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An experimental assessment of biodiversity and species turnover in terrestrial vs canopy leaf litter

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Abstract Forest canopies support diverse assemblages of free-living mites. Recent studies suggest mite species complementarity between canopy and terrestrial soils is as high as 80–90%. However, confounding variation in habitat quality and resource patchiness between ground and canopy has not been controlled in previous comparative studies. We used experimental litter bags with standardized microhabitat structure and resource quality to contrast the colonization dynamics of 129 mite species utilizing needle accumulations on the ground vs in the canopy of *Abies amabilis* trees in a temperate montane forest in Canada. Mite abundance and species richness per litter bag were five to eight times greater on the ground than in the canopy, and composition differed markedly at family-, genus-, and species-level. Seventy-seven species (57%) were restricted to either ground or canopy litter bags, but many of these species were rare ($n < 5$ individuals). Of 49 'common' species, 30.6% were entirely restricted to one habitat, which is considerably lower than most published estimates. In total, 87.5% of canopy specialists had rare vagrants on the ground, whereas only 51.9% of ground specialists had rare vagrants in the canopy. Canonical correspondence analysis of mite community structure showed high species turnover through time and a high degree of specialization for early-, mid-, and late-successional stages of litter decomposition, in both ground and canopy mites. In addition, distinct assemblages of ground-specialist mites dominated each elevation (800, 1000, and 1200 m), whereas few canopy-specialist mites had defined elevational preferences. This suggests that canopy mites may have greater tolerance for wide variation in environmental conditions than soil mites. The degree of species turnover between adjacent mountains also differed markedly, with 46.5% turnover of ground species, but 63.4% turnover of canopy species between the two montane areas. While ground and canopy assemblages are similar in total biodiversity, it appears that local mite richness (alpha diversity) is higher on the ground, whereas species turnover between sites (beta diversity) is higher in the canopy.

Keywords Acari · Colonization · Elevation · Forest canopy · Litter bag · Montane · Oribatida · Habitat specialization

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Introduction

Forest canopies intercept nutrients and detritus from host-tree and epiphyte foliage, forming discrete accumulations of suspended litter that serve as habitat and resources for microarthopods such as mites (Schowalter and Ganio 1998). Although forest canopies are known to contain a large proportion of arthropod biodiversity in tropical and temperate ecosystems (Stork et al. 1997; Basset et al. 2003), traditional canopy sampling methods have been inefficient for mite collection (Yanoviak et al. 2003). Consequently, it is only quite recently that the diversity of mites in forest canopies has been well documented (Walter and Behan-Pelletier 1999). The degree of canopy specialization in mites is remarkable (Winchester and Fagan 2000). For example, only 18% of species were found in common between the canopy and the ground oribatid mite assemblages of a Sitka spruce forest in Canada (Winchester 1997). Taxonomic distinctiveness is also pronounced for canopy mites in temperate Japan (Aoki 1973), USA (D.J. Voegtlin unpublished report 1982), northern Venezuela (Behan-Pelletier et al. 1993), and Peru (Wunderle 1992). Many species appear to be restricted to microhabitats associated with ancient forests (e.g. deep moss mats) that are not replicated in second-growth forests (Winchester and Ring 1999).

The diversity and distinctiveness of canopy mite assemblages highlight the importance of linking ground and canopy soil subsystems in ecosystem-level investigations (Wardle et al. 2003; Didham and Fagan 2004). Indirect attempts to relate responses of ground microarthropods to processes occurring in the canopy have shown that assemblage structure in terrestrial litter bags is affected by canopy defoliation, season, and changes in litter quality (Schowalter and Sabin 1991). Litter throughfall from the canopy is a major pathway of nutrient and energy flux, and significantly increases litter microarthropod densities and litter comminution on the ground (Hasegawa 2001; Reynolds et al. 2003). Despite this, most nutrient cycling research takes little or no account of the quantity of suspended litter trapped in the canopy, or of the importance of decomposition processes within canopy microhabitats (Didham and Fagan 2004).

Few studies have directly compared mite species colonizing organic litter on the ground and in the canopy simultaneously (Nadkarni and Longino 1990; Proctor et al. 2002). In many cases, a standard area or volume of canopy material is not always available, or is not directly comparable across microhabitats or sites (Behan-Pelletier and Walter 2000). In other cases, the quantity of material sampled from natural microhabitats has been standardized, but habitat structure and resource quality could not be controlled (Winchester and Behan-Pelletier 2003; Winchester unpublished data), even though these factors are important determinants of variation in mite species composition (Hansen 2000). In this study, microhabitat structure and resource quality were standardized using a series of stratified litter bag experiments to compare the diversity and composition of mites colonizing ground and canopy needle habitats simultaneously. Modelled after earlier ground litter bag experiments, this is the first direct quantitative comparison of the entire mite assemblage inhabiting both canopy and ground habitats in a temperate montane forest.

Hypotheses

Litter bag experiments were designed to test three important determinants of spatial and temporal variation in mite species composition: (1) the degree of spatial partitioning in species composition between ground and canopy (Nadkarni and Longino 1990), (2) the degree of temporal partitioning of litter resources during colonization (Schowalter and Sabin 1991), and (3) large-scale spatial turnover in species composition between elevations and mountains (Walter 1985; Lamoncha and Crossley 1998). We propose three hypotheses:

1. *Hypothesis 1*. As indicated by studies of naturally occurring litter in temperate and tropical forests, there should be a high degree of species complementarity between ground and canopy litter bags.
2. *Hypothesis 2*. Since mite densities are lower in naturally occurring canopy litter (Winchester et al. unpublished data), and canopy litter is more patchily distributed than ground litter, colonization rates in experimental litter bags should be slower in the canopy than on the ground.
3. *Hypothesis 3*. Because canopy litter habitats are more patchy and subject to greater environmental fluctuations than ground litter (Bohlman et al. 1995), canopy mites should exhibit greater dispersal abilities, and thus have lower species turnover across large spatial scales than ground mites.

Methods

Study area

Study sites were located within the Mt. Cain Coastal Montane Biodiversity Project on northern Vancouver Island, British Columbia, Canada (50°13′N, 126°18′W) (R.S. McNay et al. unpublished report 1998) (Fig. S1). Amabilis fir was chosen as the focal tree species in this study because it is one of the dominant conifers in montane areas, and canopy arthropods associated with this early- to mid-seral stage tree (mountain hemlock being the late-successional dominant) have not been documented (see ‘Supplementary materials and methods’ for further details).

Experimental protocol

Experiment I: Mt. Cain, 1997

Single-rope techniques were used to access the forest canopy. In May 1997, a total of 243 litter bags were placed in three amabilis fir trees randomly located at each of three elevations (800, 1,000, and 1,200 m) on Mt. Cain (see Fig. S1). As a common litter substrate, green amabilis fir needle/twig material was collected haphazardly from branches at a range of height from ground to canopy on several trees. The litter was thoroughly mixed and sterilized by freezing and thawing over two separate 24 h periods; then 10 g (±0.1 g) was placed in each litter bag (10×20 cm, with 0.5 mm mesh). The purpose in selecting fresh litter was to provide a standardized common substrate that would naturally be encountered and colonized by mites, both in the canopy and on the ground. Analyses emphasize community structure of mites utilizing needle litter as a food resource, although some organisms may simply use the litter bags for shelter. Styrofoam chips were used as a control to determine whether colonization was due to needle litter resource quality or microclimatic conditions created by the litter bag.

Within each tree, nine litter bags and three control bags were attached at random distances along each of three randomly chosen branches. Previous evidence suggests that some mite species may show strong vertical stratification within tree crowns (Behan-Pelletier and Winchester 1998; Schowalter and Ganio 1998), and that arthropod diversity increases with architectural complexity (Strong et al. 1984). Therefore, all branches sampled were at approximately the same height (30–35 m above ground) to standardize comparisons across trees. Three litter bags and one control bag were also staked to the forest floor beneath each tree to test for differences between ground and canopy species composition.

Three canopy litter bags and one canopy control bag were randomly selected and removed from each branch after 60, 120, and 360 days (beginning May 22, 1997). One ground bag from each tree was also removed during each sampling time. The single ground control bag was removed during one of the three sampling times, chosen at random. An equal number of litter bags were collected within each treatment subgroup (i.e. branches within trees), so that ground sampling effort was equal to within-branch canopy sampling effort at each time interval. Mite abundance varied between litter bags, but this was taken into account in the statistical analyses. A total of 108 canopy litter bags (including controls) and 12 ground litter bags (including control) were collected at each sampling period, placed in plastic Ziploc bags, and stored at 5–10°C for no more than 3 days. Mites were extracted from the needle litter over a 48-h period using a modified Lussenhop extractor that applied thermal gradients to samples (Lussenhop 1971).

Experiment II: Variation between mountains

To determine if similar colonization and elevational trends occurred at other montane sites, two adjacent mountains, Mt. Cain and Mt. Maquilla, were sampled from May through August 1998. The two mountains are 14 km apart and have comparable biogeoclimatic zones at the two elevations tested (800 and 1,200 m, respectively) (R.S. McNay et al. unpublished report 1998). On Mt. Cain the same trees were sampled as those in 1997. One canopy litter bag from each branch and one ground litter bag were removed at random after 30, 60, and 90 days (beginning May 22, 1998).

Acari species identification

Acari were selected for species-level analysis as they are a dominant faunal element of both ground and canopy habitats (Behan-Pelletier and Walter 2000). Adult and immature mites were included in all analyses, whereas exuviae and damaged or unidentifiable specimens were not (see ‘Supplementary materials and methods’ for further details).

Statistical analyses

Abundance and species richness

Abundance and richness data were log-transformed (ln $X+1$) to achieve normality. Analyses of mite abundance and species richness on Mt. Cain during 1997 were performed using nested analysis of covariance (ANCOVA) on log-transformed data with Type III sums of squares, testing the main effects of vertical stratification (CANOPY: ground and canopy), time (TIME: 60, 120, 360 days), elevation (ELEV: 800, 1,000, 1,200 m a.s.l.), and tree within elevation (TREE/ELEV: three trees per elevation). Nested analyses were used because litter bags were not independent replicates, due to possible spatial autocorrelation of bags on branches, branches within trees, and trees within elevations. ANCOVAs were performed using the model: log (abundance or richness $+1$) $\sim$ log(TIME) + CANOPY + ELEV/TREE, in SPLUS 4.5 for Windows. Abundance and species richness in control bags were analysed using the same model. If significant ($P<0.05$) spatial or temporal variation in the data was observed in the canopy control bags, the experimental canopy litter bags and the canopy control bags were compared directly using the model: log (canopy abundance or richness $+1$) $\sim$ log(TIME) + CONTROL + ELEV/TREE/BRANCH. If significant variation was observed in the ground control bags, the experimental ground litter bags and the ground control bags were compared directly using the model: log (ground abundance or richness $+1$) $\sim$ log(TIME) + CONTROL + ELEV/TREE.

Analyses of the 1998 data comparing Mt. Cain and Mt. Maquilla tested the main effects of vertical stratification (CANOPY: ground and canopy), time (TIME: 30, 60, 90 days), mountain (MTN: Mt. Cain and Mt. Maquilla), elevation within mountain (ELEV/MTN: 800 and 1,200 m a.s.l.), and tree within elevation (TREE/ELEV: three trees per elevation). ANCOVAs were performed using the model: log (abundance or richness $+1$) $\sim$ log(TIME) + CANOPY + MTN/ELEV/TREE.

Measurement of environmental variables

Thirty-two measures of spatial and temporal environmental variation were recorded for each sample, including the following variables referred to in the text: METHOD, CANOPY, MTN, ELEV, TIME, TREE, presence of bedrock (BEDROCK), site series under the biogeoclimatic ecosystem classification scheme (SERIES: 01, 06 or 31), height above ground (HEIGHT in metres), branch orientation (DIRECTN in degrees), tree diameter at breast height (DBH in cm), year of sampling (YEAR), month of litter bag placement (SET), month of collection (COLL), and other variables as described in Tables S1, S2. Variables directly associated with individual trees were measured at the time of sampling.

Multivariate analyses of species composition

Variation in mite species composition was analysed by canonical correspondence analysis (CCA) using the CANOCO (version 3.1) program. Site scores in CCA were linear combinations of environmental variables (LC site scores) (McCune 1997). Forward selection was used to test which of the 32 environmental variables explained significant variation in mite species composition. Partial CCAs (CCAs with covariables) were performed when there were inconsistencies in sampling methods or sample size between sites. For example, the number of individuals collected was highly unequal between canopy and ground, and so sample abundance (SAMPSIZE) was entered as a covariable into CCA analyses if it explained significant variation in species composition. Extraction procedure differed for one 30-day sampling period in 1998 (see ‘Supplementary materials and methods’; Table S2) so METHOD was entered as a covariable into CCA analyses if it explained significant variation in species composition.

Designating ‘specialist’ species

In conjunction with the determination of species relationships to environmental variables in CCA analyses, species significantly over-represented in particular vertical strata (i.e. canopy or ground specialists), at particular stages of succession (i.e. early-, mid- or late-successional specialists), at particular elevations (i.e. low-, mid- or high-elevation specialists), or on a particular mountain (i.e. Mt. Cain or Mt. Maquilla specialists) were determined to be ‘specialists’ by using a chi-square test with William’s correction for small sample sizes. ‘Specialization’, as designated here, may or may not reflect the level of habitat specialization of the same species at other sites, or in other studies. Equally, many true habitat specialist species may not be recognized as such in these tests due to inadequate statistical power (i.e. rarity).

Results

The mite fauna

A total of 4,783 invertebrates were extracted from 507 litter bags placed in the canopy and on the ground beneath amabilis fir trees located at Mt. Cain and Mt. Maquilla, 1997–1998. Acari (mites) dominated both canopy ($n=1{,}201$ mites) and ground ($n=1{,}310$ mites) litter bags, representing 61.7 and 63.1% of the total number of invertebrates extracted, respectively. Total mite species richness was high ($s=129$ species), with 77 species in canopy samples and 107 species in ground samples (Table S3).

The suborder Oribatida (excluding Astigmata) dominated both canopy and ground litter bags at all sites (species richness, $s=76$; number of individuals, $n=1{,}754$), followed by the suborders Mesostigmata ($s=28$, $n=315$), Prostigmata ($s=19$, $n=361$), and the oribatid clade Astigmata ($s=6$, $n=81$). In the suborders Mesostigmata and Prostigmata, total abundance and species richness were two times greater on the ground than in the canopy. Differences between the canopy and the ground fauna were apparent even at the superfamily level. Within the canopy, the most speciose superfamilies were Oripodoidea, Ceratozetoidea, and Eremaeoidea, whereas the rank-ordering of dominant superfamilies in the ground fauna was Eremaeoidea, Zerconoidea, and Ceratozetoidea (Table S3).

The abundance and richness of mites colonizing litter bags

In experiment I, in 1997, the abundance of mites colonizing litter bags increased significantly over time ($F_{1,259}=130.96$, $P<0.001$), with a similar response shown for mite species richness ($F_{1,259}=67.37$, $P<0.001$; note that species richness was strongly correlated with increasing number of individuals per litter bag, $r=0.87$, $n=243$, $P<0.0001$). However, mite abundance and richness also increased significantly over time in control bags containing Styrofoam chips. Despite this, ANCOVA models showed that abundance and richness were consistently higher in canopy litter bags vs canopy control bags (abundance: $F_{1,295}=26.57$, $P<0.001$; richness: $F_{1,295}=23.47$, $P<0.001$), as well as in ground litter bags vs ground control bags (abundance: $F_{1,28} = 30.46$, $P < 0.001$; richness: $F_{1,28} = 20.83$, $P < 0.001$). Ground litter bags showed a high initial rate of colonization compared to canopy litter bags. Moreover, mite abundance per litter bag was eight times greater on the ground than in the canopy ($F_{1,259} = 174.14$, $P < 0.001$), and mite species richness per litter bag was five times greater ($F_{1,259} = 147.80$, $P < 0.001$).

Low elevation sites generally showed greater abundance and species richness per litter bag than sites at higher elevation, although these trends were not significant (abundance: $F_{2,6} = 3.36$, $P = 0.105$; richness: $F_{2,6} = 1.69$, $P = 0.262$). Similarly, there was no spatial variation in mite abundance or species richness detected between mountains (abundance: $F_{1,104} = 0.006$, $P = 0.938$; richness: $F_{1,104} = 0.002$, $P = 0.964$). It is possible that trends at larger spatial scales were masked by highly significant variation in species richness between individual trees within sites ($F_{6,259} = 2.58$, $P = 0.019$).

Small-scale spatio-temporal variation in mite species composition: Experiment I

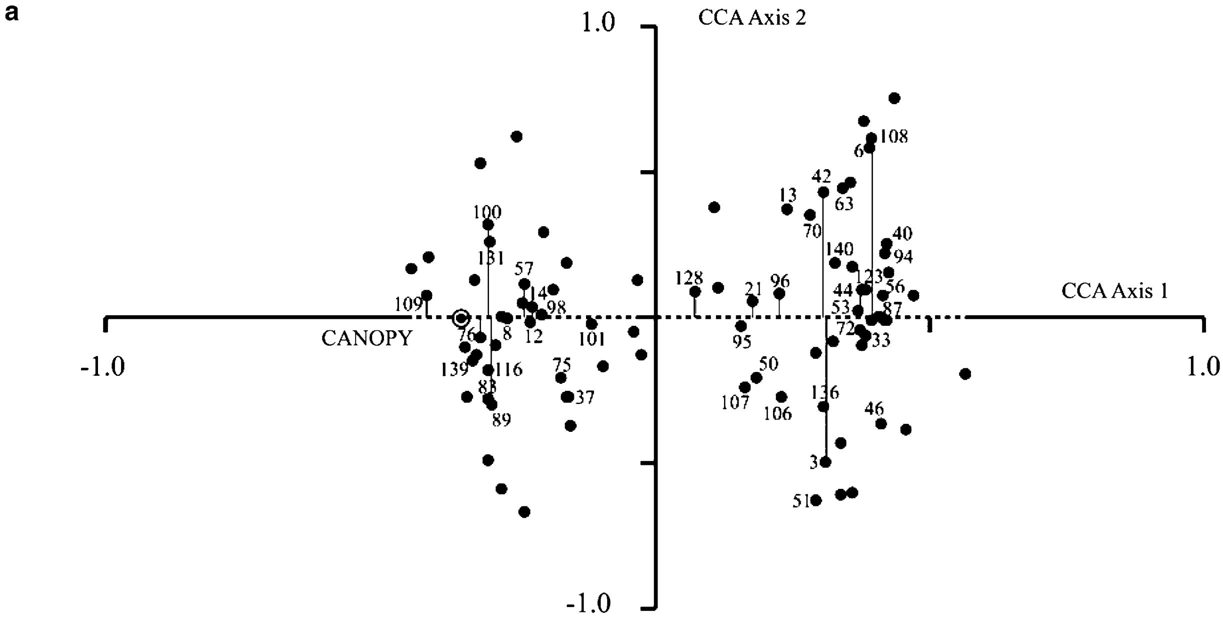
Species relationship to environmental variables

SAMPSIZE (sample abundance) explained significant variation in species composition ($\lambda = 0.52$, $P = 0.001$, explaining 4.4% of variance in the species-abundance data) and was entered as a covariable into a partial CCA analysis. In this partial CCA analysis, CANOPY (canopy vs ground treatments), TIME (the time available for colonization), ELEV1200 (high elevation site, 1,200 m), and TREE2 (variation among individual trees) explained significant variation in mite species-abundance data (Table 1a, Fig. S3). The first four partial CCA axes explained 15.8% of the variance in mite species composition ($\lambda_1 = 0.73$, $\lambda_2 = 0.49$, $\lambda_3 = 0.33$, $\lambda_4 = 0.24$ for axes 1–4, respectively) (Table S4a). All species–environment correlations were high (Table S4a) and Monte Carlo permutation tests showed that the linear combination of environmental variables represented by the first two axes explained significant variation in the species-abundance data ($P = 0.001$). Three variables, CANOPY, ELEV1200, and TREE2, explained significant variation in mite species composition at sites ordered along axis 1 ($r = -0.99$, $r = 0.16$, and $r = 0.21$, respectively, all $P < 0.05$), while CANOPY, TIME, ELEV1200, and TREE2 explained significant variation at sites ordered along axis 2 ($r = -0.02$, $r = 0.75$, $r = 0.43$, and $r = -0.27$, respectively, all $P < 0.05$) (Table S4a, Fig. S3). Therefore, the first axis represented a gradient in species composition between canopy and ground litter bags (Fig. 1), and the second axis represented a gradient in species composition in response to time available for colonization (Fig. 2).

Table 1 Environmental variables explaining significant variation in mite species composition between sites by their marginal (*left*) and conditional (*right*) effects on mite species (CCA forward selection procedure). (a) Experiment I—partial CCA with SAMPSIZE entered as a covariable, Mt. Cain, 1997 (see Table S4a and Fig. S3 for species-abundance results). (b) Experiment II—partial CCA with METHOD and SAMPSIZE as covariables, Mt. Cain and Mt. Maquilla, 1998 (see Table S4b for species-abundance results)

Marginal effects (forward: step 1)				Conditional effects (forward: continued)				
j	Variable	λ_j	*P*	*J*	Variable	λ_a	*P*	cum(λ_a)
(a) Experiment I—Mt. Cain, 1997								
2	CANOPY	0.72	0.001	2	CANOPY	0.72	0.001	0.72
16	HEIGHT	0.67	0.001	32	TIME	0.44	0.001	1.16
32	TIME	0.46	0.001	5	ELEV1200	0.34	0.002	1.50
5	ELEV1200	0.36	0.005	6	TREE2	0.29	0.020	1.79
6	TREE2	0.35	0.017					
20	DBH	0.33	0.012					
18	DIRECTN	0.26	0.241					
7	TREE3	0.21	0.679					
4	ELEV1000	0.20	0.754					
(b) Experiment II—Mt. Cain and Mt. Maquilla, 1998								
2	CANOPY	0.28	0.001	2	CANOPY	0.28	0.001	0.28
18	DIRECTN	0.24	0.001	5	ELEV1200	0.16	0.003	0.44
16	HEIGHT	0.19	0.001	3	MOUNTAIN	0.15	0.011	0.59
5	ELEV1200	0.16	0.006	32	TIME	0.15	0.045	0.74
3	MOUNTAIN	0.15	0.011					
32	TIME	0.15	0.055					
19	SERIES31	0.15	0.033					
7	TREE3	0.11	0.248					
6	TREE2	0.11	0.302					

Abbreviations and symbols: λ_j eigenvalue (fit) with variable *j* only, λ_a increase in eigenvalue (additional fit), cum(λ_a) cumulative total of eigenvalues λ_a, *P* significance level of effect, as obtained with a Monte Carlo permutation test (999 random permutations). Prior to forward selection, other environmental variables were removed due to multicollinearity among variables (see Tables S1 and S2 for a complete list)



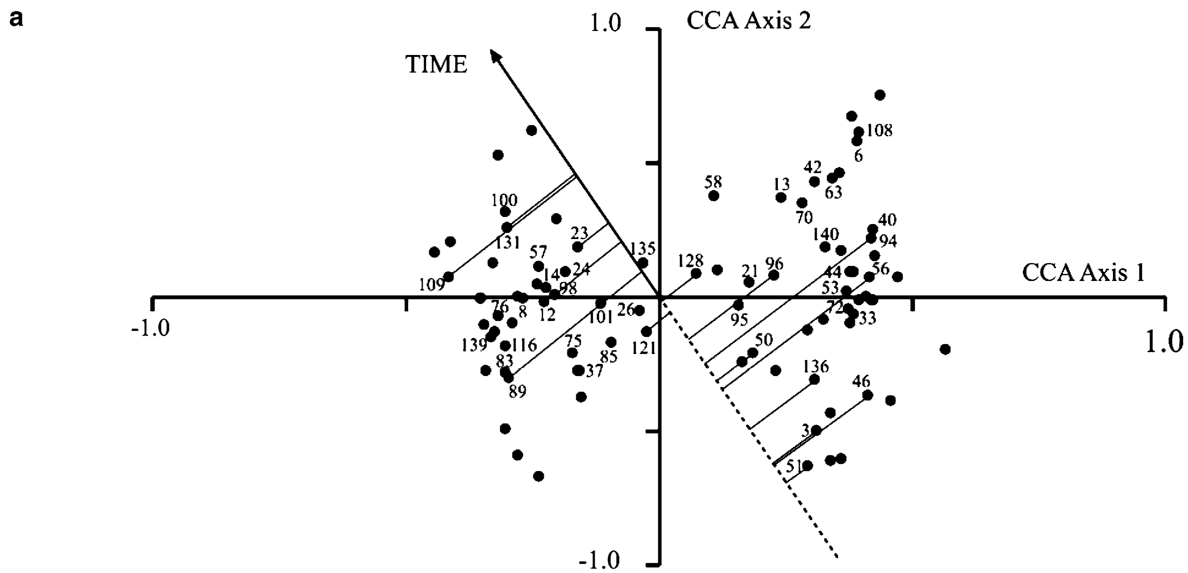
b

Canopy specialists				Ground specialists			
		Abundance				Abundance	
Species	**Code**	**Canopy**	**Ground**	**Species**	**Code**	**Canopy**	**Ground**
Dendrozetes sp.	109	155***	1	*Rhizoglyphus* sp.	3	2	59***
Scapheremaeus nr. *palustris*	89	34***	1	*Platynothrus peltifer*	87		30***
Eueremaeus acostulatus	98	39***	6	*Eremaeus* sp.	96	2	35***
Eupodes sp.	14	32**	6	*Tarsonemus* sp.	21		26***
Eueremaeus sp.	100	20**	1	*Gamasellus* sp.	42	5	36**
Bdella sp.	8	20*	4	*Phauloppia* sp.	128	6	36**
Neogymnobates marilynae	76	12*	1	*Sejus* sp.	44		16*
Zercon sp.1	57	14*	2	*Ceratoppia quadridentata*	108		13*
Alicorhagiidae Genus6	16	8		*Microzercon* sp.1	53		10
Gymnodamaeus sp.	139	6		*Eremaeus brevitarsus*	94		10
Camisia sp.	83	8	1	*Eupelops* sp.	136	3	15
Parapirnodus hexaporosus	131	10	3	Histiostomatidae Genus2	6		8
Typhlodromus sp.	37	6	1	Zerconidae Genus14	50	4	16
Jugatala tuberosa	75	7	2	*Pergamasus* sp.	33	1	10
Eupodidae Genus4	12	5	1	*Trachytes* sp.	40		7
Megeremaeus montanus	101	4	1	Zerconidae Unknown Genus	56		6
				Dentizetes rudentiger	72		6
				Urodiaspis sp.	46		5
				Bledus sp.	51		5
				Liochthonius sp.2	63		5
				Tritegeus sp.	70	2	9
				Eremaeus occidentalis	95	2	9
				Tectocepheus velatus	140	1	7
				Liacarus bidentatus	106	2	8
				Cocceupodes sp.	13	1	5
				Ceratoppia bipilis	107	1	4
				Suctobelba sp.	123	1	3

Fig. 1 **a** Mite species distributions (*filled circles*) in relation to ground vs canopy habitat preference, on Mt. Cain, 1997 (see Fig. S3 for pCCA ordination biplot). **b** Canopy and ground specialization among 'common' ($N \geq 5$) mite species. χ^2 test of significant positive deviations from expected random distribution across samples: $^{***}P < 0.001$; $^{**}P < 0.01$; $^{*}P < 0.05$ (significant negative deviations not shown). Species are ordered within categories by descending value of χ^2 statistic. See Table S3 for a complete list of species codes

Canopy habitat specialization

Numerically dominant species differed between ground and canopy litter bags. The two most abundant canopy species across all sites on Mt. Cain in 1997 were *Scapheremaeus* nr. *palustris*, and *Dendrozetes* sp., followed by *Eueremaeus acostulatus*, *Parapirnodus hexaporosus*, *Eueremaeus* sp., *Eupodes* sp., *Bdella* sp., *Jugatala*



b

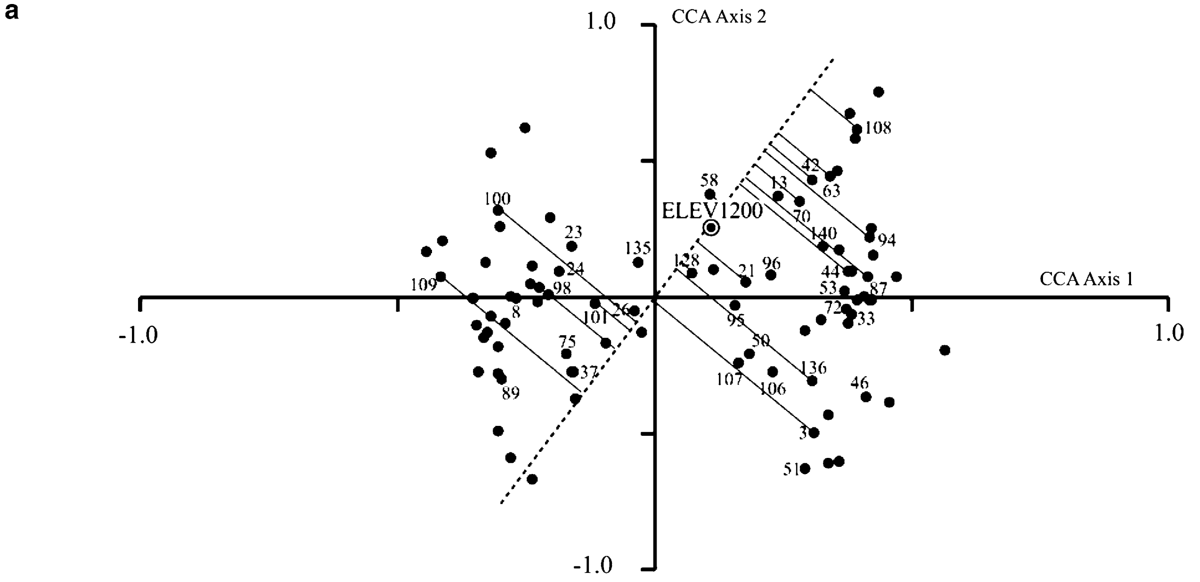
Early-succession specialists				
		Abundance		
Species	**Code**	**60 days**	**120 days**	**360 days**
[C] *Scapheremaeus* nr. *palustris*	89	19***	13	3
Eremaeus brevitarsus	94	6***		4
Urodiaspis sp.	46	4***		1
Parapirnodus hexaporosus	131	6**	6	1
Eupelops sp.	136	7**	9	2
Oppiella nova	121	3*		2
[G] *Eremaeus* sp.	96	10*	3	24
Mid-succession specialists				
[G] *Rhizoglyphus* sp.	3	4	51***	6
Zerconidae Genus14	50		13**	7
Bledus sp.	51		5*	
Zerconidae Unknown Genus	56		5*	1
[C] *Eueremaeus acostulatus*	98	3	21*	21
Megeremaeus montanus	101		4	1
Microzercon sp.1	53		6	4
Tectocepheus velatus	140	1	5	2
Pergamasus sp.	33	3	6	2
Camisia segnis	85	3	6	2
Camisia sp.	83	1	5	3

Late-succession specialists				
		Abundance		
Species	**Code**	**60 days**	**120 days**	**360 days**
[C] *Dendrozetes* sp.	109	1	18	137***
[G] *Phauloppia* sp.	128	2	2	38**
Tydeidae Genus9	23			18*
[C] *Eueremaeus* sp.	100	1	1	19
[G] *Sejus* sp.	44		1	15
[G] *Tarsonemus* sp.	21	1	3	22
[G] *Ceratoppia quadridentata*	108		1	12
[G] *Gamasellus* sp.	42	2	8	31
Tydeidae Genus10	24	1		9
Cocceupodes sp.	13			6
Liochthonius sp.2	63			5
[C] *Bdella* sp.	8	2	6	16
[C] *Zercon* sp.1	57		5	11
Histiostomatidae Genus2	6		2	6
Zercon sp.2	58	1	1	5
Scheloribates/*Oribatula* sp.	135	1	1	5
Trachytes sp.	40		3	4
Tydeus sp.	26	1	3	8
Tritegeus sp.	70	2	2	7
Eremaeus occidentalis	95	1	4	6
[C] *Eupodes* sp.	14	1	15	22
Eupodidae Genus4	12	2		4
Dentizetes rudentiger	72	2		4
[C] *Neogymnobates marilynae*	76	4	2	7

Fig. 2 **a** Mite species distributions on Mt. Cain, 1997 (*filled circles*) in relation to time available for colonization (TIME: 60, 120, and 360 days) (see Fig. S3 for pCCA ordination biplot). **b** Specialization for early vs late stages of succession among 'common' ($N \geq 5$) mite species. [C] Canopy specialist, [G] ground specialist. Details of codes and χ^2 tests of significant habitat preference as in Fig. 1 and Table S3

tuberosa, and *Neogymnobates marilynae*. By contrast, there was an almost completely distinct assemblage of species colonizing litter bags on the ground, dominated by *Tarsonemus* sp., *S.* nr. *palustris*, *Platynothrus peltifer*, *Eremaeus* sp., *Gamasellus* sp., *Rhizoglyphus* sp., *Eremaeus occidentalis*, *Tritegeus* sp., *Eupelops* sp., and *Phauloppia* sp. In total, 77 species (57%) were entirely restricted to either ground or canopy litter bags. However, many of these species were rare ($n < 5$) and putative habitat preferences are subject to extreme sample effects. If rare species are excluded ($n < 5$), then 43 of 49 common species (87.8%) showed a clear preference for either canopy or ground habitats (Fig. 1), but only 15 of these (30.6%) were entirely restricted to one habitat. Surprisingly, the six species which were found equally abundantly in canopy and ground litter bags were all relatively uncommon ($n < 10$). Consequently, the numerically dominant species differed significantly between the canopy and the forest floor.

There were a total of 16 canopy specialists recognized, although only eight of these were significantly over-represented in canopy habitats, including *Dendrozetes* sp., *S.* nr. *palustris*, *Eu. acostulatus*, *Eupodes* sp., and *Eueremaeus* sp. (χ^2 tests, all $P < 0.01$) (Fig. 1b). By contrast, there were 27 ground specialists recognized, of which eight were significantly over-represented on the



b

Low-elevation specialists				
		Abundance		
		800	**1000**	**1200**
Species	**Code**	**m**	**m**	**m**
[G] *Phauloppia* sp.	128	37**	2	3
[G] *Tarsonemus* sp.	21	24**	2	
[G] *Rhizoglyphus* sp.	3	45*	14	2
[G] *Sejus* sp.	44	15*	1	
Eupelops sp.	136	16*		2
Eremaeus occidentalis	95	10	1	
[G]*Eremaeus* sp.	96	26	3	8
Cocceupodes sp.	13	6		
Bledus sp.	51	5		
Tydeidae Genus9	23	13	1	4
Liacarus bidentatus	106	8	1	1
Microzercon sp.1	53	7	2	1
Urodiaspis sp.	46	4	1	
Ceratoppia bipilis	107	4	1	
Tydeus sp.	26	8	1	3
Zerconidae Genus14	50	12	5	3
[C] *Bdella* sp.	8	14	5	5
Tydeidae Genus10	24	6	3	1
[C] *Scapheremaeus* nr. *palustris*	89	18	12	5
Jugatala tuberosa	75	5	3	1
Scheloribates/*Oribatula* sp.	135	4	2	1
Typhlodromus sp.	37	4	1	2

Mid-elevation specialists				
		Abundance		
		800	**1000**	**1200**
Species	**Code**	**m**	**m**	**m**
[G] *Platynothrus peltifer*	87	1	22***	7
Liochthonius sp.2	63		5**	
[C] *Dendrozetes* sp.	109	95	57*	4
Dentizetes rudentiger	72	1	4	1
High-elevation specialists				
[G] *Gamasellus* sp.	42	4	8	29***
[G] *Ceratoppia quadridentata*	108			13***
[C] *Eueremaeus acostulatus*	98	10	11	24***
Zercon sp.2	58		1	6**
[C] *Eueremaeus* sp.	100	3	7	11*
Tritegeus sp.	70	1	3	7*
Megeremaeus montanus	101		1	4*
Eremaeus brevitarsus	94	1	3	6*
Tectocepheus velatus	140		3	5
Pergamasus sp.	33	4	1	6

Fig. 3 **a** Mite species distributions (*filled circles*) in relation to elevation (ELEV1200) (see Fig. S3 for pCCA ordination biplot). **b** Specialization for low, mid, or high elevation forest among 'common' ($N \geq 5$) mite species. [C] Canopy specialist, [G] ground specialist. Details of codes and χ^2 tests of significant habitat preference as in Fig. 1 and Table S3

ground, including *Rhizoglyphus* sp., *P. peltifer*, *Eremaeus* sp., *Tarsonemus* sp., *Gamasellus* sp., and *Phauloppia* sp. (χ^2 tests, all $P < 0.01$) (Fig. 1b).

Time available for colonization

Only eight species (7.3%) were equally abundant at all collection times; the majority of species showed a preference for either early-mid colonization or mid-late colonization time intervals (Fig. 2b). Seven species were statistically over-represented during the early stages of succession, including *S.* nr. *palustris*, *E. brevitarsus*, *Urodiaspis* sp., *P. hexaporosus*, and *Eupelops* sp., five species during mid-succession, including *Rhizoglyphus* sp. and Zerconidae Genus14, as well as four species during late succession, including *Dendrozetes* sp. and *Phauloppia* sp. (χ^2 tests, all $P < 0.01$) (Fig. 2b). In terms of numerical dominance, a typical 60–120–360-day colonization sequence in the canopy was characterized by *S.* nr. *palustris*, then *Eu. acostulatus*, and then *Dendrozetes* sp., whereas a typical successional sequence on the ground was characterized by *Eremaeus* sp., then *Rhizoglyphus* sp., and then *Phauloppia* sp. (Fig. 2b).

Elevation

Five species were significantly over-represented at low elevation, including *Phauloppia* sp. and *Tarsonemus* sp., three species at mid-elevation, including *P. peltifer* and *Liochthonius* sp., and eight species at high elevation, including *Gamasellus* sp., *C. quadridentata*, and *Eu. acostulatus* (χ^2 tests, all $P < 0.01$) (Fig. 3b). The majority of these species were ground specialists. In contrast, most canopy specialist species were more widely distributed across elevations, or were characteristic of high elevation sites (Fig. 3b).

Variation in mite species composition between mountains: Experiment II

Species relationship to environmental variables

METHOD and SAMPSIZE explained significant variation in species composition (cumulative $\lambda = 0.82$, $P = 0.001$, explaining 11.1% of variance in the species-abundance data) and were entered as covariables into a partial CCA. Significant variation in mite species-abundance data was explained by CANOPY (canopy vs ground treatments), ELEV1200 (high elevation site, 1,200 m), MOUNTAIN (Mt. Cain or Mt. Maquilla), and TIME (the time available for colonization) (Table 1b). The first four partial CCA axes explained 11.3% of the variance in mite species composition ($\lambda_1 = 0.29$, $\lambda_2 = 0.18$, $\lambda_3 = 0.14$, $\lambda_4 = 0.13$ for axes 1–4, respectively) (Table S4b). All species–environment correlations were high (Table S4b), and Monte Carlo permutation tests showed that the first two axes explained significant variation in species-abundance distributions ($P = 0.001$). Two variables, CANOPY and MOUNTAIN, explained significant variation in mite species composition at sites ordered along axis 1 ($r = 0.84$ and $r = -0.23$, respectively, both $P < 0.05$), while ELEV1200, MOUNTAIN, and TIME explained significant variation in mite species composition at sites ordered along axis 2 ($r = 0.55$, $r = 0.36$, and $r = -0.37$, respectively, all $P < 0.05$) (Table S4b).

Species turnover between years and between mountains

A total of 64 mite species were collected from litter bags in the canopy ($s = 27$) and on the ground ($s = 55$) at Mt. Cain 1998, and a similar total (65 species) were collected from litter bags in the canopy ($s = 29$) and on the ground ($s = 54$) at Mt. Maquilla 1998 (Fig. S2). Only 36.6% of canopy species (15 species) were collected on both Mt. Cain and Mt. Maquilla, whereas a much higher proportion of ground species (53.5%) were common to both mountains. A similar pattern was evident between years 1997–1998 on Mt. Cain (Fig. S2), indicating that the canopy is subject to a greater spatial and temporal turnover of mite species than the ground. Similar total numbers of species colonized litter bags on both mountains (Figs. S2, S4), and all common species ($n \geq 5$) except *Oribatula tibialis* and Cheyletidae Genus3 were found on both mountains. Of these species, most were considered habitat specialists. Only *Eupelops* sp. and *O. tibialis* were significantly over-represented on Mt. Cain than on Mt. Maquilla (all $P < 0.05$) (Fig. S4b). Four species, *Tarsonemus* sp., *Scheloribates* sp., *Gamasellus* sp., and *E. occidentalis*, were significantly over-represented on Mt. Maquilla (all $P < 0.05$) (Fig. S4b).

Discussion

Mite assemblages colonizing experimental litter bags differed markedly in abundance, species richness, and composition between ground and canopy habitats. The average number of mite species per litter bag was approximately 5–10 times greater on the ground than in the canopy, but this did not translate directly into a substantially larger species pool within ground habitats. In total, 107 species were found in the ground litter bags and 77 species in the canopy litter bags, although part of this difference may be explained by the higher total abundance of mites captured in ground samples. In order to account for the inconsistency between local sample diversity and total species diversity, there must have been a substantial difference in species turnover rates between litter bags in ground and canopy habitats. Community ordination analyses support this contention, with marked differences between ground and canopy assemblages in patterns of species turnover through time and across multiple spatial scales (supporting hypothesis 1). These findings have important implications for our understanding of how species diversity is partitioned within forest habitats, and for extrapolating regional or global biodiversity estimates when sampling is based almost entirely within ground habitats.

Mite colonization of litter bags is faster on the ground than in the canopy

Mites were eight times as abundant and five times as species rich in the ground litter bags as compared to the canopy litter bags, indicating that mites either occur at lower densities in the canopy and/or colonize newly available resources at much slower rates in the canopy than on the ground (supporting hypothesis 2). There are a number of plausible alternative explanations for the observed trend, including: (1) lower availability and greater patchiness of canopy litter, (2) greater abiotic extremes in the forest canopy, or (3) greater trophic specialization of canopy mites, which leads to bias in the use of single-substrate experimental litter bags. However, without further experimentation it might not be possible to clarify the relative importance of these factors.

Low and patchy resource availability in the canopy

The most parsimonious explanation for lower colonization rates, and hence lower abundance and richness in canopy litter bags, is that there is a lower absolute biomass of suspended litter in forest canopies compared to that found on the forest floor (McCune et al. 2000). Total organic matter availability is often the most important factor influencing the abundance and community structure of soil Collembola and Oribatida (Hasegawa 2001; Reynolds et al. 2003). Furthermore, litter biomass (as well as litter chemistry and the dynamics of litter decomposition) may also determine the distribution of fungal and bacterial biomass, which many mites consume (Berg et al. 1998; Hansen 2000; Osler and Beattie 2001). Consequently, lower colonization rates in the canopy may be largely due to the lower densities of individuals and species in natural habitats surrounding litter bags. Standardized sampling of naturally occurring ground and canopy habitats at other sites has shown that the density of mites in canopy litter may be an order of magnitude lower than in ground litter. For example, the mean density of mites in paired samples from a range of tropical and temperate trees was approximately 0.7 mites per gram dry weight of litter in the canopy, compared to 9.9 mites per gram on the ground below the same trees (Winchester unpublished data). These data are consistent with the densities of mites in litter bags in the present study, which averaged 1.1 mites per gram in the canopy vs 8.7 mites per gram on the ground at 800 m elevation.

In addition to lower total availability of litter resources, naturally occurring litter is much more patchily distributed in the forest canopy (Nadkarni and Longino 1990; Behan-Pelletier and Walter 2000). It is likely that increased patchiness reduces the colonization rate of newly created patches by canopy mites, although there are only limited data available on mite dispersal abilities (Aoki 1973; Ichisawa and Aoki 1998). Whether low colonization rates are a cause, or a consequence, of the lower density of mites per unit resource in the canopy is unknown.

Greater abiotic extremes in the forest canopy

Tree crowns are subject to more extreme variability in ambient insolation, wind, desiccation, and precipitation than the forest understorey (Bohlman et al. 1995). In montane forests in Costa Rica, for example, canopy organic substrate experiences periods of rapid and severe desiccation (20–40% moisture content), while forest floor soils remain at a consistently high water content (60–70%) (Bohlman et al. 1995). Such extreme variability in moisture content and other environmental conditions has been shown to have species-specific effects on mites (Berg et al. 1998). Typically, harsh environmental conditions result in lower numbers of individuals and species (e.g. Sgardelis and Usher 1994), but under certain circumstances fluctuating microclimate and greater environmental extremes may promote the coexistence of more species (Huhta and Hänninen 2001). Under these conditions, community structure may depend more on the tolerances of individual species to abiotic factors than on interactions among species (Whitford et al. 1981). Similarly, it is possible that arboreal mite communities are structured by extreme and fluctuating abiotic conditions first, and second, by habitat availability (Prinzing and Woas 2003).

Bias in the use of a single-litter substrate

There is strong evidence that multi-species leaf mixtures typically have higher mite abundance and richness than single-litter substrates (Thomas and Proctor 1997; Hansen 2000). In principle, if canopy mites were substantially more specialized in their feeding or habitat preferences than ground mites, then lower colonization rates in canopy litter bags might result from the fact that distinct subsets of species prefer amabilis fir litter compared to other litter types or microhabitats. In ground habitats of Pacific Northwest forests, Walter (1985) showed no significant difference in mite colonization rates of five litter species in single-substrate experiments, and that 66–83% of the oribatid species colonizing amabilis fir litter also colonized each of the four other litter species. However, there is no comparable evidence to indicate whether canopy mites show a higher degree of specialization than this for habitat or food resources.

In the absence of direct experimental evidence, the possibility remains that the use of sterilized single-litter substrate may introduce unintentional bias if canopy mites are indeed significantly more specialized than ground mites. However, this bias would only serve to increase the apparent degree of patchiness and species turnover between canopy habitats and ground habitats. Consequently, we may have only quantified minimum differences in colonization rates (and species turnover) between ground and canopy litter bags, and our treatment effects may be conservative.

Mite species complementarity is high between terrestrial and canopy litter

From the few studies available, ground and canopy soils are generally thought to share arthropod communities with a fundamentally similar higher-taxon structure (Nadkarni and Longino 1990). While this may be true for ordinal-level abundance of insects, we found that mite composition varied between vertical strata at all taxonomic levels from superfamily to species. There was a high degree of habitat specificity, with ground litter bags dominated by a different species assemblage (*Rhizoglyphus* sp., *P. peltifer*, *Eremaeus* sp., *Tarsonemus* sp., *Gamasellus* sp., and *Phauloppia* sp.) than that found in canopy litter bags (*Dendrozetes* sp., *S.* nr. *palustris*, *Eu. acostulatus*, *Eupodes* sp., and *Eueremaeus* sp.) (supporting hypothesis 1). Several of these canopy species have been shown to exhibit arboreal specificity in other tree species (Winchester 1997; Winchester et al. 1999), and the genera *Dendrozetes* and *Scapheremaeus* also dominate suspended litter in temperate forest canopies in Japan (Aoki 1973; Behan-Pelletier and Walter 2000).

Despite strong vertical stratification in species composition, only 30.6% of common species were entirely restricted to one habitat, which is considerably lower than most published estimates of ground-canopy specialization among mites (Behan-Pelletier and Walter 2000; Proctor et al. 2002). However, our data suggest that many species which are otherwise predominantly found in one vertical stratum, occasionally utilize other vertical strata. Whether these species simply disperse through alternative habitats, or actually feed and reproduce in both strata is unknown. Information on feeding habits is available for a few common species, but there is no robust classification of trophic guilds across mite taxa. Moreover, Schneider et al. (2004) recently showed that even different species within the same genus can occupy different trophic niches, and oribatid mites in general span three to four trophic levels. Different life-history stages may also be dependent on different habitats for food, shelter, or oviposition at different times, as has been shown for the arboreal oribatid *Humerobates rostrolamellatus* Grandjean (Murphy and Balla 1971). In addition, rare sampling occurrences may be random events with no direct bearing on species habitat preferences. When the designation of ‘specialization’ is relaxed to take rare vagrants into account, 79% of common species are considered ground or canopy specialists (with 75% or more of individuals in one vertical stratum). As the canopy may be considered the more ‘extreme’ habitat for mites, it follows that more canopy specialists may ‘utilize’ the ground habitat than ground specialists utilize the canopy habitat. As predicted, in Experiment I, 14 of the 16 canopy specialists (87.5%) had rare vagrants on the ground, whereas only 14 out of 27 ground specialists (51.9%) had rare vagrants in the canopy. The high rate of canopy specialists utilizing the ground may be a trivial consequence of random branch or litter fall (Proctor et al. 2002), but it may also indicate a relatively high rate of active dispersal. The fact that over half of the ground specialist mites were found occasionally in the canopy is surprising. Negative geotaxis would seem to be an unlikely behaviour for ground specialists. Furthermore, Proctor et al. (2002) found almost no overlap in adult oribatid species composition between ground and tree trunks in Australia, and concluded that tree trunks do not act as highways for mites. The inconsistency between this conclusion and the findings in the present study possibly stems from Proctor et al. (2002) excluding juvenile stages of mites from their analyses, or a difference in the degree of habitat specialization in temperate vs subtropical forests.

Dominant species differ over time between vertical strata

There was significant variation in mite species composition through time in both the ground and the canopy litter bags. Mites appeared to partition resource utilization to a surprisingly high degree during stages of plant succession (see Scheu and Schulz 1996). Furthermore, the dominant species in early-, mid-, and late-successional stages of litter decomposition differed significantly between vertical strata. While other successional litter-bag studies have also shown that mite species composition changes through time (Hasegawa 1997; Reynolds et al. 2003), it was unusual that oribatid mites dominated all stages of colonization in the present study. As oribatids exhibit ‘k’-style life-history traits (Norton 1994), they would normally have been expected to be slower colonizers than Mesostigmata or Prostigmata species (Osler et al. 2004). Many of the early-colonist oribatids in the present study have also been collected in aerial and ground malaise (dispersal) traps by Behan-Pelletier and Winchester (1998), but the life-history traits that might influence the colonization rates of these species are unknown. One important implication of oribatid mites dominating all stages of the litter decomposition process in the canopy is that even short-term conditioning of suspended litter may have a large impact on terrestrial nutrient recycling following subsequent litter throughfall to the ground (Reynolds et al. 2003).

Ground and canopy mites show differential species turnover across large spatial scales

Despite the high variation among individual trees within elevations, there was still a significant decrease in mite abundance and species richness with increasing elevation. More importantly, mite species composition also differed significantly across elevations, although this was largely due to higher colonization rates of a few dominant mite species in the ground litter bags at low elevation sites (*Phauloppia* sp., *Tarsonemus* sp., *Rhizoglyphus* sp., *Eremaeus* sp., *S.* nr. *palustris*, and *P. peltifer*). Walter (1985) also found that mite species composition in ground habitats changed significantly with increasing elevation. Typically, high abundance and elevational preference in these species is thought to be a result of less extreme variability in temperature and moisture regimes at lower elevations. However, more recent studies have shown that local microclimate and vegetation structure of the habitats sampled can also have a major influence on the interpretation of elevational trends (Schatz 1998).

Unfortunately, no previous studies have compared canopy mite assemblages across elevations, but in the present study very few canopy specialists favoured a particular elevational zone, and when there was an apparent preference, it was for mid- to high-elevations (e.g. *Eueremaeus* sp. *Eu. acostulatus*, and *Dendrozetes* sp.). This might suggest that canopy specialists have greater tolerance for wider variation in environmental conditions than ground specialists (at least partially supporting hypothesis 3). Stevens (1992) called the relationship between climatic tolerance and elevational distribution the 'climatic variability hypothesis', and argued that species at high elevations should be able to withstand a wider range of local abiotic conditions, and should thus have a wider elevational distribution. Gaston and Chown (1999) tested this hypothesis for dung beetles across an elevational gradient, and found that species occurring at higher altitudes did indeed have broader microclimatic tolerances and wider distribution across elevations.

In Experiment II, we explicitly tested whether the trends in mite species composition observed between ground and canopy habitats, and across elevations on Mt Cain in 1997 were generalized and repeatable over larger, regional scales. Despite the shorter colonization time and reduced number of elevations sampled on Mt Cain and Mt Maquilla in Experiment II, the same variables (ground vs canopy habitat, time available for colonization, and elevation) were again the most significant predictors of variation in mite species composition. However, the rank dominance and the relative abundance of common mite species did vary markedly between mountains, for both ground and canopy assemblages. Most importantly, the ground fauna had a lower total species turnover between mountains (46.5%) than did the canopy fauna (63.4%). This is somewhat similar to the results of Proctor et al. (2002) in which oribatid assemblages were more uniform among samples from terrestrial litter than among bark samples from tree trunks. However, even for the ground fauna, the degree of species turnover in the present study was substantially greater than in most other studies. More typically, most studies have concluded that species turnover is low for ground oribatid assemblages. For example, Osler and Beattie (2001) found no significant difference in soil oribatid assemblages between sites 1-km apart that varied dramatically in fire history and understorey vegetation structure.

In our study, the comparatively high turnover in canopy species composition between mountains is consistent with the high turnover of canopy species among individual trees within a site, but is at odds with the comparatively low turnover of canopy mites across elevations. These contrasting findings appear to contradict any simplistic notion that canopy mites should exhibit greater dispersal abilities in order to be able to colonize patchy suspended litter accumulations (rejecting hypothesis 3 as a complete explanation of spatial turnover in mite species composition). It is unclear what factors contribute to these contrasting trends in large-scale species turnover between ground and canopy specialist mites, but the answers probably lie in the mechanisms and frequency of long distance dispersal events (both within and among mountains), which are almost completely unknown for the majority of species.

Nevertheless, taken together with the observed variation in mite species richness between sites, the inference is that ground and canopy assemblages make up a similar proportion of total forest biodiversity, but that the spatial distribution of this diversity is markedly different. It appears that local mite species richness (alpha diversity) is higher on the ground than in the canopy, whereas species turnover between adjacent trees and across different sites (beta diversity) is higher in the canopy.

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