeus acostulatus Behan-Pelletier, 1993	0	1 (0.0%)
	Eueremaeus marshalli Behan-Pelletier, 1993	13 (0.2%)	0
Megeremaeidae	Megeremaeus montanus Higgins and Woolley, 1965	0	1 (0.0%)
Liacaridae	Liacarus sp. 1 nr. bidentatus Ewing, 1918	3 (0.1%)	94 (2.0%)
	Liacarus sp. 2 nr. robustus (Gervais, 1844)	0 Ó	21 (0.4%)
	Liacarus sp. 3	0	12 (0.3%)
	Liacarus sp. 4	0	1 (0.0%)
Astegistidae	Cultroribula sp. nr. bicultrata (Berlese, 1905)	0	6 (0.1%)
Peloppiidae	Ceratoppia sp.	0	54 (1.2%)
• • • • •	Paenoppia sp.	2 (0.0%)	0
Gustaviidae	Gustavia sp.	0`́	1 (0.0%)

Kodiakellidae Carabodidae Tectocepheidae Oppiidae	Kodiakella lutea Hammer, 1967 Carabodes hoh Reeves and Behan-Pelletier, 1998 Tectocepheus velatus (Michael, 1880) Oppiella nova (Oudemans, 1902) Moritzoppia sp. Multioppia sp. Ramusella (Ramusella) sp. 1 Ramusella (Insculptoppia) sp. 2	2 (0.0%) 0 303 (5.7%) 528 (10.0%) 459 (8.7%) 48 (0.9%) 17 (0.3%) 0 1 (0.0%)	0 1 (0.0%) 93 (2.0%) 439 (9.4%) 0 0 0 8 (0.2%) 1 (0.0%)
Quadroppiidae Suctobelbidae	Quadroppia quadricarinata (Michael, 1885) Suctobelbella sp. 1 Suctobelbella sp. 2 nr. longicuspis Jacot, 1937 Suctobelbella sp. 3 Suctobelbella sp. 4 Suctobelbella sp. 5 Suctobelbella sp. 6 Suctobelbella sp. 7 Allosuctobelba sp. nr. gigantea (Hammer, 1955)	357 (6.8%) 14 (0.3%) 47 (0.9%) 0 357 (6.8%) 0 12 (0.2%) 0	172 (3.7%) 53(1.1%) 6 (0.1%) 4 (0.1%) 134 (2.9%) 279 (5.9%) 14 (0.3%) 14 (0.3%) 10 (0.2%)
Autognetidae	Autogneta sp. nr. longilamellata (Michael, 1885)	3 (0.1%)	1 (0.0%)
Thyrisomidae	Banksinoma lanceolata (Michael, 1885)	3 (0.1%)	0
Achipteriidae	Achipteria sp. nr. curta Aoki, 1970 Dentachipteria sp. Anachipteria acuta (Ewing, 1918)	1 (0.0%) 0 2 (0.0%)	2 (0.0%) 177 (3.8%) 1 (0.0%)
Phenopelopiidae	Eupelops sp.	0	1 (0.0%)
Scheloribatidae	Scheloribates sp.	540 (10.2%)	28 (0.6%)
	<i>Parapirnodus coniferinus</i> Behan-Pelletier et al., 2002	4 (0.1%)	6 (0.1%)
Oribatulidae	Oribatula sp.	120 (2.3%)	0
	Phauloppia sp.	6 (0.1%)	1 (0.0%)
Oripodidae	Benoibates sp.	1 (0.0%)	0
Chamobatidae	Chamobates sp.	1 (0.0%)	1 (0.0%)
Ceratozetidae	Ceratozetes pacificus Behan-Pelletier, 1984	167 (3.2%)	18 (0.4%)
	Sphaerozetes winchesteri Behan-Pelletier, 2000	42 (0.8%)	0
Mycobatidae	Mycobates acuspidatus Behan-Pelletier, 2001	0	1 (0.0%)
Galumnidae	Pilogalumna sp.	5 (0.1%)	0
Total adult oribatids		5273	4693

References

- Anderson, J.M., 1977. The organization of soil animal communities. Ecol. Bull. 25, 15–23.
- André, H.M., 1985. Associations between corticolous microarthropod communities and epiphytic cover on bark. Holarctic Ecol. 8, 113–119.
- Aoki, J.-I., 1973. Soil mites (oribatids) climbing trees. In: Daniel, M., Rosicky, B. (Eds.), Proceedings of the Third International Congress of Acarology, Prague, 31 August–6 September, Junk, Hague, 1971, pp. 59–65.
- Barker, M., Standridge, N., 2002. Ropes as mechanisms for canopy access. In: Mitchell, A.W., Secoy, K., Jackson, T. (Eds.), The Global Canopy Handbook. Global Canopy Programme, Oxford.
- Behan-Pelletier, V.M., Walter, D.E., 2000. Biodiversity of oribatid mites (Acari: Oribatida) in tree canopies and litter. In: Coleman, D.C., Hendrix, P.F. (Eds.), Invertebrates as Webmasters in Ecosystems. CAB International, Wallingford, pp. 187–202.

- Behan-Pelletier, V.M., Winchester, N.N., 1998. Arboreal oribatid mite diversity: colonizing the canopy. Appl. Soil Ecol. 9, 45–51.
- Behan-Pelletier, V.M., Paoletti, M.G., Bisset, B., Stinner, B.R., 1993. Oribatid mites of forest habitats in northern Venezuela. Trop. Zool. (special issue) 1, 39–54.
- Behan-Pelletier, V.M., Clayton, M., Humble, L., 2002. Parapirnodus (Acari: Oribatida: Scheloribatidae) of canopy habitats in western Canada. Acarologia 42, 75–88.
- Buddle, C.M., Beguin, J., Bolduc, E., Mercado, A., Sackett, T.E., Selby, R.D., Varady-Szabo, H., Zeran, R.M., 2005. The importance and use of taxon sampling curves for comparative biodiversity research with forest arthropod assemblages. Can. Entomol. 137, 120–127.
- Colwell, R.K., 2005. EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples. Version 7.5. Persistent URL <purl.oclc.org/estimates>.

- Colwell, R.K., Coddington, J.A., 1994. Estimating terrestrial biodiversity through extrapolation. Philos. Trans.
 R. Soc. London B 345, 101–118.
- Fagan, L.L., Winchester, N.N., 1999. Arboreal arthropods: diversity and rates of colonization in a temperate montane forest. Selbyana 20, 171–178.
- Franklin, J.F., Van Pelt, R., 2004. Spatial aspects of structural complexity on old-growth forests. J. Forest. 102, 22–27.
- Karasawa, S., Hijii, N., 2004. Effects of microhabitat diversity and geographical isolation on oribatid mite (Acari: Oribatida) communities in mangrove forests. Pedobiologia 48, 245–255.
- Krantz, G.W., 1978. A Manual of Acarology. Oregon State University, Corvallis.
- Lindo, Z., Visser, S., 2004. Forest floor microarthropod abundance and oribatid mite (Acari: Oribatida) composition following partial and clear-cut harvesting in the mixedwood boreal forest. Can. J. For. Res. 34, 998–1006.
- Meidinger, D., Pojar, J., 1991. Ecosystems of British Columbia. BC Ministry of Forests, Victoria, British Columbia.
- Nadkarni, N.M., 1994. Diversity of species and interactions in the upper tree canopy of forest systems. Amer. Zool. 34, 70–78.
- Nadkarni, N.M., Longino, J.T., 1990. Invertebrates in canopy and ground organic matter in a neotropical montane, Costa Rica. Biotropica 22, 286–289.
- Nadkarni, N.M., Matelson, T.J., 1991. Fine litter dynamics within the tree canopy of a tropical cloud forest. Ecology 72, 2071–2082.
- Nicolai, V., 1993. The arthropod fauna on the bark of deciduous and coniferous trees in a mixed forest of the Itasca State Park, MN, USA. Spixiana 16, 61–69.
- Paoletti, M.G., Taylor, R.A.J., Stinner, B.R., Stinner, D.H., Benzing, D.H., 1991. Diversity of soil fauna in the canopy and forest floor of a Venezuelan cloud forest. J. Trop. Ecol. 7, 373–383.
- Perry, D.R., 1978. A method of access into the crowns of emergent and canopy trees. Biotropica 10, 155–157.
- Petersen, H., Luxton, M., 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. Oikos 39, 287–388.
- Primer 5 for Windows, 2001. Version 5.2.2. Primer-E Ltd.
- Prinzing, A.J., 2001. Use of shifting microclimatic mosaics by arthropods on exposed tree trunks. Ann. Entomol. Soc. Am. 94, 210–218.
- Prinzing, A.J., 2005. Corticolous arthropods under climatic fluctuations: compensation is more important than migration. Ecography 28, 17–28.
- Prinzing, A.J., Woas, S., 2003. Habitat use and stratification of Collembola and oribatid mites. In: Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L. (Eds.), Arthro-

pods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy. Cambridge University Press, Cambridge, pp. 271–281.

- Proctor, H.C., Montgomery, K.M., Rosen, K.E., Kitching, R.L., 2002. Are tree trunks habitats or highways? A comparison of oribatid mite assemblages from hooppine bark and litter. Aust. J. Entomol. 41, 294–299.
- Schowalter, T.D., 1989. Canopy arthropod community structure and herbivory in old-growth and regenerating forests in western Oregon. Can. J. For. Res. 19, 318–322.
- Seyd, E.L., Seaward, M.R.D., 1984. The association of oribatid mites with lichens. Zool. J. Linn. Soc. 80, 369–420.
- Siepel, H., 1996. The importance of unpredictable and short-term environmental extremes for biodiversity in oribatid mites. Biod. Letters 3, 26–34.
- Simberloff, D., 1976. Experimental zoogeography of islands: effects of island size. Ecology 57, 629–648.
- Spain, A.V., Harrison, R.A., 1968. Some aspects of the ecology of arboreal cryptostigmata (Acari) in New Zealand with special reference to the species associated with *Olearia colensoi* Hook.f. N. Z. J. Sci. 11, 452–458.
- SPSS for Windows, 2001. SPSS Advanced Statistics 11.0. SPSS Inc., Chicago, Illinois.
- Wallwork, J.A., 1983. Oribatid mites in forest systems. Annu. Rev. Entomol. 28, 109–130.
- Walter, D.E., O'Dowd, D.J., 1995. Beneath biodiversity: factors influencing the diversity and abundance of canopy mites. Selbyana 16, 12–20.
- Wardle, D.A., Yeates, G.W., Barker, G.M., Bellingham, P.J., Bonner, K.I., Williamson, W.M., 2003. Island biogeography and ecosystem functioning in epiphytic soil communities. Science 301, 1717–1720.
- Winchester, N.N., Behan-Pelletier, V.M., 2003. Fauna of suspended soils in an Ongokea gore tree in Gabon. In: Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L. (Eds.), Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy. Cambridge University Press, Cambridge, pp. 102–109.
- Winchester, N.N., Behan-Pelletier, V.M., Ring, R.A., 1999. Arboreal specificity, diversity and abundance of canopy-dwelling oribatid mites (Acari: Oribatida). Pedobiologia 43, 391–400.
- Wunderle, I., 1992. Arboricolous and edaphic oribatids (Acari) in the lowland rainforest of Panguana, Peru. Amazoniana 12, 119–142 (translated from German to English by the Government of Canada).
- Yanoviak, S.P., Walker, H., Nadkarni, N.M., 2004. Arthropod assemblages in vegetative vs. humic portions of epiphyte mats in a neotropical cloud forest. Pedobiologia 48, 51–58.