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Canopy Oribatida: Tree specific or microhabitat specific?

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ABSTRACT

A diverse assemblage of oribatid mites inhabits the canopy of coniferous trees in western North America. We tested the hypothesis that oribatid mites are microhabitat specific in old-growth Douglas fir, Western hemlock and western redcedar at the Wind River Crane Canopy Research Facility, Washington, USA. The upper 3 m of canopy of the three tree species were accessed using the canopy crane. Oribatida were extracted from 4 to 12 g dwt samples of alecterioid and foliose lichens using the twig-washing technique. Overall species richness was low, 16 species representing 11 families, with no species unique to this site. Species were absent from samples taken contemporaneously from the forest floor. All oribatid species were found in foliose lichens, whereas only nine species, in seven families, were recovered from alecterioid lichens. Oribatid species richness was lichen specific depending on the tree species. On Western hemlock both lichens supported similarly rich communities, but on Douglas fir and western redcedar foliose lichens supported the richer community.

1. Introduction

An abundant, free-living mite fauna inhabits temperate and tropical canopies [25]. When adequate sampling methods are used, mites of the suborder Oribatida are often found to be more numerous than other arboreal arthropods, including insects, and often as species rich [3]. For example, Oribatida represented 86% of the arthropods of lichens on the bark of Red oak in USA [24], 34% of arthropods extracted from bark and epiphytes in a beech-hornbeam forest [1], and about 60% of microarthropods extracted from suspended soils of western redcedar [12].

The litter oribatid mite fauna traditionally has been considered the source of canopy diversity, with specimens dispersing from the litter and reaching the canopy by climbing the trunk highway. This view overlooks the distinctness of the arboreal oribatid fauna, emphasized since the early 1960s [3]. More recently, the myth of tree trunks as highways has been challenged, with only one, of 31 oribatid morphospecies found in both ground litter and bark habitats [19]. Furthermore, a clear separation of the corticolous and ground oribatid mite community is evident at the 4 m height on the trunk of western redcedar [13].

The distinct assemblage of oribatid mites that inhabits the canopy of coniferous trees in western North America has been used as one of arguments for conservation of these old-growth forests [27]. There is evidence that oribatid assemblages are microhabitat specific first and only secondarily tree species specific in mature forests [17,26]. We tested the hypothesis that oribatid mites are microhabitat specific in

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the canopy of old-growth forest by examining assemblage structure on two different lichen functional groups (alecterioid and foliose lichen) in the canopy of three conifer species, Western hemlock, Douglas fir and western redcedar at the Wind River Crane Canopy Research Facility, Washington, USA. This Facility provides access to a range of mature coniferous tree species all located in the same landscape. Of the four functional groups of lichens in conifers at this site [15] only alecterioid and foliose lichens were available for destructive sampling in the upper canopy.

2. Materials and methods

2.1. Site description

Wind River Crane Canopy Research Facility (WRCCRF) is located within the Gifford Pinchot National Forest, Washington, USA (45°49′N, 121°57′W) at an elevation of 355 m. This area is dominated by 275–500-year-old Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco) (DF) and Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (WH), with the tallest trees averaging 55–65 m (maximum 67 m). Other tree species include western redcedar (*Thuja plicata* Donn) (RC). WRCCRF old-growth forest is located within the Wind River valley on gentle topography (<10% slope). The 4-ha crane plot was installed in 1994. The canopy crane has a height of 87 m (http://depts.washington.edu/wrccrf/), and its gondola can be maneuvered throughout the forest canopy.

Epiphytes in the canopy of trees at the WRCCRF were described in Ref. [15]. Alecterioid lichens are pendulous species and include mainly *Alectoria* sp. and *Usnea* sp. at this site, whereas foliose lichens included *Hypogymnia* and *Platismatia* spp.

2.2. Acari sampling and extraction

Three samples, ca. 10 cm × 10 cm, of each of alecterioid and foliose lichens were removed from branches and/or trunk in the upper 3 m of canopy of each of three tree species: Douglas fir (trees 1030, 1014, 1037), Western hemlock (trees 1048, 1054, 1225) and western redcedar (trees 119, 137, 3096) on 29 September 2000, using canopy crane access. Trees were chosen for similarity in height and diameter at breast height (DBH). Data for each tree are given in Table 1. Replication was three samples of each of two types of lichen/tree × three tree species × three trees of each species = 54 samples.

Individual lichen samples were washed for 24 h in a weak NaOH and water solution (10 NaOH pellets/4 L water). The samples were sieved through screens of 1 cm^2 and 52 μm. Arthropods were sorted from the retained debris, and stored in 75% EtOH. The lichen for each sample was oven dried and weighted to provide dry weight. Adult and immature oribatid mites were identified to species, and abundances 10 g^{-1} given in Table 1 include all stages present.

Ten litter and soil samples of approximately 10 cm × 10 cm × 5 cm depth were taken in the 4 ha canopy plot on the same date as the canopy samples and mites were extracted using modified Berlese funnels.

2.3. Statistical analysis

Statistics were performed and figures generated using R 1.9.1 [20]. Comparisons of log-transformed oribatid species richness (g dwt^{-1}) between tree species and lichen types were performed by analysis of variance (ANOVA) using a linear mixed effects model (function lme of package nlme) with the subject tree entered as a random effect and lichen type repeated within subject tree. Untransformed data are presented in figures as means ± standard error. No suitable transformation of oribatid mite abundance (g dwt^{-1}) could be found (based on Bartlett's test for homogeneity of variance and inspection of residuals), thus a Kruskal–Wallis rank sum test (K–W) was used (function kruskal.test) to compare oribatid abundance between tree species for each lichen type independently. Post hoc comparisons were performed as pairwise *t*-tests with *p*-values adjusted for multiple comparisons using the fdr method [5].

Canonical correspondence analyses (CCA) [6] was performed using function CCA of package vegan. Oribatid species of low occurrence (singletons and doubletons) were removed from the data set prior to analysis. Abundance of oribatid species was entered as raw values and the effect of lichen dry weight and tree subject sampled from were partialled out as a co-variables. Lichen type, tree species and tree DBH were entered as environmental factors. Significance of results was determined using Monte Carlo permutations (1000). CCA plots were not scaled and only environmental factors with a significance of $P < 0.1$ are shown.

Table 1 – Wind River Crane Canopy Research Facility tree data, mean size of lichen samples and mean oribatid abundance (DBH, diameter (cm) at breast height (1.3 m)

	Tree Number (cm)	DBH (cm)	Height (m)	Foliose lichen g dwt ($n = 3$)	Oribatida (10 g dwt^{-1})	Alecterioid lichen g dwt ($n = 3$)	Oribatida (10 g dwt^{-1})
Douglas fir	1030	111	53.3	5.6	135	14.2	12
	1014	93.4	50.6	6.5	148	8.1	36
	1037	112.8	54.5	5.1	33	8.4	8
Western hemlock	1048	97.4	53.5	13.9	82	8.2	7
	1054	84.9	48.2	9.9	139	3.9	10
	1225	87.3	49.6	7	80	11.7	5
Redcedar	119	126.5	48.0	5.1	43	5	3
	137	144	54.3	10.9	11	7.3	1
	3069	114.5	44.4	4.8	30	4.7	2

3. Results

3.1. Oribatid assemblage structure

Oribatid mites dominated the arthropod fauna of both foliose and alecterioid lichen types, in terms of species richness and abundance. Sixteen oribatid species in 11 families were recorded (Table 2); however, data for the three species of *Camisia* were combined, as immatures are difficult to separate. Abundance ranged from an average of one oribatid mite 10 g dwt^{-1} in alecterioid lichen on western redcedar to 148 oribatid mites 10 g dwt^{-1} dwt in foliose lichen on Douglas fir (Table 1). None of the oribatid species found in foliose or alecterioid lichens was found in samples taken contemporaneously from forest floor soil and litter in the 4 ha crane site.

3.2. Habitat specificity

Among Oribatida, *Camisia* spp. had the highest frequency, followed by *Mycobates acuspidatus*, and were found in both lichen types on all tree species, but relative abundance of *Camisia* spp. was higher on alecterioid lichens, whereas that of *M. acuspidatus* was higher on foliose lichens (Table 2). Seven species were only recorded from foliose lichens of which *Eueremaeus acostulatus* and *Anachipteria* sp. had a frequency of >25% (Table 2).

There was an interaction between tree species and lichen type ($t_{39} = -3.00$, $P = 0.005$; Fig. 1) in terms of oribatid species richness (S). Oribatid S was similar in alecterioid lichens from all tree species, but significantly higher in foliose lichens on DF compared with WH ($t_{16} = -3.43$, $P = 0.006$). Oribatid S in foliose lichens from RC was intermediate between DF and WH.

The abundance of oribatid mites was greater on foliose compared with alecterioid lichens ($\chi^2_1 = 26.1083$, $P < 0.001$; Fig. 2). There was some evidence that abundances differed between tree species as well ($\chi^2_2 = 4.66$, $P = 0.097$).

Canonical correspondence analysis indicated that oribatid communities were significantly influenced by the environmental factors of lichen type and DBH of host trees, but not tree species ($F_{3,\ 10} = 0.744$, $P < 0.01$; Fig. 3). However, only 17% of the total variance in the data was explained by this relationship. Lichen type correlated significantly with the first two canonical axes ($r^2 = 0.32$, $P < 0.002$) as did DBH ($r^2 = 0.39$, $P < 0.002$).

4. Discussion

4.1. Abundance and species richness

Abundance of oribatid mites in the lichens was high, up to 36 specimens 10 g dwt^{-1} and up to 148 specimens 10 g dwt^{-1} in alecterioid and foliose lichens, respectively, in contrast to 43 oribatid mites 1000 g dwt^{-1}, collected by direct sorting from

Table 2 – Relative frequency (%) of oribatid species in canopy samples and relative abundance (%) by lichen type (foliose, alecterioid) and tree species (DF: Douglas fir, WH: Western hemlock; RC: redcedar)

Lichen		Foliose			Alecterioid		
Oribatida	Frequency ($n = 54$)	DF ($n = 3$)	WH ($n = 3$)	RC ($n = 3$)	DF ($n = 3$)	WH ($n = 3$)	RC ($n = 3$)
Camisiidae							
Camisia spp. (*C. horrida* (Hermann), *C. carrolli* André, *C. segnis* (Hermann))	100	6.7	31.5	21.7	42	32	67
Neoliodidae							
Platyliodes macroprionus Woolley & Higgins	22.2	–	0.3	4.5	–	1.8	–
Eremaeidae							
Eueremaeus acostulatus Behan-Pelletier	33.3	7.1	0.3	10.7	–	–	–
Carabodidae							
Carabodes willmanni Bernini	11.1	0.2	–	–	–	12.3	–
Cymbaeremaeidae							
Ametroproctus reticulatus Aoki & Fujikawa	16.7	0.4	2.1	–	–	–	–
Scapheremaeus nr. *palustris* (Sellnick)	38.9	1.0	0.1	3.2	5.5	–	–
Licneremaeidae							
New genus	5.6	–	0.1	–	–	–	–
Achipteriidae							
Anachipteria sp.	38.9	17.8	0.1	22	–	–	–
Oribatulidae							
Phauloppia sp.	83.3	11.7	9.8	11.9	5.3	19	–
Scheloribatidae							
Parapirnodus hexaporosus Behan-Pelletier et al.	16.7	0.3	0.1	5	–	–	–
Scheloribates sp.	5.6	0.2	–	–	–	–	–
Ceratozetidae							
Jugatala tuberosa Ewing	5.6	0.1	–	–	–	–	–
Neogymnobates marilynae Behan-Pelletier	72.2	3.8	0.3	8.5	22	7	25
Mycobatidae							
Mycobates acuspidatus Behan-Pelletier et al.	83.9	50.7	55	17	25	28	8
Oribatid S/microhabitat		12	11	9	5	6	3

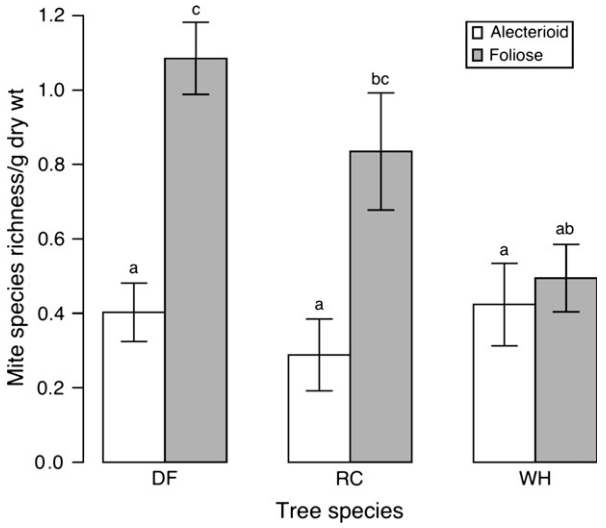

Fig. 1 – Oribatid mite species richness (g dwt^{-1} of lichen) sampled from alecterioid and foliose lichens from the canopies of three species of trees at the Wind River Crane Canopy Research Facility (WRCCRF). Bar heights are means ± 1 standard error. Bars labeled with the same letter were not significantly different ($\alpha = 0.05$). DF = Douglas fir; RC = redcedar; and WH = Western hemlock.

conifer needles [22]. Abundance in these canopy lichens is comparable to that recorded from boreal forest soil [14]. As none of these canopy species was found on the forest floor, and no forest floor species were found in these canopy lichens, faunistic similarity was zero, a very low similarity for temperate forests [18].

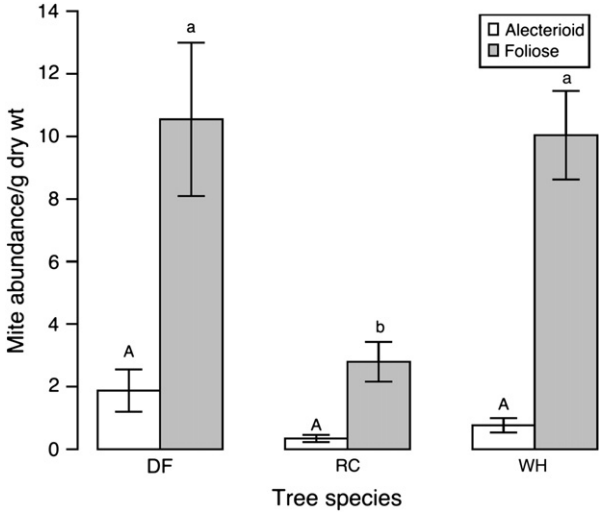

Fig. 2 – Oribatid mite abundance (g dwt^{-1} of lichen) sampled from alecterioid and foliose lichens from the canopies of three species of trees at the Wind River Crane Canopy Research Facility (WRCCRF). Bar heights are means ± 1 standard error. Bars labeled with the same letter, within lichen type, were not significantly different ($\alpha = 0.05$). DF = Douglas fir; RC = redcedar; and WH = Western hemlock.

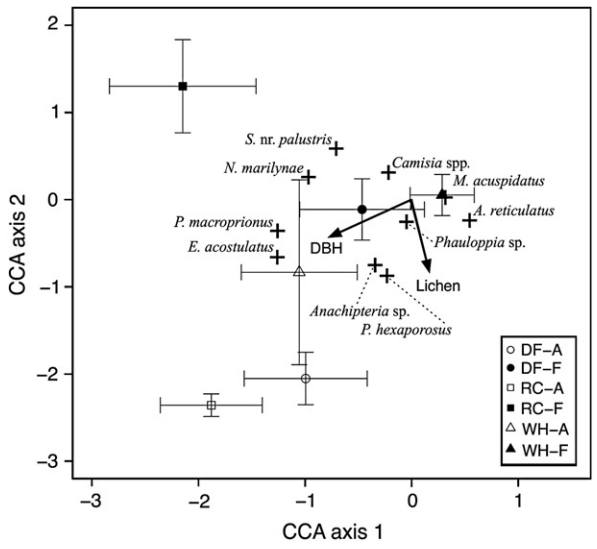

Fig. 3 – First two canonical axes representing the relationship between oribatid mite communities and tree species identity, lichen type (lichen) and diameter at breast height (DBH). Mean sample scores ± 1 standard error are plotted for alecterioid (A) and foliose (F) lichens per tree species (DF = Douglas fir; RC = redcedar; WH = Western hemlock). Plus symbols (+) represent species (see Table 2 for full species names) and vector lines are environmental factors significant at $\alpha = 0.05$.

4.2. *Assemblage structure*

None of the oribatid species collected is unique to the WRCCRF, almost all have been collected from other coniferous canopy habitats [10]. All but two species were represented by both adults and immatures indicating completion of their life-cycles in the lichen environment.

The association of certain oribatid mites with lichens, both as food, and habitat is well known and has been reviewed [23]. Evidence for close lichen–oribatid mite interaction is the vectoring of viable ascospores and photobiont cells of lichen by a lichen feeding oribatid species [16]. The dominant oribatid genus in alecterioid lichens in this study, *Camisia*, also dominates needles and twigs of old-growth Douglas fir [7]. *Camisia* species are parthenogenic, and thus can easily colonize new canopy microhabitats [1]. Species are widely distributed geographically, but are restricted to arboreal habitats [2]. The species *Camisia carrolli* is more abundant in the upper canopy of Douglas fir, but it is more abundant in the lower canopy of Western hemlock [22]. The dominant species in foliose lichens, *M. acuspidatus*, has been collected from twigs and lichens in upper and lower canopy of old-growth Western hemlock and Pacific silver fir [4].

4.3. *Microhabitat specificity*

Oribatid species richness was lichen specific depending on the tree species. On Western hemlock both lichens supported similarly rich communities, but on Douglas fir and redcedar foliose lichens supported the richer community. Similarly,

overall canopy arthropod abundance and community structure were distinct between the four tree species at WRCCRF [22]. Oribatid diversity in the upper canopy was influenced by DBH with WH > DF > RC, but not by overall tree height. This specificity may be related to tree age, data for which were not available for individual trees. The assumption is that older trees have time to develop a more species rich fauna that provides a more diverse pool to colonize microhabitats as these develop over time. The effect of tree age on oribatid assemblage structure is controversial, e.g., *C. carrolli* and five other mite species collected from old-growth (>400 yr.) Douglas fir were absent from regenerating 10 year old trees [21], however, density, diversity, and community structure of Oribatida on the bark of oak trees were not affected by forest age [9]. DBH may also reflect canopy complexity, e.g., there is a strong correlation between DBH and number of large branches for Douglas fir [8]. Structural complexity influences lichen distribution and abundance [8], with the assumption of a more diverse fauna associated with this complexity.

The results of this study support the evidence [11] for sampling multiple microhabitats for assessing overall canopy biodiversity, or for comparing tree canopies. Although often found on the same branches, alecterioid and foliose lichen microhabitats have different oribatid assemblages.

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