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The Canopy Starts at 0.5 m: Predatory Mites (Acari: Mesostigmata) Differ between Rain Forest Floor Soil and Suspended Soil at any Height

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ABSTRACT

Suspended soils in forest canopies are thought to harbor a substantial fraction of canopy biomass and many arboreal specialists, but do forest floor generalist predators with high vagility also use this habitat? We tested the hypothesis of no difference between forest floor and suspended-soil predatory mite faunas (Acari: Mesostigmata) in an Australian rain forest. Our results show that instead of being habitat generalists, many predatory mites partition soil into two main strata: soil suspended aboveground irrespective of height (0.5–20 m) and soil on the ground. Of 53 species of Mesostigmata in suspended soil, 53 percent (28 species) were absent from or rarely found on the ground. This increased to 60 percent (15/25 species) if only common species are considered. Among these 15 'suspended-soil specialists', all but the three least abundant were found throughout the arboreal strata. Moreover, ten species also occurred in litter accumulated on the surface of decaying logs or boulders close to the forest floor. Thus, although the arboreal predatory mite fauna is distinct from that on the forest floor, it is not restricted to the high canopy: even slightly elevated substrate appears acceptable as habitat for these suspended-soil specialists. Our data suggest that a substantial portion of a rain forest's soil and litter fauna is held above the forest floor.

Key words: arboreal arthropods; biodiversity conservation; bird's nest ferns; epiphytes; habitat partitioning; habitat specificity; vertical stratification.

Canopies are vital for the maintenance of diversity in rain forests: the majority of tropical forest vertebrates use canopy resources either directly or after it has fallen to the forest floor (Kays & Allison 2001) and 10 percent of invertebrate species may be restricted to arboreal habitats (Ozanne *et al.* 2003). Obvious canopy habitats include epiphytes and the flowers, leaves, and branches of the canopy trees; however, soil also is suspended in the forest canopy. Several studies have documented the impact of aboveground deposits of soil and litter on nutrient cycling and their role as habitat and foraging substrate for canopy-dwelling organisms (Longino & Nadkarni 1990, Paoletti *et al.* 1991, Basset 2001, Ellwood & Foster 2004, Nadkarni *et al.* 2004, Roisin *et al.* 2006). This 'suspended soil' is typical of rain forest canopies where moss carpets and large epiphytes foster the accumulation of dead organic matter (Ellwood & Foster 2004, Nadkarni *et al.* 2004). It can represent tonnes of dry matter per hectare of forest and supports rich arthropod faunas that are numerically dominated by mites (Arachnida: Acari) (Paoletti *et al.* 1991, Walter & Behan-Pelletier 1999, Yanoviak *et al.* 2003, Fagan *et al.* 2006). Among these arboreal mites are the Mesostigmata, which are often the most numerous and diverse, albeit smallest, predatory arthropods in soil environments (Walter *et al.* 1988, Paoletti *et al.* 1991).

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Soil and litter faunas may represent a major fraction of species richness in any terrestrial ecosystem (André *et al.* 2002). The few studies that have compared assemblages of invertebrates in suspended soil and on the ground suggest that >30 percent of species of ants, beetles, springtails, and oribatid mites found in suspended soil are restricted to or prefer this habitat to the forest floor (Longino & Nadkarni 1990, Rodgers & Kitching 1998, Behan-Pelletier & Walter 2000, Karasawa & Hijii 2006, Lindo & Winchester 2006, Karasawa *et al.* 2008). In contrast, preliminary work on mesostigmatic mites in western Canada indicates that most species found in suspended soil are also common forest floor dwellers (Fagan *et al.* 2006).

To determine if this apparent exception holds in another forest type, we sampled three subtropical rain forest sites in eastern Australia and tested these hypotheses: (1) irrespective of height, suspended soil is inhabited by a subset of the forest floor Mesostigmata rather than a unique assemblage of aboveground specialists and (2) Mesostigmata in suspended soil are more heterogeneous than in forest floor samples.

METHODS

Mite collecting.—Sampling was conducted at three sites (Site 1: 28°13′45″ S, 153°07′25″ E, 875 m asl; Site 2: 28°14′10″ S, 153°08′25″ E, 950 m asl; Site 3: 28°12′35″ S, 153°11′30″ E, 900 m asl) that were 2–6 km apart in montane subtropical rain forest (complex notophyll vine forest; Webb *et al.* 1984) in Lamington National Park in southeast Queensland, Australia, an extensive rain forest area of $> 100\,km^2$ on red basaltic soils. The upper canopy is mostly 25–30 m high with some emergents reaching *ca* 50 m. Average annual precipitation is 1800–2300 mm (Busby 1986).

Each 2-L suspended-soil sample was composed of 1-L of litter and humus trapped inside a large bird's nest fern (BNF) (*Asplenium australasicum*), and 1-L from the fern's rootball (living and decaying rhizoids). Ferns higher than 2 m were reached using the single-rope climbing technique. Fern height was measured at the level of the crown, where litter is trapped. Only one sample was taken per tree. At each site (1 ha), five to eight samples of both suspended soil and ground samples were taken at each sampling period. In Site 1, samples ($N = 6$) were taken on 17 March 2002. In Sites 2 ($N = 23$) and 3 ($N = 21$), samples were taken during four periods: 20–21 April, 17–18 May, and 17–18 October 2002, and 9–10 August 2003 (Site 2); and 14–27 April, 11 June, and 1–22 November 2002, and 26–27 July 2003 (Site 3). Each 1.5-L ground sample was composed of 1-L litter and 0.5-L underlying soil randomly taken from the sites.

To examine whether species occurring in BNFs high in trees also occur in other types of suspended soil, samples of *ca* 1 L each were haphazardly taken at Sites 2 and 3 between 20 April 2002 and 9 August 2003 from: (1) small BNFs at 0.6–2 m high (mainly rootball material) ($N = 10$); (2) elkhorn ferns (*Platycerium bifurcatum*) (rootball only) at 4 and 18 m high ($N = 2$); (3) litter and humus in tree forks, 6–21 m high ($N = 5$); (4) small BNFs attached to boulders ($N = 2$); and (5) epiphytes (BNFs, *P. bifurcatum*, or *Platycerium superbum*) fallen on the ground (mainly rootball material) ($N = 15$). Finally, samples were taken from litter and humus accumulated on the surface of logs (> 25 cm diam; $N = 20$) and boulders (smallest width > 25 cm; $N = 10$) (hereinafter 'low suspended soil').

Samples were transferred to the laboratory in plastic bags, extracted using Berlese–Tullgren funnels, and adults of all nonparasitic Mesostigmata, excluding Uropodina, were identified to species or morphospecies using differential-interference contrast microscopy, appropriate literature (*e.g.*, Lee 1970, Halliday *et al.* 1998), and the reference collection at the University of Queensland. Voucher specimens are deposited in the University of Queensland Insect Collection.

Species richness.—Overall species richness of BNFs vs. ground was compared using rarefaction curves (100 randomizations) and computed using EstimateS 7.5 (Colwell 2005). Number of species and individuals per sample were compared for each site with a two-sample *t*-test. Before analysis, number of individuals was log-transformed ($\ln x$) to achieve normality. The effect of height of BNF on species richness per sample was assessed using simple linear regression.

Species composition.—Comparison of species composition between BNF and forest floor samples in each site was performed using the Bray–Curtis (distance) coefficient, based on log-transformed ($\ln x+1$) abundances. Coefficient values range from 0 (no difference for any species) to 1 (no species shared at all). A matrix of Bray–Curtis distances between all possible pairs of samples was created, followed by an ordination of the samples with semi-strong hybrid multi-dimensional scaling (SSH MDS) using the software PATN (Belbin 1995). Analysis of similarity (ANOSIM) was then conducted using PATN to test for significant dissimilarity between BNF and ground.

To test for a height effect on species composition, Bray–Curtis distances were plotted against vertical distance between paired BNF or BNF/ground samples. Significance was tested using a Mantel test (using PopTools, Hood 2006) for BNF/BNF and a linear regression for BNF/ground samples. For the regression, we compared the average Bray–Curtis distance between a given BNF sample and all ground samples with the height of the BNF sample.

We examined the effect of sampling time by plotting the mean Bray–Curtis distances between pairs of BNF/BNF, ground/ground, and BNF/ground samples against the number of months between sampling periods. For Site 3, samples taken during 14–27 April 2002 and 1–22 November 2002 were coded as 20 April and 11 November, respectively, for the analysis. An analysis of variance (ANOVA) followed by a Bonferroni–Dunn *post-hoc* test was used to test for significance.

Heterogeneity.—Heterogeneity in species composition was compared between BNF and ground using: (1) mean Bray–Curtis distances among samples within each habitat (two-sample *t*-test) and (2) the distribution of proportion of samples in which a given species occurred (= species frequency) in each habitat. We considered a habitat with a higher proportion of rare species more heterogeneous than a habitat with many common species, because in the former, two given patches are likely to have more distinct species composition than in the latter.

Species' habitat preferences.—Common species were separated into three categories: (1) suspended-soil specialists: found in ≥ 10 percent of BNF samples and for which ≥ 90 percent of all occurrences (occurrence = presence in a sample) were in BNF; (2) ground specialists: found in ≥ 10 percent of ground samples and for which ≥ 90 percent of all occurrences were on the ground; and (3) generalists: found in ≥ 10 percent of both BNF and ground samples and for which < 90 percent of all occurrences were in BNF and < 90 percent on the ground.

To test whether species showed a preference for litter trapped in the epiphyte's crown litter or rootball, the abundance of specialists and generalists occurring in ≥ 20 percent of BNF samples was compared using a Wilcoxon signed-rank test. A second Wilcoxon test was performed to test whether ground specialists and generalists occurring in ≥ 20 percent of ground samples preferred litter or soil. For this second test, abundance data from soil samples was multiplied by two to reduce the bias due to difference in sample volume (1-L vs. 0.5-L for litter and soil, respectively).

The *t*-tests, ANOVA, regression, χ^2, and Wilcoxon signed-rank tests were conducted using StatView (SAS Institute 1998). Summary statistics are presented as means $\pm$ SD.

RESULTS

Species richness.—In total, 9401 mites representing 23 families of Mesostigmata were identified to 140 species-level taxa (Table S1).

The majority of individuals, 7870 (120 species), were collected from the forest floor and large BNFs, while 1531 mites (including 20 additional spp.) were found in other samples of suspended soil. Most of the 140 species collected (78%) appear to be undescribed.

Rarefaction curves indicate that overall species richness is about twice as high on the ground: for ≥500 individuals collected, the ratio of species richness of ground to BNF stabilizes between 1.89 and 1.92 (Fig. S1). In total, 53 species from 17 families were found in BNF, whereas 97 species from 14 families were found on the forest floor. Significantly more species occurred in ground vs. BNF samples at all sites; however, number of individuals collected was not significantly different at any site (Table 1). The number of species per sample did not decline but appeared to increase with height of BNF (Fig. S2), a relationship which was significant at Site 3 ($r^2 = 0.42$, $P = 0.0014$), but not at Sites 1 or 2 ($r^2 = 0.065$, $P = 0.62$; and $r^2 = 0.048$, $P = 0.31$, respectively).

Species composition.—Mite assemblages were fairly similar between sites. No species were exclusive to Site 1, and 80.3 percent of species found in ≥10 percent of samples (57/71 species) occurred at both Sites 2 and 3.

We found little overlap in species composition between large BNFs and the forest floor. Among 120 species collected, 70 species (58.3%) were found only or almost only (≥90% of occurrences) on the ground and 28 were found only or almost only in BNFs (23.3%). This leaves only 22 species (18.3%) found in both habitat types (excluding eight habitat specialists that had individuals in the nonpreferred habitat).

The ordinations show a clear distinction between BNF and ground assemblages at each site (Fig. 1), and ANOSIM reveals that these distinctions are highly significant ($P = 0.0013$, $P < 0.0001$, and $P < 0.0001$ for Sites 1, 2, and 3, respectively).

The height of BNFs did not have any clear effect on species composition (Fig. 1). If there was a height effect, one would expect low samples (*e.g.*, 1–3 m high) to be positioned closer to ground samples, which is not the case. Indeed, Bray–Curtis distances do not show an increase with vertical distance between BNF samples (Fig. S3A; Mantel test: $P = 0.29$, $P = 0.25$, $P = 0.70$ for Sites 1, 2, and 3, respectively). There is also no trend in Bray–Curtis distances between BNF and ground samples (Fig. S3B; regression test: Site 1: $r^2 = 0.32$, $P = 0.24$; Site 2: $r^2 = 0.09$, $P = 0.17$; Site 3: $r^2 = 0.06$, $P = 0.27$); ground samples were consistently different from BNF samples (Bray–Curtis distances often reaching 1.0; Fig. S3B), regardless of the height above ground.

Time of sampling had minimal effect on species composition. Bray–Curtis distances between habitats ranged 0.92–0.97 across temporal distance for both sites (Fig. S4). Bray–Curtis distances within habitats, although clearly lower (0.53–0.74), varied more with time. For Site 2, the coefficient was lowest for the 0 and 0.9 mo of temporal distance (0.57–0.59 for BNF vs. BNF; 0.53–56 for ground vs. ground); for BNF vs. BNF, means for 5 and 9.7 mo (0.70 for both) were significantly different from the mean at 0 mo (0.59; $P < 0.0001$). For ground vs. ground, means at 5–15.6 mo (0.64–0.74) were all significantly different from the mean at 0 mo (0.56; all $P < 0.002$). For Site 3, there were no significant differences from the mean at 0 mo (0.54–0.67 for BNF vs. BNF; 0.61–0.71 for ground vs. ground).

Heterogeneity.—Mean Bray–Curtis distances among BNF samples were almost equal to those among ground samples in Sites 1 and 2, but were significantly lower at Site 3: Site 1, BNF = 0.55 ± 0.12, ground = 0.56 ± 0.10 ($t_{0.05, 28} = 0.26$, $P = 0.79$); Site 2, BNF = 0.65 ± 0.13, ground = 0.64 ± 0.14 ($t_{0.05, 504} = -0.62$, $P = 0.53$); Site 3, BNF = 0.62 ± 0.14, ground = 0.67 ± 0.10 ($t_{0.05, 418} = 3.77$, $P = 0.0002$).

Species in BNFs were found in more samples on average (10.4 samples) than species on the forest floor (8.9). BNFs did not have a higher proportion of rare species than the ground: 35.8 percent of species collected in BNFs were found in one or two samples only, as opposed to 38.1 percent of species collected on the ground. Also, suspended-soil specialists did not seem to be either rarer or more common than generalists or ground specialists (Fig. S5).

Species' habitat preferences.—A total of 15 species of suspended-soil specialists occurred in 12–70 percent of BNF samples, with only five species occurring in 2–4 percent of forest floor samples (Table S2); 39 ground specialists occurred in 10–92 percent of forest floor samples, and only three of them were found in 2–4 percent of BNF samples; seven generalists were found in ≥10 percent of both BNF and ground samples.

Most suspended-soil specialists and generalists were distributed throughout the canopy, from BNFs near the ground up to as high as we climbed, > 20 m (Fig. 2). Most of the 15 suspended-soil specialists from large BNFs were found in other types of suspended soil, including small BNFs at 0.6–2 m high on tree trunks (12 species; Table S2); litter perched on tree fork (six); *Platycerium* ferns attached to tree trunks (five) or fallen on the ground (three); small BNFs attached to boulders (11; Fig. 2); and 10 species occurred in low suspended soil (five on logs and nine on boulders), including five commonly so (Table S2).

Some generalists were found in small BNFs at 0.6–2 m high on tree trunks (three species); tree fork litter (three); fallen BNFs or *Platycerium* ferns (six); small BNFs attached to boulders (four; Fig. 2); litter on logs (all seven species) and boulders (four; Table S2; Fig. 2).

Of 39 ground specialists, only three were found in BNF samples, and such occurrences were all low (< 2 m; Table S2; Fig. 2).

TABLE 1. *Number of species and individuals collected in bird's nest fern (BNF) and forest floor samples in Lamington National Park, Australia. Significant differences between BNFs and forest floor are as follows:* *P < *0.01,* **P < *0.001* (t-*test*).

	Number of species		Number of individuals	
Site (*N*)	Forest floor	BNFs	Forest floor	BNFs
1 (6)	16.0 ± 4.8*	7.2 ± 1.6	76.8 ± 43.1	56.5 ± 28.1
2 (23)	16.5 ± 5.0**	11.6 ± 3.5	58.6 ± 30.5	79.7 ± 73.0
3 (21)	18.2 ± 5.1**	11.2 ± 3.5	90.4 ± 63.6	93.6 ± 54.5

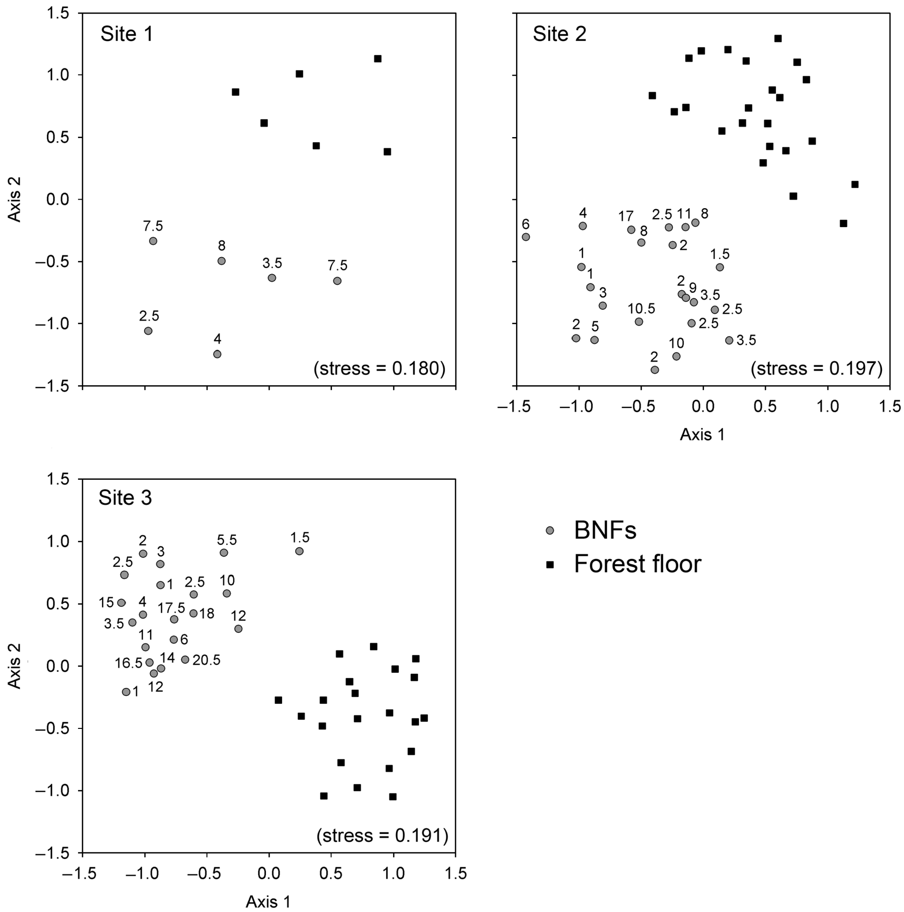

FIGURE 1. Two-dimensional ordinations of ground and large bird's nest fern (BNF) samples from the three rain forest sites, based on log-transformed abundance data of species. Numbers indicate the height (m, rounded to unity or half unity for clarity) of BNFs aboveground.

No ground specialist was found in arboreal suspended soil higher than 2 m.

Some species differentiated among the subhabitats within BNFs, and within the forest floor. Most (nine) suspended-soil specialists and four generalists were more abundant in litter from the BNF's crown, while three suspended-soil specialists were more abundant in the rootball ($P < 0.05$; Table S2). Twelve ground specialists and three generalists were significantly more abundant in litter while two ground specialists preferred soil.

DISCUSSION

Vertical partitioning of habitat occurs in many arboreal taxa, with most species preferentially distributed in one or a few layers of a forest's vertical profile (*e.g.*, birds: Karr 1971; ants: Brühl *et al.* 1998; epiphytes: Nieder *et al.* 2000; phytophagous insects: Basset *et al.* 2003). Here, we show that in an Australian rain forest a clear-cut dichotomy occurs between Mesostigmata on the forest floor and those in aboveground soil deposits whatever their height or location. A similar dichotomy was found for corticolous oribatids in Canada between 0–4 m (mixed fauna) and 6–36 m (specialized arboreal fauna; Lindo & Winchester 2007).

As our suspended-soil specialists showed no preference for where the humus had accumulated, these predatory mites do not appear to be associated with canopy ferns *per se*, but rather favor microhabitat conditions generally found in dead organic material aboveground. Similarly, Travé (1963) observed that many oribatid species occur on lichen or mosses on both tree trunks and rock surfaces. These two habitats are both more variable in terms of humidity and temperature than the forest floor (Travé 1963), as is suspended soil (Bohlman *et al.* 1995). Hence, generalists and aboveground specialists may tolerate better microclimate extremes than ground specialists (Behan-Pelletier & Walter 2000). It is possible that some species feed preferentially on prey that are habitat specific themselves. Ground and aboveground Mesostigmata, however, appear to feed largely on the same broad groups, such as nematodes, collembolans, and/or soft-bodied mites (Beaulieu & Walter 2007), all of which abound in soil habitats irrespective of their location (Paoletti *et al.* 1991, Wardle *et al.* 2003, Yanoviak *et al.* 2003).

Higher heterogeneity in suspended soil than on the ground has been observed in Collembola (Rodgers & Kitching 1998) and oribatid mites (Fagan *et al.* 2006, Lindo & Winchester 2006). Oribatid assemblages on tree trunks also were observed to be more heterogeneous than their ground counterparts (Proctor *et al.* 2002).

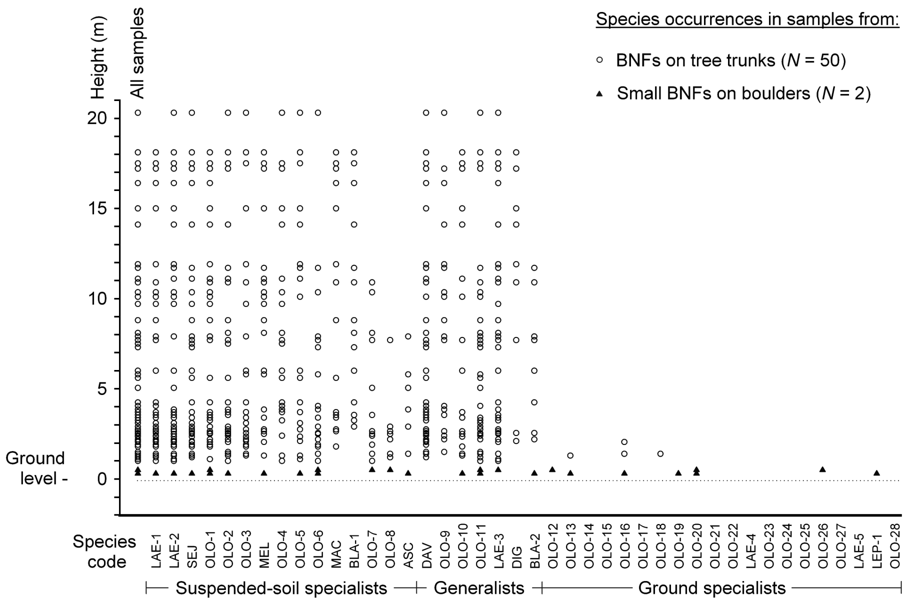

FIGURE 2. Vertical distribution of occurrences in bird's nest fern (BNF) samples (each circle or triangle represents a sample where species was present) of suspended-soil specialists, generalists, and ground specialists. Abundances and species names are shown in Table S2. The first column represents a hypothetical species that would be present in all samples. Only the 20 most common species of ground specialists are shown for simplicity.

In our study, suspended-soil Mesostigmata were no more heterogeneous than those on the forest floor. We suspect this is because Mesostigmata are highly vagile generalist predators, and thus, may be less subject to local population extinctions.

Our data suggest that over 20 percent of all predatory Mesostigmata in Lamington rain forest are dependent on suspended soil. If these results also apply to other soil invertebrate groups, then epiphytes and dead organic matter perched aboveground may be essential for a substantial portion of soil-dwelling rain forest fauna, which itself makes up a significant share of local and global biodiversity (André *et al.* 2002, Ellwood & Foster 2004). This aboveground diversity is likely to be largely lacking in secondary forests, where epiphytes and suspended soil represent a tiny fraction of the volume developed in primary forests (Nadkarni *et al.* 2004). Hence, ancient forests and their canopies should be a priority target for biodiversity conservation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *List of species collected in Lamington National Park, southeast Queensland, Australia.*

TABLE S2. *Habitat distribution of suspended-soil specialists, generalists, and ground specialists collected in Lamington National Park, Australia.*

FIGURE S1. Rarefaction curves for all species of mesostigmatic mites collected from large BNFs and forest floor (data from all three sites pooled).

FIGURE S2. The number of species of mesostigmatic mites per sample from BNFs as a function of height of sample.

FIGURE S3. Bray–Curtis distance for pairwise comparisons of (A) BNF samples as a function of the vertical distance between samples and (B) BNF vs. ground samples as a function of height of BNF samples.

FIGURE S4. Mean Bray–Curtis distances for pairwise sample comparisons as a function of the temporal distance between the times at which the two samples were taken.

FIGURE S5. Distribution (%) of species of suspended-soil specialists, generalists, and ground specialists in forest floor and BNF samples.

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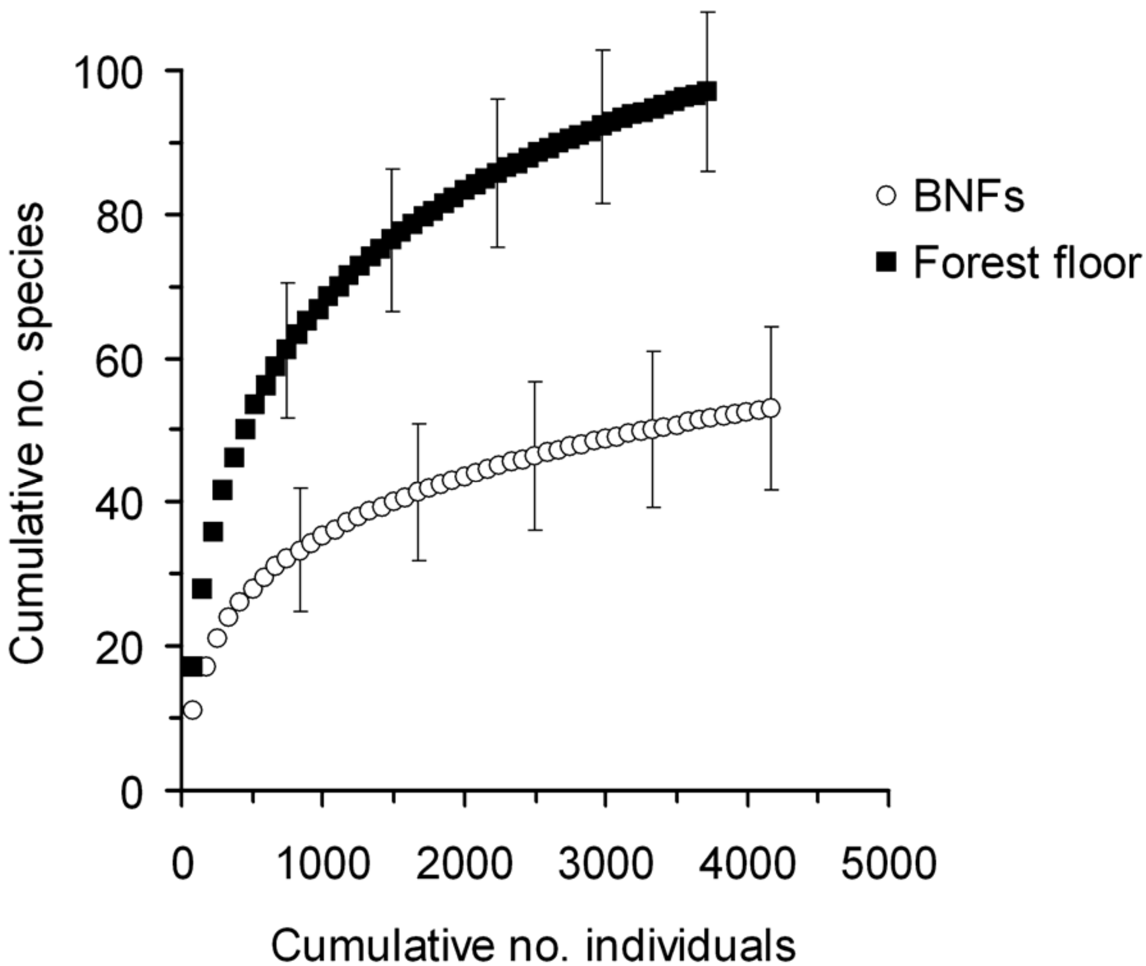

FIGURE S1. Rarefaction curves for all species of mesostigmatic mites collected from large BNFs and forest floor (data from all three sites pooled). The 95% CIs are shown.

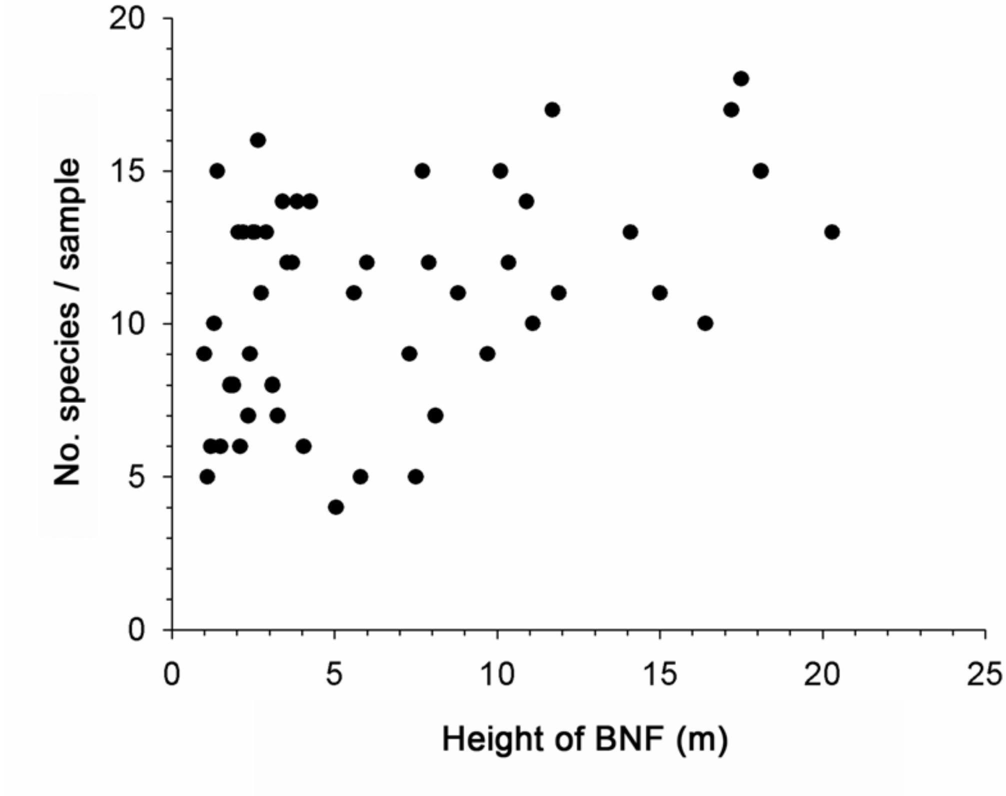

FIGURE S2. The number of species of mesostigmatic mites per sample from BNFs as a function of height of sample (data from all three sites pooled).

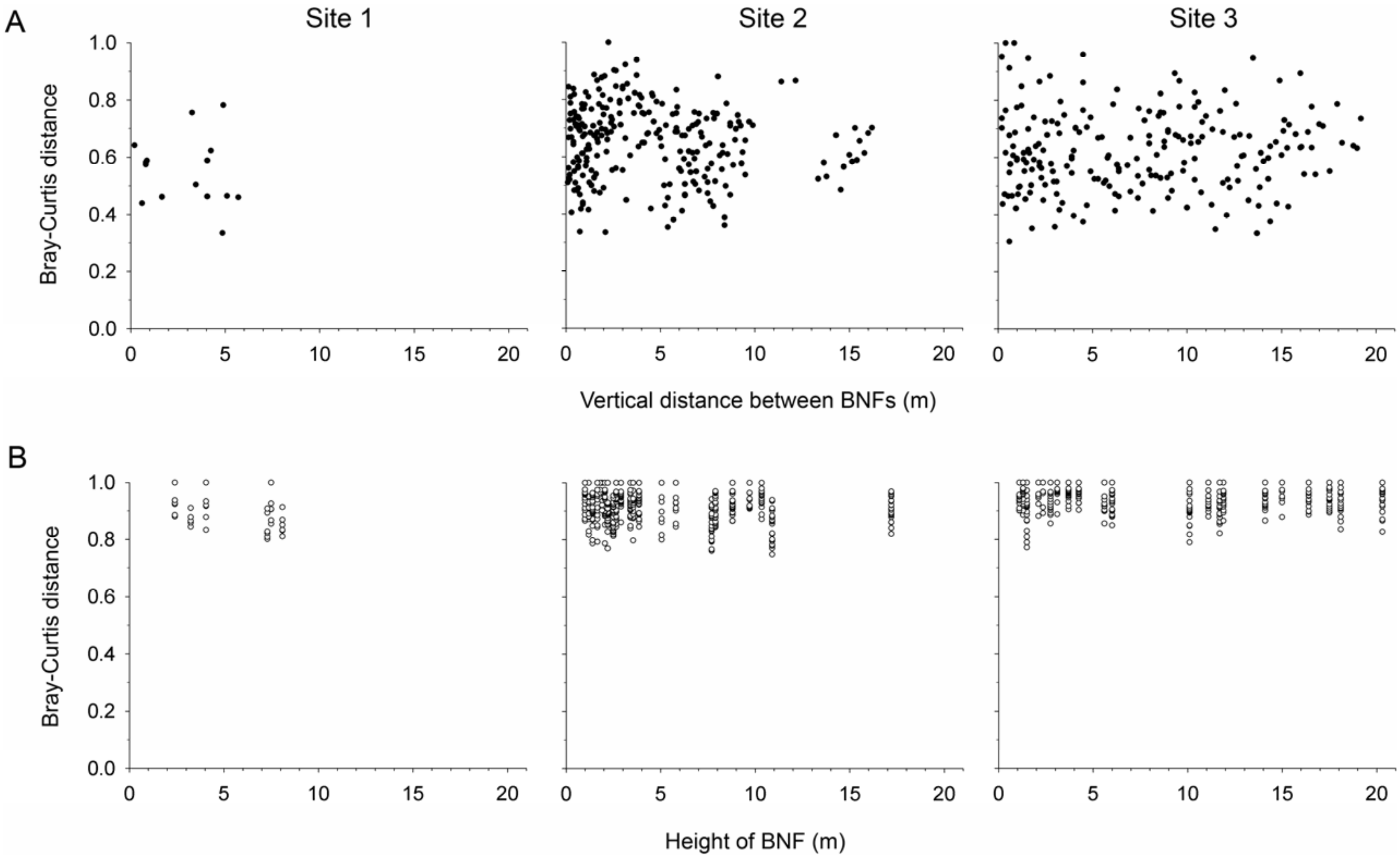

FIGURE S3. Bray-Curtis distance for pairwise comparisons of (A) BNF samples as a function of the vertical distance between samples and (B) BNF vs. ground samples as a function of height of BNF samples.

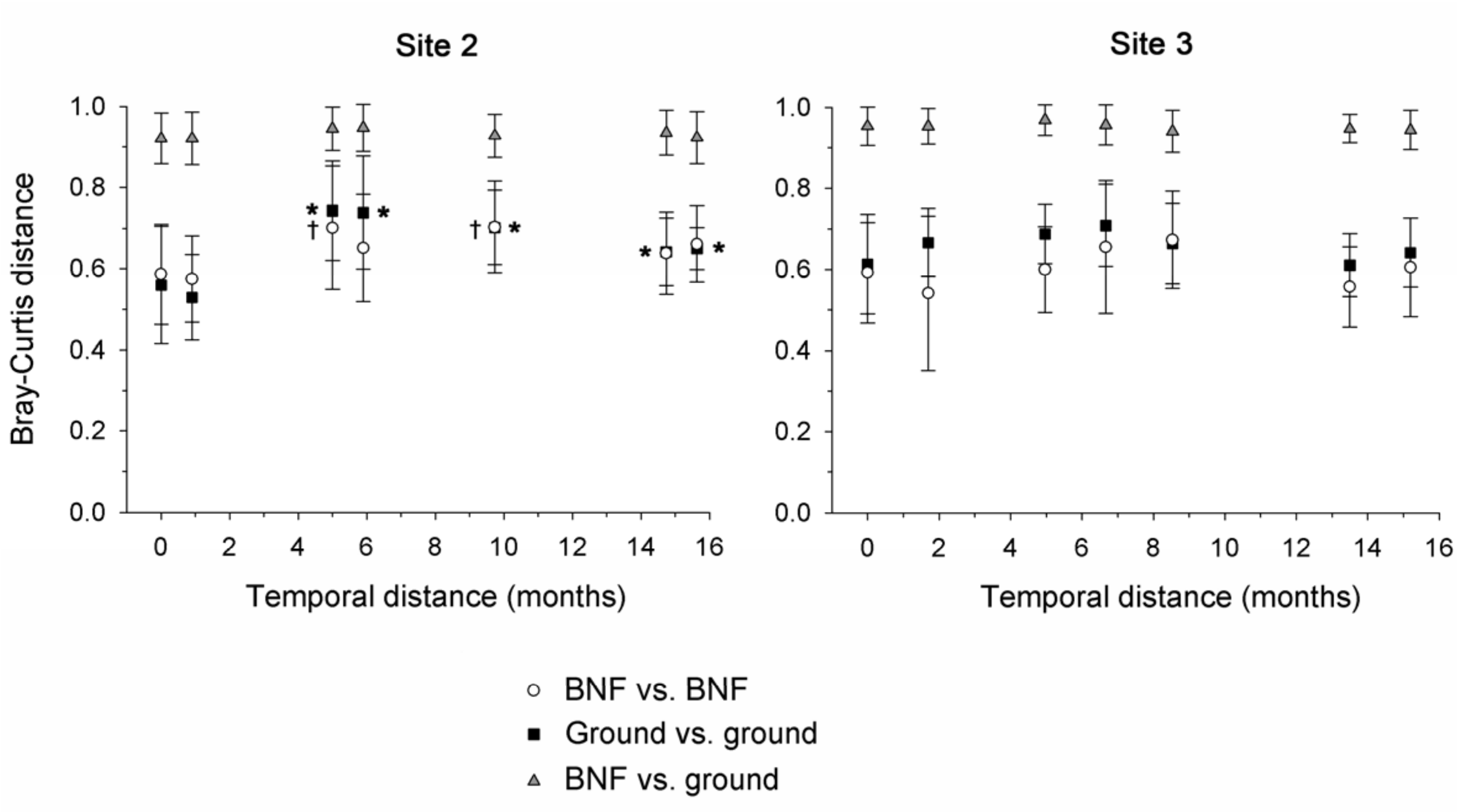

FIGURE S4. Mean Bray-Curtis distances for pair-wise sample comparisons as a function of the temporal distance between the times at which the two samples were taken. Error bars represent ± SD. Asterisks (for ground vs. ground) and † (for BNF vs. BNF) indicate that the mean was significantly different from the mean at 0 month (0 month = samples compared were taken at the same date; ANOVA followed by a Bonferroni-Dunn post-hoc test).

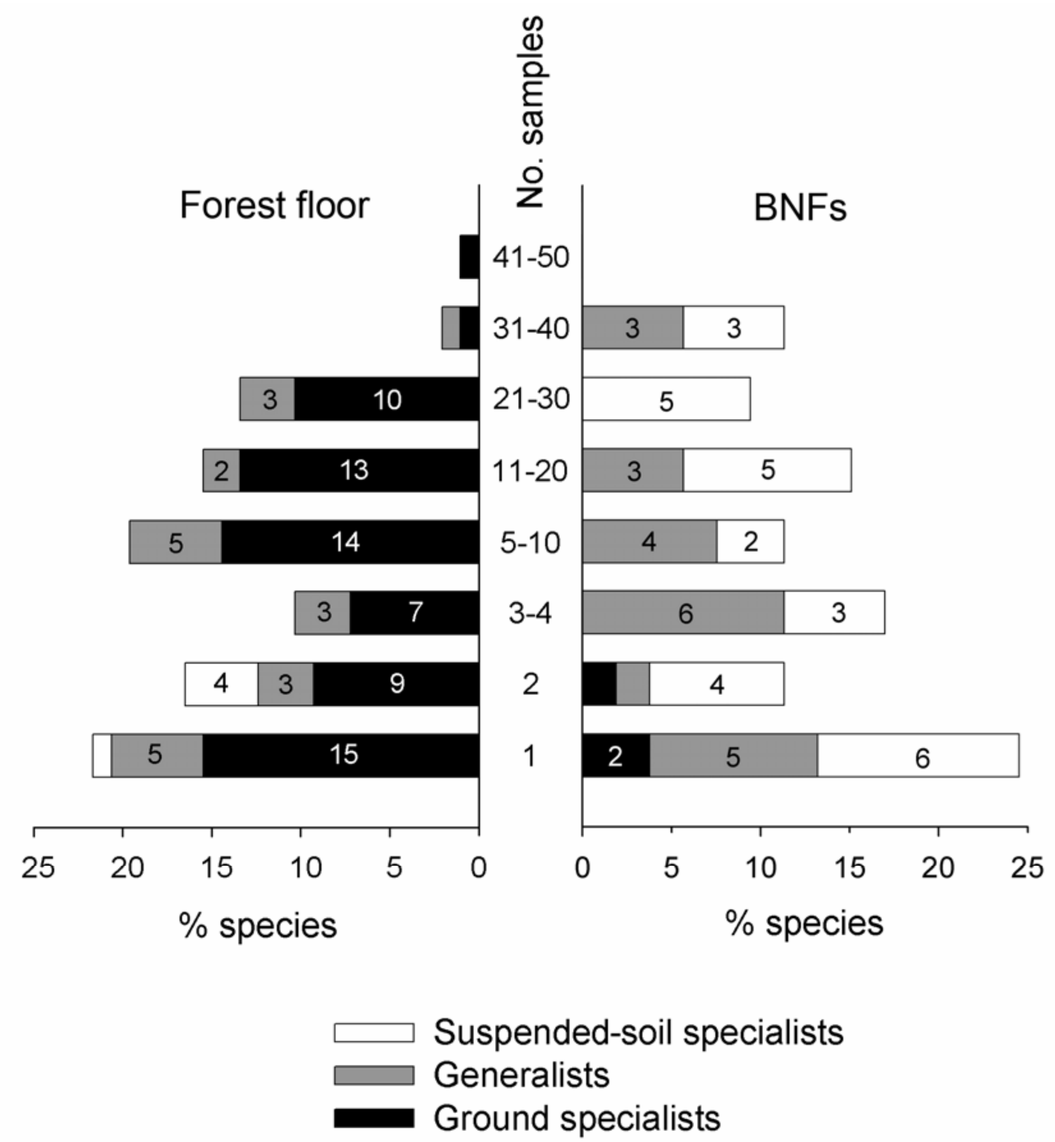

FIGURE S5. Distribution (%) of species of suspended-soil specialists, generalists and ground specialists in forest floor (including common and rare species) and BNF samples. The numbers inside bars indicate the number of species represented (bars without numbers are represented by one species).

TABLE S1. *List of species collected in Lamington National Park, southeast Queensland, Australia.* Numbers indicate the percentage of samples in which species were present (in parentheses: total abundance). Codes for ecological categories are as follows: SS = suspended-soil specialists, FF = forest floor specialists, gen = generalists; "n. sp." and "n. gen." stand for "new (undescribed) species" and "new genus"; species likely to be invertebrate paraphages or parasites (*), or vertebrate parasites (**) were excluded from the analysis.

			Arboreal suspended soil				Fallen epiphytes		Low suspended soil		
	Ecological category	**Forest floor**	**BNFs** (1-20.5m)	small BNFs (0.6-2m)	elkhorn ferns (4, 18m)	Tree forks (6-21m)	Fallen BNFs	Fallen elkhorn/ staghorn ferns	Logs	Boulders	BNFs on boulders
Species		(*n* =50)	(*n* =50)	(*n* =10)	(*n* =2)	(*n* =5)	(*n* =8)	(*n* =7)	(*n* =20)	(*n* =10)	(*n* =2)
Ameroseiidae											
Epicriopsis walteri Halliday		2 (1)									
Neocypholaelaps rotundus (Womersley)		2 (1)	4 (4)								
Ameroseiidae sp. A		2 (1)									
Ascidae											
Arctoseius n. sp. nr *memnon* Halliday, Walter & Lindquist			8 (5)			20 (2)					
Asca sp. 4	SS		12 (22)	10 (3)		20 (2)				30 (4)	50 (1)
Asca sp. 5										20 (10)	100 (3)
Gamasellodes adriannae Walter			2 (1)	10 (6)					5 (2)		
Iphidozercon foveatus Gwiazdowicz & Halliday		8 (13)							10 (2)		
Iphidozercon walteri Gwiazdowicz & Halliday			4 (3)								
Xenoseius n. sp. 1			2 (1)								
Xenoseius n. sp. 4									10 (8)		
Xenoseius n. sp. 5							13 (6)		10 (14)		
Zerconopsis n. sp. nr *pristis* Halliday, Walter & Lindquist									5 (1)		
Asternoseiidae											
Asternoseius n. sp. 1		2 (1)		10 (1)			13 (1)			10 (1)	50 (5)
Blattisociidae											
Arrhenoseius gloriosus Walter & Lindquist	SS		28 (114)				13 (1)				
Cheiroseius sp. 1	gen	64 (167)	16 (53)			20 (2)		14 (3)	10 (12)	10 (3)	50 (3)
Cheiroseius sp. 6										10 (1)	
Cheiroseius sp. 7						20 (1)					
Lasioseius boomsmai Womersley									5 (1)		
Lasioseius zalucki Walter & Lindquist		2 (1)	6 (5)							20 (8)	
Lasioseius sp. 2		2 (1)	2 (1)						10 (2)	10 (1)	
Cercomegistidae											
Cercomegistus n. sp. 1						20 (1)					
Davacaridae											
Acanthodavacarus klompeni Walter	gen	16 (29)	74 (557)				25 (7)		10 (10)		
Davacarus lindquisti Walter										10 (5)	
Digamasellidae											
Dendrolaelaps sp. A									35 (29)		
Dendrolaelaps sp. 2									5 (8)		
Dendrolaelaps (?Dendrolaelaspis) sp. 1	gen	28 (104)	18 (52)						10 (4)		
Diplogyniidae											
Cryptometasternum derricki Womersley									5 (5)		

Species	Ecological category	**Forest floor**	Arboreal suspended soil				Fallen epiphytes		Low suspended soil		
			BNFs (1-20.5m)	small BNFs (0.6-2m)	elkhorn ferns (4, 18m)	Tree forks (6-21m)	Fallen BNFs	Fallen elkhorn/ staghorn ferns	Logs	Boulders	BNFs on boulders
Cryptometasternum queenslandense Womersley		4 (2)									
Heatherellidae											
Heatherella callimaulos Walter		12 (9)	2 (1)								50 (2)
Ichthyostomatogasteridae											
Asternolaelaps australis Womersley & Domrow			4 (5)								
Iphiopsididae											
Iphiolaelaps ?myriapoda Womersley	*		4 (2)								
Scissuralaelaps sp.nr *grootaerti* Fain			2 (2)								
Conolaelaps sp. nr *coniferus* (Canestrini)	*		2 (2)								
Laelapidae											
Cosmolaelaps (*acuta* group) sp. 1		4 (2)	6 (27)					14 (1)			
Cosmolaelaps (*acuta* group) sp. 2						20 (1)					
Cosmolaelaps (*cuneifer* group) sp. 1		2 (1)	2 (8)						5 (1)		
Cosmolaelaps (*cuneifer* group) sp. 2		4 (2)	12 (13)				13 (1)	14 (10)	20 (13)	10 (1)	50 (1)
Cosmolaelaps (*cuneifer* group) sp. 3		2 (1)									
Cosmolaelaps sp. A				10 (23)					20 (14)		
Cosmolaelaps sp. nr *multisetosus* Domrow	gen	48 (98)	62 (402)			40 (9)		14 (1)	50 (80)	10 (2)	50 (3)
Gaeolaelaps sp. 1			6 (3)						5 (4)		
Gaeolaelaps sp. 2		2 (1)									
nr *Gaeoalelaps* sp. A			2 (1)					14 (1)			
Mesolaelaps bandicoota (Womersley)	**		2 (1)								
Pseudoparasitus annectans (Womersley)	SS	4 (3)	70 (313)	20 (2)	50 (5)	80 (8)	38 (6)		5 (1)	30 (3)	50 (5)
Pseudoparasitus sp. 1	FF	28 (32)									
Stratiolaelaps lamington Walter & Campbell	SS		70 (659)	20 (6)	50 (2)						50 (1)
Stratiolaelaps womersleyi Walter & Campbell	FF	42 (63)									
Leptolaelapidae											
Hunteracarus womersleyi Costa		4 (5)									
Hunteracarus n. sp. 1		2 (1)								10 (3)	
Hunteracarus n. sp. 2		4 (17)							5 (1)	10 (1)	
N. gen. 1 sp. 1	FF	20 (18)									
N. gen. 1 sp. 2	FF	12 (15)								10 (1)	
Genus 2 sp. 1	FF	26 (73)							5 (3)	40 (7)	50 (1)
Genus 2 sp. 2		2 (1)									
Macrochelidae											
Macrocheles novaezelandiae Emberson		16 (14)	6 (7)							10 (1)	
Macrocheles spiculata Halliday	SS		30 (114)								
Melicharidae											
Proctolaelaps nesbitti Womersley	SS	2 (3)	42 (226)				13 (1)			10 (5)	50 (3)
Proctolaelaps pygmaeus (Müller)		4 (3)	28 (29)			40 (5)					
Nothogyniidae											
Nothogynus klompeni Walter & Krantz										10 (1)	

Species	Ecological category	**Forest floor**	**Arboreal suspended soil**				**Fallen epiphytes**		**Low suspended soil**		
			BNFs (1-20.5m)	small BNFs (0.6-2m)	elkhorn ferns (4, 18m)	Tree forks (6-21m)	Fallen BNFs	Fallen elkhorn/ staghorn ferns	Logs	Boulders	BNFs on boulders
Ologamasidae											
Acugamasus n. sp. 3	SS	4 (5)	58 (156)	50 (47)	50 (1)	20 (2)	63 (27)	57 (10)	30 (13)	10 (1)	50 (1)
Acugamasus n. sp. 4		8 (4)	16 (14)	10 (1)	100 (5)		38 (3)	57 (8)	60 (50)	70 (30)	50 (7)
Acugamasus n. sp. 5									5 (1)		
Antennolaelaps affinis Womersley		8 (6)					13 (1)				
Antennolaelaps n. sp. nr *convexa* Womersley	FF	22 (37)									
Antennolaelaps n. sp. nr *testudo* Lee		4 (5)								10 (1)	
Antennolaelaps n. sp. 2		50 (66)	8 (24)				25 (4)	14 (4)	15 (10)	10 (1)	50 (5)
Antennolaelaps n. sp. 3		2 (1)	8 (4)	10 (1)	100 (2)		13 (2)	57 (11)	35 (13)	30 (3)	
Antennolaelaps n. sp. 4	FF	10 (6)					13 (1)		20 (4)	20 (3)	50 (1)
Athiasella n. sp. 2		6 (3)									
Athiasella n. sp. 3	FF	92 (378)							15 (7)	20 (2)	50 (1)
Athiasella n. sp. 4	FF	52 (56)					13 (1)	29 (2)	5 (1)		
Athiasella n. sp. 7	SS	4 (3)	38 (138)	20 (26)		20 (1)	38 (9)	43 (38)	45 (61)	60 (16)	50 (6)
Athiasella n. sp. 8		2 (3)									
Athiasella n. sp. 10	SS		24 (66)	30 (14)	50 (1)				10 (17)		50 (3)
Athiasella n. sp. 11	FF	24 (37)									
Athiasella n. sp. 13	SS		46 (147)	20 (3)			25 (6)	14 (7)		10 (11)	
Athiasella n. sp. 14		6 (28)								20 (9)	50 (16)
Athiasella n. sp. 15	FF	24 (28)									
Athiasella n. sp. 18	FF	52 (133)	4 (36)						10 (3)	20 (6)	50 (3)
Athiasella n. sp. 23	FF	10 (11)									
Caliphis novaezelandiae Womersley	FF	20 (17)		10 (4)					15 (6)	30 (10)	
Caliphis queenslandicus Womersley	SS		60 (243)	10 (1)			13 (3)			40 (54)	50 (4)
Caliphis tamborinensis (Womersley)	SS	4 (2)	36 (45)	30 (5)		60 (19)	13 (2)			20 (3)	50 (6)
Caliphis n. sp. nr *queenslandicus*	FF	32 (42)									50 (1)
Euepicrius n. sp. 1	FF	30 (43)								10 (1)	
Euepicrius n. sp. 2		30 (37)	6 (3)						10 (4)		
Euepicrius n. sp. 3	gen	16 (14)	34 (59)	10 (4)			13 (1)	14 (2)	5 (1)	10 (2)	50 (1)
Euepicrius n. sp. 4		6 (7)	2 (1)							10 (2)	
Euepicrius n. sp. 5	FF	10 (9)									
Euepicrius n. sp. 6		4 (5)									
Euepicrius n. sp. 7	FF	42 (68)							5 (5)	30 (7)	
Gamasellus n. sp. nr *discutatus* (Lee)	FF	24 (30)					13 (1)	29 (13)	15 (8)		
Gamasellus sp. A		2 (1)									
nr *Gamasellus* sp. 1		2 (1)									
Gamasiphis nr *australicus* Womersley n. sp. 1	FF	32 (66)							5 (1)		
Gamasiphis nr *australicus* n. sp. 2	SS		42 (102)	30 (9)	50 (5)		13 (1)		15 (6)	10 (5)	
Gamasiphis nr *australicus* n. sp. 5	FF	44 (342)						14 (1)	5 (2)	10 (1)	
Gamasiphis nr *australicus* n. sp. 6	FF	52 (204)					25 (5)	14 (1)	5 (6)	10 (1)	
Gamasiphis nr *australicus* n. sp. 8	SS		14 (18)	10 (13)			13 (5)				50 (4)
Gamasiphis n. sp. nr *fornicatus* Lee	FF	48 (106)							5 (4)	10 (1)	100 (6)

			Arboreal suspended soil				Fallen epiphytes		Low suspended soil		
Species	Ecological category	**Forest floor**	**BNFs** (1-20.5m)	small BNFs (0.6-2m)	elkhorn ferns (4, 18m)	Tree forks (6-21m)	Fallen BNFs	Fallen elkhorn/ staghorn ferns	Logs	Boulders	BNFs on boulders
Gamasiphis n. sp. 12	FF	10 (17)					13 (1)			10 (1)	
Gamasiphis n. sp. 13		4 (6)									
Gamasiphoides n. sp. 1	FF	68 (181)	2 (1)							10 (2)	50 (2)
Gamasiphoides n. sp. 2	FF	20 (15)						14 (1)	5 (5)	20 (5)	50 (2)
Gamasiphoides n. sp. 6			6 (3)			20 (6)	13 (2)			10 (1)	
Gamasiphoides n. sp. 9										30 (9)	
Gamasiphoides n. sp. 13		2 (2)									
?*Gamasiphoides* sp. 1		8 (5)	2 (1)					14 (2)	10 (2)		50 (1)
Geogamasus n. sp. 1	FF	24 (17)									
Geogamasus n. sp. 2	gen	16 (14)	36 (116)	20 (8)	50 (1)		13 (2)	29 (12)	5 (2)		
Geogamasus n. sp. 3	FF	60 (367)					38 (4)			10 (2)	
Geogamasus n. sp. 4		6 (11)									
Laelaptiella anomala Womersley	gen	46 (170)	62 (195)	60 (21)		60 (32)	75 (22)	29 (5)	35 (43)	60 (47)	100 (13)
Onchogamasus n. sp. 3		4 (3)									
Onchogamasus n. sp. 5		8 (6)						14 (1)	5 (2)		
Onchogamasus n. sp. 10	FF	16 (11)									
Oriflamella lutulenta Halliday	FF	38 (48)									
Pyriphis n. sp. 1	FF	32 (49)							5 (1)	10 (2)	
Pyriphis n. sp. 3		2 (2)						14 (2)			
Pyriphis n. sp. 4	FF	10 (18)									
Pyriphis n. sp. 5		6 (4)									
Queenslandolaelaps n. sp. 1	FF	48 (124)					13 (2)	57 (20)	5 (5)	10 (1)	50 (1)
Queenslandolaelaps n. sp. 3		4 (3)									
Gamasiphinae n. gen. 1 sp. 1	FF	50 (68)	2 (1)						5 (2)		
Ologamasinae n. gen. 2 sp. 1	FF	10 (6)									
Sessiluncinae n. gen. 3 sp. 1		4 (2)									
Sessiluncinae n. gen. 4 sp. 1	FF	24 (32)							10 (4)		
Sessiluncinae n. gen. 5 sp. 1	FF	12 (7)									
Sessiluncinae n. gen. 6 sp. 1	FF	10 (8)									
N. gen. 7 sp. 1		2 (2)									
N. gen. 8 sp. 1	FF	20 (21)									
Ologamasidae sp. A		2 (1)									
Phytoseiidae											
Amblyseius (*sturtii* group) sp. 1		2 (1)									
Amblyseius deleoni Muma & Denmark									5 (1)	10 (1)	
Neoseiulella (*cottieri* group) n. sp. 1			2 (6)	10 (1)							
Neoseiulella n. sp. nr *armidalensis* Schicha & Elshafie										10 (1)	
Podocinidae											
Podocinum n. sp. 1			4 (18)						5 (1)		
Promegistidae											
Promegistus armstrongi Womersley	*	4 (2)									
Sejidae											
Sejus n. sp. A	SS		68 (130)	30 (3)		60 (9)					50 (2)

			Arboreal suspended soil				Fallen epiphytes		Low suspended soil		
Species	Ecological category	**Forest floor**	**BNFs** (1-20.5m)	small BNFs (0.6-2m)	elkhorn ferns (4, 18m)	Tree forks (6-21m)	Fallen BNFs	Fallen elkhorn/ staghorn ferns	Logs	Boulders	BNFs on boulders
Triplogyniidae											
Funkotriplogynium iagobadius Seeman & Walter									5 (3)		
Uropodellidae											
N. gen. sp. 1			4 (6)								
Veigaiidae											
Veigaia sp. 1			2 (1)								
Total no. individuals (excl. parasites)		3708	4162	202	22	100	128	156	509	300	114
Total no. species		97	53	22	8	15	29	23	54	51	32

TABLE S2. *Habitat distribution*[a] *of suspended-soil specialists, generalists, and ground specialists collected in Lamington National Park, Australia.*

				Arboreal suspended soil				**Fallen epiphytes**		**Low suspended soil**	
	Species code[b]	Species	**Forest floor** (*n* =50)	**BNFs** (1-20.5m) (*n* =50)	small BNFs (0.6-2m) (*n* =10)	elkhorn ferns (4, 18m) (*n* =2)	Tree forks (6-21m) (*n* =5)	Fallen BNFs (*n* =8)	Fallen elkhorn/ staghorn ferns (*n* =7)	Logs (*n* =20)	Boulders (*n* =10)
Suspended-soil specialists	LAE-1	*Stratiolaelaps lamington*		70 (659)$^{L+}$	++	+					
	LAE-2	*Pseudoparasitus annectans*	4 (3)	70 (313)$^{L+}$	++	+	++++	++		5 (1)	30 (3)
	SEJ	*Sejus* n. sp. A		68 (130)$^{L+}$	++		++++				
	OLO-1	*Caliphis queenslandicus*		60 (243)$^{L+}$	+			+			40 (54)
	OLO-2	*Acugamasus* n. sp. 3	4 (5)	58 (156)^{R}	+++	+	++	++++	+++	30 (13)	10 (1)
	OLO-3	*Athiasella* n. sp. 13		46 (147)^{L}	++			++	+		10 (11)
	MEL	*Proctolaelaps nesbitti*	2 (3)	42 (226)$^{L+}$				+			10 (5)
	OLO-4	*Gamasiphis* nr *australicus* n. sp. 2		42 (102)^{R}	++	+		+		15 (6)	10 (5)
	OLO-5	*Athiasella* n. sp. 7	4 (3)	38 (138)	++		++	++	+++	45 (61)	60 (16)
	OLO-6	*Caliphis tamborinensis*	4 (2)	36 (45)$^{L+}$	++		++++	+			20 (3)
	MAC	*Macrocheles spiculata*		30 (114)$^{L+}$							
	BLA-1	*Arrhenoseius gloriosus*		28 (114)$^{L+}$				+			
	OLO-7	*Athiasella* n. sp. 10		24 (66)^{R}	++	+				10 (17)	
	OLO-8	*Gamasiphis* nr *australicus* n. sp. 8		14 (18)	+			+			
	ASC	*Asca* sp. 4		12 (22)	+		++				30 (4)
Generalists	DAV	*Acanthodavacarus klompeni*	16 (29)	74 (557)$^{L+}$				++		10 (10)	
	OLO-9	*Geogamasus* n. sp. 2	16 (14)	36 (116)	++	+		+	++	5 (2)	
	OLO-10	*Euepicrius* n. sp. 3	16 (14)	34 (59)$^{L+}$	+			+	+	5 (1)	10 (2)
	OLO-11	*Laelaptiella anomala*	46 (170)$^{L+}$	62 (195)$^{L+}$	++++		++++	++++	++	35 (43)	60 (47)
	LAE-3	*Cosmolaelaps* sp. nr *multisetosus*	48 (98)	62 (402)$^{L+}$			+++		+	50 (80)	10 (2)
	DIG	*Dendrolaelaps (?Dendrolaelaspis)* sp. 1	28 (104)$^{L+}$	18 (52)						10 (4)	
	BLA-2	*Cheiroseius* sp. 1	64 (167)$^{L+}$	16 (53)			++		+	10 (12)	10 (3)

				Arboreal suspended soil				Fallen epiphytes		Low suspended soil	
	Species code[b]	Species	**Forest floor**	**BNFs** (1-20.5m)	small BNFs (0.6-2m)	elkhorn ferns (4, 18m)	Tree forks (6-21m)	Fallen BNFs	Fallen elkhorn/ staghorn ferns	Logs	Boulders
Ground specialists	OLO-12	*Athiasella* n. sp. 3	92 (378)[L+]							15 (7)	20 (2)
	OLO-13	*Gamasiphoides* n. sp. 1	68 (181)[L+]	2 (1)							10 (2)
	OLO-14	*Geogamasus* n. sp. 3	60 (367)[L]					++			10 (2)
	OLO-15	*Gamasiphis* nr *australicus* n. sp. 6	52 (204)[L+]					++	+	5 (6)	10 (1)
	OLO-16	*Athiasella* n. sp. 18	52 (133)[L+]	4 (36)						10 (3)	20 (6)
	OLO-17	*Athiasella* n. sp. 4	52 (56)					+	++	5 (1)	
	OLO-18	Gamasiphinae n. gen. 1 sp. 1	50 (68)[L+]	2 (1)						5 (2)	
	OLO-19	*Queenslandolaelaps* n. sp. 1	48 (124)[S]					+	+++	5 (5)	10 (1)
	OLO-20	*Gamasiphis* n. sp. nr *fornicatus*	48 (106)							5 (4)	10 (1)
	OLO-21	*Gamasiphis* nr *australicus* n. sp. 5	44 (342)[L+]						+	5 (2)	10 (1)
	OLO-22	*Euepicrius* n. sp. 7	42 (68)[L+]							5 (5)	30 (7)
	LAE-4	*Stratiolaelaps womersleyi*	42 (63)								
	OLO-23	*Oriflamella lutulenta*	38 (48)								
	OLO-24	*Gamasiphis* nr *australicus* n. sp. 1	32 (66)							5 (1)	
	OLO-25	*Pyriphis* n. sp. 1	32 (49)[L]							5 (1)	10 (2)
	OLO-26	*Caliphis* n. sp. nr *queenslandicus*	32 (42)[L]								
	OLO-27	*Euepicrius* n. sp. 1	30 (43)								10 (1)
	LAE-5	*Pseudoparasitus* sp. 1	28 (32)								
	LEP-1	Genus 2 sp. 1	26 (73)[L]							5 (3)	40 (7)
	OLO-28	*Athiasella* n. sp. 11	24 (37)								
	OLO-29	Sessiluncinae n. gen. 4 sp. 1	24 (32)							10 (4)	
	OLO-30	*Gamasellus* n. sp. nr *discutatus*	24 (30)					+	++	15 (8)	
	OLO-31	*Athiasella* n. sp. 15	24 (28)								

				Arboreal suspended soil				Fallen epiphytes		Low suspended soil	
	Species code[b]	Species	**Forest floor**	**BNFs** (1-20.5m)	small BNFs (0.6-2m)	elkhorn ferns (4, 18m)	Tree forks (6-21m)	Fallen BNFs	Fallen elkhorn/ staghorn ferns	Logs	Boulders
Ground specialists	OLO-31	*Athiasella* n. sp. 15	24 (28)								
	OLO-32	*Geogamasus* n. sp. 1	24 (17)[S+]								
	OLO-33	*Antennolaelaps* n. sp. nr *convexa*	22 (37)								
	OLO-34	N. gen. 8 sp. 1	20 (21)								
	LEP-2	N. gen. 1 sp. 1	20 (18)[L]								
	OLO-35	*Caliphis novaezelandiae*	20 (17)		+					15 (6)	30 (10)
	OLO-36	*Gamasiphoides* n. sp. 2	20 (15)						+	5 (5)	20 (5)
	OLO-37	*Onchogamasus* n. sp. 10	16 (11)								
	LEP-3	N. gen. 1 sp. 2	12 (15)								10 (1)
	OLO-38	Sessiluncinae n. gen. 5 sp. 1	12 (7)								
	OLO-39	*Pyriphis* n. sp. 4	10 (18)								
	OLO-40	*Gamasiphis* n. sp. 12	10 (17)					+			10 (1)
	OLO-41	*Athiasella* n. sp. 23	10 (11)								
	OLO-42	*Euepicrius* n. sp. 5	10 (9)								
	OLO-43	Sessiluncinae n. gen. 6 sp. 1	10 (8)								
	OLO-44	*Antennolaelaps* n. sp. 4	10 (6)					+		20 (4)	20 (3)
	OLO-45	Ologamasinae n. gen. 2 sp. 1	10 (6)								

[a] Numbers and + (5-19%), ++ (20-39%), +++ (40-59%), ++++ (60-80%) indicate the percentage of samples in which species were present (in parentheses: total abundance) (for elkhorn ferns: + indicates that species was present in 1 sample out of 2). n = number of samples taken. Preferences (P<0.05) for litter (L), fern rootball (R) or soil (S) are indicated after ground and/or BNF values (Wilcoxon signed rank test; + indicates that P<0.005).

[b] Species codes indicate families as follows: ASC=Ascidae, BLA=Blattisociidae, DAV=Davacaridae, DIG=Digamasellidae, LAE=Laelapidae, LEP=Leptolaelapidae, MAC=Macrochelidae, MEL=Melicharidae, OLO=Ologamasidae, SEJ=Sejidae