Nested patterns of community assembly in the colonisation of artificial canopy habitats by oribatid mites

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An observed species–area relationship (SAR) in assemblages of oribatid mites inhabiting natural canopy habitats (suspended soils) led to an experimental investigation of how patch size, height in canopy and moisture influence the species richness, abundance and community composition of arboreal oribatid mites. Colonisation by oribatid mites on 90 artificial canopy habitats (ACHs) of three sizes placed at each of three heights on the trunks of ten western redcedar trees was recorded over a 1-year period. Fifty-nine oribatid mite species colonised the ACHs, and richness increased with the moisture content and size of the habitat patch. Oribatid mite species richness and abundance, and ACH moisture content decreased with increasing ACH height in the canopy. Patterns in the species richness and community composition of ACHs were non-random and demonstrated a significant nested pattern. Correlations of patch size, canopy height and moisture content with community nestedness suggest that species-specific environmental tolerances combined with the differential dispersal abilities of species contributed to the non-random patterns of composition in these habitats. In line with the prediction that niche-selection filters out species from the regional pool that cannot tolerate environmental harshness, moisture-stressed ACHs in the high canopy had lower community variability than ACHs in the lower canopy. Colonising source pools to ACHs were almost exclusively naturally-occurring canopy sources, but low levels of colonisation from the forest floor were apparent at low heights within the ACH system. We conclude that stochastic dispersal dynamics within the canopy are crucial to understanding oribatid mite community structure in suspended soils, but that the relative importance of stochastic dispersal assembly may be dependent on a strong deterministic element to the environmental tolerances of individual species which drives non-random patterns of community assembly.

Community structure is the product of the complex interplay between stochastic demographic processes, dispersal limitation and deterministic niche processes (Gilbert and Lechowicz 2004). Although neutral theory proposes that many community patterns can be explained by sole recourse to stochastic processes of births, deaths, colonisation (speciation) and extinction (i.e. ‘ecological drift’), numerous empirical studies suggest that species–environment relationships are also important determinants of community structure, at least at small spatial scales. For example, in a meta-analysis of 158 community studies Cottenie (2005) found that purely neutral processes seemed to be important in only a limited fraction (ca 8%) of real metacommunities in temperate ecosystems. Most communities actually had a significant environmental (niche-limitation) component influencing community structure and dynamics (Cottenie 2005). At the same time, though, Cottenie (2005) found that dispersal trait-type was the most important determinant of metacommunity type. Taken together, these findings suggest that community structure at a local scale is determined by the relative balance between species traits, species–environment relationships and the spatial structure of the landscape, as well as stochastic dispersal and demographic processes. However, the conditions under which different processes predominate remain poorly understood.

Recently, Chase (2007) proposed the hypothesis that the relative importance of stochastic ecological drift versus environmental (niche-selection) filtering depends on the harshness of the environmental filter operating in local habitats. Harsh environmental conditions, such as drought, may act as a filter for species assembly and community composition (Chase 2007), preventing the colonisation of species from the regional pool that are unable to tolerate moisture-stressed environmental conditions in the local habitat patch, thus resulting in a more deterministic community structure (Chase 2007). Conversely, the relative importance of ecological drift should be greater when niche-selection is weak and priority effects are strong, leading to dispersal-assembled communities (Chase 2007). Whether this hypothesis holds across a range of systems beyond the experimental pond mesocosms of Chase (2007) remains unknown.

Here, we examine how habitat variables such as patch size, isolation and moisture availability affect colonisation dynamics and the resulting abundance, species richness and...
community composition of a group of microarthropods (oribatid mites) in an experimental arboreal ecosystem. Other microarthropod studies (Gilbert et al. 1998, Gonzalez et al. 1998, Gonzalez and Chanetton 2002, Hoyle and Harborne 2005, Schneider et al. 2007, Starzomski and Srivastava 2007) have primarily focused on the effect of patch size, isolation and habitat quality on extinction-driven patterns in diversity. However, few studies have explored how patch size, isolation and habitat quality variables affect colonisation processes in moss–microarthropod systems (Rantalainen et al. 2005, Domes et al. 2007), and only one study has tested these factors experimentally in forest canopy habitats (Wardle et al. 2003). In this study we use an experimental system of artificial canopy habitats (ACHs) to investigate local environmental conditions and regional dispersal processes contributing to the community assembly of arboreal oribatid mites, and have the following hypotheses:

1. Following the predictions of the ‘target effect’ (Gilpin and Diamond 1976) and island biogeography theory (MacArthur and Wilson 1967), we hypothesise that larger ACHs close to a colonising source will contain the greatest species richness and abundance. Here, we use sequential general linear models to test the contribution of habitat size, height and moisture content on oribatid mite species richness and abundance. We quantify the species–area relationship (SAR) in ACHs, and discriminate between random processes of colonisation and habitat selection/environmental tolerance using a random placement model (Coleman 1981, Coleman et al. 1982) as a null model for the SAR.

2. We measure the species compositional variability among ACHs, and test whether variation in patterns of community composition demonstrate significant nestedness in community structure, whereby the species present in the species-poor ACHs are non-random subsets of the species present in richer ACHs (Patterson and Atmar 1986). In line with the prediction that niche-selection filters out species from the regional pool that cannot tolerate environmental harshness, we hypothesise that species compositional variability will decrease in ACHs under increased environmental stress (low moisture). We hypothesise that an observed nested pattern will be correlated with differences in habitat properties (size, height, moisture) between ACHs (Hylander et al. 2005), combined with interspecific variation in tolerances to environmental conditions (Worthen et al. 1998).

3. Finally, we compare the species composition of oribatid mites colonising ACHs with previously described assemblages from naturally occurring canopy suspended soils, bark habitats, litterfall and forest floors to elucidate the source pool of colonists in the ACH experimental system. We hypothesise that the source pool of oribatid mite colonists in ACHs will be naturally occurring canopy habitats rather than the forest floor.

**Material and methods**

**Study site and experimental design**

The experiment was performed in the temperate rain forest of the Walbran Valley on the southwest coast of Vancouver Island, British Columbia, Canada (48°39’N, 124°35’W). The valley lies within the Coastal Western Hemlock biogeoclimatic zone where summers are wet, humid and cool, and winters are mild and wet. The mean annual precipitation is 2990 mm (Environment Canada 2008). Conifers dominate this rain forest and include western hemlock *Tsuga heterophylla*, Sitka spruce *Picea sitchensis*, Amabilis fir *Abies amabilis* and western redcedar *Thuja plicata*. The western redcedar trees used in the experiment were part of a project that involved extensive sampling of forest floor litter/soil (Lindo and Winchester 2008), bark (Lindo and Winchester 2007b), litterfall within the canopy (Lindo and Winchester in press) and suspended soil habitats (Lindo and Winchester 2007a) over three years.

Artificial canopy habitats (ACHs) were constructed of 2.5-cm thick untreated, western redcedar wood planks of three sizes: 16 × 16 cm (small, 256 cm²), 22.5 × 22.5 cm (medium, 512 cm²), and 32 × 32 cm (large, 1024 cm²). The sizes of the ACHs were determined so that the surface area of each size class was double the prior size class. Each plank was attached to a metal bracket and had a 7 cm border of steel mesh (1 mm) to enclose the substrate. Single rope climbing methods were used to access the trunks of ten western redcedar trees. At heights of 5, 15 and 30 meters above ground, one pre-constructed plank of each size class was affixed to the trunk resulting in nine planks placed in each tree (3 sizes × 3 heights × 10 trees = 90 planks total). Where trunk reiterations occurred, the largest trunk was used. Planks were attached to the trunk by the bracket using screws long enough to affix the plank, without penetrate the cambium layer of the tree. Pre-sterilized substrate (soil and moss) was added to the attached planks. Artificial canopy habitats were filled with 5 cm soil substrate, and topped with 2 cm moss to emulate naturally occurring suspended soil habitats (small ACH = 0.465 l soil, medium = 0.929 l, large = 1.858 l). Substrates were sterilized by microwaving each aliquot for 5 min, which proved to be 99.4% efficient at removing microarthropods in previous trials. Artificial canopy habitats were left, open-topped, for colonisation by microarthropods for a period of one year (23 July 2005–25 July 2006).

Substrate was collected from ACHs while they were still attached to the tree. Mesh borders were cut and folded back so that the substrate could be scraped into plastic bags before dismantling the ACH. One ACH was damaged and contents lost during the first six months of the experiment, and there was evidence of vertebrate disturbance in some ACHs. Contents of ACHs were brought back to the lab and microarthropods were extracted over 48 h using modified
Berlese funnels. All microarthropods were preserved in 75% EtOH. Moisture content of ACH substrates (expressed as percent dry weight (dw)) was estimated gravimetrically by measuring the mass of the substrate prior to and following extraction of microarthropods (% moisture = ((wet weight (g) – dw (g))/dw (g)) x 100). All extracted oribatid mites were counted and adult oribatid mite species were identified to species. Representative specimens were slide mounted using Hoyer’s medium and a reference collection was deposited at the Canadian National Collections in Ottawa, Canada.

Data analysis

A type I sums-of-squares general linear model (GLM) with two categorical predictor variables, ACH size and height in canopy, and two continuous predictor variables, substrate dry weight and moisture content, was created for each of the dependent variables, oribatid mite species richness and overall abundance. In preliminary models, random variability among the 10 trees on which ACHs were placed was accounted for by entering ‘Tree’ as a random block variable into the GLM. However, the block (Tree) effect was non-significant (p > 0.05 for both richness and abundance models) and was subsequently excluded from the final models. Type I GLMs give importance to the sequential ordering of variables, allowing us to test the degree of intercorrelation among measured variables. For example, we can order the continuous predictor variables ahead of the categorical treatment variables to see if they remove (i.e. explain) the variance associated with the treatments, which then become non-significant. A post-hoc Scheffe’s test was used on significant categorical predictor variables to determine which ACH size or height class differed. The GLMs were conducted in Statistica 7.0 (StatSoft Inc. 2004) using an alpha of 0.05.

We characterized the observed SAR for oribatid mites colonising the ACHs using nonlinear estimation of parameters for a power function regression model in Statistica 7.0. This design follows a type 3 SAR curve (Rosenzweig 1995) where ACHs are spatially separated isolates, with each ACH appearing only once in the analysis. This model used dry weight of ACH substrate instead of surface area or volume, although all three independent variables gave near identical parameter estimates, and only differed in the model fit (R² value). Substrate dry weight gave the best R² values due to the continuous (vs categorical) nature of this variable. We tested whether the observed SAR was due to random placement of individuals using the Coleman method (Coleman 1981, Coleman et al. 1982) to generate an expected species–area curve. This method predicts the expected number of species occurring in a particular ACH based on the total abundance of each species, and the total amount of ACH substrate sampled using the equation:

\[ s(\alpha) = S - \sum (1 - \alpha)^{n_i} \]

where \( s \) is the expected species richness for a patch, \( \alpha \) is the relative size of that patch proportional to the total of all patches, \( S \) is the total number of species collected among all patches, and \( n_i \) is the total number of individuals of the \( i \)th species. Random placement is rejected when greater than one third of the observed SAR data points lie outside one standard deviation of the expected curve.

Community composition of adult oribatid mites in ACHs was evaluated using non-metric multidimensional scaling (NMDS) (Clarke 1993) which arranged the ACHs with respect to the rank order of similarity in community composition based on Bray–Curtis similarity of square root transformed oribatid mite species abundance data. We used the MVDisp program in Primer 5 (Primer-E Ltd. 2001) to calculate a multivariate dispersion index (a measure of community variability) for ACHs within height classes (5, 15, 30 m). Nested oribatid mite assemblage patterns in ACHs were analysed using the program Binmatnest (Rodríguez-Girónés and Santamaría 2006) using the recommended parameter specifications (PopSize = 30, TourSize = 7, nbGen = 2000). Binmatnest permutes the rows and columns of a presence-absence species-by-sample (ACH) data matrix to create an optimally ordered (nested) matrix. Both rows (species) and columns (ACHs) are ordered so that ACHs decrease in species richness, and species decrease in occurrence. The degree of nestedness in this maximally packed matrix is represented by the nestedness temperature (T), which ranges from 0 (no deviation from perfect nestedness), to 100°C (complete deviation). The significance of the observed maximally nested matrix is determined by testing it against the mean T value of 10,000 randomly drawn matrices. The probability of detecting nested community patterns depends on the metric used to calculate nestedness and the randomization or null model used to test for significance in the pattern of nestedness. Recently, many studies have suggested that the detection of nestedness has high type I error (Greve and Chown 2006, Rodríguez-Gironés and Santamaría 2006, Ulrich and Gotelli 2007), and the selection of the appropriate null model is an important consideration (Timi and Poulin 2007). Binmatnest provides three null models ranging in their probability of type I and II error rates, with null model 3 suggested as conservative and most reliable (Rodríguez-Gironés and Santamaría 2006). The three null model statistics provided by Binmatnest in this study gave very similar results, differed slightly in the estimated mean temperature, but had identical p-values, therefore we show only the results from null model 3. Spearman rank correlations were then used to test the relationship of the nested ACH order with the variables size (dry weight substrate), height and moisture content. A significant correlation between rank order in Binmatnest and independent ACH variables indicates a possible influence of that factor on the observed nested structure (Rodríguez-Gironés and Santamaría 2006).

We explored the source pool of oribatid mites colonising ACHs by comparing the community composition of ACHs with previously known assemblages associated with canopy suspended soil, bark, litterfall and forest floor soils at the same study location using classic and non-parametric similarity indices (Chao et al. 2005) and the Shared Species Statistics in EstimateS (Colwell 2005). The source pool information is summarised from previous sampling on the same trees at the same study location during the same years as this experimental ACH study. Canopy suspended soils and forest floors were sampled repeatedly over two and a half years using core sampling of substrate (Lindo and...
Winchester 2007a, 2008), the bark community was sampled from scrapings of bark from 0 to 36 m along the vertical profile of trunks in the same year as the ACH placement (Lindo and Winchester 2007b), and litterfall was collected over the same year to assess the aerially distributed oribatid mite community (Lindo and Winchester in press).

**Results**

A total of 59 species of oribatid mites colonised artificial canopy habitats (ACHs). Dry weight, moisture content, and height of ACHs contributed significantly to the variation in oribatid mite species richness (Table 1). The dry weight of ACH substrate accounted for a significant amount of richness variation associated with the size categories of ACH substrate (Scheffe’s test showed 30 m ACHs had contributed significantly to the variation in oribatid mite species richness (Table 1). The dry weight, height of ACHs contributed significantly to the variation in canopy habitats (ACHs). Dry weight, moisture content, size and height on oribatid mite abundance using a type I sums-of-squares GLM.

The type 3 species–area curve for oribatid mites that colonised the 89 artificial canopy habitats is described by a power function between species richness and the dry weight of ACH substrate (\(S = 0.223 \times \text{dw}^{0.616} \pm 0.1063\), \(R^2 = 0.313, p < 0.001\) (Fig. 1). The distribution of oribatid mite species richness in ACHs was non-random since more than one third of the observed data points (68/89 points = 76%) were greater than one standard deviation from the expected species–area curve. Residual values (observed – expected) for each ACH were plotted against substrate dry weight and we found that species richness was generally less than expected for most ACHs; this pattern was most pronounced in 30 m ACHs (Fig. 2).

The ACH communities at 30 m clustered tightly (dispersion index = 0.486) in the NMDS ordination space, whereas ACHs at 5 m and 15 m were more dispersed (dispersion index = 1.439 and 1.105, respectively) (Fig. 3). Oribatid mite assemblages were significantly nested (\(T = 6.806\)) compared with the null model average temperature (\(T = 21.371\), variance = 2.825, \(p < 0.001\) (Fig. 4). Spearman’s rank correlation indicated that ACH order, as determined by Binmatnest, was significantly correlated with the dry weight of the ACH substrate (\(R = -0.419, p < 0.001\), height (\(R = 0.479, p < 0.001\)), and moisture content (\(R = -0.402, p = 0.001\).

The number of oribatid mite species in common between the ACHs and natural source areas (i.e. suspended soil, bark, litterfall and forest floor habitats) ranged from 37 to 46 species, while extrapolated estimates of the total number of shared species that might exist, if sampling effort had been greater, were much higher (45–80 species). Classic similarity indices showed the highest similarity of ACH community composition with bark habitat, while the Chao abundance-based similarity indices, which take into account the number of unseen shared species, showed ACH communities were most similar to oribatid mite communities from natural suspended soil habitats (Table 3).

**Discussion**

The effect of patch size, height and moisture content

Habitat patch size (dry weight) played an important role in determining the richness and community structure of arboreal oribatid mites colonising ACHs. The relationship

![Figure 1. Observed species richness (S) of oribatid mites after 1 year as a function of the amount of colonising space (substrate dry weight, dw) in artificial canopy habitats. Fitted line is \(S = 0.223 \times \text{dw}^{0.616} \), \(R^2 = 0.313, p < 0.001\) (n = 89). Legend is: ○ 5 m ACH, + 15 m ACH, ▲ 30 m ACH.](image-url)
between substrate dry weight of ACHs and oribatid mite species richness was modelled by a positive, power-law equation SAR for this experimental system, as also observed for arboreal oribatid mites in naturally-occurring canopy suspended soils at the same study location (Lindo and Winchester 2007a). Dispersal ability or mode may interact with habitat patch size as larger areas have greater ‘findability’ for dispersing organisms (Finn and Giller 2000) and intercept more individuals (i.e. the target effect; Gilpin and Diamond 1976, Buckley and Knedlhans 1986). Furthermore, edge effects may have contributed to the SAR, as an increased influence of edges (e.g. moisture limitation, temperature extremes) has been shown to exaggerate area-effects on populations in small habitat patches (Murcia 1995, Didham et al. 1998, Ewers et al. 2007). This study, however, failed to show a significant interaction between patch size and moisture for oribatid mite richness or abundance in ACHs, which would support increased habitat stability with increased habitat patch size.

Placement height of ACHs within the canopy had a significant effect on the richness, abundance and composition of colonising arboreal oribatid mites. Canopy habitats in high tree crowns are generally drier than habitats at lower tree levels (McCune 1993), and moisture contents of ACHs showed a strong, negative relationship with height, suggesting that moisture conditions in ACHs at 30 m were unfavourable for oribatid mite species colonisation and/or establishment. Similarly, Karasawa and Hijii (2006) attributed the significant negative relationship between height and density of oribatid mites in litter patches of arboreal bird’s nest ferns to the lower moisture content at greater heights above ground. Moisture regimes and humidity of microhabitats are fundamental factors influencing the diversity, abundance and distribution of oribatid mites (Siepel 1996), and drought extremes in the upper canopy and 30 m ACHs most likely limit the abundance and richness of these oribatid mite assemblages.

Nested patterns of community assembly

Oribatid mite assemblages in smaller, higher, drier ACHs were strongly nested subsets of species found within larger, lower, moister ACHs. Patch size, height in the canopy and moisture content of ACHs all contributed to the observed patterns of non-randomness in species richness and composition of oribatid mites, as indicated by a significant deviation from the SAR random placement model and significant patterns of nestedness. Patterns in nested community structure among habitat patches have been shown to be associated with extinction (Wright et al. 2007), colonisation (Loo et al. 2002), and the vagility of species (Cook and Quinn 1995, Greve et al. 2005). Nestedness can also occur without significant differences in dispersal ability or extinction (McLain and Pratt 1999) and it is likely that many processes act in conjunction to contribute to patterns of nestedness. For example, both colonisation and extinction processes would play a role if ACHs and natural suspended soil patches were too small to sustain oribatid mite populations without recurring colonisation events (i.e. rescue effects; Brown and Kodric-Brown 1977) when deterministic extinction due to abiotic conditions is
Figure 4. Maximally ordered matrix of oribatid mite species occurrence in artificial canopy habitats (ACHs). Each column of the matrix represents a separate ACH with height (m) and size class (small, medium, large) indicated, and each row represents an oribatid mite species. Black spaces indicates species presence, white spaces indicates species absence.
patterns of nested community structure have been shown to increase under stressful and desiccating conditions, suggesting non-random species loss due to species-specific environmental tolerances to drought (Worthen et al. 1998). Moisture stressed conditions at the 30 m ACHs may be the ‘environmental filter’ preventing a large proportion of the regional species pool from colonising 30 m ACHs and resulting in more deterministically-structured communities that are more similar to one another than communities within the 5 or 15 m height classes (Chase 2007). Previously known canopy-specific species (Lindo and Winchester 2008) such as Eupterotegaeus rhamphosus, Epidamaeus nr floccosus, and Scheloribates (Scheloribates) sp. were found in all ACH patches including small, desiccated patches high in the canopy, demonstrating that canopy-specific species are drought tolerant and well-adapted to utilizing patchily-distributed, environmentally-challenging habitats (Behan-Pelletier and Walter 2000). Many species that only occurred on large, low, moister ACHs were small (e.g. Suctobelbella spp. 1, 4), and not well sclerotized (e.g. Liochthonius spp. 1, 3) suggesting lower moisture availability in the higher canopy likely decreased the probability of establishment and increased deterministic extinction rates at 30 m for these species, supporting the idea that species-specific tolerances to drought contributed to patterns of nestedness. At the local community scale, this suggests that community assembly depends not only on the stochastic dispersal of individuals, but also on their ability to establish in a given biotic and abiotic environment.

### Source pool for ACH colonists

Interestingly, height in the canopy still had a significant negative effect on richness and abundance of oribatid mites in ACHs, even after the effect of the vertical moisture gradient was removed. Island biogeography theory (MacArthur and Wilson 1967) predicts that richness should decrease with increasing distance (isolation) from a colonising source, which would only support the observed trend of lower species richness in the 30 m ACH height class if the likely dispersal source for ACHs was the ground. However, this was clearly not the case, as the data showed that the species composition of oribatid mite assemblages in ACHs was most similar to that in naturally-occurring suspended soils, followed by bark, and litterfall, rather than to the forest floor community. The forest floor is least likely to be the primary colonising source pool for ACH immigrants, but it is worth noting that eight species that had previously been shown to be ‘ground-specific’ (Lindo and Winchester 2008) were collected in ACHs. Most of these ground-dwelling species had low abundance in ACHs (1, 2 or 3 individuals, except L. bidentatus with 29 individuals), and all were found exclusively at 5 m in height. Previous work on vertical patterns of oribatid mite communities living on bark of western redcedar showed a transition zone in richness, abundance and composition between heights of 4 and 6 m above ground, and suggested ground species may expand their range into bark habitats up to these heights (Lindo and Winchester 2007b). This transition zone may represent a biome shift in demographic or environmental requirements of individual species, particularly moisture availability (Lindo and Winchester 2007b).

As a result of the dispersal source for ACH communities being the canopy, rather than the ground, the mechanism for decreased species richness and abundance with increasing ACH height remains undetermined, but may be linked to arboreal oribatid mite dispersal mode. There are two potential dispersal modes for oribatid mite colonists from canopy source pools: passive tree-to-tree dispersal via abiotic dispersal vectors or aerial planktonic drift through the atmosphere (Lindo and Winchester 2008); and active cursorial dispersal among habitat patches within a tree via bark environments (Lindo and Winchester 2007b). The relationships between habitat patch size and height with

### Table 3. Similarity of oribatid mite assemblages in artificial canopy habitats (ACHs = 59 species) with potential source pool areas for oribatid mite colonisers of ACHs.

<table>
<thead>
<tr>
<th>Potential source pool</th>
<th>Suspended soil</th>
<th>Forest floor</th>
<th>Bark</th>
<th>Litterfall</th>
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<tbody>
<tr>
<td>Observed species richness</td>
<td>83</td>
<td>99</td>
<td>62</td>
<td>56</td>
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<tr>
<td>Observed number of shared species</td>
<td>46</td>
<td>41</td>
<td>41</td>
<td>37</td>
</tr>
<tr>
<td>Estimated shared species</td>
<td>57.79</td>
<td>50.03</td>
<td>44.68</td>
<td>80.34</td>
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<tr>
<td>Classic similarity indices</td>
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<td></td>
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<td></td>
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<tr>
<td>Morisita-Horn</td>
<td>0.44</td>
<td>0.11</td>
<td>0.69</td>
<td>0.36</td>
</tr>
<tr>
<td>Bray-Curtis</td>
<td>0.14</td>
<td>0.08</td>
<td>0.51</td>
<td>0.21</td>
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<tr>
<td>Jaccard</td>
<td>0.48</td>
<td>0.35</td>
<td>0.51</td>
<td>0.47</td>
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<tr>
<td>Sørensen</td>
<td>0.65</td>
<td>0.52</td>
<td>0.68</td>
<td>0.64</td>
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<tr>
<td>Chao abundance-based indices of similarity</td>
<td></td>
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<tr>
<td>Chao-Jaccard index</td>
<td>0.88</td>
<td>0.66</td>
<td>0.78</td>
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<tr>
<td>Chao-Sørensen index</td>
<td>0.94</td>
<td>0.80</td>
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<tr>
<td>Chao-Jaccard estimate</td>
<td>0.91</td>
<td>0.73</td>
<td>0.80</td>
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<td>0.95</td>
<td>0.84</td>
<td>0.89</td>
<td>0.92</td>
</tr>
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</table>


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1. Gonzalez 2000
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3. Arce and Wilson 1967
4. Chase 2007
5. Worthen et al. 1998
7. Lindo and Winchester 2007b
species richness, as well as the associated immigration patterns in habitat patches, are likely to differ between these dispersal modes. For example, passive dispersal via an abiotic dispersal vector predicts that the probability of encountering a habitat patch is a function of the surface area of the patch (Bowman et al. 2002), that species are not likely to differ in their dispersal ability, and that patch connectivity should be a function of height, as gravity dictates a downward dispersal trajectory (Okubo and Levin 1989). By contrast, in an active cursorial dispersal mode, the probability of encountering a habitat patch is a function of the patch perimeter (or linear attachment of ACH with trunk), species may differ in their ability to disperse over bare bark habitats (Prinzing 2005), and patch connectivity is a function of nearest neighbour distance and bare microhabitat complexity within a tree, but is not necessarily a function of patch height in a tree. These predictions suggest that litterfall as an abiotic vector for arboreal oribatid mite dispersal would result in both a positive relationship of species richness with habitat patch size, and a negative relationship of species richness and abundance with height, which is supported by our findings.

Conclusions
Community assembly was determined to a large extent by the stochastic dispersal of oribatid mites from naturally-occurring canopy source pools, but there was no strong indication of dispersal limitation (most of the species previously found in surrounding natural habitats were found in at least one ACH), despite the fact that oribatid mites are small, wingless and not typically considered to be highly dispersive. Under some conditions, local environmental factors such as habitat patch size, height in canopy and moisture stress also had a significant effect on community assembly processes. In particular, there was a strong deterministic element to the desiccation tolerance of early colonists, leading to significant nestedness in community structure under adverse environmental conditions. As suggested by Chase (2007), the relative importance of stochastic ecological drift versus environmental niche-selection does appear to depend on the harshness of the environmental filter operating in local habitats. The results of this study give greater mechanistic understanding of the ecological processes underlying community assembly dynamics of arboreal oribatid mites (reviewed by Behan-Pelletier and Walter 2000). We encourage further research to concentrate on understanding the species-specific mechanisms of dispersal in arboreal oribatid mites, and the processes that govern their dispersal ability, which will be critical in explaining species distribution patterns.

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