Local–regional boundary shifts in oribatid mite (Acari: Oribatida) communities: species–area relationships in arboreal habitat islands of a coastal temperate rain forest, Vancouver Island, Canada

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ABSTRACT

Aim This study investigates the species–area relationship (SAR) for oribatid mite communities of isolated suspended soil habitats, and compares the shape and slope of the SAR with a nested data set collected over three spatial scales (core, patch and tree level). We investigate whether scale dependence is exhibited in the nested sampling design, use multivariate regression models to elucidate factors affecting richness and abundance patterns, and ask whether the community composition of oribatid mites changes in suspended soil patches of different sizes.

Location Walbran Valley, Vancouver Island, Canada.

Methods A total of 216 core samples were collected from 72 small, medium and large isolated suspended soil habitats in six western redcedar trees in June 2005. The relationship between oribatid species richness and habitat volume was modelled for suspended soil habitat isolates (type 3) and a nested sampling design (type 1) over multiple spatial scales. Nonlinear estimation parameterized linear, power and Weibull function regression models for both SAR designs, and these were assessed for best fit using $R^2$ and Akaike’s information criteria ($\Delta AIC$) values. Factors affecting oribatid mite species richness and standardized abundance (number per g dry weight) were analysed by ANOVA and linear regression models.

Results Sixty-seven species of oribatid mites were identified from 9064 adult specimens. Surface area and moisture content of suspended soils contributed to the variation in species richness, while overall oribatid mite abundance was explained by moisture and depth. A power-law function best described the isolate SAR ($S = 3.97 \times A^{0.12}$, $R^2 = 0.247$, $F_{1,70} = 22.450$, $P < 0.001$), although linear and Weibull functions were also valid models. Oribatid mite species richness in nested samples closely fitted a power-law model ($S = 1.96 \times A^{0.39}$, $R^2 = 0.854$, $F_{1,18} = 2693.6$, $P < 0.001$). The nested SAR constructed over spatial scales of core, patch and tree levels proved to be scale-independent.

Main conclusions Unique microhabitats provided by well developed suspended soil accumulations are a habitat template responsible for the diversity of canopy oribatid mites. Species–area relationships of isolate vs. nested species richness data differed in the rate of accumulation of species with increased area. We suggest that colonization history, stability of suspended soil environments, and structural habitat complexity at local and regional scales are major determinants of arboreal oribatid mite species richness.

Keywords Boundary shift, canopy, habitat islands, oribatid mites, scale dependence, species–area relationship, suspended soil, western redcedar.
INTRODUCTION

The positive relationship between species richness and area is well established in community ecology (Connor & McCoy, 1979; Rosenzweig, 1995; Drakare et al., 2006). Generally this species–area relationship (SAR) is described using the power-law equation \( S = cA^z \), where \( S \) is the number of species, \( A \) is a unit of area, and \( c \) and \( z \) are constants (Arrhenius, 1921). The power-law function is linear on a log-log plot, and the slope (\( z \)) of the SAR typically varies between 0.1 and 0.4, depending on the system or taxon under observation (Rosenzweig, 1995).

The interpretation of \( z \), and whether there is a biological meaning, is highly debated (Martin, 1981; Abbott, 1983; Matter et al., 2002), but factors believed to influence \( z \) include latitude, habitat complexity, habitat isolation, species source pool size, body size and dispersal capability (Martin, 1981; Abbott, 1983; Gentile & Argano, 2005; Drakare et al., 2006).

The traditional power-law equation fits most SAR data (Connor & McCoy, 1979; Szinglo & Storch, 2004); however, species–area curves may differ depending on the manner in which samples are collected and analysed (Rosenzweig, 1995; Scheiner, 2003). Data collected from isolates (discrete habitat patches such as ponds, mountain tops or islands) give true SARs, and differ from nested SARs where survey areas are defined by the sampling design and areas of greater size are accumulated through sampling (Drakare et al., 2006). Furthermore, SARs sampled over large, nested spatial scales are shown to be triphasic (Hubbell, 2001), and the slope of the SAR scale-dependent.

The SAR has been clearly demonstrated for many taxa (Drakare et al., 2006), but the causal mechanisms of the observed relationship are less clear. Three main hypotheses proposed to explain SARs are habitat heterogeneity (Lawton & Schröder, 1977; Southwood, 1996); the balance between colonization–extinction dynamics that forms the core of the equilibrium theory of island biogeography (MacArthur & Wilson, 1967); and as a sampling artefact (Connor & McCoy, 1979). Traditionally, island biogeography theory has been used to predict species assemblages in a mainland-island system, but has also been applied to ‘habitat islands’ (Haila, 2002), extending colonization–extinction dynamics into a metacommunity framework where local habitat patches are linked by dispersal to other habitat patches within a region (Wilson, 1992; Leibold et al., 2004; Cadotte & Fukami, 2005; Koelle & Vandemeer, 2005). Examples of natural metacommunities exist in the form of ponds (Rundle et al., 2002), dung, carrion or fungal fruiting bodies (O’Connell & Bolger, 1997) (patches are discrete but ephemeral), reefs (Gennon et al., 2004), alpine meadows or hydrothermal vents (Tsurumi, 2003) (patches are permanent but with less defined boundaries), lakes (Havel & Shurin, 2004), moss- and lichen-encrusted boulders (Weibull & Rydin, 2005), or suspended soils in temperate and tropical rain forest canopies (Lindo & Winchester, 2006) (patches are permanent and discrete). In ancient western redcedar trees (*Thuja plicata* D. Don) of North American temperate rain forests, suspended soils form high above the forest floor (c. 35 m) and occur as discrete patches of habitat ranging in surface area from 100 to 20,000 cm² (Lindo & Winchester, 2006). Suspended soils are habitat islands of accumulated organic matter and epiphytes, separated from one another within a tree crown by a barren bark matrix and between trees by the atmosphere (Moffet, 2000; Wardle et al., 2003). These habitats contain an abundant and species-rich community of arboreal microarthropods dominated by oribatid mites (Acari: Oribatida), many species of which are undescribed and not found on the forest floor (Behan-Pelletier et al., 1993; Winchester et al., 1999; Fagan et al., 2006).

This study investigates the species–area relationship in the acarine suborder Oribatida inhabiting 72 suspended soil habitat islands in the canopy of six western redcedar trees in a temperate rain forest of Canada. As oribatid mites inhabit three-dimensional soil space, we use volume of suspended soil patch size in our SAR models. We evaluate the shape and slope of the SAR for a data set of isolates (individual suspended soil habitat islands), use multivariate regression models to elucidate factors affecting richness and abundance patterns, and ask whether community composition of oribatid mites changes in suspended soil patches of different sizes. We then compare the isolate SAR with a nested data set collected over three spatial scales (core, patch and tree level), and investigate whether scale dependence is exhibited and if local–regional boundary shifts are detectable when successively larger areas of suspended soil habitats are sampled. We hypothesize that the species richness of oribatid mites within suspended soil habitats is likely to be dependent on correlates of patch size such as surface area, depth, volume and moisture. Additionally, species may respond differently to the same level of habitat size (Didham et al., 1998). Differences in community composition within an SAR framework may be due to species–time relationships (White et al., 2006) (large suspended soil patches may have existed for longer); differences in species responses to edges (Bender et al., 1998) (as the harshness of the soil environment will be buffered in larger habitat islands); or differences in competitive abilities (poor competitors are less abundant in large patches) or reproductive modes (Schneider et al., 2007) among species.

METHODS

Study site and sampling design

The study site was located in the temperate rain forest of the Walbran Valley on the south-west coast of Vancouver Island, British Columbia, Canada (48°39′N, 124°35′W). The valley lies entirely within the Coastal Western Hemlock biogeoclimatic zone (Meidinger & Pojar, 1991) where the climate is characterized by wet, humid, cool summers and mild winters, and where a mean annual precipitation of 2990 mm is typical for the area (Environment Canada, 2006). Conifers are dominant in this rain forest and include western hemlock (*Tsuga heterophylla* (Rafn.) Sarg.), Sitka spruce (*Picea sitchensis* (Bong) Carr.), Amabilis fir (*Abies amabilis* (Dougld.) Forb.) and western redcedar (*Thuja plicata* D. Don).
In Pacific Northwest forests, ancient western redcedar have a distinct morphology of trunk reiterations referred to as a candelabra structure. The multi-furcated trunk morphology promotes the accumulation of organic matter and the formation of numerous discrete, isolated patches of suspended litter and soil of varying size. Suspended soils typically do not form without trunk reiterations or substantially-sized limbs to accumulate organic matter, and as such, suspended soils are not usually encountered below 20 m above the ground. The six western redcedar trees sampled in this study were c. 50 m high, and the diameter of the trunks at breast height (d.b.h.) ranged from 213–365 cm (mean d.b.h. = 271 cm ± 52 SD). The majority of limbs and trunk reiterations occurred between 20 and 45 m above ground level.

Suspected soils in six western redcedar trees were sampled from 5 to 10 June 2005. Suspected soils within each tree were classified by their surface area into three size classes that were selected a priori to incorporate the range of suspected soil patches available (small = 750 cm$^2$, medium = 2500 cm$^2$, large = 7500 cm$^2$). We randomly chose four suspected soil habitats of each size class within each tree and extracted three replicate subsamples from the centre of each habitat patch using individual PVC corers (160 series, 3.175 cm diameter). A total of 216 core samples were collected (72 from each size class). Access to the canopy was by single-rope techniques that have been modified over the previous 10 years in association with the canopy research program at the University of Victoria (Lindo & Winchester, 2006). Each suspected soil habitat patch (72 in total) was measured for surface area (cm$^2$), height from ground (m) and average depth (cm) in the field. Moisture content (%) was determined gravimetrically from soil cores in the laboratory. Oribatid mites were extracted from soil core samples into 75% EtOH using Berlese funnels for 48 h (Norton & Kethley, 1988). Extracted oribatid mites were quantified by number of individuals per g dry weight, and all adult oribatid mites were identified to species. Representative specimens were slide-mounted using Hoyer’s medium (Krantz, 1978) and a reference collection is deposited at the Canadian National Collection of Insects, Arachnids and Nematodes in Ottawa, Canada.

Data analyses

This study incorporates a randomized block design where four replicate suspected soil patches within three size classes are sampled within each of six trees serving as replicate blocks. All response variables (height, moisture, surface area, depth, volume, total microarthropod and oribatid mite abundance, oribatid mite species richness) conformed to normality, and analysis and patch-level data are averaged for within patches (one to three cores across 72 patches sampled) and within trees (1–12 patches sampled in six trees). Nonlinear estimation parameterized, linear, power and Weibull function regression models for the multiple scale SAR, which were assessed for best fit using $R^2$ and $\Delta$AIC values.

RESULTS

Suspended soil habitats sampled within each of three size classes (small, medium, large) at a range of heights within the canopy of six western redcedars were significantly different...
from one another with respect to average surface area and volume of the suspended soil sampled (Table 1). There was a significant difference in average soil depth among the different size classes, with the large suspended soil habitats being significantly deeper than the small or medium suspended soil habitats. Moisture content among the different size classes showed similar results, with the large suspended soils being significantly wetter than the small and medium suspended soil patches. All suspended soils were sampled from 17.5 to 44.7 m above the ground, and there was no relationship between the size of the suspended soil and the height at which it occurred within the canopy (Table 1).

Sixty-seven species of oribatid mites were identified from 9064 adult specimens collected from 216 cores sampled from 72 suspended soil habitat islands (see Appendix S1 in Supplementary Material). Oribatid mite species richness was significantly greater in the large suspended soil size class when compared with the small and medium size classes; however, there was no difference in richness between the medium and small size classes (Table 1; Fig. 1).

![Cumulative species richness](image)

**Figure 1** Coleman rarefaction curves (average of 50 randomizations without sample replacement ± SD) for adult oribatid mites (Acari: Oribatida) identified from 72 core samples in three a priori determined size classes of suspended soil habitat in six western redcedar trees in the Walbran Valley of Vancouver Island, Canada.

Microarthropod and oribatid mite abundance did not differ significantly among size classes (Table 1). Surface area and moisture content of suspended soil contributed to the variation in oribatid mite species richness ($R^2 = 0.337$, $F_{2,65} = 17.554$, $P < 0.001$), while overall oribatid mite abundance was best explained by a multiple regression model including moisture, depth, and surface area of the suspended soils ($R^2 = 0.244$, $F_{3,68} = 7.334$, $P < 0.001$). The regression model that accounted for the most variation in total microarthropod abundance included moisture and depth of the suspended soils ($R^2 = 0.278$, $F_{2,69} = 13.305$, $P < 0.001$).

Rarefaction curves indicated that species richness of oribatid mites in suspended soils increases with larger soil patches, and all curves followed a similar trajectory (Fig. 1), but estimates of species richness in the medium size class sometimes exceeded those of the large suspended soil patches due to the high variance associated with the medium-sized patches (Table 2). The five most abundant species, *Quadroppia quadricarinata* (Michael), *Oppiella nova* (Oudemans), *Tectocepheus velatus* (Michael), *Scheloribates* sp. and *Archiphthiracarus* sp. 1 collectively accounted for > 50% of the total number of individuals identified. Three of the 10 most abundant oribatids (*Archiphthiracarus* sp. 1, *O. nova*, *Suctobelbella* sp. 5) showed significant increases in standardized and relative abundance with increasing size of suspended soil patch (Table 3). The relative abundance of *T. velatus* decreased with increasing patch size class.

The SAR constructed for the 72 suspended soil habitat islands (isolate data) was best described by the power-law function ($S = 3.97 \times A^{0.12}$, $R^2 = 0.247$, $F_{1,70} = 22.450$, $P < 0.001$) (Fig. 2), although linear and Weibull functions were also valid models (AAIC value < 2.00) (Table 4). Oribatid mite species richness data arranged by nested samples of volume from 47 to > 10,350 cm$^3$ across suspended soil habitats in western redcedar trees also closely fit a power-law model ($S = 1.96 \times A^{0.39}$, $R^2 = 0.854$, $F_{1,18} = 2693.600$, $P < 0.001$) (Fig. 3). The same data provided a poorer fit to a linear or Weibull function (Table 4). The nested SAR constructed over spatial scales of core, patch and tree levels proved to be scale-independent.

### Table 1 The effect of suspended soil patch size on physical and microarthropod variables in western redcedar trees of the Walbran Valley, BC, Canada.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Small ($\text{m}$)</th>
<th>Medium ($\text{m}$)</th>
<th>Large ($\text{m}$)</th>
<th>$F_{2,10}$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height (m)</td>
<td>32.2 (6.6)</td>
<td>31.3 (6.6)</td>
<td>34.1 (5.7)</td>
<td>1.509</td>
<td>0.230</td>
</tr>
<tr>
<td>Moisture (%)</td>
<td>69.1 (48.9)$^b$</td>
<td>82.6 (52.5)$^b$</td>
<td>123.3 (47.9)$^a$</td>
<td>12.154</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Surface area ($\text{cm}^2$)</td>
<td>378 (167)$^b$</td>
<td>2733 (1659)$^b$</td>
<td>7933 (4950)$^a$</td>
<td>47.791</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Depth (cm)</td>
<td>5.00 (2.0)$^b$</td>
<td>5.74 (1.7)$^b$</td>
<td>7.46 (1.9)$^a$</td>
<td>10.742</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Volume ($\text{cm}^3$)</td>
<td>1951 (1209)$^c$</td>
<td>16,387 (12,749)$^b$</td>
<td>55,500 (32,972)$^a$</td>
<td>44.063</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Microarthropod abundance</td>
<td>17.69 (14.8)</td>
<td>17.20 (15.1)</td>
<td>18.79 (9.6)</td>
<td>0.102</td>
<td>0.903</td>
</tr>
<tr>
<td>Oribatid abundance</td>
<td>9.36 (8.4)</td>
<td>8.36 (6.3)</td>
<td>11.12 (6.3)</td>
<td>1.016</td>
<td>0.369</td>
</tr>
<tr>
<td>Oribatid species richness</td>
<td>9.58 (4.0)$^b$</td>
<td>10.75 (3.5)$^b$</td>
<td>14.08 (3.0)$^a$</td>
<td>10.984</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>

Values are means (SD). Different superscript letters denote significant differences among treatments based on an LSD post hoc test.

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DISCUSSION

We describe a positive SAR between oribatid mites and increasing size (volume) of isolated suspended soil habitats in western redcedar tree crowns, and attribute this association to patch size characteristics such as depth, moisture and surface area. Increased stability of soil microclimates with increasing depth (Wallwork, 1983), greater moisture-holding capacity of large suspended soil patches (Siepel, 1996), and vertical stratification of species associated with differences in the structural aspects within different suspended soil layers (Yanoviak et al., 2004) are parameters that contribute to increased species richness of soil microarthropods. These correlates to diversity are supported in this study, where increased depth and moisture content are positively related to large suspended soil habitat patches, and are significant factors that contribute to increased species richness and abundance of oribatid mites.

The 67 species of oribatid mites collected from suspended soils associated with western redcedar canopies in the Walbran Valley on Vancouver Island increased the known arboreal species of this system by 12 species, and exceeded previously calculated species richness estimates from this forest ecosystem (Lindo & Winchester, 2006). Rarefaction curves and richness estimators suggest that more species are likely to be encountered with increased sampling, particularly in medium-sized suspended soil patches. The heterogeneity observed at the medium-sized patch class is also observed as a slightly steeper rise in the medium size class rarefaction curve, although the inequality in sampling effort (number of individuals caught) between the medium and large size classes may promote a biased effect (Buddle et al., 2005).

High species richness is associated with accumulations of organic matter and the formation of well developed suspended soil habitat patches (Wunderle, 1992; Behan-Pelletier et al., 1993; Lindo & Winchester, 2006), and we show further that

### Table 2

<table>
<thead>
<tr>
<th>Number of individuals</th>
<th>Total</th>
<th>Small</th>
<th>Medium</th>
<th>Large</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observed species richness</td>
<td>67</td>
<td>40</td>
<td>48</td>
<td>57</td>
</tr>
<tr>
<td>Jackknife 1st order</td>
<td>78.94 (±3.64)</td>
<td>46.90 (±2.50)</td>
<td>61.81 (±3.88)</td>
<td>69.82 (±3.80)</td>
</tr>
<tr>
<td>Jackknife 2nd order</td>
<td>80.97</td>
<td>48.92</td>
<td>74.64</td>
<td>71.91</td>
</tr>
<tr>
<td>Chao 1</td>
<td>77.29 (±7.79)</td>
<td>46.00 (±6.48)</td>
<td>64.67 (±14.84)</td>
<td>64.56 (±5.96)</td>
</tr>
</tbody>
</table>

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

### Table 3

The effect of suspended soil patch size on the abundance (number per 100 g dry weight) and relative abundance (percentage of total) of the 10 most common oribatid mite species in western redcedar trees of the Walbran Valley, BC, Canada.

<table>
<thead>
<tr>
<th>Species</th>
<th>Small</th>
<th>Medium</th>
<th>Large</th>
<th>F_{3,10}</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Archphthiracarus sp. 1</td>
<td>7.29 (17.3)</td>
<td>17.31 (55.2)</td>
<td>70.74 (135.9)</td>
<td>3.948</td>
<td>0.025</td>
</tr>
<tr>
<td>Trhypochthonius tectorum (Berlese, 1896)</td>
<td>33.14 (116.8)</td>
<td>27.13 (81.7)</td>
<td>2.27 (7.7)</td>
<td>0.977</td>
<td>0.383</td>
</tr>
<tr>
<td>Eupterotegaes rhamphosus Higgins and Woolley, 1963</td>
<td>20.82 (30.8)</td>
<td>34.62 (59.7)</td>
<td>15.21 (21.0)</td>
<td>0.598</td>
<td>0.553</td>
</tr>
<tr>
<td>Tectocepheus velatus (Michael, 1880)</td>
<td>81.89 (91.5)</td>
<td>50.04 (126.6)</td>
<td>39.93 (31.8)</td>
<td>0.357</td>
<td>0.701</td>
</tr>
<tr>
<td>Ophiella nova (Oudemans, 1902)</td>
<td>28.61 (65.1)</td>
<td>33.49 (71.1)</td>
<td>120.83 (172.8)</td>
<td>5.382</td>
<td>0.007</td>
</tr>
<tr>
<td>Moritzoppia sp.</td>
<td>21.63 (34.0)</td>
<td>41.47 (103.9)</td>
<td>42.55 (80.7)</td>
<td>1.677</td>
<td>0.196</td>
</tr>
<tr>
<td>Quadropria quadricarinata (Michael, 1885)</td>
<td>137.34 (264.7)</td>
<td>95.79 (121.0)</td>
<td>80.91 (91.5)</td>
<td>0.060</td>
<td>0.942</td>
</tr>
<tr>
<td>Suctobelbella sp. 5</td>
<td>16.65 (24.5)</td>
<td>18.54 (30.9)</td>
<td>43.38 (49.7)</td>
<td>4.184</td>
<td>0.020</td>
</tr>
<tr>
<td>Oribatula sp.</td>
<td>33.06 (85.9)</td>
<td>24.93 (87.2)</td>
<td>16.27 (31.8)</td>
<td>0.235</td>
<td>0.791</td>
</tr>
</tbody>
</table>

Values are means (SD). Different superscript letters denote significant differences among treatments based on an LSD post hoc test.
oribatid mite community composition in suspended soil habitats changes as a function of habitat patch size. The species driving community composition patterns tended to be the most abundant species in all size class patches, and the abundances of three species (O. nova, Archiphthiracarus sp. 1, Suctobelbella sp. 5) increased with size class. A nested community structure (Lomolino, 1996) was not observed, although the same three species had greater population sizes and standardized abundance in larger suspended soil patches. This increase in population size with increased area is consistent with island biogeography theory (MacArthur & Wilson, 1967; Martin, 1981), but may also be indicative of species-specific habitat associations. For example, phthiracarroid mites such as Archiphthiracarus sp. 1 are specialist decomposers of woody material (Niedbała, 1998), and may be more abundant in large soil patches as a result of increased woody material accumulation, or feeding on the host branch (if it is a suitable feeding resource for this species).

Spatial heterogeneity of the soil environment is one explanation for the high level of diversity observed in many soil microarthropod communities (Giller, 1996), and support for the habitat heterogeneity hypothesis is shown in increased diversity and abundance of arboreal mites associated with greater structural complexity of leaves in an Australian subtropical rain forest (Walter & O’Dowd, 1995). Furthermore, we observed that larger suspended soil patches supported a greater diversity of epiphytes (such as ferns, herbaceous plants and small conifer saplings) when compared with smaller suspended soil patches. The roots and root exudates associated with these plants can influence soil microarthropod composition (Lindo & Visser, 2003) by increasing food resources, such as ectomycorrhizal fungi associated with root tips (Schneider et al., 2005).

Table 4 The species–volume relationship (SVR) as described by linear, power-law and Weibull functions for arboreal oribatid mite communities in western redcedar trees at single and multiple spatial scales.

<table>
<thead>
<tr>
<th></th>
<th>d.f.</th>
<th>$R^2$</th>
<th>$P$</th>
<th>$\Delta$AIC</th>
<th>a</th>
<th>b</th>
<th>c</th>
</tr>
</thead>
<tbody>
<tr>
<td>Single-scale SVR</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Linear: $S = a + b \times A$</td>
<td>1,70</td>
<td>0.203</td>
<td>$&lt; 0.001$</td>
<td>1.74</td>
<td>$6 \times 10^{-5}$</td>
<td>10.03</td>
<td></td>
</tr>
<tr>
<td>Power: $S = a \times A^b$</td>
<td>1,70</td>
<td>0.247</td>
<td>$&lt; 0.001$</td>
<td>0.00</td>
<td>0.12</td>
<td>3.97</td>
<td></td>
</tr>
<tr>
<td>Weibull: $S = a \times [1 - \exp(-b \times A^c)]$</td>
<td>2,69</td>
<td>0.246</td>
<td>$&lt; 0.001$</td>
<td>2.00</td>
<td>103.60</td>
<td>0.04</td>
<td>0.12</td>
</tr>
<tr>
<td>Multiple-scale SVR</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Linear: $S = a + b \times A$</td>
<td>1,18</td>
<td>0.854</td>
<td>$&lt; 0.001$</td>
<td>20.1</td>
<td>19.58</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td>Power: $S = a \times A^b$</td>
<td>1,18</td>
<td>0.987</td>
<td>$&lt; 0.001$</td>
<td>0.00</td>
<td>1.96</td>
<td>0.39</td>
<td></td>
</tr>
<tr>
<td>Weibull: $S = a \times [1 - \exp(-b \times A^c)]$</td>
<td>2,17</td>
<td>0.927</td>
<td>$&lt; 0.001$</td>
<td>16.4</td>
<td>1075.1</td>
<td>$-0.05$</td>
<td>$-0.01$</td>
</tr>
</tbody>
</table>

Single spatial scale type 3 SVR for 72 individual suspended soil habitat islands. Multiple spatial scale for type 1 nested SVR with 19 cumulative sample points.
in larger patches may be inferior competitors, flourishing in less species-rich environments. *Tectocephus velatus* and *Q. quadrarcarinata*, both cosmopolitan species found in high abundance in many habitats (Behan-Pelletier, 1997), are known to inhabit high-disturbance areas, are generalist colonizer/early successional species, and are able to exploit new habitats (Maraun & Scheu, 2000). Their decreasing abundance with increasing patch size is perhaps indicative of soil patch age and stability.

Recent literature has focused on reproductive modes as a possible explanation for the distribution patterns for oribatid mites (Cianciolo & Norton, 2006; Schneider et al., 2006). This study estimated that 43% of species collected were asexually and 45% sexually reproducing, but 12% were undetermined (based on designations by Norton et al., 1993; Cianciolo & Norton, 2006). General trends in reproduction mode show that the average number of asexual species in suspended soil patches increases with increasing patch size; however, the proportion of number of individuals with an asexual reproductive mode decreased with patch size. In this study, we posit that increased stability and habitat heterogeneity are positively correlated with increased size of suspended soil patch where depth and moisture holding capacity increases, and edge effects are reduced. This may lead to increased asexuality being an artefact of species lineage, rather than a determinant of oribatid mite species distribution. Increased habitat complexity in larger suspended soils could increase the proportion of asexual species by increased prevalence of lower oribatid lineages (Macropylina), which are more commonly asexual (Norton et al., 1993). This study has a higher occurrence of lower oribatids than other canopy studies; for example, 19.5% of all species recorded in this study are Enarthronota, compared with the 9% known from other canopy studies (Behan-Pelletier & Walter, 2000). A lower relative proportion of Brachypylina (higher taxonomic lineages) oribatid mites (66%) are also observed, compared with the 74% of previously known canopy species (Behan-Pelletier & Walter, 2000).

Schneider et al. (2006) found no effect of habitat loss or isolation on the abundance or richness of oribatid mites during a field mesocosm experiment. They attributed these results to oribatid mites being generalist feeders, utilizing microhabitats, and having a high occurrence of asexual reproduction (thelytokous parthenogenesis; Norton, 1994), which enabled effective reproduction rates without having to find a mate. However, our study suggests that naturally occurring habitat patches developed over a long period (upwards of 1400 years; Parish & Antos, 2004), promote habitat heterogeneity which was correlated with patch size. Colonization processes in our study were more likely to be the driving structural force in our assemblages, compared with extinction processes associated with induced habitat loss in Schneider et al. (2006). Colonization history, structural complexity and environmental stability are all major determinants of species richness (Southwood, 1996). The role of community assembly history (Chase, 2003) and an interactive effect of time in SARs (species–time relationships; Adler et al., 2005) have been demonstrated recently. Structural complexity in forest ecosystems increases with time (Franklin & Van Pelt, 2004), and in the canopy is observed in increasing formation, structural complexity and stability within suspended soil habitats, which provides for increased species colonization potential (habitat template *sensu* Southwood, 1996).

The shape of the observed SAR in oribatid mite communities of isolated suspended soils was described adequately by a power-law function, followed closely by a linear fit to the data. The Weibull function (Tjørve, 2003; Jiménez-Valverde et al., 2006) and the asymptotic nature of this curve is a useful tool in providing estimates of regional species richness (Jiménez-Valverde et al., 2006), although we found it provided no greater resolution of fit than the power or linear functions. Different models were tested to fit the SAR data (He & Legendre, 1996) and our results support Connor & McCoy (1979), who found a linear or a power-law function to best describe their observed data sets. The power-law function is robust enough to describe most SARs (Sizling & Storch, 2004) and is also useful in comparing slopes of log-log plotted SARs. The biological meaning of $z$ is much debated (Martin, 1981; Abbott, 1983; Matter et al., 2002), and generally varies between 0.1 and 0.4. Diversity in isolates depends on the rates at which species colonize patches from nearby areas and then become extinct. Very isolated islands exhibit even lower $z$ values because colonization is from neighbouring islands rather than a mainland source pool, which typically has lower richness, decreasing the overall potential species richness, spatial turnover and thus $z$. Our $z$ value of 0.12 is low, but comparable with other type 3 SAR (Rosenzweig, 1995) data sets of island birds (Matter et al., 2002), plant species across 49 islands (Hovestadt et al., 2005), island snail populations (Nilsson et al., 1988), phytoplankton communities of freshwater and marine habitats (Smith et al., 2005), and oribatid mites in experimentally fragmented moss mats on boulders (Hoyle, 2004). Low $z$ values are attributed to the sampling design, and also to aggregated distributions (Turner & Tjørve, 2005), low trophic levels and generalist feeders (Holt et al., 1999), and small body size (Matter et al., 2002) characteristics of oribatid mites (Gillier, 1996).

It is necessary to differentiate between SAR sampling designs of nested and independent data sets (Drakare et al., 2006), as the two sampling designs can produce dramatically different SARs. Nested sampling designs (type 1 *sensu* Rosenzweig, 1995) often show greater goodness of fit to power-law functions and higher values of $z$ (slope) than data collected from isolates (Drakare et al., 2006). This was observed in our comparison of SAR slopes for oribatid mites in suspended soils of western redcedar when SARs were constructed from isolate data ($z = 0.12$, power-law $R^2 = 0.247$) and nested data ($z = 0.39$, power-law $R^2 = 0.987$). Data points in nested designs are non-independent and species richness always increases with increasing area, whereas in isolate data species richness is free to fluctuate, lowering potential conformity to any one model. Goodness of fit for isolate data sets can be decreased further via the small island effect (MacArthur &
Wilson, 1967), where species richness often does not correlate with island size for groups of very small isolates, due to either a species-specific minimum area effect or low habitat heterogeneity within isolates.

The form of an SAR reflects the geographical, evolutionary and ecological context of the species considered (Drakare et al., 2006), and also changes as a function of spatial scale (Rosenzweig, 1995). This change in form reflects changes in the biological determinants of richness (Shmida & Wilson, 1985). At small spatial scales, the SAR is sensitive to the identity of each new individual encountered (Hubbell, 2001), and may not conform to an overall power-law function (Sízling & Storch, 2004). The slope of the SAR, or rate of increase in species richness, decreases as the area sampled increases (species richness asymptotes as the community is almost completely sampled at a regional spatial scale) and SARs conform to the power-law equation. The goodness of fit to a power-law model in this study may represent the nested SAR of the cumulative patch/tree system as a regional spatial scale for areas up to 10,350 cm². Our nested data set had a relatively high z value of 0.39, although this is comparable with other fine-scale studies (Fridley et al., 2005). The steepness of slope (z) at the regional spatial scale is influenced by several factors, including dispersal ability (Durrett & Levin, 1996; Hubbell, 2001; Hovestadt & Poethke, 2005), source pool size (Martin, 1981), habitat availability and isolation, and competition between species (Abbott, 1983; Gentile & Argano, 2005). In nested data sets, low dispersal of organisms increases z values because of greater heterogeneity produced through high species turnover and greater endemic species (Drakare et al., 2006). The prevalence of arboreal specialists in this system (Lindo & Winchester, 2006), high between-tree beta diversity (Z.L., unpublished data), and high observed z values at the regional scale support endemism, facilitated by isolation, and suggest within-tree dispersal but limited tree-to-tree dispersal for arboreal oribatid mite communities.

The third phase of the triphasic SAR pattern shows increases in the rate of species accumulation (slope) as major dispersal barriers are crossed and new communities are sampled (Hubbell, 2001). We suggest that these changes can elucidate the absolute spatial scales where local, regional and global boundaries exist for different groups of organisms, and we predict that a triphasic curve should emerge for arboreal oribatid mites at larger spatial scales, for example at the scale of watersheds. Unfortunately, estimates of species richness for oribatid mites are poorly parameterized (Behan-Pelletier, 1993), with even less known with respect to the arboreal fauna. The spatial scale of dispersal limitation in arboreal arthropods, and the extent to which dispersal limitation inflates beta diversity, is important in conservation strategies for the identification of biodiversity hot-spots (Gering et al., 2003). We suggest that more detailed studies relating to beta diversity over larger spatial scales (for example, among trees vs. among sites vs. among watersheds) are needed to explore dispersal limitation in arboreal oribatid mites.

**ACKNOWLEDGEMENTS**

The authors gratefully acknowledge the contribution of Kevin Jordan (Arbornaut Access) for his expertise in canopy sampling and Richard Ring for his continued support and encouragement. This manuscript was greatly improved by comments from Raphael Didham and anonymous reviewers. This research is funded by a grant to Z.L. (332720-06) and N.N.W. (238631-06) from the Natural Sciences and Engineering Research Council of Canada.

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BIOSKETCHES

Zoë Lindo is a PhD candidate at the University of Victoria. This manuscript is part of her thesis, which describes the community structure of oribatid mites in arboreal habitats and forest floors in an ancient temperate rain forest ecosystem. Her research interests include patterns of beta diversity, and dispersal of oribatid mites in canopy habitats.

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Editor: P. John Lambshead