Out on a limb: microarthropod and microclimate variation in coastal temperate rainforest canopies

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Abstract. 1. Species richness of microarthropods in coastal temperate rainforests of western North America is enhanced by the presence of heterogeneous arboreal habitats (moss mats). We studied the relationship between species traits and microclimate as a structuring mechanism for understanding this high diversity.

2. To examine whether community composition is associated with distinct microclimate zones we used Non-metric Multidimensional Scaling ordination of environmental and community data. To link the traits of arboreal microarthropod species with observed environmental variables we used a trait-based approach of RLQ and fourth-corner analysis.

3. Distinct microclimatic zones were observed in the canopy ecosystem stemming from gradients of moisture, temperature, and climatic stability associated with height in canopy and distance from trunk. Associated with these gradients is the growth and development of epiphytic bryophytes such as moss mats and suspended soils, which in turn, influence canopy microclimates.

4. Microarthropod fauna displayed a community-level response to microclimate gradients which was mediated and partially explained by a trait-based analysis. A general decline in species richness was associated with harsher microclimate conditions. While many species possessed desiccation resistance traits under low-moisture conditions, we posit that other species were able to persist by compensatory movements at very small spatial scales.

5. In conclusion this study highlights the importance of environmental buffering associated with greater epiphytic biomass for preserving canopy microarthropod biodiversity, but also how developing an understanding of the species trait distributional shifts can enhance our understanding of communities under different environmental conditions, and for predicting future communities under global environmental change.

Key words. Arboreal communities, microarthropods, microclimate, microhabitat, trait analysis.

Introduction

Spatial heterogeneity of soil environments is the leading hypothesis to explain the high diversity of soil organisms observed (e.g. microhabitats at small spatial scales) (Giller, 1996; Bardgett, 2002; Nielsen *et al.*, 2010). This high biodiversity of small, typically ground-dwelling organisms extends to other, non-typical 'soil' ecosystems, such as well-developed moss-based canopy habitats in coastal temperate coniferous rainforest of western North America (Lindo & Winchester, 2006). Here, the presence, abundance, and complexity of microhabitats within the canopy ecosystem, in particular the suspended soils, support high species richness. While the observed species richness on the forest floor is greater than in the canopy system (Lindo & Winchester, 2009), these habitats contribute significantly to forest-level biodiversity because the number of canopy dwellers and canopy specialists is estimated to be 40% and 20% of the total diversity, respectively

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(Lindo & Winchester, 2006, 2008). This pattern is not unique to these forests as the proportion of shared species between canopy and forest floor systems has repeatedly been observed between 30% and 50% (Aoki, 1973; Wunderle, 1992; Karasawa & Hijii, 2004; Beaulieu *et al.*, 2010).

Historically, the mechanism structuring canopy-dwelling diversity has been attributed to the dispersal ability of forest floor-dwelling species (Aoki, 1973). More recently, studies have attributed lower species richness in arboreal habitats to patchy habitat availability (Lindo & Winchester, 2007b; Rodgers & Kitching, 2012), differences in the quality of the organic matter associated with these two habitats (Nadkarni & Longino, 1990), and greater abiotic extremes in the canopy (Lindo *et al.*, 2008). In particular, moisture regimes and the relative humidity of microhabitats are fundamental factors influencing microarthropod communities (Siepel, 1996), and low-moisture conditions in the arboreal habitat is proposed as the limiting factor in canopy species richness (Lindo *et al.*, 2008). Recently, the idea that canopy-dwelling species are actually 'forest floor avoiders' (Beaulieu *et al.*, 2010) has been proposed, where species climate tolerances lead to a species sorting pattern of community assembly (Leibold *et al.*, 2004).

While dispersal-limitation (spatial processes) structure communities at large spatial scales (Lindo & Winchester, 2009), significant contributions from environmental variations associated with moisture, correlated with canopy habitat height, support the idea that differences in microclimate at small spatial scales (i.e. within-tree variation) may have a strong effect on arboreal community diversity. This is consistent with an observed 'break-point' in community composition along the vertical axis of tree trunks at approximately 5 m above ground in coastal temperate rainforest ecosystems (Lindo & Winchester, 2007a), and at 0.5 m above the forest floor in more arid subtropical forest regions (Beaulieu *et al.*, 2010). For temperate coniferous forests, canopy specialists exist at heights >5 m, whereas forest floor species are found on tree trunks, but at heights <5 m (Lindo & Winchester, 2007a). This change in community composition is attributed to changes in microclimate associated with the loss of understory shading, rather than any overt differences in tree trunk structure acting as a dispersal barrier (Lindo *et al.*, 2008). Yet, at the same time, climate conditions within canopy systems have been little explored (but see Campbell & Coxson, 2001; Rambo & North, 2009; Dial *et al.*, 2011; Gehrig-Downie *et al.*, 2011).

In this study, we recorded temperature and relative humidity in the canopy ecosystem over 1 year, and sampled the microarthropod communities within the canopy of Sitka spruce [*Picea sitchensis* (Bong) Carr.] trees across three watershed estuaries in the coastal temperate rainforest of western Canada. Sitka spruce is a widespread coastal temperate rainforest tree species known for great height (>90 m) and high canopy moss-mat biomass (Winchester & Ring, 1999; Ellyson & Sillett, 2003) (Fig. S1). Here, we examine (i) whether small-scale (within-tree)

environmental differences are detectable and form distinct microzones within a tree, (ii) whether diversity of canopy microarthropod communities change with changes in microclimate, and (iii) whether there are species-level traits that are associated with environmental variables in canopy microzones. We hypothesise that the availability of microclimates may dictate within-tree diversity and contribute to forest-level diversity patterns, whereas species-specific traits may dictate community composition, as the ability of a species to persist or perish under a set of environmental factors depends on intrinsic and extrinsic attributes such as desiccation tolerance (Lindo *et al.*, 2008).

Methods

Study system and sampling design

This study was conducted in the coastal temperate rainforest within Clayoquot Sound UNESCO Biosphere Reserve on the west coast of Vancouver Island, Canada. Samples and measurements are associated with >500-year-old Sitka spruce [*Picea sitchensis* (Bong) Carr.] trees within the alluvial flood plain of three watershed estuaries: Sydney (49º30′72″N, 126º17′60″W), Watta (49º27′20″N, 126º01′94″W), and Moyeha (49º24′69″N, 125º54′87″W). Twelve trees in each watershed were randomly selected within the context of suitability for single rope climbing techniques. Microclimate and microarthropod data were collected at two heights within the canopy, either 30 m or 15 m, and at two distances along branches, either 0 m (trunk) or 2 m (branch) away from the trunk (total nine trees sampled for each height-by-distance combination). Total tree height and tree diameter at breast height (DBH) were recorded for the 36 sample trees. All trees sampled were over 30 m in height, but smaller trees were used for 15 m treatments because moss availability decreases within the top few metres of a tree, and we chose to collect data from abundant moss mats on healthy limbs. As such, trees used for 30 m treatments tended to be larger [ave. DBH 1.52 m (±0.3 SD), ave. height 52.5 m (±9.6 SD)] than trees used for 15 m treatments [ave. DBH 1.06 m (±0.3 SD), ave. height 41.2 m (±8.2 SD)], although these differences are statistically non-significant (see statistical analysis). Microclimate measurements were gathered using Hobo Pro v2 dataloggers installed in July 2008 (started recording July 10, 2008) and collected in June 2009 (stopped recording June 5, 2009). Temperature and relative humidity were recorded every 0.5 h for 330 days.

Moss substrate samples (approx. 10 g dwt) were collected from moss mats directly adjacent to the dataloggers in June 2009 using a standardised circular coring tool (7 cm diameter). Microarthropods from moss samples were extracted within 24 h on Tullgren funnels for 48 h, and collected into 70% EtOH. Moisture content of the moss samples was estimated gravimetrically by weighing

the sample prior to and following extraction [moisture content % = (wet weight (g) − dry weight (g)/dry weight (g)) × 100]. Microarthropods were sorted into major taxonomic groups: mites (Acari: Mesostigmata, Astigmata, Prostigmata, Oribatida), springtails (Collembola: Arthropleona, Symphypleona), and other microarthropods which included adult and immature Coleoptera, Diptera, Araneae, Pseudoscorpiones, Thysanoptera, Myriapoda, Psocoptera, Hymenoptera, Homoptera. Mites and springtails accounted for over 97% of the total individuals collected and were further identified to morphospecies and species. Mites were identified using Krantz and Walter (2009) and keys therein, whereas springtails were identified using Christiansen and Bellinger (1998).

Statistical analyses

Each sample (Hobo data or moss core sample for fauna) is an independent replicate of a treatment (in this case, microzone within a tree), and replication was performed by sampling multiple trees (nine trees per treatment ($n = 9$) across four treatments = 36 trees sampled in total). Each tree was sampled only once at the treatment (microzone) it was designated. All microclimate data conformed to parametric assumptions. Microarthropod data (species richness and abundance) were standardised to the number of species or individuals per 100 g dry weight (dwt) moss, and log transformed prior to analyses. We used a generalised random block design to test the effect of watershed (block), height, and distance on microclimate and microarthropod data. A separate multivariate analysis of variance (MANOVA, full-factorial mixed-model) was used to analyse each of the temperature, humidity, and microarthropod abundance data, due to the non-independence of variables within each. The following dependent variables were examined for the effect of height and distance from trunk: Temperature–minimum temperature, maximum temperature, average daily temperature, and standard deviation (SD) of temperature; Relative humidity–minimum relative humidity, average daily relative humidity, SD of relative humidity, and the number of days humidity reached 100%; Microarthropod abundance (no. individuals per g dwt moss) – Oribatida, Mesostigmata, Prostigmata, Collembola, and other microarthropods. A two-way, full-factorial ANOVA was used to test the effects of height and distance on absolute moisture content of the moss habitat, and total species richness (no. species per g dwt moss). These tests were performed using Statistica 7.0 (StatSoft Inc, 2004).

To examine whether small-scale (within-tree) environmental differences form distinct microclimate zones, we used a Non-metric Multidimensional Scaling (NMDS) plot based on Euclidean distance similarity of environmental variables among sample locations followed by a one-way analysis of similarities (ANOSIM) using each height-by-distance combination as independent treatments in Primer 5 (2001). Community composition of the microarthropods was explored in a similar manner, using Bray-Curtis pair-wise similarity matrix on square root transformed standardised species abundances followed by one-way ANOSIM and plotted using NMDS. The NMDS method uses the ranks of the Bray-Curtis similarities to construct the ordination plot, and the realisation of the NMDS is assessed by a stress value.

We use two methods to link the traits of microarthropod species to our environmental variables: RLQ analysis (Dolédec *et al.*, 1996) and fourth-corner analysis (Legendre *et al.*, 1997; Dray & Legendre, 2008). RLQ analysis consists of a co-inertia analysis of the joint structure of three matrices, and is a measure of how robust relationships are under random permutation of matrix rows and columns. The three matrices were as follows: the species abundance-by-site matrix (L), the environmental factors-by-site matrix (R), and the species abundance-by-trait state matrix (Q). Matrices L and R are linked by shared rows (sites), whereas the L and Q matrices are linked by shared columns (species). A total of 36 trees, 20 species (representing >90% of the total abundance), 44 environmental factor states, and 20 trait states were included in the RLQ analysis (Supplementary Tables S1 and S2). All species trait and environmental states were expressed as dummy variables.

The first step in RLQ analysis is three separate ordinations of the R, L, and Q matrices, respectively. The species matrix (L), containing the standardised abundance of the 20 most abundant species at each sample location, was analysed by correspondence analysis (CA). The environmental factor matrix (R) and the traits state matrix (Q) were both analysed using principal component analysis (PCA), using CA site scores as row weightings for the PCA of R, and CA species scores as column weightings in the PCA of Q (Hausner *et al.*, 2003). A single inertia analysis (RLQ analysis) was then conducted on the cross-matrix, and overall significance of the relationship between environmental factors and species traits was assessed by 999 Monte Carlo permutations of the rows in R and Q with the total inertia in the RLQ analysis (Dolédec *et al.*, 1996). The total inertia of the RLQ analysis was then compared with the inertia of the unconstrained, separate analyses to evaluate the per cent of the variation in the separate analyses that is accounted for by the RLQ analysis. Subsequently, fourth-corner analysis (Legendre *et al.*, 1997; Dray & Legendre, 2008) was used to quantify and test the relationship between environmental variables and species trait states. The fourth-corner statistic corresponds to a Pearson product-moment correlation measuring the link between species abundances, environmental treatment variables, and species traits. RLQ and fourth-corner analyses were conducted using the ade4 package (Chessel *et al.*, 2004) in R version 2.14.1 (R Development Core Team, 2011).

Results

The moss-habitat microclimate within large, old Sitka spruce trees differed depending on the height from ground and distance from the trunk, with the biggest difference

Table 1. Average temperature (*T*) and relative humidity (RH) (±SE) as measured in four different areas (30 m or 15 m height; beside trunk, or 2 m out from trunk on a branch) of the canopy of Sitka spruce trees. Values are averaged across three watershed estuary sites on the west coast of Vancouver Island, Canada. Total number of trees measured was 36 trees over 330 days.

	Temperature (°C)			
	Maximum *T*	Minimum *T*	Average *T*	SD* *T*
30 m trunk	34.63 (1.5)	−5.17 (0.2)	7.97 (0.1)	5.85 (0.1)
30 m branch	36.62 (2.0)	−5.65 (0.1)	7.84 (0.1)	6.06 (0.1)
15 m trunk	31.50 (1.0)	−5.20 (0.1)	7.57 (0.2)	5.75 (0.0)
15 m branch	36.15 (1.9)	−5.58 (0.1)	7.51 (0.1)	5.94 (0.1)

Height: $F_{4,29} = 5.70$, $P = 0.002$
Distance: $F_{4,29} = 6.60$, $P = 0.001$

	Relative humidity (%)			
	Minimum RH	Average RH	SD* RH	100% Days
30 m trunk	16.21 (0.8)	89.12 (0.6)	14.82 (0.4)	31.56 (7.5)
30 m branch	15.71 (2.1)	91.15 (0.6)	14.52 (0.8)	75.56 (15.1)
15 m trunk	18.53 (0.8)	91.73 (0.8)	12.80 (0.9)	40.11 (19.1)
15 m branch	17.59 (1.2)	93.45 (0.3)	11.63 (0.5)	68.00 (16.6)

Height: $F_{4,29} = 5.13$, $P = 0.003$
Distance: $F_{4,29} = 3.41$, $P = 0.021$

*SD is the average standard deviation of temperature/relative humidity measured over 330 days for each treatment, and is used as an index of climate variability. Statistics given are from full-factorial MANOVA general linear model. Height × Distance interactions are non-significant ($P > 0.05$), and not shown.

being between 30 m areas near the trunk versus lower canopy (15 m) areas on branches, 2 m away from the trunk (Table 1). In general, temperature increased with height and distance from the trunk, microclimate stability decreased with height, and moisture availability/relative humidity decreased with height and increased with distance from the trunk (Fig. 1). We found that the average temperature was warmer at 30 m than 15 m (Univariate results presented from MANOVA: $F = 32.14$, $P < 0.001$), as was the maximum temperature reached, and the variability of temperature greater at 30 m. The high canopy was significantly less humid on average than at 15 m (Univariate $F = 15.40$, $P < 0.001$), and also had lower minimum humidity, and greater variability in humidity (Univariate $F = 13.78$, $P < 0.001$). Distance from trunk was a significant variable in both temperature and relative humidity measures. Maximum temperatures (Univariate $F = 4.413$, $P = 0.046$), minimum temperatures (Univariate $F = 42.97$, $P < 0.001$), and the variation in temperature (Univariate $F = 7.47$, $P = 0.012$) were significantly greater at 2 m away from the trunk. Relative humidity was on average lower near the trunk (Univariate $F = 8.91$, $P = 0.005$), but there was greater variability further away from the trunk; 2 m away from the trunk recorded nearly twice as many 100% relative humidity days (Univariate $F = 5.58$, $P = 0.024$). The absolute moisture content of the moss at the time of collection was significantly reduced at 30 m (39.7%) compared with 15 m (77.2%) in the canopy (ANOVA; $F = 6.49$, $P = 0.016$). These differences in microclimate factors lead to significantly different environmental zones within trees (ANOSIM Global

$R = 0.089$, $P = 0.030$), whereby near the trunk at 30 m was significantly different than further out on the branch at 30 m, or 15 m near the trunk (pair-wise comparisons $P = 0.048$, 0.005, respectively) (Fig. 2a).

Total species richness and overall abundances of canopy-dwelling microarthropods were significantly greater at 15 m than 30 m (Richness: $F_{1,32} = 6.853$, $P = 0.013$; Abundance: Wilk's $\lambda = 0.675$, $F_{5,28} = 2.70$, $P = 0.041$). Average species richness for each height-by-distance combination was as follows: 15 m trunk = 19.0 (±1.2 SE), 15 m branch = 19.8 (±1.6 SE), 30 m trunk = 16.8 (±2.4 SE), and 30 m branch = 13.3 (±1.0 SE). Trends in abundance were driven by the most abundant group, Oribatid mites, and other microarthropods (Univariate abundance result for Oribatida; $F = 9.08$, $P = 0.005$, other microarthropods; $F = 11.03$, $P = 0.002$). There were significant univariate height-by-distance interactions for abundances of Mesostigmata and Collembola (Univariate results $F = 6.945$, $P = 0.013$, $F = 4.41$, $P = 0.047$, respectively), whereby abundances were highest near the trunk at 30 m, and at 2 m from the trunk in the lower canopy (Fig. 3). ANOSIM revealed significant differences in community composition (Global $R = 0.254$, $P = 0.001$) among all pair-wise combinations with the exception of near the trunk at 30 and 15 m (Fig. 2b).

In the RLQ analysis, random permutations (999) of the rows of the R and Q tables indicated a significant ($P = 0.033$) association of the co-structure between species traits and environmental variables. The first two axes of the RLQ analysis extracted 56% and 33% of the total variance of the cross-matrix of the species traits and
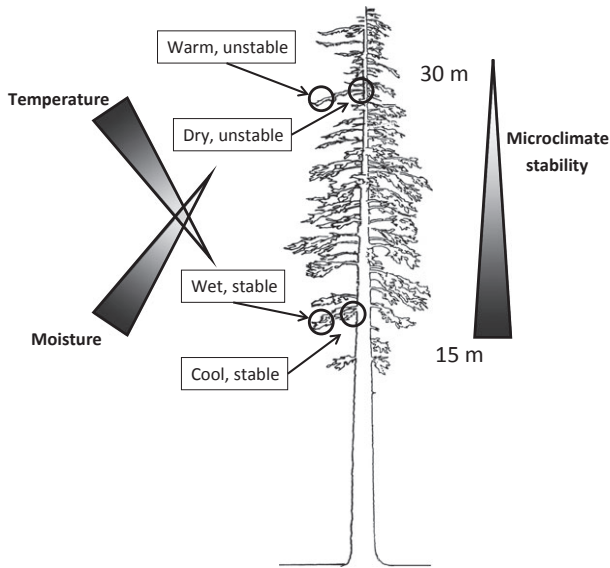
Fig. 1. General microclimate trends observed within canopy habitats of Sitka spruce trees on the west coast of Vancouver Island, Canada. Temperature and relative humidity were measured in four different canopy zones (30 m or 15 m height; beside trunk or 2 m out from the trunk) in 36 trees across three watershed estuary over 330 days. Microclimate zones within the canopy were observed, but overlap among the zones suggest a gradient of environmental conditions associated with exposure (sun, wind, and rain) and the development of moss microhabitat.

environmental variables, respectively. The proportion of variance accounted for by the RLQ analysis was compared with that resulting from the separate analyses of the individual matrices. Here, the RLQ axis 1 accounted for 57% and 90% of the potential variability of the first axis in the separate analyses of the environmental variables and species traits (i.e. the ratio between the variance of the environmental/trait characteristics in RLQ and the variance of the environmental/trait characteristics in the separate analysis). Because the RLQ analysis maximises the covariance between the species traits and the environmental variables, species abundance explained less variance in the first axis (63%). Both the first and second RLQ axes accounted for a moderate amount of the variance among the environmental dataset; axis 1 separated 30 m sampling locations with low moisture (negative values), from 15 m sampling locations with greater moisture (positive values), whereas watershed differences were associated with axis 2 – Sydney watershed (negative values) had more variable climate conditions, whereas the Moyeha and Watta watersheds (positive values) experienced milder and warmer temperatures (Fig. 4a). For the species trait dataset, the first RLQ axis separated two groups of smaller bodied Oribatida mite species based on desiccation tolerance; desiccation tolerant members of the family Oppiidae (negative values) versus low-to-moderate desiccation tolerance in members of the families Tectocepheidae (*Tectocepheus velatus*) and Oribatulidae (*Phauloppia*
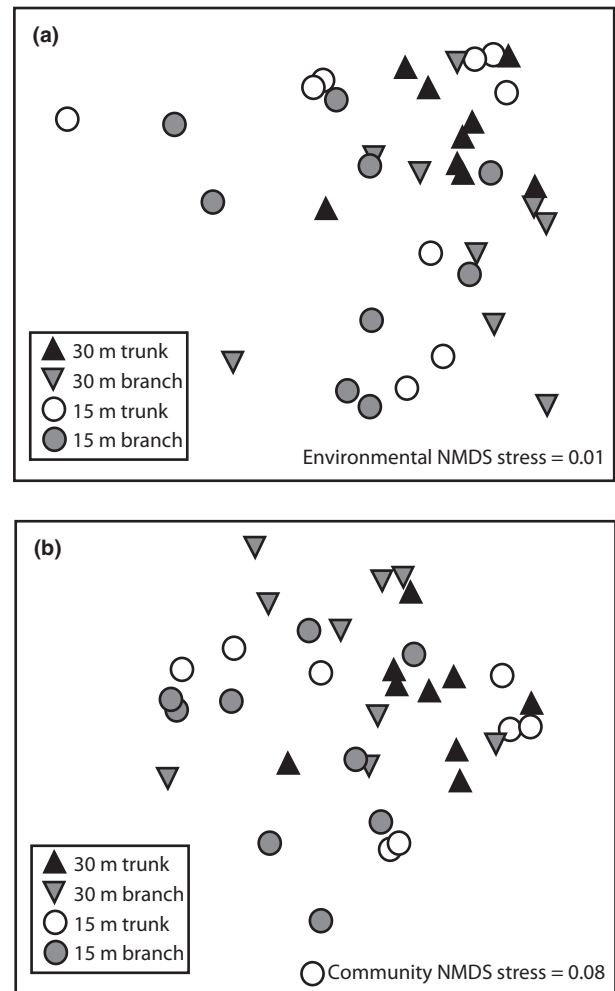

Fig. 2. (a) Non-metric Multidimensional Scaling plot of environmental variables, and (b) community composition of the microarthropods within canopy habitats of Sitka spruce trees on the west coast of Vancouver Island, Canada. Environmental conditions near the trunk at 30 m are considered a distinct microclimate zone, which contained a qualitatively different microarthropod community.

sp.) (positive values). The second axis of the trait dataset separated species that were well-sclerotised (Oribatida) from soft-bodied Collembola and Prostigmata species (Fig. 4b). Fourth-corner analysis revealed numerous correlations between environmental characteristics and species trait states that were significantly different from expected based on permutation tests (Fig. 4c). The highest correlation was a negative correlation between well-sclerotised species (mainly Oribatida) and warm average temperatures ($P < 0.001$).

Discussion

Microclimate zones within the canopy of conifer trees in a coastal temperate rainforest were observed, but overlap
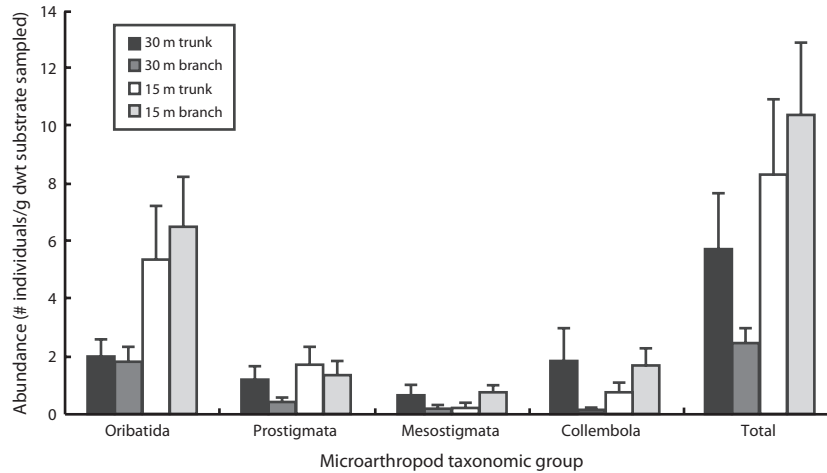
Fig. 3. Average abundance (no. individuals per g dwt canopy substrate) (±SE) for microarthropod groups sampled from canopy microclimate zones of Sitka spruce trees on the west coast of Vancouver Island, Canada.

among the zones suggest a gradient of environmental conditions associated with exposure (sun, wind, and rain). These factors are likely inter-related and further associated with age of the tree and the development stage of both the forest stand (Dial *et al.*, 2011) and the canopy moss microhabitat itself. Arboreal epiphytic bryophytes are strongly regulated by moisture and temperature (Proctor, 1982), and the vertical stratification of arboreal bryophytes has been well established for temperate coniferous forests in North America (McCune *et al.*, 1997; Sillett & Rambo, 2000; Campbell & Coxson, 2001; Sillett & Antoine, 2004; Heithecker & Halpern, 2006; Rambo & North, 2009) and Central and South American cloud forests (Gehrig-Downie *et al.*, 2011; Romanski *et al.*, 2011). These studies suggest that humidity as related to rainfall and mist/fog availability is the most important factor for growth of dominant canopy moss species (e.g. *Isothecium myosuroides*) (Smith, 1982). Access to light availability higher in the canopy may also increase moss growth, but increased exposure to wind higher in the canopy likely decreases the retention of moisture in the moss system (Romanski *et al.*, 2011). Retention of moisture by mosses also increases with depth of underlying suspended soils (Lindo & Winchester, 2007b). Thus, there is likely a positive feedback of increased moisture retention in the lower canopy that would facilitate moss growth, and in turn, retain greater suspended soil moisture. Differences in environmental variables observed between heights are influenced by differences in exposure from branches located above and the extent and development of moss patches; whereas differences in environmental variables between trunk and branch are less influenced by exposure, and more strongly related to the development of moss patches, as depth of moss decreases considerably on limbs directly adjoining the trunk. In turn, moss growth and suspended soil development is likely an underlying factor separating environmental conditions on 15 m branch samples from 30 m trunk sampling sites.

We found separation of microarthropod communities among microzones sampled associated with environmental factors, driven largely by decreased species richness and abundance at 30 m due to reduced moisture availability in the moss substrate (Siepel, 1996; Lindo & Visser, 2003; Chisholm *et al.*, 2011). Similar to environmental conditions, however, microarthropod communities did not completely form separate communities associate with *a priori* microclimate zones. This is likely due to community composition depending on moss depth as a buffer for temperature and moisture conditions at depth within the moss system (Lindo *et al.*, 2008), and the factors affecting moss-mat development as previously described. The RLQ analysis helped reveal some of the variation in both environmental and species data, as many species traits were associated with the microclimate variables observed. The first RLQ axis in both the environmental and trait datasets separated sites and species based on moisture conditions and desiccation tolerance. But it also became apparent that differences in environmental conditions among watersheds contributed to the variation associated with height and distance factors. Although these results were not observed as a significant block effect in the parametric analyses, they appear to play a role in the relationship between species traits and environmental conditions in the RLQ analysis. In particular, the secondary axes of the RLQ can be explained by a less species rich community in the Watta/Moyeha watersheds, which experienced warmer and milder climate conditions compared with the Sydney watershed which is known for its high diversity (Lindo & Winchester, 2009). This trend of high diversity in the Sydney watershed was observed in our trait-based analysis whereby well-sclerotised, larger bodied species with low vagility (suborder Oribatida) were grouped along the second RLQ axis associated with environmental conditions specific for the Sydney.

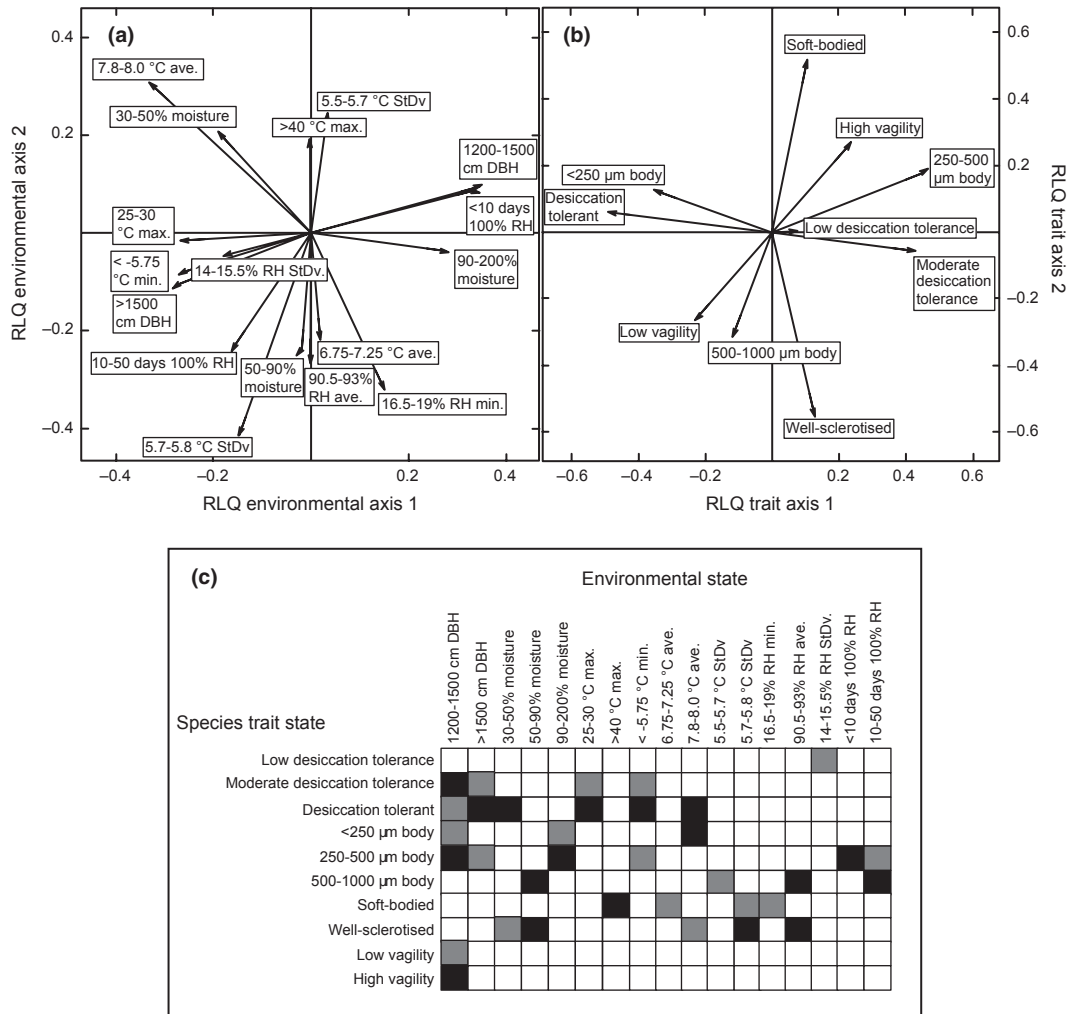Surprisingly, many soft-bodied species (Collembola, Prostigmata) were found in the warmest, low-moisture

Fig. 4. Results of RLQ analysis: (a) microclimate environmental states, (b) microarthropod species trait states (only traits with significant and positive correlation values with an environmental variable are shown), and (c) results of fourth-corner permutation test displaying significant correlation of species trait state with environmental variable state (black is positive correlation, grey is negative correlation; all correlations are significant at $P < 0.05$). Please refer to environmental and species trait information in Supplementary Tables S1 and S2.

conditions, suggesting that other physiological mechanisms allow for these organisms to retain moisture under harsh conditions (Wauthy & Vannier, 1988; Elnitsky *et al.*, 2008). For instance, the desiccation resistance of the red velvet mite (*Balaustium* sp. (Prostigmata: Erythraeidae) (Hedges *et al.*, 2012) has been attributed to glands (urnulae) which secrete a waterproofing barrier that potentially reduces water loss in this species (Yoder *et al.*, 2008). It remains unknown whether moss-dwelling members of the Tydeidae possess similar physiological mechanisms. Results are similar to Lindo *et al.* (2012) who found small, soft-bodied Prostigmata to be the most desiccation resistant among a forest floor microarthropod community, and Prinzing (2001, 2005) suggests that microarthropods use compensatory movement among microhabitats to cope with fluctuating climate conditions; species may migrate to moist microsites during drought periods. It was expected

that increased variability (in temperate and moisture) would select for species with specific characteristics associated with vagility and desiccation tolerance. For microarthropods, however, compensatory redistribution may occur at the scale of centimetres (Prinzing, 2005), which may explain why few environmental variables correlated significantly with vagility. Regardless, the ability of a species to respond in a compensatory way to changes in climate or move to more suitable environmental conditions (species sorting) is an important factor in climate change models for biodiversity (Urban *et al.*, 2011).

Epiphytes in the arboreal system of coniferous coastal temperate rainforests are primarily bryophytes, and were the target of our sampling. They have been shown to have high microarthropod species diversity which increases with extent and development of the moss mats (Lindo & Winchester, 2007b), and the moss mats themselves have been

shown to correlate with tree size (age) and climate gradients (temperature and humidity) associated with height in trees. We add to this observation in two ways. First, although we show that temperature and moisture conditions differ among the within-tree microzones, the response of the fauna is more likely dependent on the climate conditions and buffering capacity within the moss mat itself – which is dependent on the size (extent and depth) of the moss mat. Second, we incorporate distance from trunk as a variable in our observations of microclimate within a tree. This is important as we show that whereas temperature increases with distance from the trunk, moisture content of the moss mat also increases due to greater depth of moss out on a limb, compared to directly adjacent to the trunk.

Interestingly, significant correlations of species traits and tree size and age (DBH) were observed, suggesting that older trees contained greater numbers of small, poorly sclerotised species. These relationships are likely mediated via climate stability dependent on formation and depth of the moss substrate (the 'bryosphere' sensu Lindo & Gonzalez, 2010), and species ability to redistribute among microsites, as previously discussed. Moss mats within conifer trees of the coast temperate rainforest are related to the age and development stage of both the tree and the forest stand (Franklin & Van Pelt, 2004), which suggests that large, old trees with high moss biomass are important for microarthropod biodiversity within canopy systems.

Acknowledgements

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12010:

Figure S1. Canopy climber in a mossy Sitka spruce [*Picea sitchensis* (Bong) Carr.] tree on the west coast of Canada.

Table S1. Twenty most abundant species and their trait states, collected from canopy habitats of Sitka spruce trees on the westcoast of Vancouver Island, Canada, used in RLQ analysis.

Table S2. Environmental states [temperature (*T*) and relative humidity (RH)] as measured in four different areas of the canopy of 36 Sitka spruce trees on the westcoast of Vancouver Island, Canada, used for RLQ analysis.

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