

# Scale dependent diversity patterns in arboreal and terrestrial oribatid mite (Acari: Oribatida) communities

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In naturally fragmented, isolated, or patchily distributed habitats that contain non-vagile organisms, we expect dispersal to be limited, and patterns of diversity to differ from similar, yet continuous habitats. We explored the alpha-beta-gamma relationship and community composition of oribatid mites (Acari: Oribatida) inhabiting spatially discrete canopy suspended soils, and compared the patterns of diversity with the continuous forest floor soils over two years. We explored dispersal limitation for oribatid mites in the canopy by using additive partitioning of species richness at multiple spatial scales. ANOSIM was used to demonstrate differences in oribatid mite community composition between the canopy and forest floor habitats over different sampling periods. Community composition of oribatid mites differed significantly between canopy and forest floor habitats, by season and yearly sampling period. Oribatid mite richness and abundance were positively correlated with substrate moisture content, particularly in the canopy. Richness and abundance of ground oribatid mites was greater in September than in June, a trend that is reversed in the canopy, suggesting canopy oribatid mite species may have altered life histories to take advantage of earlier moisture conditions. Alpha diversity of oribatid mites in the canopy was lower than the ground at all sampling levels, and not significantly different from a random distribution in either habitat. Beta diversity was greater than expected from a random distribution at the patch- and tree-level in the canopy suggesting dispersal limitation associated with physical tree-to-tree dispersal barriers, and limited dispersal among patches within a tree. Beta diversity at the tree-level was the largest contribution to overall species richness in both canopy and ground habitats, and was also greater than expected on the ground. These results suggest that factors other than physical dispersal barriers, such as aggregation, habitat availability, and environmental factors (moisture), may limit the distribution of species in both habitats.

Recent research in community ecology has attempted to integrate local and regional processes, focussing on the roles that spatial configuration of habitat patches, dispersal of species, and colonization history have on species richness, abundance and community composition (Holyoak and Loreau 2006). In this context, community ecology places importance to the spatial scale at which regional and local factors affect diversity. In spatially discrete habitats, dispersal is a key process linking multiple spatial scales and is an important mechanism leading to colonization and maintenance of diversity within spatially-structured communities (Mouquet and Loreau 2003). Local communities linked by dispersal within a region are termed a metacommunity (Hanski and Gilpin 1991, Wilson 1992, Leibold et al. 2004), and the growing field of metacommunity ecology provides a framework to understand how assemblages of organisms are distributed in space by focusing on the ecological processes of species interactions and dispersal. Although, empirical findings suggest current metacommunity paradigms (Leibold et al. 2004) do not yet satisfactorily explain dynamics in patch systems (Vandvik and Goldberg

2006, Ellis et al. 2006, Vanschoenwinkel et al. 2007). Differential dispersal rates affect species interactions and community composition, acting as diversity-maintaining or diversity-generating processes (Vandvik and Goldberg 2005). Theoretical models have shown that increased dispersal has a unimodal effect on alpha diversity, an overall decreasing effect on beta diversity, and a delayed decreasing effect on gamma diversity (Mouquet and Loreau 2003). At high dispersal rates the effect of spatial subdivision is reduced and the metacommunity collapses into a single large community with local scale processes determining community composition (Mouquet and Loreau 2003). These predictions are supported empirically by Cadotte (2006) and the studies therein.

Dispersal is limited in naturally fragmented, isolated, or patchily distributed habitats that contain sessile or non-vagile organisms, surrounded by highly contrasting environmental matrices (e.g. islands, ponds, reefs), (Shepherd and Brantley 2005). In turn, we would expect lower alpha diversity within habitat patches, and higher beta diversity among habitat patches compared to a similar, continuous

habitat. For example, Tsurumi (2003) found gamma diversity of benthic invertebrates at hydrothermal vents was similar in patchy versus continuous habitats, but beta diversity was greater in patchy areas, while alpha diversity was greater in continuous habitat. Additionally, patchy habitats may also experience increased influence of edges creating unfavourable abiotic conditions, such as moisture limitation or temperature extremes, further limiting local diversity (Ewers and Didham 2006).

Here we explore the alpha-beta-gamma relationship for a prototypical metacommunity of arboreal habitats called suspended soils. Suspended soils are accumulations of decomposing organic matter and epiphytes within tree crowns (Moffet 2000). In western redcedar trees of the Pacific Northwest, suspended soils are spatially discrete habitats, separated from one another within the tree crown by a barren bark matrix and between trees by the atmosphere (Lindo and Winchester 2007a). The inhabitants of suspended soil habitats are a species-rich community of microarthropods dominated by oribatid mites (Acari: Oribatida) (Behan-Pelletier et al. 1993, Lindo and Winchester 2006). Oribatid mites are slow-moving (Berthet 1964), and non-phoretic (but see Norton 1980). Observed abundance and richness patterns of oribatid mites in epicorticolous habitats (Lindo and Winchester 2007b), and in aerially circulated substrates like litter and litterfall (Lindo and Winchester 2008) suggest between-suspended soil patch (bark) and between-tree (atmosphere) dispersal barriers are prominent. We investigate evidence of dispersal limitation in the canopy by comparing patterns of oribatid mite diversity in the fragmented arboreal suspended soil habitat with patterns of diversity in continuous forest floor soil habitats.

The objective of this paper is to examine oribatid mite community composition and the relationship between alpha-beta-gamma diversity in each habitat (canopy suspended soil and forest floor soil). We explore how diversity components change over a moderate spatial scale using a nested hierarchical sampling design, testing for scale-dependence in the observed alpha and beta species richness at each hierarchical level, and ask whether oribatid mite communities in arboreal suspended soils show evidence of dispersal limitation demonstrated as higher between-patch and between-tree-levels of beta diversity compared to forest floor communities. Additionally, we use measures of moisture content to hypothesize that canopy suspended soils and forest floor soils will differ in overall abundance, richness and composition of microarthropods, and this difference will be more pronounced during times of moisture limitation in the canopy.

## Materials and methods

### Study area and sampling design

The study area is located in the temperate rainforest of the Walbran Valley on the southwest coast of Vancouver Island, British Columbia, Canada (48°39'N, 124°35'W). The Walbran Valley is typical of the Coastal Western Hemlock biogeoclimatic zone (Meidinger and Pojar 1991) and the dominant conifers are: western hemlock *Tsuga heterophylla*,

sitka spruce *Picea sitchensis*, silver fir *Abies amabilis*, and western redcedar *Thuja plicata*. The study area within the Walbran Valley has a high density of ancient (>800 yr) western redcedar trees that have a distinct, multi-furcated trunk morphology resembling a candelabrum. The branching structure of trunk reiterations allows for the accumulation of organic matter within tree crowns, and forms many discrete, isolated patches of arboreal habitat referred to as suspended soils (Lindo and Winchester 2006). Suspended soils are typically located high in the canopy (ca 35 m) and range in size from 100 to 20 000 cm<sup>2</sup> (Lindo and Winchester 2007a). Substrate from individual suspended soils and forest floor locations associated with six western redcedar trees were repeatedly sampled for oribatid mites bi-annually (June and September) over two and a half years (Sept. 2004–Sept. 2006). The suspended soils and forest floor locations are described in Lindo and Winchester (2006).

Based on the natural spatial discreteness of the arboreal suspended soil habitat system, we partitioned the sampling of suspended soil and forest floor locations into four nested spatial levels: 1) the smallest spatial sampling level consisted of individual core samples (160 series PVC corers, 3.175 cm diameter, average depth 7 cm) of substrate from suspended soil patches or forest floors (core-level); 2) the next spatial level (patch-level) included the three replicate core samples nested within individual suspended soil patches or cardinal localities on the forest floor, 1.5 m from the base of the tree trunk; 3) the tree-level spatial scale included the four spatially discrete habitat patches (suspended soils in the canopy of each tree and four cardinal locations on the forest floor surrounding each tree); and 4) the largest hierarchical spatial scale (habitat-level) consists of all samples pooled within the arboreal or terrestrial system among all six western redcedar trees sampled within the study area. One hundred and forty-four core samples were collected during each sampling period (72 from the canopy, 72 from the forest floor) for a total of 720 core samples collected over five sampling periods (Sept. 2004, June 2005, Sept. 2005, June 2006, Sept. 2006). The same suspended soil patches and forest floor locations associated with each tree were re-sampled at each collection time. Sampling depleted the soil within patches, however, the size of the samples were relatively small with respect to the overall size of the patch. Patches were selected a priori so they were large enough to support repeated sampling and to ensure that sampling had little effect on the overall structural integrity of the suspended soil patch.

Microarthropods were extracted from soil core samples using modified Berlese funnels (Lindo and Winchester 2006). Moisture content of each core sample was estimated gravimetrically by measuring soil weight prior to (wet weight) and following (dry weight) microarthropod extraction. Extracted microarthropods were sorted into three taxonomic groups, mites (Acari), springtails (Collembola) and other microarthropods. The Acari were further identified to suborder (Mesostigmata, Prostigmata, Astigmata and Oribatida) and all adult oribatid mites were identified to species. Voucher specimens are deposited at the Canadian National Collections in Ottawa, Canada.

## Statistical analyses

The generally accepted forms of the alpha-beta-gamma relationship are  $\gamma = \alpha \times \beta$  (Whittaker 1960) and  $\gamma = \alpha + \beta$  (Lande 1996) where  $\alpha$  is the local richness of sites within the region, and  $\beta$  is a measure of the variation in species composition among sites. Using the additive form of the relationship, all components of total diversity share the same units (number of species) (Lande 1996), and additive partitioning methods (Gering and Crist 2002) can be used to explore the relative contribution of alpha and beta diversity to gamma diversity. Using the additive partitioning approach (Lande 1996), total oribatid mite diversity (gamma diversity ( $\gamma$ )) within each habitat during each sampling period was calculated as the sum of alpha diversity ( $\alpha_1$ ) within each core sample, beta diversity ( $\beta_1$ ) among core samples, beta diversity ( $\beta_2$ ) among patches, and beta diversity ( $\beta_3$ ) among trees:

$$\gamma_{\text{(total diversity)}} = \alpha_{1(\text{within cores})} + \beta_{1(\text{among cores})} + \beta_{2(\text{among patches})} + \beta_{3(\text{among trees})}$$

Alpha diversity can also be calculated at each hierarchical level because within- and between-community diversity are linked additively to form the next highest level (Wagner et al. 2000), so that  $\alpha_1 + \beta_1 = \alpha_2$  or, more generally,  $\alpha_n = \alpha_{n-1} + \beta_{n-1}$ . We used PARTITION (Veech and Crist 2007) to perform these calculations and to test for the presence of any scale dependent spatial patterns of oribatid mite species richness across hierarchical levels for the canopy and forest floor data sets. Specifically, we test the null hypothesis that the observed alpha and beta species richness at each hierarchical level were not significantly different from those obtained from a random distribution of oribatid mite species among samples at all hierarchical levels (i.e. no scale-dependence). We used the complete randomization procedure option in PARTITION to generate 10 000 random distributions of oribatid mite species among samples at all hierarchical levels to form the null distribution of each alpha and beta estimate for each level within the hierarchy. PARTITION then tests the observed diversity components (alpha, beta) at each level to the expected mean diversity component values generated by assessing the proportion of null values that were greater or less than the actual estimate. Our highest hierarchical scale of analysis was at the habitat scale (canopy, ground) rather than the total diversity for the entire data set that would include both arboreal and ground habitats (whole site), which would bias within-habitat scale comparisons because

we know arboreal and ground habitats differ significantly in species composition (Lindo and Winchester 2006).

A repeated measures nested analysis of variance (RM-ANOVA) was used to test the main effects of habitat (canopy, ground) (nested with tree) and sampling time on the abundance and richness of oribatid mites, and moisture content of the soil core samples followed by a Scheffé's post hoc test on the significant variables. Oribatid mite abundance and richness was standardized on a number per g dry weight basis, and tested for normality using Leven's test. Oribatid mite species richness was  $\log(x+1)$  transformed to correct for non-normal data. Pearson's correlation analyses were performed to assess the relationship between abundance, richness and moisture content for canopy suspended soil and forest floor habitats for pooled sample times. All analyses were performed using STATISTICA 7.0 (StatSoft 2004) with an alpha value of 0.05.

Examination of the differences in species composition between canopy suspended soils and forest floor soils is not covered by additive partitioning methods, therefore, community composition of oribatid mites inhabiting canopy suspended soils and forest floors during the five sampling periods was analysed using standardized abundances (number per g dry weight) of all species recorded for canopy and forest floor samples. We created a community compositional similarity matrix based on Bray-Curtis similarity of square root transformed oribatid mite species for each habitat at each sampling period in PRIMER 5 (Primer-E, primer for windows, ver.5.2.2). Assessment of significance of the random occurrence of a priori main factor effects (habitat, season, year) was based on analysis of similarities (ANOSIM) with 10 000 randomized permutations.

## Results

A total of 118 oribatid mite species from 35 451 individuals were recorded from the canopy suspended soil (83 species, 19 055 individuals) and forest floor (94 species, 16 396 individuals) habitats (Appendix 1). Habitat (canopy, ground) was not a significant factor affecting oribatid mite abundance, however, there was a significant effect of time and a habitat-by-time interaction (Table 1). A significant difference in abundance in canopy habitats occurred during September 2004 and September 2006 (Fig. 1A). Habitat, time and a habitat-by-time interaction were significant factors affecting the richness of oribatid mites (Table 1). Richness was significantly greater in the

Table 1. Results of repeated measures nested ANOVA; effect of habitat (canopy versus ground) and sampling time on oribatid mite species abundance, richness and moisture content of the suspended soil and forest floor substrates.

Variable	Source of variation (DF)	SS	F	p
Total abundance	Habitat (6,36)	945.09	1.881	0.111
	Time (4,144)	936.81	16.223	<0.001
	Time $\times$ Habitat (24,144)	737.60	2.129	0.003
Species richness	Habitat (6,36)	30.70	5.896	<0.001
	Time (4,144)	10.49	10.902	<0.001
	Time $\times$ Habitat (24,144)	11.91	2.062	0.005
Moisture content	Habitat (6,36)	$109 \times 10^4$	27.148	<0.001
	Time (4,144)	$62 \times 10^4$	118.710	<0.001
	Time $\times$ Habitat (24,144)	58 284	1.835	0.016

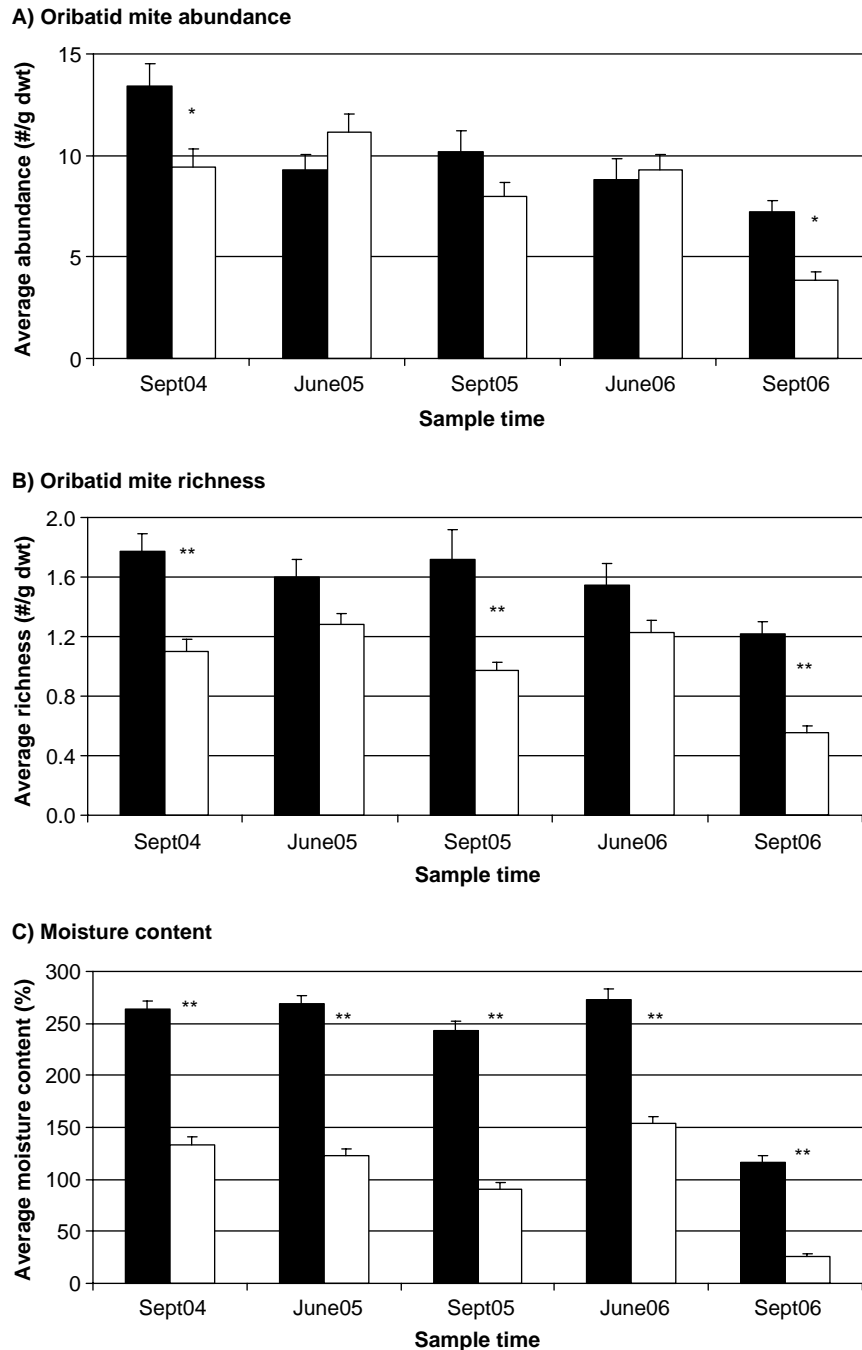


Fig. 1. Average (A) oribatid mite abundance (number individuals per g dry weight of substrate), (B) oribatid mite species richness and (C) moisture content (percentage of dry weight) in canopy suspended soil and forest floor habitats over five sampling periods. Bars are SE. \*denotes significant difference between canopy and ground habitats during individual sampling periods (\* $p < 0.05$ , \*\* $p < 0.001$ ). Legend is: ■ forest floor, □ suspended soil.

forest floor soils compared to the canopy suspended soils (Fig. 1B). With the exception of September 2006, ground and canopy habitats showed reverse seasonal trends, albeit weak, with richness being greater in September vs June in ground habitats and greater in June vs September in canopy habitats. For both ground and canopy habitats, richness was significantly reduced in the September 2006. Moisture content of the canopy and ground soils differed significantly, with consistently greater moisture content found in forest floor soils (ca 2 times greater than in the canopy

suspended soils). A significant decrease in moisture content in both the canopy and the ground occurred in September 2006 (Table 1, Fig. 1C). Oribatid mite abundance and species richness were significantly, positively correlated with the moisture content of the substrates over all sampling times (abundance: suspended soil  $R^2 = 0.384$ ,  $p < 0.001$ , forest floor  $R^2 = 0.227$ ,  $p < 0.001$ ; richness: suspended soil  $R^2 = 0.355$ ,  $p < 0.001$ , forest floor  $R^2 = 0.125$ ,  $p = 0.018$ ). Community composition of oribatid mite assemblages in canopy suspended soils and forest floor soils were

significantly different (41% similarity) based on ANOSIM in the Bray-Curtis similarity matrix (Global  $R = 1.00$ ,  $p = 0.008$ ) (Fig. 2). ANOSIM showed no significant effect of time (season or year) on community composition.

Alpha, beta and gamma diversity were greater in forest floor soils when compared to canopy suspended soils at all spatially nested levels (core, patch, tree, habitat) with the exception of tree-level beta diversity, which was similar between the two habitats (Table 2). Beta diversity at the tree-level was the largest contribution to overall species richness in both arboreal and ground habitats, and contributed 50% on average of the total species richness in the canopy and 40% on the forest floor (Fig. 3). The observed beta diversity at the tree-level ( $\beta_3$ ) was significantly greater than expected from random for canopy and forest floor habitats at all sampling times (Table 2). Beta diversity at the patch-level ( $\beta_2$ ) was significantly greater than random in canopy habitats at all times except September 2006, and ground habitats in all but June 2005 and September 2006 (Table 2).

## Discussion

Higher oribatid mite species richness and abundance in forest floor soils when compared with canopy habitats is well documented (Behan-Pelletier and Walter 2000) and supported in this study. Regardless, we report the second highest record of oribatid mite species richness in a canopy habitat world-wide. The parameters that contribute to increased richness in forest floor soils (depth, heterogeneity, moisture-holding) also apply to the various canopy habitats (e.g. branch tips, lichens, moss mats, suspended soils), but on a smaller localised scale, and records of high species richness and abundance of oribatid mites in rainforest canopies is always associated with the presence of complex and heterogeneous habitats such as suspended soils (Wunderle 1992, Behan-Pelletier et al. 1993). Observed seasonal variation in oribatid mite species richness and abundance, although confounded by yearly variations in this study, may be related to specific life history of species or seasonal reproduction (Siepel 1994), combined with an interactive effect of moisture availability, particularly in the

canopy compared to the forest floor. The peak richness and abundance earlier in the season (June) for canopy oribatid mites suggests they may have altered life histories (Norton 1994) compared to ground species to take advantage of early moisture conditions. Moisture regimes and humidity of microhabitats are fundamental factors influencing the diversity, abundance and distribution of oribatid mites (Siepel 1996). Reductions in both abundance and richness of the canopy oribatid mite community occurred during September 2006, and forest floor and suspended soils were extremely dry during this sampling period, compared with other sampling times. The amount of rainfall in July and August of 2006 was exceptionally low, only 12% of the average rainfall during the same months in 2004 and 2005, producing extremely dry conditions at the time of sampling in September 2006 (Environment Canada 2007).

We observed habitat (ground, canopy) and seasonal trends in the community composition of oribatid mites. Community dissimilarity (high complementarity) is well documented in oribatid mite canopy/ground comparison studies (Wunderle 1992, Behan-Pelletier et al. 1993, Winchester et al. 1999, Karasawa and Hiji 2004), and the number of unique canopy species (20% of total) 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, corroborating earlier findings (Lindo and Winchester 2006). The Bray-Curtis indices for arboreal and terrestrial habitats over five sampling periods show low (41%) overall similarity, but similarity is high among the different sampling periods within each habitat.

Exploring how overall patterns of community composition and diversity change across spatial and temporal scales is important for conservation of biodiversity as it may reveal the sources of diversity (Veech et al. 2002) and elucidate the processes that create or maintain diversity (Gering et al. 2003, Noda 2004). Using the additive diversity partitioning approach, total oribatid mite diversity (gamma diversity ( $\gamma$ )) within each habitat during each sampling period was decomposed into alpha and beta diversity components at the level of core sample, patch and tree. Greater forest floor gamma diversity was facilitated by the higher observed

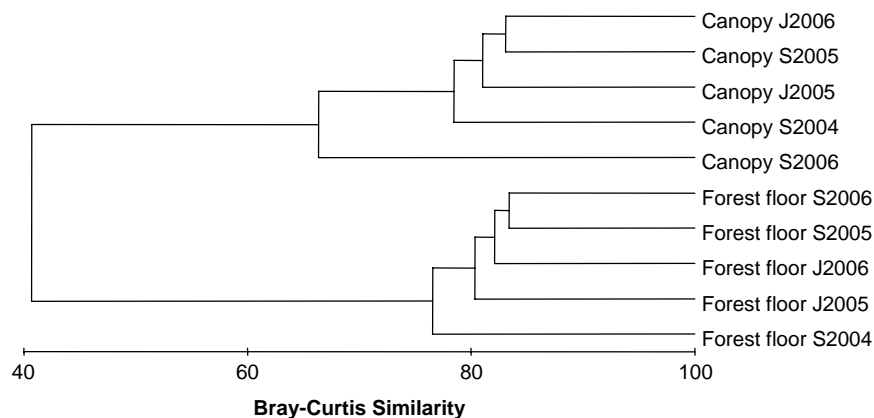


Fig. 2. Similarity dendrogram of oribatid mite community composition in canopy suspended soils and the forest floor soils associated with western redcedar trees in the Walbran Valley, Vancouver Island, Canada. Values are based on Bray-Curtis percent similarity indices of 118 oribatid mite species abundances collected over five sampling periods (J = June, S = September; 2004–2006).

Table 2. Additive partitioning results for oribatid mite communities in canopy suspended soil and forest floor soils. Significance of observed diversity partitioning is based on expected values generated from 10 000 random permutations using PARTITION software. Values represent absolute ( $\gamma$ ) or average ( $\beta_3$ ,  $\beta_2$ ,  $\beta_1$ ,  $\alpha_1$ ) richness components within each hierarchical sampling scale.

	Total ( $\gamma$ )	Tree ( $\beta_3$ )	Patch ( $\beta_2$ )	Core ( $\beta_1$ )	Core ( $\alpha_1$ )
Canopy suspended soils					
September 2004	55	27.3**	11.8**	4.3	11.6
June 2005	57	29.0**	12.9**	4.6	10.5
September 2005	45	21.8**	9.9**	4.0	9.3
June 2006	51	24.9**	11.3**	4.2	10.6
September 2006	47	25.4**	10.0	3.7	7.9
Forest floor soils					
September 2004	71	29.9**	16.3**	9.2	15.6
June 2005	63	27.3**	15.1	7.9	12.7
September 2005	63	24.3**	16.4*	8.1	14.2
June 2006	63	26.3**	16.9*	8.0	11.8
September 2006	58	23.0**	13.9	7.7	13.4

\*denotes significantly different from expected (\* $p < 0.05$ , \*\* $p < 0.001$ ).

alpha diversity in forest floor habitats at all nested sublevels (core, patch and tree) compared to the canopy habitat. Factors which contribute to high forest floor gamma diversity, as discussed previously (increased area, depth, spatial heterogeneity, moisture-holding), are generated at these smaller spatial scales and demonstrate the interactive relationship between local and regional diversity.

How gamma diversity is partitioned into alpha and beta diversity components depends on the absolute spatial scale of observation (Loreau 2000, Stendera and Johnson 2005), and has been linked to particular ecological processes, such as dispersal (Gering and Crist 2002), or life history characteristics such as niche-breadth (Summerville et al. 2006). Observed alpha diversity at all levels in both habitats conformed to the expected values of a null distribution, but the observed beta diversity at the patch-level and at the tree-level were often greater than expected in both habitats. We expected patch- and tree-level beta diversity to be high in the canopy because the canopy habitat is more spatially heterogeneous with discrete patches of habitat creating increased dispersal barriers for oribatid mites compared to

the forest floor. A clear dispersal barrier for canopy suspended soil-dwelling oribatid mites exists at the tree-to-tree-level, suggesting high beta diversity at the tree-level in the canopy is generated by dispersal limitation (Freestone and Inouye 2006). Cursorial movement by canopy oribatid mites to travel from tree-crown to tree-crown is not likely since there is low similarity of canopy/ground communities and many species are restricted to one habitat or the other (Lindo and Winchester 2006, 2007b). Oribatid mites are not known phoronts (but see Norton 1980, and Krivolutsky and Lebedeva 2004), thus a passive dispersal mechanism such as aerial plankton or an abiotic dispersal vector (Lindo and Winchester 2008) is a more probable means of tree-to-tree dispersal. Similarly, low oribatid mite species richness and abundance in epicorticolous habitats between suspended soil patches (Lindo and Winchester 2007b) suggests limited cursorial inter-patch dispersal within trees.

Greater tree- and patch-level beta diversity may indicate dispersal limitation in the canopy, however, we observed higher than expected tree- and patch-level beta diversity in

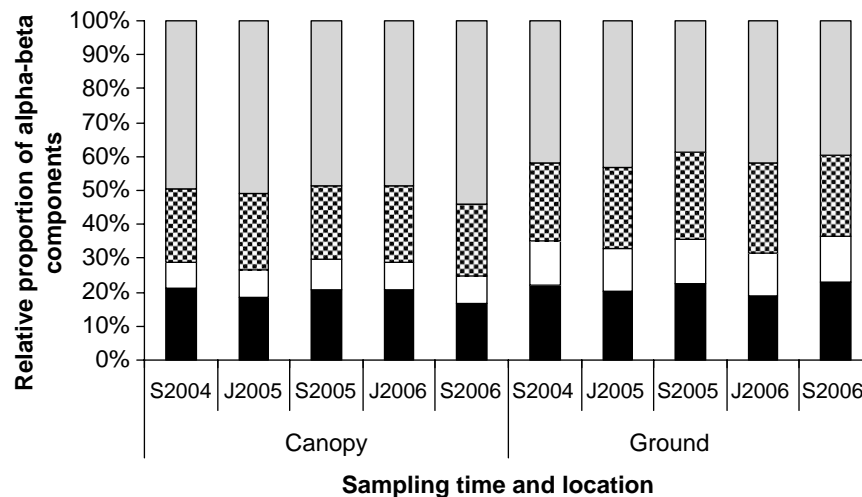


Fig. 3. Proportion of diversity components alpha and beta to overall gamma diversity of oribatid mites in canopy and ground habitats associated with western redcedar trees on Vancouver Island, British Columbia, over five sampling periods (see Fig. 2). Legend is: ■ core ( $\alpha_1$ ), □ core ( $\beta_1$ ), ■ patch ( $\beta_2$ ), ■ tree ( $\beta_3$ ).

the continuous forest floor habitat. Consequently, we must acknowledge that factors other than dispersal barriers may limit the distribution of species in both habitats. These factors may include the availability of suspended soil habitat (Lindo and Winchester 2007a), intraspecific aggregation (Veech 2005), or species-specific microhabitat associations (niche-partitioning). Aggregation of individuals within a species has been shown to decrease alpha diversity and inflate beta diversity (Veech 2005), and soil microarthropods with their small body size and low mobility are known aggregates (Giller 1996). Additionally, higher beta diversity on the forest floor may be maintained by species-specific microhabitat associations (Aoki 1967), even at spatial scales as small as the patch-level. Thus, we need explicit information on species-specific dispersal characteristics, and short and long-range dispersal patterns, as well as factors that control and maintain intraspecific aggregation patterns for oribatid mites to distinguish among potential processes limiting diversity. Additionally, while the canopy and ground oribatid mite communities share some species in common (ca 40% of the total system species richness), the suspended soils and forest floors differ in the majority of their constituent species, therefore closer examination of shared taxa or experimental manipulations within each community are needed to explicitly test dispersal limitation.

Fagan et al. (2006) found that the oribatid mite community in a montane forest canopy had greater beta diversity and lower alpha diversity than ground habitats, which they attributed to low and patchy resource availability and greater abiotic extremes in the canopy. If habitat patches are relatively permanent and large with respect to the tempo-spatial scale of the organism, a species could persist by remaining within the patch without dispersal from external sources. We believe this may be the case for very large suspended soil patches as community heterogeneity increases with decreasing size of suspended soil patch (Lindo and Winchester 2007a), and very small patches are likely too small to sustain populations without reoccurring colonization events, particularly if extinction is driven by deterministic means such as abiotic conditions of low moisture. The difference in alpha and beta diversity patterns in arboreal and terrestrial oribatid mite communities thus may be related to processes that drive these local-scale extinction processes (Layou 2007), in combination with physical dispersal limitations and aggregation tendencies.

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